DOES NAVIGATION WITHOUT VISUAL CLUES EXIST IN ROBINS?

by

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INTRODUCTION

Kramer's discovery of birds being able to display migratory orientation in a circular cage has provided us with a new valuable tool in the study of bird navigation (Kramer 1949, 1950 a, b, 1951). I propose to call in future all types of such cages Kramer-cages, as a memory to this brilliant investigator.

Kramer found that caged day migrants were disorientated when the sun was hidden behind clouds. In a similar way Sauer (1957) observed oriented movements of night migrants only when the stars were visible. Orientation, dependent on visibility of sun or stars could also be demonstrated in the initial directions taken by homing or migrating birds after release (Matthews 1955, Kramer 1957, Bellrose 1958). This evidence led to the formulation of navigation theories based on sun and stars as the only visual clues (Matthews 1951, Pennycuck 1960, Sauer 1960).

Although a sun compass could be demonstrated (Hoffmann 1954, 1960), the Kramer-school rejected these navigation theories for both experimental and theoretical reasons (Kramer 1957, Hoffmann 1958, Wallraff 1960 b, c, Schmidt-Koenig 1960, 1961 b). No alternative theory could be given, but Kramer (1953) introduced the map-and-compass concept. In this opinion the sun is used as a compass only, even in homing or goal orientation. The basis of the orientation, however, is the "map", i.e. the ability of the bird to react to certain geophysical clues. Although the nature of these clues is unknown, it is improbable that they would lead the bird in a straight course towards the goal. The bird is therefore supposed to discover the direction of this straight line from the "map" and then to keep this direction with its sun-compass. This theory implicates that, although with unclouded skies a quicker return is possible, the bird might be able to come home also when celestial bodies are invisible. It has only to follow the geophysical clues that form his "map".

In this light it seems of utmost importance to find out whether orientation without visual clues is really possible. At the moment there are
several claims in the literature that this is the case. When studying the behaviour of starlings in a Kramer-cage I found that one bird in the course of 2½ weeks gradually improved its orientation under heavily overcast conditions (Perdeck 1957). The landscape was masked and the cage was turned during the tests. Acoustical orientation, however, could not be excluded. Schmidt-Koenig (1958) also obtained direction-finding of pigeons in cage experiments under overcast conditions, whereas both Hitchcock (1955) and Wallraff (1960a) reported overcast releases of homing pigeons, where initial orientation was accurate. In these cases one cannot exclude the possibility that the birds were still able to locate the sun, owing to a presumably greater ability to distinguish tones of grey, as compared with man.

Gerdes (1962) placed Black-headed Gulls, freshly taken from their nests in Kramer-cages at various distances and directions from the colony. The escape movements of the birds were home-directed, not only in overcast conditions (without sight on landmarks, of course), but also indoors in a lecture room of rather symmetrical structure. Thus, incidentally, Gerdes was the first to demonstrate homing orientation in a caged bird. Fromme (1961; Merkel & Fromme 1958) studied Robins and Whitethroats in Kramer-cages with automatic registration. The movements of nightly migratory restlessness were oriented in the direction to be expected according to the season under the following conditions.

1. With sight on the sky only, both under starry and heavily overcast conditions (autumn, Robin).
2. Outdoors, but cage evenly illuminated (spring, Robin).
3. In a forcing house and a big tent, cage evenly illuminated (spring, Robin).
4. In a cellar, without windows (spring, Robin; autumn, Whitethroat). Orientation broke down in a climatic room with steel walls, but there was still some orientation when not all doors were closed (Robin, autumn). In this room at least at the place where the cage stood, the earth’s magnetism was not disturbed.

These experiments indicate strongly that Robins and probably also Whitethroats were able to find their direction of migration without visual clues from celestial bodies.

A confirmation of both Gerdes’ and Fromme’s results was needed. In this paper experiments with Robins similar to those of Fromme, are reported.
ACKNOWLEDGEMENTS

The registration apparatus was built by my assistant Mr. A. J. de Zwart. He was aided in electrical matters by Mr. J. Veringa.

The manuscript was read by Prof. Dr. H. Klop, Dr. H. N. Kluijver and Dr. G. V. T. Matthews; I am grateful for their remarks. Dr. Matthews kindly revised the English text and drew my attention to some deficiencies in Fromme’s paper (see under Discussion).

APPARATUS AND EXPERIMENTAL SITUATION

The experiments were carried out in a temporary home of the Vogeltrekstation, a wooden bungalow north of Arnhem in the direct surroundings of which no heavy buildings or factories occur.

![Diagram](image)

**Figure 1.** Plan of building.

The Kramer-cage was placed in a room of $2 \times 3$ m, height 2.75 m, with one window and two doors (room A in Fig. 1). Light from outside the room was excluded. The cage itself consists of two main parts: an outer and an inner cage (Fig. 2A). The outer one is hexagonal, each of the six sides 55 cm high and 66 cm wide. The cage has a wooden frame and bottom. The sides are exchangeable. During these experiments they were from hard board. On top an opaque (milky) plexiglass plate of 3 mm thickness is placed. A bulb of 15 Watt is hanging 35 cm above
the centre of the top plate, the light being subdued by transparent paper. By this bulb the interior of the cage is very evenly illuminated. On the bottom a contact apparatus for automatic registration is mounted. From the inside of the cage only a ring of 16 buttons is visible, each button connected with a registration device and corresponding to one point of the compass (Fig. 2B).

During the experiments the bird is housed permanently in the inner cage, that can be moved in and out the outer cage freely. This has the advantage that the bird is not seriously disturbed when changing from resting place to experimental situation. This inner cage is circular with a diameter of 62 cm and a height of 38 cm. It consists of a metal frame and is covered with nylon network (Fig. 2C). The metal bottom of the cage has 16 holes corresponding with the buttons of the outer cage which protrude into the inner cage when it is brought in position. Each button then raises a small lid at the end of which a perch is fastened. The circle formed by all perches together has a diameter of 47 cm. In the middle of the cage food and water for the bird are placed, as symmetrically as possible, generally by placing a small water-container in the middle of the food tray.

When the bird alights on one of the 16 perches, the button is pressed down and, by means of a microswitch (Fig. 2E) an electrical contact is made, resulting in the shifting of one figure of an electrical counter. The 16 microswitches correspond to 16 counters and the position of the microswitches is fixed and set in the real compass directions beforehand. The outer cage, together with inner cage and buttons, can be turned by hand. After each turn one has only to care for a good connection between buttons and microswitches. Then the movements of the birds are directly registered in the true compass directions (Fig. 2F). The counters have to be read at the beginning and at the end of each separate experiment.

The microswitches were also connected with a chronograph, which continuously records the activity of the bird. The observer together with counters and chronograph remained during the experiments in the adjacent room, at B in Fig. 1. He entered the experimental room only to shift the position of the cage and to make observations on the behaviour of the bird. When the observer was in the experimental room, the apparatus was stopped.

The bird remained in the experimental situation for several days. At night only the 15 Watt bulb was burning, during the day the normal room illumination was added, consisting of two fluorescence lights,
FIGURE 2. A. Kramer-cage, outer cage partially dismantled. B. Bottom of cage, inner cage removed, showing buttons. C. Inner cage with perches hold up by buttons. D. Inner cage with registration apparatus (chronograph, set of counters and voltage regulator). E. Connection of buttons with microswitches. F. Electrical counters for each point of the compass. Master counter on top. Chronometer is used to measure time spent by bird on perches.
each 40 Watt, attached to the ceiling (not immediately over the Kramer-cage). The night-day rhythm was held constant, but was not the same in all experimental periods: the night lasted from 6.45 p.m. till 6.00 a.m. (March 29 till April 10) or 6.30 p.m.-5.00 a.m. (April 10-13) or 5.30 p.m.-4.00 a.m. (April 13-22). This shift was made in order to have the birds more active in the first part of the night, the most convenient time to watch. A definite effect was, however, not observed. When the daylight switched on, the counters stopped automatically.

Since we know that caged birds very quickly orient themselves to irregularities of the cage (although it is built as symmetrically as possible) frequent turning of the cage is of paramount importance. During the experiments the cage was turned after a certain number of contacts (measured by a master-counter, that registered the contacts from all perches), the number per unit of time depending on the activity of the bird. In the beginning the cage was turned alternatively, 90° and 180°, resulting in four different positions, at right angles to each other. Later 16 different positions were used, always in groups of 4, with 2 pairs of opposite directions at right angles (e.g. a certain part of the cage was pointing into different directions in this order: N, S, E, W; NNW, SSE, ENE, WSW; etc.) In each experiment, lasting 2-5 hours, the position of the cage was altered 12-16 times. When an experiment was finished the apparatus was left on and next morning the counters gave data on the behaviour of the bird in a fixed cage position.

The birds

Three Robins (*Erithacus rubecula*) were used. They will be indicated by the letters A, B, and C.

Robin A was caught near The Hague on September 29, 1962. Inspection of the ossification of the skull through the skin revealed that it was a bird of the year. Robin B was caught at Meppel on Febr. 16, 1963, and Robin C at Oosterbeek (near Arnhem) on Febr. 18, 1963. The age of these two birds is unknown. Robin A could be a passage-migrant, B and C wintering birds, from north-eastern countries. The experiments were carried out in the period of spring migration (March, April).

All birds showed a distinct activity at night that can without doubt be interpreted as migratory restlessness (Fig. 3).

The movements of the birds within the cage could be watched through a small hole in one of the sides of the cage. Sometimes the bird flew from a perch to the top of the cage, circled around and alighted on
another perch. Or it behaved like a flycatcher, returning to the same or a neighbouring perch. More commonly however, swinging movements from perch to perch, net to net or perch to net between more or less opposite parts of the cage were observed. But the behaviour varied a great deal and more random movements were common. Visits to food and water vessel in the centre were dispersed between flights. It is important to note that, when perching, the bill was pointing mainly towards the outside of the cage. Thus, although only positions in the

Figure 3. Activity of the birds during 24 hours. On the ordinate activity is plotted, expressed as the number of 2-minute periods per hour in which at least one movement of the bird was registered (maximum 30). The graphs are the mean of at least four complete 24 hour periods.
cage were registered, these positions often indicate the direction of the body axis of the bird. Quivering movements with the wings were often observed. They are probably intention movements of flying and comparable with the typical wing fluttering described by KRAMER (1949). Occasionally the bird called with a short, high-pitched note.

**STATISTICS**

The randomness of the movements was tested by the vector method as described in SCHMIDT-KÖNIG (1961 a: 242). This test appears to be very sensitive. But it has the disadvantage that an orientation in two opposite directions (that might occur easily in a caged bird) is not detected. Therefore the experiments were also tested with a variant of the KOLMOGOROV-SMIRNOV test, adapted to the circular distribution (KUIPER 1960).

The paper of KUIPER is difficult to understand for a non-mathematician. I therefore give a short recipe of this test, which I owe to Mrs. E. M. GRUYSCASIMIR. Cumulate the values of the various directions from a certain arbitrary starting direction. Calculate the theoretical cumulative distribution under random conditions, each direction having then the value of N (total number of observations) divided by the number of directions. Compare the experimental and the theoretical cumulative distribution and pick out the two directions with the maximum positive and the maximum negative difference between experimental and theoretical values. The sum of the absolute value of these two differences divided by N is called $V$. Calculate $V \times \sqrt{N}$. Compare this value with Table 1. When it is greater than the value from the table (chosen according to significance level $P$ and value of $N$), the distribution deviates significantly from the theoretical random distribution.

<table>
<thead>
<tr>
<th>$N$</th>
<th>$10$</th>
<th>$20$</th>
<th>$30$</th>
<th>$40$</th>
<th>$100$</th>
<th>$\infty$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$.10$</td>
<td>1.4877</td>
<td>1.5322</td>
<td>1.5503</td>
<td>1.5608</td>
<td>1.5839</td>
<td>1.6196</td>
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<tr>
<td>$.05$</td>
<td>1.6066</td>
<td>1.6564</td>
<td>1.6760</td>
<td>1.6869</td>
<td>1.7110</td>
<td>1.7473</td>
</tr>
<tr>
<td>$.01$</td>
<td>1.8391</td>
<td>1.9027</td>
<td>1.9253</td>
<td>1.9375</td>
<td>1.9637</td>
<td>2.0010</td>
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</table>

3) In the original paper the figure 1.9153 is given; this is a printing error.

**RESULTS**

Details of the 13 experiments are given in Table 2 and in Fig. 4. The mainly random character of the movements is clear. The vector test,
FIGURE 4. Directions of birds in turned Kramer-cage in 13 experiments (percentage distribution). Sum of all experiments in graph S (right, bottom). Outer circle represents length of radii in purely random distribution. Details of each experiment in Table 2 (number of experiment in centre).
however, revealed a significant deviation (P < 0.05) from random distribution in 4 experiments (No. 2, 3, 6, 7). This deviation was already obvious during the experiments. A critical re-examination of the set-up was therefore made. Nothing asymmetrical was found, but it was suggested that the bird in the Kramer-cage had an auditory contact with the

two other Robins that, while not being used were placed in room C and D (fig. 1). The piercing calls may have been heard through the two doors separating the birds. Therefore, from April 10/11 onwards the other Robins were removed from the building (except in one night, April 18/19, when this was forgotten). Now significant deviations from random movements did not occur any longer. Out of 8 experiments made when other Robins were in the same house, 4 showed significant non-random movements, but they were random in all 5 experiments with no other Robins in the house. An influence of the other birds is therefore not unlikely. The position of the other Robins in relation to the Kramer-cage was between SE and S by E. The mean direction in the four non-random movements was E, SE by S, SW by S and W (calculated by vector addition).

### Table 2

<table>
<thead>
<tr>
<th>Experiment</th>
<th>Robin</th>
<th>Date</th>
<th>Time</th>
<th>Total number of observations</th>
<th>P Vector test</th>
<th>Kui-per test</th>
<th>Other Robins in same building</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>B</td>
<td>21/3</td>
<td>20.07-23.47</td>
<td>988</td>
<td>&gt;.10</td>
<td>&gt;.10</td>
<td>present</td>
</tr>
<tr>
<td>2</td>
<td>C</td>
<td>1-2/4</td>
<td>21.30-0.22</td>
<td>688</td>
<td>&lt;.05</td>
<td>&gt;.10</td>
<td>present</td>
</tr>
<tr>
<td>3</td>
<td>C</td>
<td>2-3/4</td>
<td>20.48-0.41</td>
<td>735</td>
<td>&lt;.05</td>
<td>&gt;.10</td>
<td>present</td>
</tr>
<tr>
<td>4</td>
<td>C</td>
<td>3-4/4</td>
<td>20.00-1.00</td>
<td>833</td>
<td>&gt;.10</td>
<td>&gt;.10</td>
<td>present</td>
</tr>
<tr>
<td>5</td>
<td>C</td>
<td>4-5/4</td>
<td>21.15-0.45</td>
<td>816</td>
<td>&gt;.10</td>
<td>&gt;.10</td>
<td>present</td>
</tr>
<tr>
<td>6</td>
<td>A</td>
<td>8-9/4</td>
<td>19.24-0.40</td>
<td>880</td>
<td>&lt;.005</td>
<td>&gt;.05</td>
<td>present</td>
</tr>
<tr>
<td>7</td>
<td>A</td>
<td>9-10/4</td>
<td>21.56-1.35</td>
<td>813</td>
<td>&lt;.05</td>
<td>&gt;.10</td>
<td>present</td>
</tr>
<tr>
<td>8</td>
<td>A</td>
<td>10-11/4</td>
<td>21.08-02.11</td>
<td>814</td>
<td>&gt;.10</td>
<td>&gt;.10</td>
<td>not present</td>
</tr>
<tr>
<td>9</td>
<td>A</td>
<td>11-12/4</td>
<td>20.22-23.23</td>
<td>394</td>
<td>&gt;.10</td>
<td>&gt;.10</td>
<td>not present</td>
</tr>
<tr>
<td>10</td>
<td>B</td>
<td>13-14/4</td>
<td>21.13-1.46</td>
<td>513</td>
<td>&gt;.10</td>
<td>&gt;.10</td>
<td>not present</td>
</tr>
<tr>
<td>11</td>
<td>C</td>
<td>18/4</td>
<td>20.48-23.14</td>
<td>485</td>
<td>&gt;.10</td>
<td>&gt;.10</td>
<td>present</td>
</tr>
<tr>
<td>12</td>
<td>C</td>
<td>19/4</td>
<td>20.28-22.11</td>
<td>511</td>
<td>&gt;.10</td>
<td>&gt;.10</td>
<td>not present</td>
</tr>
<tr>
<td>13</td>
<td>C</td>
<td>21/4</td>
<td>20.03-21.55</td>
<td>500</td>
<td>&gt;.10</td>
<td>&gt;.10</td>
<td>not present</td>
</tr>
</tbody>
</table>

All experiments together (S) 8970 >.05 >.10
If all experiments are taken together (Fig. 4 S) the probability of a random movement is still more than 0.05. Application of the test of Kuiper did not reveal significant orientation in any of the experiments (Table 2, column 7).

Our conclusion is that these three Robins did not choose a consistent direction in the situation described.

**DISCUSSION**

The experiments were planned as a repetition of similar ones reported by Fromme (1961). The findings of this author were not confirmed. I cannot give an explanation for this. Since I had no opportunity to check the orientation of my Robins under more natural conditions, one might argue that they could not orientate at all. The characteristic migrational restlessness renders this rather unlikely.

The method used by Fromme was not quite the same. Fromme used 8 perches instead of 16, his cage was octagonal instead of hexagonal and the arrangement of the perches were at least in most cases radial instead of tangential. It seems improbable that these and similar details have
been of influence. More important could have been the fact that FROMME did not turn the cage frequently. He mentions that each night the cage was set in another position. Also a constantly turning cage was used, but the number of experiments made with a turning and a fixed cage are not given. We found that in a fixed cage the bird showed a tendency to move in a hexagonal pattern, reflecting the form of the cage (Fig. 5). Such deviations from random movements cannot bring about a distinct orientation in one direction. Sometimes one of the six peaks was missing or was very short. This is probably caused by a series of swinging movements from the side wall of the cage to the opposite perch, since hanging from the network is not registered. An apparent orientation results, that would not have been found with a turning cage. When all our data with a fixed cage are added the picture is again a random one. FROMME’s figures are always based on a number of days. Therefore his less frequent turning of the cage is not likely to be responsible for the difference between his and my results.

Dr. G. V. T. MATTHEWS wrote me, that after a careful examination of FROMME’s paper he had little faith in FROMME’s conclusions. He gives two main reasons. Firstly FROMME presents his results in graphical form and as deviations from the expected level. In this way any deviation is exaggerated, especially when only the zone immediately above and below the 100% level is shown. When the data are replotted in the more usual way, as circular diagrams, the degree of orientation is much less clear. Secondly the statistics used by FROMME can be questioned. Analysis of variance of average percentages is a dubious procedure. In any case such an analysis only shows that the values of some directions are larger than others, not that there is a significant accumulation in a general direction. A recalculation of FROMME’s data with the vector test or the KUIPER test is necessary (this requires the original figures that are not given in the paper). If after this recalculation an orientation in FROMME’s critical experiments can still be demonstrated I would suggest that auditory stimuli, not unknown factors, such as the “map” factors postulated by KRAMER, are responsible.

**Summary**

Three Robins tested during spring migration in a Kramer-cage indoors, with all visual clues excluded, moved at random in the cage during their nightly period of migratory restlessness. This result is in contrast with the claim of FROMME (1961), that Robins can orient in a similar situation.

**Samenvatting**

De proeven van FROMME (1961), die er op wezen dat Roodborsten zich binnenshuis, zonder gebruik te maken van visuele kenmerken, in de te verwachten trekrichting konden oriënteren, werden herhaald. De resultaten van FROMME konden niet worden bevestigd: drie Roodborsten, beproefd
tijdens het voorjaar in een met die van Fromme vergelijkbare proefopstelling, bewogen zich op ongerichte wijze in de kooi gedurende hun nachtelijk periode van trekontrust.

REFERENCES


SCHMIDT-KOENIG, K. 1961a. Die Sonne als Kompasz im Heimorientierungssystem der Brieftauben. Z. Tierpsychol. 15: 221-244.


