THE EXPERIMENTAL INVESTIGATION OF NAVIGATION IN HOMING PIGEONS

By G. V. T. MATTHEWS
Department of Zoology, University of Cambridge

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(With Twelve Text-figures)

INTRODUCTION

There are two main problems in bird navigation, concerned respectively with natural migration journeys and with 'homing' to an area after being artificially transported away from that area. The latter more complete problem is the concern of the present work. The term 'navigation' is used here in the sense of the dictionary definition, 'the art or science of directing the movements of vessels on the sea...or in the air', and this is taken to exclude 'pilotage' which is defined as 'the steering of ships...wherever local knowledge is required'. Thus if it should be shown that birds only returned regularly from areas already known to them, and that returns from unknown areas were attributable to chance wanderings, then the term 'navigation' would have to be dropped. One school of thought to-day holds this opinion with some minor concessions. The other holds that at least some of the facts of homing cannot be dismissed on this basis, and a number of explanatory theories have been put forward. It is not the purpose of the present paper to provide full chapter and verse for the controversy that has been going on for more than eighty years. Griffin (1944) provides an adequate summary, and Matthews (1950) has discussed it in rather more detail.

One of the main causes of this prolonged debate has been the dearth of detailed, critically assembled facts. In particular, the difficulty of delimiting the area known to any particular bird has resulted in ambiguous interpretations of such facts as we do possess. This difficulty is much easier to overcome in the case of homing pigeons, particularly with young birds only a few months old. It is therefore surprising that this obvious experimental animal has been so little used by investigators. There is, of course, a vast popular literature, mostly highly uncritical. Accounts of the usual training and performances have been given, among others, by Riviere (1923), Knieriem (1943) and Nicol (1945). Field tests of a general nature have been carried out by Thauzies (1909), Riviere (1929), Gibault (1930, 1933), Grundlach (1932), Heinroth (1941) and Platt & Dare (1945), with conflicting results. A number of other experimenters have used pigeons to test particular theories, taking small numbers of unknown strains and histories, and employing them with little knowledge of their capabilities under normal conditions.

The present work was therefore undertaken first to provide a quantity of statistically satisfactory experimental data on the homing behaviour of pigeons under various conditions. Secondly, it was intended to investigate some of the theories of special navigational ability, if a straightforward explanation of the accumulated facts was not possible.

MATERIAL AND METHODS

It was necessary to rear large numbers of pigeons from proven racing stock, to use them in their first year, operating from a well-equipped loft where they were carefully handled. Field Station facilities were not then available, and the very essential breeding, rearing and initial training was carried out by three breeders of long standing with large establishments of successful strains, viz. L. A. Meredith at Easton, Norwich, in 1948 (25 birds), P. Cope at Duxford, Cambridge (34 birds), and L. R. Duke at Sawston, Cambridge (26 birds) in 1949, and P. Cope at Duxford (73 birds) in 1950.

The birds were hatched in two 'rounds', early in March and in Mid-April, so that all were 3–4 months old when the experiments were begun. By then they were accustomed to handling, travelling in baskets, re-entering the loft on their return and the other incidentals of the work, by several releases in groups up to 10 miles from the loft in one 'training' direction. A series of controlled experimental releases were then carried out.

The birds were fed on the afternoon prior to the test. They were then taken in a closed van (except for tests, A and B, in which rail transport was used) to Cambridge, and then on to the release point in the early hours of the morning, arriving about 0500 G.M.T. The greater part of the journey was thus done in the dark, and in addition the baskets containing the birds were covered with opaque black cloth. Water was provided but no food. On release, therefore, these young birds were required to exhibit a very simple form of homing—to 'home plus food'. No sexual motives governed their return.

Release points were chosen to give a clear all round view, no trees or buildings near enough to block out a pigeon flying at 100 ft. up to two miles away. The latter was found to be the approximate limit for following a single bird in 16 × 40 binoculars.

Each bird was tossed straight up into the air, the liberator facing in different directions during the course of releases. The bird was then followed in the binoculars until it had vanished from sight, when the next was released. In this way, in most of the experiments, the birds were operated as individuals and complication of results by group effects was avoided. As there is a strong tendency for single birds to join up with any strong-flying group of pigeons, no releases were made on Saturdays, or other days on which mass pigeon-racing was in progress.

The straight-line homing speeds of birds returning on the day of release were calculated. These, together with the proportion of stragglers and losses, form a useful index of success on any one test. Winds and other meteorological conditions must be considered when comparing one test with another. Small differences in homing speed may be due to actual differences in flight speed, but in the main will reflect the extent of deviation from the straight track home, or of halts by the way.

As each bird was lost from view in the binoculars, its bearing was noted. This 'Vanishing Point' is not necessarily representative of the course being flown, since the majority of birds, having circled once or twice, make off in one general direction, at the same time flying a series of wide zigzags or horizontal loops. The vanishing point is generally reached when the bird turns end-on to the observer, and is therefore likely to indicate the limits of the sideways search about the general line of flight. As an individual index the vanishing point may thus be somewhat misleading, but with a number of birds, a departure 'fan' is obtained whose orientation may be interpreted with confidence. Throughout the series of tests this index bore a general positive relation to homing success. Thus for all birds released singly more than 48 miles from the loft we have:

Vanishing point	Sorties	Homing speed	Returned 2nd day (%)	Stragglers and lost (%)
Within 30° of home line	222	Av. 24·5	12	9
More than 30°	363	Av. 19·8	9	21

The time from release to vanishing would depend partly on atmospheric conditions (although visibility was reasonable in all tests), on the attitude of the bird relative to the observer and on any tendency to wait for a companion. It has, however, been called 'Orientation Time', and this would seem to be justified as there is a positive correlation with the accuracy of the initial direction taken:

Orientation time (min.)	Sorties	Vanishing points within 30° of home line (%)
1½–3½	244	45
–5½	168	36
Over 5½	173	30

Similarly, a positive correlation with homing success can be demonstrated.

For the great majority of sorties these three indices of performance are available, showing the degree of uncertainty on release, the accuracy of the initial course and the success in regaining home. They are represented in histogram form for the important tests in Figs. 2–12, the detailed information being too bulky to include. That for 1948 and 1949 is available elsewhere (Matthews, 1950).

For ease of subsequent reference a list of the tests carried out is given in Table 1, the results and interpretations being discussed later as appropriate. The relation of the release points to home is shown in Fig. 1. This paper is thus based on the performances of 158 individual pigeons, in a total of 902 sorties. Only 153 of the latter were in groups of three to eight birds.

BEHAVIOUR OF PIGEONS WHEN RELEASED ON A 'TRAINING LINE'

It has been known for centuries that fewer losses and faster returns will result when pigeons are 'trained' by being released at increasing distances in one general direction only. All pigeon racing is based on this procedure, likewise the use of pigeons as

Table 1

Test	Date	No. of birds	Distance and bearing of home
1948: A	4. viii	24	55 miles 052° T.
B	18. viii	9	55 miles 052° T.
1949: 1	17. vii	50 (in groups)	24 miles 161° T.
2	21. vii	60	24 miles 161° T.
3	24. vii	18 (in groups)	
		38	49 miles 159° T.
4	27. vii	53	49 miles 159° T.
5	5. viii	52	78 miles 160° T.
6	10. viii	48	78 miles 160° T.
7	17. viii	45	127 miles 158° T.
8	29. viii	47	79 miles 070° T.
9	4. ix	33	69 miles 345° T.
1950: 10	11. vii	66 (in groups)	25 miles 164° T.
11	18. vii	61	25 miles 164° T.
12	25. vii	10	49 miles 085° T.
13	25. vii	44	53 miles 157° T.
14	1. viii	43	
		3 (in group)	53 miles 157° T.
15	4. viii	10	62 miles 079° T.
16	4. viii	32	87 miles 154° T.
17	10. viii	33	87 miles 154° T.
18	18. viii	35	130 miles 161° T.
18*a*	18. viii	8 (in group)	49 miles 143° T.
19	22. viii	16	
		8 (in group)	13 miles 186° T.
20	24. viii	30	81 miles 070° T.
20*a*	24. viii	10	53 miles 064° T.
21	1. ix	16	68 miles 344° T.

message carriers. As a first step it was therefore necessary to investigate the factors governing this technique, and particularly to find out whether a tendency to fly in the one particular direction was established, and if so how the birds recognized that direction. There was the added advantage that such a procedure resulted in most of the birds becoming used to flying long distances without covering more than a narrow tract of country.

A series of tests were therefore carried out on one line bearing north-north-west from the loft. In the first the birds were released in groups, thereafter as individuals. They were released a second time at each stage before proceeding to the next. The distance between stages was successively increased, for instance, from 15 to 28, 34 and 43 miles in 1950, and similarly in 1949.

A general orientation of the departure 'fan' about the home/training direction could be discerned, and became clearer with each new stage up the line, an increasing proportion of birds being with a narrow arc:

Birds within 30° *of home line*

1949	Test 3	27%	1950	Test 13	21%
	5	50%		16	50%
	7	54%		18	53%

Also see and compare Fig. 2 with Fig. 4, and Fig. 3 with Fig. 9. The average orientation time varied about 5 min. without showing a steady decrease, suggesting that the orientation process was a fairly constant one. The average speed of return increased through the series, e.g. 17·8, 20·2 and 30·9 m.p.h. in tests 3, 5 and 7. This reflects an increase in flying speed and strength, in confidence and 'desire' to reach home, and in the proportion of the track previously flown over.

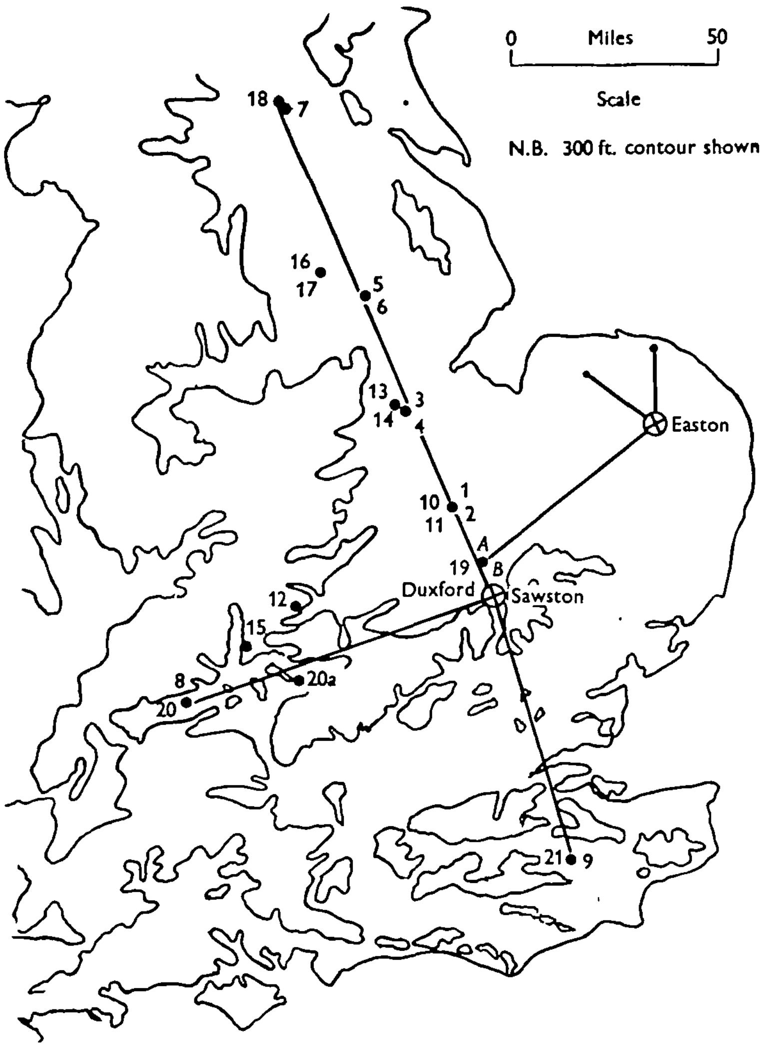

Fig. 1. Relation of release points to home lofts.

In the conditions under which pigeon races are carried out—mass releases of birds of mixed histories and training—leadership by experienced birds and other group effects undoubtedly play a part. As the present tests were expressly designed to eliminate these factors nothing much can be said on this score. In Test 3, however, eighteen birds were released in three groups, the remainder singly. The groups were lost from sight twice as quickly (despite their greater visibility) as the single birds, and closer to the home direction (11°, 17° and 33° off, v. 27% within 30°). They also returned faster, 28·0 v. 17·8 m.p.h. The group effects resulting in this superior performance probably include the satisfaction of the desire for company, competitive striving, and cancelling out of diverging flight lines (groups rarely circle, and make off with few changes of direction). That some birds will follow the lead of their more confident fellows is suggested by the performance of these

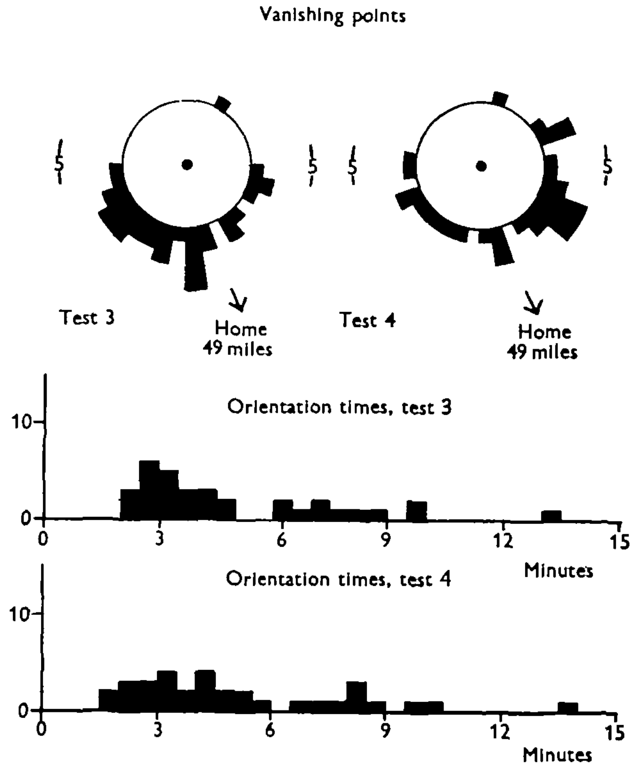

Fig. 2. Effect of overcast skies on a repeat release from a point on the training line.

grouped birds when released singly at the same point in Test 4. Ten reached vanishing point in 2·8–5·8 min., but seven others were very slow to depart, taking from 8·2 to 31·0 min. It seems probable that the latter had 'gone with the crowd' on their first release and had difficulty in picking up a line of flight on the second occasion.

The arrangement of these unidirectional releases made it most unlikely that any pigeon had been to a release point prior to the first test there. It also seems probable that the fairly moderate intervals between successive stages would be sufficient to prevent the viewing of known horizons. The pigeons flew relatively low, 100–200 ft., giving a horizon at 12–18 miles. In Test 5 owing to a strong head wind they flew very low, 30–70 ft., with a horizon at 7–10 miles. Yet a good concentration of vanishing points was still recorded in the home direction. Similarly, the coast line was sufficiently distant, and its nearest points had no constant orientation relative to the training line.

The present results suggest that pigeons do not possess a 'photographic' memory of the general features of the landscape. When released a second time at the same point, the concentration of vanishing points may show some, though no very great,

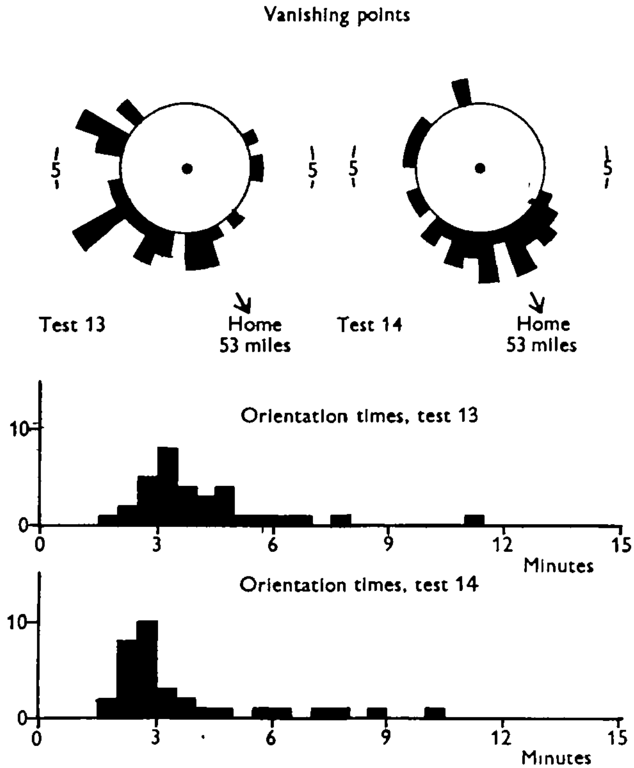

FIG. 3. Effect of overcast skies on an initial release from a point on the training line.

improvement, e.g. Tests 5 and 6, 45 % v. 55 % within 30°. In other cases there was no improvement, e.g. Tests 16 and 17, both had 57 % within 30°, or a poorer performance may result, e.g. Tests 3 and 4, 33 % v. 24 %. It might be added here that pigeons have shown themselves to be slow learners in laboratory tests involving the use of visual clues (Matthews, 1950). It is probable, however, that general features of the landscape may influence the initial flight direction, especially in the early stages of training. Thus a low ridge lay to the south of the release point in Tests 10 and 11, while in Test 13 a similar ridge lay to the west. Fig. 3 suggests that a number of birds were attracted to the west in the latter test.

Overcast skies were found to have some effect on orientation in the training direction. In 1949, thirty-three birds were released singly in both Tests 3 and 4, and in 1950 another thirty-three were released singly in both Tests 13 and 14. All were thus in the same stages of training and were released in the same landscape, but with widely differing cloud conditions. Test 3 was made in bright sunshine with 2/10th to 5/10th cloud, but in Test 4 the sky was overcast and the sun only visible very occasionally as a shrouded disk. Despite the presumed assistance of previously seen landmarks the birds gave a poorer performance in orientating on their second release. In 1950 the *first* release was made with the sky overcast and the sun infrequently visible as a disc, while the repeat release was in bright sunshine with 2/10th to 6/10th cloud. With this sequence a considerable improvement resulted. Results for the two sets of tests were:

Test	Orientation time	Within 30° of home
3	5·1	11
4	5·5	8
13	4·1	8
14	3·7	18

They are shown graphically in Figs. 2 and 3.

Schneider (1906) suggested that, as racing pigeons were usually released early in the morning, the position of the sun in azimuth would provide a relatively constant directional clue. Fixed-angle learning is within a pigeon's capacity, as it has been shown in laboratory experiments (Matthews, 1950) that they could learn to go to food placed at 090°, 180° and 360° to an artificial sun. Test 7 was designed to test this theory. The release points in Tests 1–6 and 7 (see Fig. 1, Table 1) were all within a degree or two of a straight line from the loft. Further, each individual pigeon was released as nearly as possible at the same Greenwich mean time in each of Tests 1–6. The *maximum* deviation from the individual mean time of release varied from 2 to 33 min., with an average value of 12 min. In all tests (except Test 4, a repeat) the weather was sunny with well-broken cloud. In Test 7, twenty-two birds were released 6 hr. earlier or later than their previous mean time of release, and twenty-three control birds were released at their normal time. In the course of 6 hr. the sun's position in azimuth changes through 90°, and the early and late birds would be expected to depart to the east and west instead of to the south, *if* they had learnt to fly at a fixed angle to the sun. Fig. 4 makes it clear that no such effect was obtained. Only two birds were within 30° of the fixed-sun-time direction, and these can be considered as the limits of scatter about the true home line. Comparing overall performances we have:

No. birds	Orientation time	Within 30° of home	Homing speed	2nd day	Stragglers
22 early and late	4·7	10	30·3	4	—
23 normal	5·4	13	31·3	1	1

The radical alteration in time of release may therefore have occasioned some confusion, but without directional significance. If these birds were using the sun to find the home/training direction, they must be able to appreciate and allow for its movement across the sky, without having witnessed that movement.

There remained the possibility that pigeons might fly at a fixed angle to the sun at an early stage of their training. This was tested in the course of releases off the training line which are discussed later (see Fig. 6). In Test 12, ten pigeons that had only flown twice from 25 miles were released 6–7 hr. later than their individual release time in Test 11. None vanished within 30° of the fixed-sun-time line.

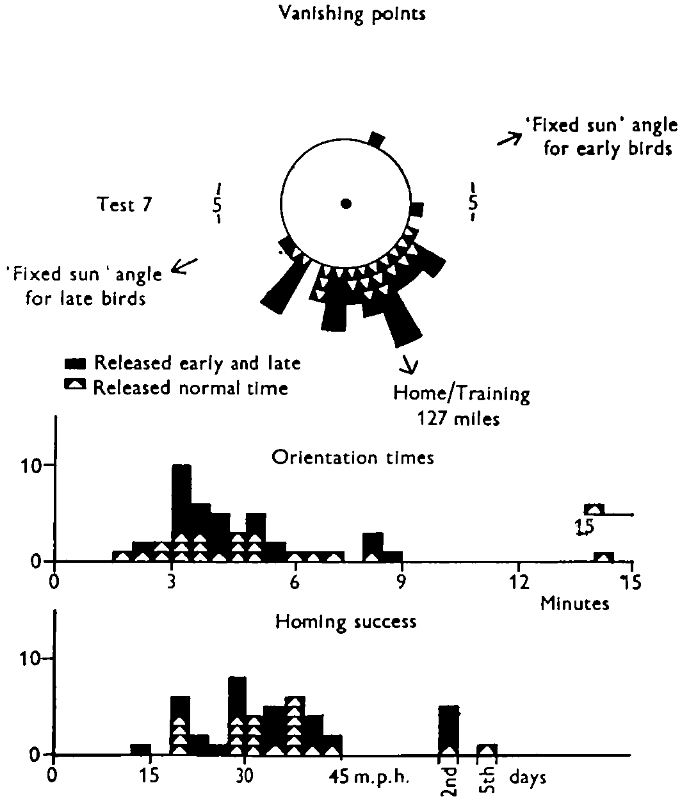

FIG. 4. Absence of a fixed sun-time-direction relation.

A further ten were used in Test 15, having flown 25 miles twice and 53 miles twice on the training line. The maximum deviation from the individual mean time of release in Tests 11, 13, 14 varied from 2 to 10 min. In Test 15 they were released between 5 and 7 hr. later. Two of these vanished within 30° of the fixed-sun-time line, but no significance can be attached to this as the general departure 'fan' was wide.

These results strongly suggest that at no stage in their training do young pigeons learn to fly at a *fixed* angle to the sun's position in azimuth.

BEHAVIOUR OF PIGEONS WHEN RELEASED OFF THE TRAINING LINE

There are many instances known in which pigeons have homed successfully from directions other than that of training, but these were generally accidental or the result of emergencies. Thus in Test 3 one bird arrived with a 'foreign' group at their loft in Birmingham. Released there at 18.50 the next day, it reached its home, 90 miles away in a novel direction, before 0730 the next morning. A few experiments have been reported that suggested that pigeons were not entirely dependent on the training line (Thauzies, 1909; Riviere, 1929; Gibault, 1933; Heinroth, 1941). The data provided was limited or otherwise unsatisfactory however,

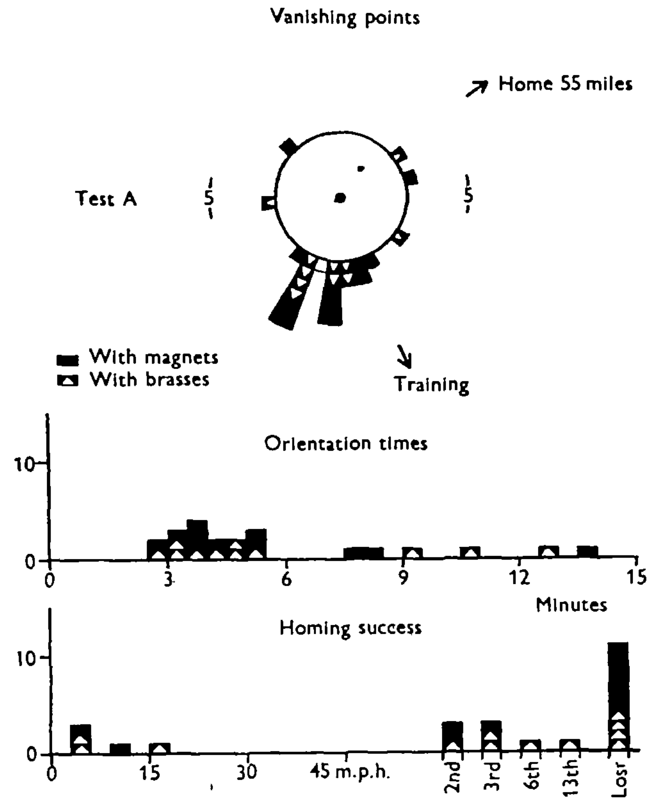

FIG. 5. Partially trained pigeons: orientation in training direction. Absence of effect by magnets.

and had little weight when compared with the heavy emphasis on one-direction flights in pigeon racing. A series of tests have therefore been carried out to determine whether pigeons, after varying amounts of training, could distinguish the home direction from the training direction when the two were no longer coincident.

In Test A, twenty-four pigeons that had had a minimum of training—grouped releases up to 16 and 18 miles north and north-west of the loft—were released singly 55 miles south-west, the home line now making an angle of 107° with the training line. The results (see Fig. 5) were:

No. birds	Orientation time	% Within 30° of		Homing speed	2nd day (%)	Stragglers (%)	Lost (%)
		Training	Home				
24	5·8	39	9	9·2	12	21	46

These birds showed a strong tendency to start out in the training direction, resulting in slow, straggling returns and the loss of nearly half their number. Two did start out in the home direction, both returned, one giving the highest speed of the test. Eight of the survivors were released again at the same point (Test B). The training line was abandoned, but no concentration in the home direction was observed. Homing success was, however, much improved, all save one returning on the day at an average speed of 21·7 m.p.h.

Four more tests were carried out with birds that had had more training, details of this and the results being tabulated below:

Test	No. birds	Previous training to N.N.W.	Release point	Angle between home/training lines
12	10	25, 25 miles	49 miles W.	079°
15	10	25, 25, 53, 53 miles	62 miles W.	082°
8	47	24, 24, 49, 49, 78, 78, 127 miles	79 miles W.S.W.	090°
9	33	Ditto and test 8	69 miles S.S.E.	175°

The relation of release points to the training line can be seen from Fig. 1. All releases were in sunny conditions with well-broken cloud. Results:

Test	Orientation time	Within 30° of		Homing speed	2nd day (%)	Stragglers (%)	Lost (%)
		Training (%)	Home (%)				
12	5·8	20	40	22·6	30	Nil	30
15	4·1	10	30	26·9	30	10	20
8	3·3	23	30	23·2	25	9	13
9	4·5	Nil	35	17·7	21	3	6

These are expressed in histogram form in Figs. 6, 7 and 8.

These birds showed a stronger tendency to start in the home direction than in the training direction, the homeward orientation of the departure 'fan' being very clear in the last two tests. That shown in Fig. 8 is a striking testimonial to the almost complete abandonment of the training line. This is in complete contradistinction to the results of Test A. There were also fewer losses and faster returns. Before the implications of these results can be fully discussed it is very necessary to see whether there is any likelihood of the birds having had previous experience of the release points.

Pigeons on exercise are rarely absent for more than an hour or two, all of which may not be spent in flight. As they prefer to fly in groups it is unlikely that odd birds could slip away without being noticed. These groups are sometimes identified up to 10 miles from the loft, but again may be seen passing over the same locality several times. It is most unlikely that systematic probing in all directions is carried out. Very rarely young pigeons are seized with an unexplained panic and refuse to return to the loft for several hours. There was one such occurrence with the Duxford birds in 1949 (twenty-two used in Test 8 and fourteen in Test 9). Although they were out for a total of 7 hr. we can state with fair certainty that they did not go much more than 20 miles from the loft. This is based on resightings in the neighbourhood, and by odd birds dropping from the flock into 'foreign' lofts. It is quite certain that they could not have reached either of the release points for Tests 8 and 9. It is therefore probable that young pigeons will become familar with country round the loft to a maximum radius of 20 miles only.

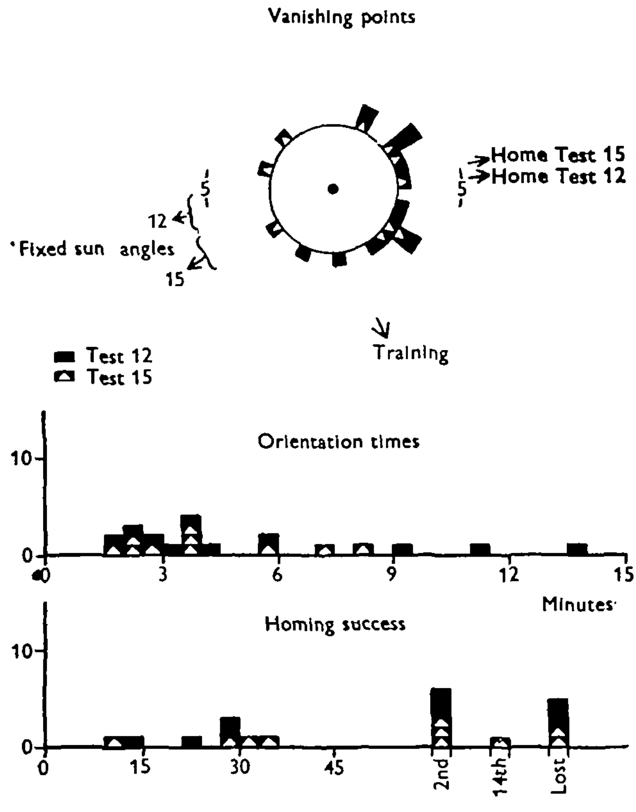

FIG. 6. Partially trained pigeons: orientation predominantly homewards. Absence of fixed sun-time-direction relation.

If the one-direction training had succeeded in its purpose the majority of the pigeons should have had no experience of country far to the west and south of the training line. In particular, birds that returned at high speeds could have deviated little from the straight training line. Those that in any one test did not return on the day might possibly have reached the critical release points. In Tests 12 and 15 only one bird was in this category, and this was lost on the critical test. The birds in Test 8 may similarly be divided into two categories. The second was extended to include birds that on any one test had been absent for longer than the time required to fly at 30 m.p.h. from the release point in question to the release point for Test 8 and on to the loft. In the same way birds in Test 9 may be divided into two categories to which the release point might respectively be considered unknown ('U') and possibly known ('K'). The division is here based on the performances in test 8, since it is from this release that stragglers were more likely to have reached the southern point. Comparing the performances of the two categories we have:

Test	No. birds	Orientation time	Within 30° of home (%)	Homing speed	2nd day (%)	Stragglers (%)	Lost (%)
8	23 'U'	3·1	35	24·8	22	9	9
	24 'K'	3·5	25	21·3	29	8	17
9	20 'U'	4·0	53	19·3	5	5	5
	13 'K'	5·3	8	12·9	46	Nil	8

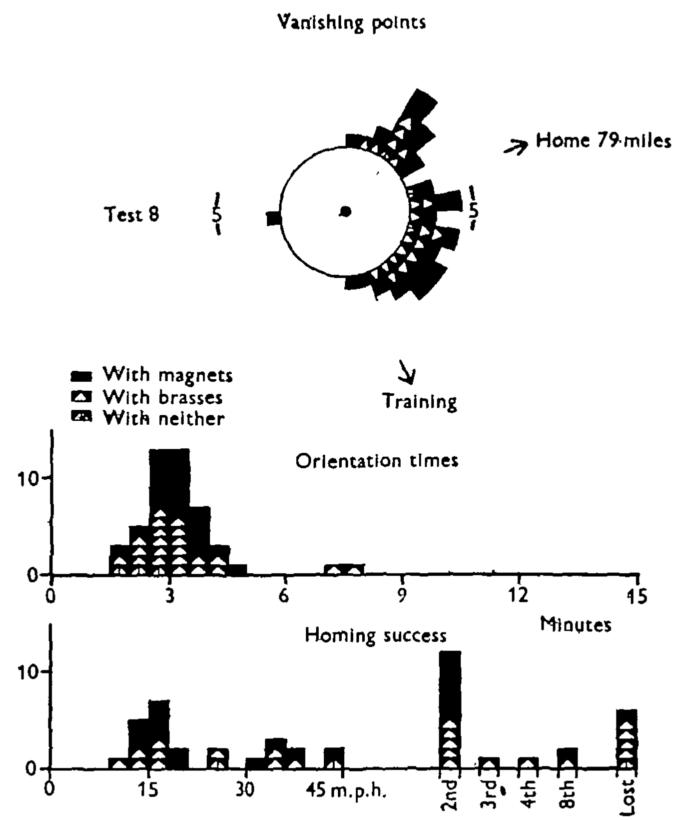

FIG. 7. Trained pigeons: orientation predominantly homewards. Absence of effect by magnets.

In both tests those birds that might possibly have had previous experience of the release point did considerably poorer in all respects than those which could not have had such experience, i.e. no question of knowledge of the surroundings can be invoked to explain the results.

It can therefore be stated that when young pigeons in various stages of training were released in unknown areas off the training line they showed a pronounced homeward orientation. This constitutes, perhaps, the most concrete evidence yet brought forward for the existence in birds of some form of true navigation in two co-ordinates.

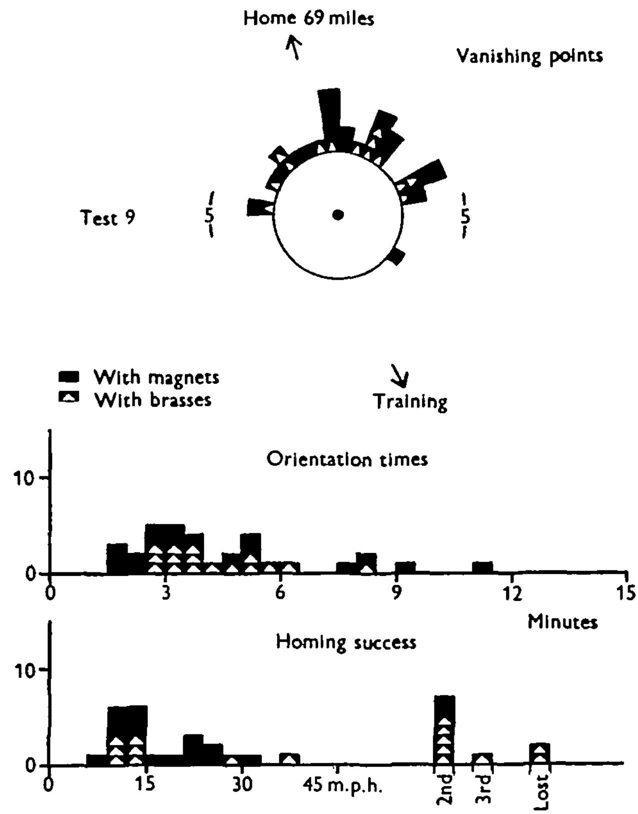

FIG. 8. Homeward orientation by trained pigeons. Absence of effect by magnets.

INDIVIDUAL VARIATION IN NAVIGATIONAL ABILITY

It has been shown that pigeons with blameless training histories put up the better performances off the training line, and this suggests that individual variation in navigational ability exists. If certain birds were superior performers in all respects it would be expected that they would do well no matter in which direction they were taken. The performance of thirty birds that took part in all the three major tests of 1949, Tests 7, 8 and 9, can be examined from this point of view. On the basis of their homing success in the last two tests they may be divided into three subequal categories:

'Good': day returns at high speed (av. over 24 m.p.h.)—9 birds.

'Moderate': day returns at low speed (av. below 24 m.p.h.)—8 birds.

'Poor': returned 2nd day or later in Test 8 and/or 9—13 birds.

Overall performances in the three main tests were:

	Orientation time			Within 30° of home (%)		
	Test 7	Test 8	Test 9	Test 7	Test 8	Test 9
Good	4·1	3·0	4·1	78	55	63
Moderate	4·2	3·2	4·1	63	12	25
Poor	6·1	3·4	5·7	60	23	17

	Homing speed		
	Test 7	Test 8	Test 9
Good	35·5	31·3	25·1
Moderate	28·2 and 2 on 2nd	15·9	11·1
Poor	25·7	13.3 and 7 on 2nd, 1 on 3rd	14.6 and 7 on 2nd, 2 lost

The nine 'good' birds gave better performances in *all* respects than the rest when released in unknown areas on an extension of the training line, at right angles to it or in the opposite direction. Again, in most respects the 'moderate' birds were consistently better than the 'poor'. The comparison cannot be carried back in detail to earlier releases at unknown points owing to insufficient data. The results obtained with these birds in Tests 3 and 5 may, however, be combined:

	Sorties	Orientation time	Within 30° of home (%)	Homing speed
Good	14	4·6	50	19·0 and 1 on 3rd and 4th
Moderate	14	4·1	36	18·6 and 1 on 2nd
Poor	21	4·8	45	19·9 and 1 on 2nd and 4th

In these earlier tests therefore no great differences are shown, nor would they be expected, as any special navigational ability would be of less importance on shorter flights over the training line. It is of interest to note, however, that only 14 % of the good sorties started out more than 45° off the home line, as opposed to 53 % of the other two groups.

When thirteen birds not used in all three major tests are classified rather arbitrarily on their partial performances, we find that of the sixty pigeons used in 1949, 18% were 'good', 15% 'moderate' and 38% 'poor', the rest being lost. This emphasizes the small proportion of pigeons that can be expected to become able navigators. The important conclusion is thus reached that there is undoubtedly a wide variation in individual navigational ability among pigeons that have received identical treatment. This indicates that the problems of bird navigation are unlikely to be solved by mass experiments that cannot distinguish individual performance from the effects of chance. Also solitary records of outstanding performances cannot be ignored. It complicates the experimental technique required, especially in the case of wild birds, and it may be that, for the present, work with pigeons is the only practical approach. It suggests an explanation for the conflicting results obtained in this field. In particular, the very different results obtained in Test A as compared with the other releases off the training line can be examined. Either the different lots of birds had equal potentialities but had developed them to different degrees, or they may have inherently possessed unequal potentialities.

The small increase of known territory prior to Test 12, as compared to Test A, would only benefit birds flying in roughly the home direction. This applies to a lesser extent to the other releases off the training line. It is possible, however, that there is a maturation of some navigational faculty during training, other than that of flying in the training direction. There is plenty of evidence that young pigeons that have received no training will fail to home from distances easily flown by trained birds of the same age. A few returns of untrained birds have been reported, but as they stand they could be attributed to chance. The present results indicate that if maturation through training occurs, it is very rapid during the early stages (e.g. between the equivalents of Test A and Test 12) and relatively slow thereafter. Possibly continuous training in one direction may actually blunt the development of any more advanced navigational faculties.

Another possibility is that some innate faculty develops independently of training, by a natural maturation process. The majority of the birds used in Test 12 were of the same age as those in Test A, but we may compare the performances of birds from two breeding 'rounds' of the same stock used on the same tests after the same training. No consistent differences in orientation behaviour were found; in particular, there was no tendency for the older birds to show stronger homeward orientation. On the training line the homing success of the two rounds was very similar, losses being equal, e.g. for Duxford stock:

Round	Age at first single release	1949		1950	
		Used	Lost (%)	Used	Lost (%)
I	20, 19 weeks	13	23	27	41
II	15, 14 weeks	19	26	28	36

In the case of the critical western releases, however, the round II birds had higher losses:

Test	Round	Age at test (weeks)	Used	Lost (%)	Stock
A	I	18	18	33	Easton
	II	13	6	83	Easton
12 and 15	I	20, 22	6	17	Duxford
	II	15, 17	8	50	Duxford
8	I	25	9	11	Duxford
	II	21	13	23	Duxford
20 (see p. 530)	I	24	10	10	Duxford
	II	20	9	66	Duxford

No other differences in the performances of the two stocks is to be discerned, th Duxford survivors in 1949 being classified:

Round	Good	Moderate	Poor
I	2	3	4
II	1	3	6

It is probable therefore that the difference between the two age groups is one of stamina, upon which heavy calls would be made on the critical releases, and is not due to any differential maturing of the navigational faculty.

There remains the possibility that the birds were of unequal inherent potentialities. There was no selection of the birds used in critical tests. In Tests 12 and 15 the birds were taken at random, in the other tests the whole available stock was used. Any natural selection of bad homers by losses on the training line was similar in all cases, amounting to 20% before Test A, 12% before Test 15 and 22% before Test 8. The suggestion is therefore that the Easton stock contained a smaller proportion of potentially able navigators. This cannot be checked directly, as the Easton birds were not subjected to full classification trials. We can, however, compare the performances of first round birds from two different stocks, Duxford (13) and Sawston (21), in 1949. These were subjected to the same tests under the same conditions throughout. Three Duxford birds (23%) were lost on the training line against one Sawston (5%). Both stocks lost one bird on Test 8. The survivors were classified:

Stock	Good	Moderate	Poor
Duxford	2 (15%)	3	4
Sawston	7 (33%)	3	9

These are indications that the Sawston stock contained proportionately more able navigators. It is therefore possible that the Easton stock contained even less than the Duxford stock, and so produced the observed difference in results. It would seem that the less able navigators can learn to fly in the training direction, but do not develop the more subtle faculty that permits them to determine the homeward direction. Insufficient controlled data are yet available to make a detailed analysis of pigeon-breeding records a rewarding one. It is of interest to note that ten of the birds classed as 'good' had sibs of the same age. Two were classed as 'moderate', five 'poor' and three were lost.

The probability that different stocks of wild birds may also contain different proportions of able navigators is an interesting speculation that cannot be developed further in this paper.

INVESTIGATION OF THE POSSIBLE FACTORS CONCERNED IN THE ORIENTATION OF PIGEONS IN THE HOMEWARD DIRECTION

It has been shown that at least a proportion of pigeons are capable of orientating themselves in the general direction of home, whether or not this coincides with the line on which they have been trained. They are further able to maintain this general direction over long stretches of unknown country. Such achievements clearly require a different order of navigational ability to that for flying in one particular direction only. Many theories have been put forward, and some have been examined experimentally in the course of the present work.

Any idea of random scatter from the release point may be excluded, likewise a spiralling out therefrom. Random search for known landmarks may also be discounted, for though a certain amount of search is carried out, it is largely confined to sideways sweeps about a general line of flight. While it is possible that air masses and wind directions would be of some help if they remained very constant, the rapidly changing weather conditions over England preclude such assistance in the present experiments. The pigeons homed successfully with head, beam and tail winds. Sensitivity to any of the effects produced by the earth's rotation may be discounted on theoretical grounds. Vague theories of 'space sense' and telepathy need not concern us here. The theory of a sensitivity to the earth's magnetic field has been resurrected by Yeagley (1948) and may be considered in more detail.

The original idea of some form of direct sensitivity has been replaced by one of indirect sensitivity, requiring the detection of minute electrical changes in the bird's body produced by its passage through the earth's field. The somewhat regular variation in the latter would then provide an indication in one co-ordinate of the relative positions of release point and home. There are strong theoretical objections to this modified theory which have been discussed in detail by Wilkinson (1948). Yeagley attached magnets to the wings of pigeons, thereby superimposing a pulsating field. He claimed that the performance of ten such birds was considerably worse than that of ten controls. The difference was not statistically significant and the loss in flight of several magnets suggests that they may have been unskilfully attached (sewn through the metacarpal joints) while brass control bars were put on by one used to such work. On this inadequate basis Yeagley embarked on a massive series of experiments, using hundreds of pigeons, which gave results he interpreted as showing that they navigated by means of a grid, one co-ordinate of which was provided by the detection of the vertical component of the earth's magnetic field, the other by detection of the Coriolis forces consequent on the earth's rotation. The planning of the experiments left much to be desired, observational bias was not prevented and the method of interpretation was faulty. The various experimental flaws that invalidate Yeagley's claims have been pointed out by Thorpe (1948). The 'magnetic wing' experiment was repeated by Gordon (1948) with entirely negative results. However, it was later found (Griffin in litt. 1949) that at least some of the pigeons had been previously used over the test course, and this throws doubt on the whole experiment. The theory was further tested on three of the critical releases off the training line in the present series.

Two methods of imposing a fluctuating field near the bird were used. In Test A (p. 517, Fig. 5) 4 g. steel magnets of 40 by 4 mm. cross-section and magnetic moment 100 gauss/cm.^{3} were hung round the birds' necks and in flight differential accelerations caused them to swing with an amplitude of at least 30°. A fluctuating voltage was thus induced in the head region of approximately 0·30 μV./cm., six times the minimum required to confuse measurement of the 'natural' induced voltage if we require a navigational accuracy of 25 miles. Similar brass rods were attached to the control birds, all being put into position the evening prior to release. In Test 8 (p. 520, Fig. 7) and Test 9 (p. 521, Fig. 8) Alnico magnets 20 by 3 mm. cross-section, weight 1½ mg., magnetic moment 100 gauss/cm.^{3}, were used. One was stuck with Bostik along the quill of the outer primary of each wing at the base of the barbs. Similar brass bars were mounted on controls. On the outspread wing the magnets were about 15 cm. from the mid-line, and with a wing beat frequency of 3/sec. and an amplitude of 7 cm. they would induce a fluctuating voltage varying between 0·16 and 0·11 μV. in the head region. Attachments were made 6 days before Test 8, and the birds given two 10-mile group flights from the training direction and also daily exercise. This accustomed them to flight with the additional weights without requiring them to exercise any special navigational faculties. No attachments were lost during the tests. Birds were released singly, two magnet releases

Test	Total	Orientation time	Within 30° of home	Homing speed	2nd day	Stragglers	Lost
A	12 magnet	5·7	1	8·4	2	1	7
	12 brass	5·9	1	9·7	1	4	4
8	22 magnet	3·3	9	22·5	7	1	1
	22 brass	3·4	5	21·9	5	3	4
9	17 magnet	4·6	8	17·8	2	Nil	Nil
	16 brass	4·5	3	17·3	3	1	2

being followed by two control releases giving the above results. There is no evidence at all that the magnets had any influence on the ability to orientate in the homeward direction and return home when released off the training line. In Test A, where the majority of birds orientated in the training direction, the magnets were also without effect, six birds with magnets vanishing within 30° of the training line as against three controls. We may therefore conclude that the detection and measurement of the earth's magnetic field plays no part in the simple or advanced types of navigation that have been demonstrated in the present tests. As the results are so entirely conclusive it is to be hoped that this theory will be finally discarded.

Generally connected with the magnetic theory have been many reports of birds disorientated by local electrical disturbances produced by thunderstorms, radio transmissions or radar. It is possible that such disturbances could, in certain circumstances, be detected by birds, but this would not necessarily prove that navigation was affected. As a test of any gross effects of radar, fifteen pigeons were released singly at R.A.F. Station, Waterbeach, Cambridgeshire, by kind permission of the Commanding Officer. The release (Test 19) was *in known country*, and the birds were subjected to 3 and 10 cm. beams from G.C.A. apparatus. Each bird was minutely observed through powerful glasses, but no change in demeanour was seen when entering or leaving the 3 cm. beam, nor when momentarily hit or followed continuously by the 10 cm. beam. There were no unusual evolutions nor any abnormal delay in departure, orientation time averaging 4·2 min. Pigeons held, or standing within a foot of the 3 cm. aerials, gave no reaction. A swallow flew steadily and unconcernedly across the path of both beams. Such a test is not, of course, entirely conclusive, but if any organ or faculty is to be thrown out of gear by radar transmissions there should have been some indication of this even if the bird was not actively using them.

The theory of displacement recording by time/acceleration measurement is also of respectable antiquity. The crude version requiring the outward path to be retraced is logically unsatisfactory, and the circumstances of Tests 12 and 15 form an experimental test. The birds were taken along two sides of a triangle, the apex of that in Test 12 being the release point for Test 13, and in Test 15 that for Test 16 (see Fig. 1). Seven of the birds homed at speeds that showed that they must have completed the third side of the triangle. The more refined version requiring the maintenance of a constant appreciation of the home direction by a process of triangulation is theoretically most unlikely to be within the power of the organs at an animal's disposal. A number of attempts have been made to disrupt the normal function of the proposed mechanism (especially of the semi-circular canals). However, critical examination of the evidence shows that in all cases the possibility of birds homing by sight and search alone has not been excluded. Further tests were therefore made in the present series.

Pigeons were carried to the release points in a large lightproof drum turning horizontally at four revolutions a minute. The drum being slightly unstable, changes in speed and direction of the transporting vehicle caused it to press on its bearings and produce a momentary slowing. The outward journey through space of the individual birds was thus remarkably complicated by an irregularly varying rotation, about 1200 revolutions on the longest journey. In Test 18 seventeen birds were released 130 miles north-north-west (after training up to 87 miles north-north-west) following rotation on the outward journey of 4 hr. 55 min. Eighteen birds were carried in the usual covered baskets to act as controls. The rotated birds included all those that had been used in Tests 12 and 15, and thus had less experience of the training line. In Test 20 the birds were released 81 miles from the loft at right angles to the training line, sixteen being rotated for 4 hr. 10 min. and fourteen taken as controls. The latter included all the birds that had been rotated previously, i.e. none of the rotated birds in Test 20 had any previous experience of western releases. Lastly, in Test 21 the survivors were released 68 miles in the opposite direction to that of training, eight being rotated for 3 hr. 50 min. and eight taken as controls. In all cases birds were released singly, two rotated being followed by two controls. The results for these three tests are given below (see also Figs. 9, 10):

Test	Total	Orientation time	Within 30° of home	Homing speed	2nd day	Stragglers	Lost
18	17 rotated	4·5	8	20·9	2	3	Nil
	18 controls	5·1	10	20·1	2	1	2
20	16 rotated	6·6	5	15·7	2	3	5
	14 controls	6·8	2	19·5	4	3	4
21	8 rotated	9·5	1	10·4	Nil	1	2
	8 controls	5·5	2	15·0	2	1	3

As no significant differences are to be discerned between the two categories, it can be said that rotation on the outward journey does not affect navigation from an unknown point on an extension of the training line or in radically different directions. It is therefore extremely unlikely that navigation in pigeons makes use of any time/acceleration mechanism. An absolutely final answer would require similar critical

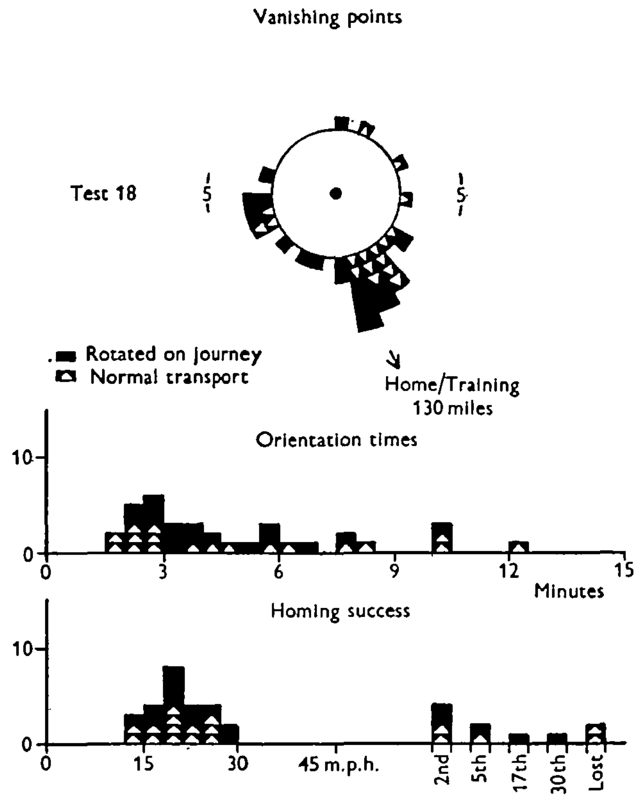

Fig. 9. Absence of effect by rotation on outward journey in release on training line.

releases of pigeons in which the probable receptors for acceleration measurement—the semicircular canals—had been destroyed. Such operative procedure is undesirable, as the effects may be more widespread than anticipated, and only negative results would be acceptable. Transport under heavy anaesthesia would be another test, again not absolutely final. The observation that most pigeons doze or sleep on the outward journeys is in itself an argument against a displacement-measuring mechanism.

We have seen (p. 514) that overcast skies had an adverse effect on orientation at a point on the training line, and the suggestion was that the pigeons were using the sun's position to determine the training direction. Test 7 (p. 516) showed that they must then be capable of taking large changes in azimuth into account and of at least ignoring large changes in altitude, and still be able to determine a particular direction.

This raises the query whether a pigeon could 'fix' its position by the classical method of mariners—latitude from the sun's altitude and longitude by time differences as observed from its position in azimuth. It is improbable that a pigeon could do this from a glimpse of the sun on any day of the year, as this would require a detailed knowledge of the apparent changes in the sun's position throughout the year. The observed general homeward orientation would, however, be explained if the birds

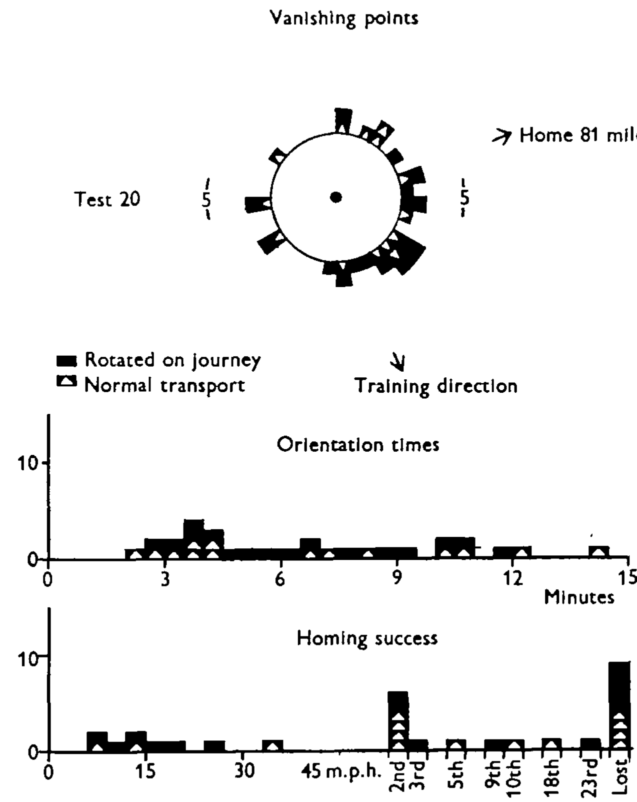

FIG. 10. Absence of effect by rotation on outward journey on release off training line. (Effect of overcast see Fig. 11.)

could detect a gross difference between displacement north or south and east or west of the loft. To use the information available from the sun's position at the time of release (varying between 0530 and 1300 G.M.T.) the birds would be required to (1) estimate the highest point of the sun's arc; (2) measure the sun's altitude at that point and the time (according to some independent chronometer) at which it would be reached (alternatively, the angle in azimuth that the sun's observed position made from the estimated south point might be measured); (3) compare these measurements with those obtaining at the loft on, say, the previous day; (4) interpret the difference between the two sets of measurements.

The arc traced out by the sun and the speed at which it moves along that arc remains practically constant from day to day, though, of course, the amount of the arc above the horizon changes progressively. Given an intimate knowledge of these factors it would theoretically be possible to estimate the highest point, and when it would be reached, from an observation of the sun's movement over a part of the arc. But, as the birds were unable to see the sun before release, the time available is only the average orientation time, during which the sun would have moved only about two diameters along its arc. Further, with displacements from the loft of the present order, the maximum angular differences from home conditions would be less than four diameters, and time differences less than 8 min. Measurements would have to be accurate to well within these limits. There is little evidence of any independent time-keeping mechanism in birds, and none as to its accuracy, but some form of physiological chronometer cannot be ruled out of hand. It should be noted that there are no definite physical limitations in the organ concerned with angular measurements, the bird's eye having a high resolving power, being adapted for the detection of movement and suffering no inconvenience from glare.

Even if the necessary measurements could be made they would still have to be compared with those made previously, requiring a remarkable spatio-temporal memory. The interpretation of the differences would also be difficult to credit. By being trained to the north the birds previously had actual experience only of a decrease in altitude and a slight decrease in azimuth. The interpretation of a large decrease in azimuth in Test 8 and an increase in altitude in Test 9 would necessitate advanced reasoning on the part of the birds or inherited information to cope with all possible combinations. It may be noted, however, that learning and individual experience does not seem to play as great a part in pigeon navigation as might be thought. This is suggested by the general lack of continuous improvement in navigational ability with further training (p. 518), and by the results of preliminary laboratory experiments (Matthews, 1950) which have indicated that navigational ability is not positively correlated with the ability to learn simple problems using visual clues.

While this simplest use of the sun's position for pure navigation would seem to be improbable, it is important that the theory should be tested experimentally. Work on these lines has not proceeded very far as yet. It is difficult to obtain completely overcast conditions with suitable flying weather in summer, as anticyclonic conditions do not produce the well-known 'gloom' seen in winter. Cyclonic overcast is frequently broken and of short duration. However, the effects of overcast on two critical releases off the training line have now been observed. In Test 20 (Fig. 11) thirteen birds were released singly with a high thin overcast and 9/10th to 10/10th low thick cloud cover. A rainstorm now developed lasting an hour, seventeen birds then being released singly under 8/10th low thick cloud. In Test 21 (Fig. 12) sixteen birds were released under low overcast conditions, though while eight of these were being released the sun was very faintly visible through the momentarily lightened clouds. The results in these tests may be compared with those made at the same places in 1949, Test 8 and Test 9. In the former the sun was visible throughout the releases, the only cloud being high thin stratus 5/10th to 8/10th, while there was brilliant sunshine with cloud never exceeding 3/10th in the latter.

Test	Conditions	Orientation time	Within 30° of (%)		Homing speed	1st day (%)	Total
			Training	Home			
20	Overcast	7·8	38	15	10·9	38	13
20	8/10th	5·7	41	29	24·4	24	17
8	Sun	3·3	23	30	23·2	53	47
21	Overcast	8·6	37	37	12·2	25	8
21	Overcast, sun visible as a disk	6·1	25	Nil	11·5	63	8
9	Sun	4·5	Nil	35	17·7	70	33

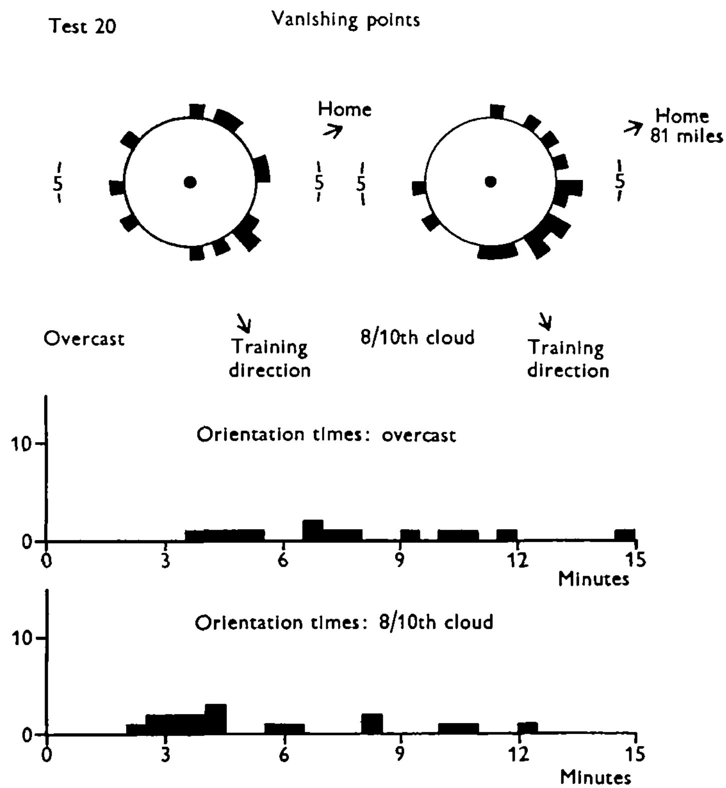

FIG. 11. Effect of overcast conditions on orientation in a release off the training line.

The comparisons certainly suggest that conditions of heavy cloud were having an adverse effect on orientation, though all the trends are not consistent. The increase of average orientation time with increasing cloud cover is noticeable in releases from both points. In Test 20 birds released under complete overcast returned slower, having shown poorer homeward orientation, than those released under 8/10th cloud. For Test 21 the few birds available does not make any strict comparison between the two groupings possible, but again more were back on the first day when they had been released with the sun visible as a disc. In both these tests there was a noticeably high proportion near the training line, which might be determined roughly from the sun's general position even when its co-ordinates could not be determined with accuracy. Only one bird started in this direction on both occasions, so there was no inability to fly in any direction other than this. Too much stress cannot be laid on homing success when comparing Test 20 with Test 8, as several heavy

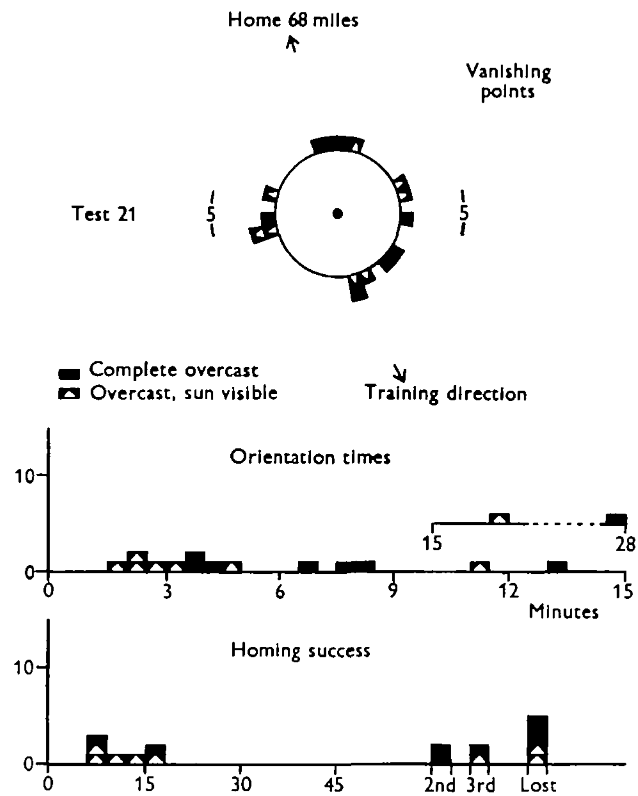

FIG. 12. Effect of overcast on release in opposite direction to training line.

thunderstorms developed across the homeward track accompanied by gale-force winds. For Test 21, however, flying conditions were excellent, and the overcast broke during the afternoon. There was a slight head wind instead of a tail wind as in Test 9, both of Force 2–3.

It is, of course, possible that the poorer showing in the 1950 tests was due to there being a smaller proportion of able navigators than in 1949. There can be no direct check of this, but it is unlikely to be more than a part of the answer. Thus a number of the birds used in Test 20 had previously homed well from releases off the training line (Tests 12 and 15). In the other major release, to the north, the performances in the two years was similar—compare Fig. 4 with Fig. 9; a rather poorer homing performance in 1950 being explained by bad weather conditions which developed across the track. In any case there are still the differences within the tests themselves to be explained.

We have therefore at least a suggestion that overcast has a disorientating effect on pigeons released off the training line. Clearly more work is required to confirm or deny this, but as it is the only positive indication that has been obtained this should be well worth while. The requirements for rough sun navigation outlined above are also open to experimental investigation, particularly the necessity for an accurate physiological time sense and for a recent experience of sun conditions at the home loft. If it should be shown that pigeons are dependent on the sun for navigation this would fit in well with the fact that they will not home at night or in dense fog. It is true that much migration in wild birds takes place at night or beneath overcast, but if, as much contemporary work suggests, migration over unknown country is in a general *direction* only, the latter could have been determined at sunset or by a short glimpse of the sun respectively. In homing experiments with wild birds no returns have been made at such speeds as would have necessitated flying through the night.

RECORDING OF THE HOMEWARD TRACK IN PIGEONS

It would clearly be useful if we could have an accurate account of the homeward track, particularly when (as with wild birds) the overall speed is small and evidence is required as to how much exploration has taken place. However, the most interesting pigeons are those that home swiftly from various directions and can have deviated little from the straight line. Determination of the track components would still be of value, especially when assessing the efficacy of any method of disorientating the birds. Developments could also be applied to wild birds.

Griffin (1949 in litt). and Hitchcock (1950) have been successful in following flocks of pigeons by means of aircraft. The wide individual variation in navigational ability suggested by the present work makes it doubtful whether the tracking of flocks would produce results of sufficient interest. Accordingly, attempts have been made to follow individual pigeons and small groups, by the courtesy of the Officer Commanding, Cambridge University Air Squadron, and with the enthusiastic co-operation of his officers. Three types of aircraft were tried, the most useful being an Auster Mark VI, which has a low stalling speed, good all round visibility and carries two observers. That available lacked both intercommunication and wireless contact with the ground. The trials involved three individual pigeons and fifteen groups of three birds. None of those available had much white in their plumage, and the light 'mealy' birds, otherwise the most visible, were quickly lost over ripening corn. Great difficulty was experienced in holding the birds in sight during their frequent sharp changes of course, and in the event no group was followed for for more than 10 min.

Automatic recorders of the track, attached to the bird itself, would be most useful. A start has been made with the flight duration recorder designed by Wilkinson (1950). This was used in Test 8 in 1949 and on a larger scale in 1950. Attention has been directed to full trials of the apparatus itself, and the elimination of various snags and inadequacies that were not at first apparent. The number of satisfactory flight records is limited and does not merit publication at present. General conclusions to date are that young pigeons will fly for up to 6 hr. on the day of release, those returning after a longer interval generally having been down for some of the time, though one continuous flight of 10½ hr. is recorded. In the case of those returning on the second or subsequent days the average daily flight has been about 4 or 5 hr., even in one that returned on the 18th day.

REVIEW OF RESULTS, AND CONCLUSIONS

This series of experiments has shown that pigeons are capable not only of learning to fly in a fixed direction on release in unknown country, but of orientating in the homeward direction when released off the training line. The latter ability varies widely between individuals and probably has an inherited basis.

Several of the theories that have been put forward are too unsatisfactory theoretically to need further investigation. Others can be considered to have been eliminated by the present work, at least in the case of pigeons. They are: random or systematic search for landmarks, use of atmospheric clues, measurement and interpretation of the earth's magnetic field, and displacement recording by a time/acceleration mechanism. It has been shown, however, that overcast skies had an apparently disorientating effect on pigeons released on and off the training line. The use of the sun to obtain the training direction would be quite reasonable, though it has been shown that it is not by means of any constant sun-time angle. Suggestions have been put forward for a rough form of true navigation involving the measurement of the sun's position in two co-ordinates. This seems to be most unlikely but not wholly impossible. Much more work in this direction is clearly required.

The present research has thus by no means solved the problems of bird navigation. It has, however, shown that there *are* problems to be solved, and indicated a possible line towards their solution.

SUMMARY

1. A series of field experiments were carried out in 1948, 1949 and 1950 to establish the facts of navigation in homing pigeons and to begin an investigation of the factors involved.

2. A total of 158 pigeons aged 3–4 months were used in twenty-three tests involving a total of 902 sorties, all but 153 being by birds released singly.

3. Three indices of performance were used, giving the degree of uncertainty on release, the accuracy of the initial course and the success in regaining home.

4. It was shown that pigeons are able to fly in one particular direction when released at a series of unknown points at increasing distances north-north-west of the loft. The following of experienced birds or the use of distant landmarks were excluded.

5. Overcast skies had a disorientating effect on these training-line releases. It was shown that if the sun was being used to determine the training direction, it was not by any simple fixed-angle relationship to home. The birds could take large

changes of azimuth into account, and at least ignore changes in altitude, without having witnessed the sun's movement.

6. Releases were also carried out in unknown areas at right angles to or in the opposite direction from the training line. Some of the birds flew in the training direction and homed badly. But a good proportion showed a definite orientation in the home direction and returned with fair success.

7. This true navigational ability was shown to vary widely amongst individual pigeons. The proportion of able navigators also varied in different stocks. There is little evidence of a continuous maturation of the faculty with experience and none with age. There are suggestions that it is not connected with a learning process.

9. The established facts require more than a random or systematic search for landmarks, or the use of atmospheric clues as an explanation.

10. It is shown by experiment that pigeons do not depend on the interpretation of the earth's magnetic field to be able to orientate in the training or in the home direction.

11. Other experiments show that a displacement recording mechanism based on time/acceleration measurements is extremely unlikely.

12. The only positive lead obtained is a definite suggestion that overcast had a disorientating effect on pigeons released *off* the training line. This requires detailed confirmation. The simplest way in which a pigeon could obtain a rough estimate of its position relative to home by measuring the sun's co-ordinates is considered.

13. Attempts to follow individual pigeons or groups of three by aircraft have so far been unsuccessful. An automatic flight recorder has been used successfully to some extent.

I should like to acknowledge my outstanding debt to Dr W. H. Thorpe for his constant encouragement and facilitation of my work. Dr D. H. Wilkinson has been an invaluable guide in matters physical, especially magnetic problems, and actively helped in several field tests. The experiments would have been impossible without the part played by Messrs P. Cope (and his loftman, S. Small), L. R. Duke and L. A. Meredith in rearing the birds and undertaking their preliminary training. For practical advice and assistance I am indebted to Drs R. H. J. Brown and M. G. M. Pryor. I am most grateful for the stimulation of personal discussion of this research with Prof. J. Gray, Drs H. B. Cott, R. G. Newton, A. Landsborough Thomson and Messrs W. B. Alexander and R. E. Moreau. Similarly, I have benefited from correspondence with Profs. D. R. Griffin, H. B. Hitchcock and V. C. Wynne-Edwards. The work was part of a programme of research carried out while I was in receipt of a Maintenance Grant from the Ministry of Education. Part of the experimental expenses in 1949, and all those in 1950, were met by a grant from the Royal Society. I should like to express my deep gratitude to both these bodies.

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