

An Approach Toward an Analysis of the Pattern Recognition Involved in the Stellar Orientation of Birds

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AT PRESENT, there seems to be no reason to doubt that birds make use of the stars as orientational cues during their nocturnal migrations (refs. 1 and 2). Probably the stars are not the only orientational cues (refs. 3 to 5), but we will not be concerned with the problem of other parameters here. Instead, we will deal with the mechanism of pattern recognition as a requirement of stellar orientation. Before it is possible to analyze it in detail, however, it is necessary to obtain a general view of the capabilities of the birds. As yet, not much more has been achieved.

The experimental method of the analysis was described earlier in detail (refs. 6 and 7); thus, a short outline may suffice. A bird is attached to a turntable with its head in the center. Its visual field is limited by a black cylinder shielding the horizon and lower parts of the sky, normally up to 40°. The turntable rotates with a speed varying between about 1 and 4 minutes per cycle. A conditioning stimulus consisting of a weak electrical shock is applied whenever the bird's axis points in a certain direction. After a pe-

riod of training, an increase in heart rate anticipating the shock can be recorded, provided that the stimulus situation enables the bird to recognize the direction at which the shock is given. Accordingly, in critical tests without any shock, we get a maximum frequency of heart beats whenever the animal is passing the training direction. An electronic system controls the experiment automatically, and the data are recorded on paper tape and analyzed by a computer.

Figure 1 illustrates the kinds of data yielded by this technique. It shows three procedural steps of the analysis of 60 test cycles without shock. In part A, the original curves of heart rate are plotted with frequency (beats/sec) as the ordinate. Clearly there is a general maximum in the training direction, but the field covered by the individual curves is rather large. This results mainly from the variability in the basic heart rate and in absolute amplitude of the training responses at different times. Compensation for these variables results in normalized curves (B) with relative units at the ordinate,

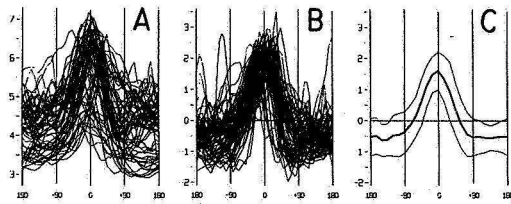


FIGURE 1. Heart rates of European teal (*Anas crecca*) during 60 test cycles without shock under the condition to which it had been trained (30 cycles clockwise and 30 counterclockwise). 0° at abscissa stands for training direction. (A) Original curves with frequency of heartbeats per sec as the ordinate. (B) Same data after normalization. This was done by calculating mean level and standard deviation for each individual cycle. Deviation of each point from the mean level was determined and divided by standard deviation. Zero stands for mean value of all individual curves. (C) Mean curve \pm standard deviation derived from part B.

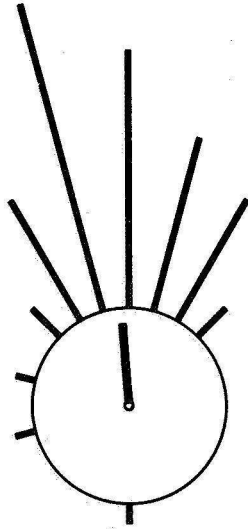


FIGURE 2. Frequency distribution of the maxima of 60 curves shown in figure 1. Training direction points upwards. Smallest length of a line refers to one maximum. Mean vector calculated from this distribution is drawn in the center. Radius of the circle coincides with greatest possible length of this vector, i.e., $a = r = 1$. (These are the basic data of the tests summarized in figure 9A.)

zero being the mean heart rate per cycle. The result of this procedure is a concentration of the curves, and the training effect becomes clearer. Part C shows the mean curves and standard deviations derived from part B.

Another much simpler kind of analysis of the same data is shown in figure 2. In this case, the direction of the maximum in each cycle is determined, and the diagram shows the frequency distribution of these 60 directions. From this distribution a mean vector can be calculated, the direction and length of which summarize conveniently the result of a particular experiment.

It has been shown that the orientational cues are picked up visually either from the natural night sky or from an artificial sphere in a planetarium (refs. 6 and 7). Besides corroborating this fact, the experiments presented here concern the effect of manipulation of the projected star patterns on the orientational responses of birds.

RESULTS

Simulated Natural Patterns

The following series of experiments with a mallard (*Anas platyrhynchos*) were conducted under a planetarium sphere simulating the natural starry sky at the same longitude during the respective time of day and season. Latitude was adjusted to 40° north, while the real place was at 48° . The lower parts of the sky up to the height of Polaris were blocked from view by the shielding cylinder. The results are shown in figure 3.

In series I, beginning in June, the bird was trained for 6 hr in the first part of the night. During these 6 hours the projected sphere rotated from hour angle of Aries 210° to 300° . At irregular intervals varying between about 15 min and 2 hr, the training program was interrupted, and a critical test

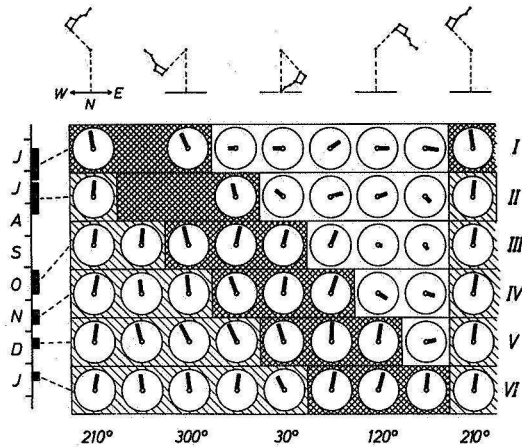


FIGURE 3. Mallard R, tests under simulated natural skies adjusted to 8 hour angles of Aries with 45° ($= 3$ hr) intervals. Respective position of Ursa Major together with Polaris is shown for illustration. During each of the series I to VI (time scale at the left: June to Jan.), bird was trained within interval indicated by cross-hatchings under a sphere continuously rotating from the respective left-hand to right-hand position. Parallel hatchings indicate former training conditions, while no hatching stands for conditions not yet used for training. Mean vectors are shown, as explained in figure 2, the training direction (west) pointing upwards. Sample size for each diagram varied between 40 and 80 test cycles.

was inserted. Normally it consisted of 10 cycles, five clockwise and five counterclockwise. These tests were made at one of eight positions of the sky around the total 360° of hour angles. In series II, the 6 hour training period was shifted 45° or 3 hours clockwise, and so on to series VI conducted in January, when the circle was closed; i.e., all test positions were covered by training.

Within the respective training phase (in fig. 3 marked by cross-hatchings), the maxima of heart rate were concentrated around the training direction. At the right of this phase, i.e., under skies not yet used for training, the bird appeared disoriented or ill-

directed. However, under skies formerly used for training at the left, it responded as well as under the current training patterns.

Before the experiments, this adult mallard was living under open air conditions. Thus, it has had the opportunity to observe the night sky. It was not a matter of course, therefore, that it did not correctly respond under stellar patterns not yet used for training. There are at least two possibilities why it did not. Either the bird did not identify the planetarium sky with the natural starry sky, or it merely failed to transpose the compass direction at which the shock was applied, from the training condition to the test condition where it had never been shocked so far.

More remarkable than this negative result may be the positive one. Once trained under a certain segment of the stellar sphere, the bird kept in mind the respective configurations while learning additional patterns. At the end of the experiments, this mallard mastered all meridian positions at latitude 40° N. In series VI, the time between training and testing at hour angle of Aries 210° was about half a year.

As a byproduct of these series, we are led to the conclusion that the circadian clock is not involved in this kind of orientation. During training, the stellar sphere was always in phase with the bird's clock, but during testing it was out of phase up to 12 hr back and forth. Provided that the bird was already familiar with the respective patterns, it never deviated from its normal direction of response (ref. 8). This is in accordance with the findings of Matthews (ref. 9) and Emlen (ref. 10). It seems doubtful, however, whether the stellar orientation is generally independent from time (or longitudinal) shifts because there are other findings suggesting that time relations might be taken into account either in certain species or (and) under certain circumstances (refs. 1 and 11

to 14). But this is not a question to be discussed here, for it involves not only the determination of a specific compass direction but also the choice of the desired direction itself during actual migration.

Artificial Patterns

Is directional training only possible under natural or simulated natural skies? Or is it possible under any arbitrary "starry sky" too? With the planetarium projector we are using (shown in ref. 7), it is easy to produce distributions of stellar patterns never and nowhere occurring in nature. For this purpose, the 31 single projectors composing the whole sphere were interchanged. Thus, the interrelations between the stars within an individual projector field remained constant, but the fields were mixed up, and all stars were dislocated with respect to the celestial coordinates.

It has been shown earlier that training under such conditions is indeed possible (ref. 7). However, at that time the question still remained open whether there might be a gradual difference between the performances under a simulated natural sky and under a totally artificial sky. Because of the interindividual variability of training performances, the same individuals had to be used under both conditions. Figure 4 shows, in a mallard as well as in a European teal (*Anas crecca*), that there are no marked differences between the orientational responses under both kinds of starry skies.

Mode of Learning and Mistaking

How do the birds learn, and what do they learn? This question is far from being solved, and the experiments to be described now can just show one of the starting points for further analysis.

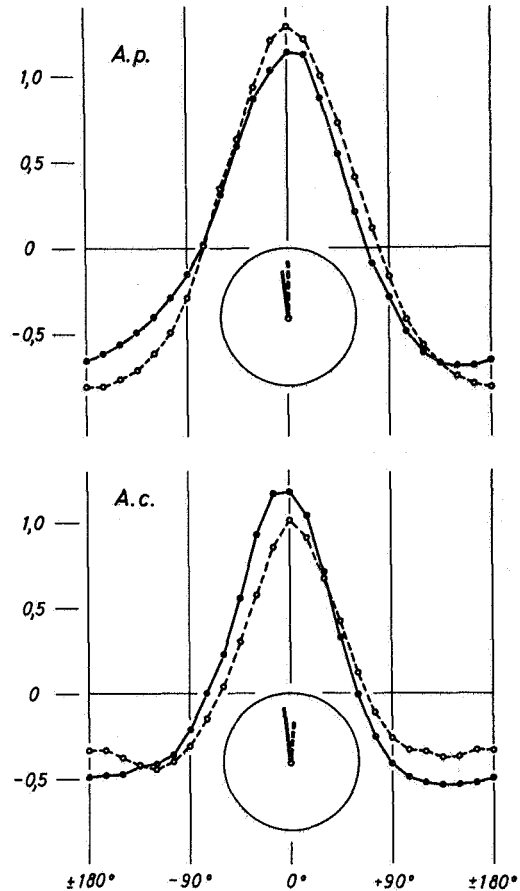


FIGURE 4. Mallard Q (top) and teal A (bottom), mean heart rates and mean directions of the maxima under simulated natural skies (solid lines) and under artificial skies (broken lines). Curves are derived as in figure 1C, and the vectors as in figure 2. Each curve and each vector, respectively, represents 320 test cycles with several adjustments of the projector. (These are overall means of the parts marked by cross-hatchings in figures 7 and 8, series I, II, and IV, plus 40 cycles in series IV with the sphere actually moving.)

Figure 5 contains the most interesting parts of a series of tests made with a teal. Two meridian positions of the simulated natural sky are involved, hour angles 60° apart from each other. In series I, the bird was

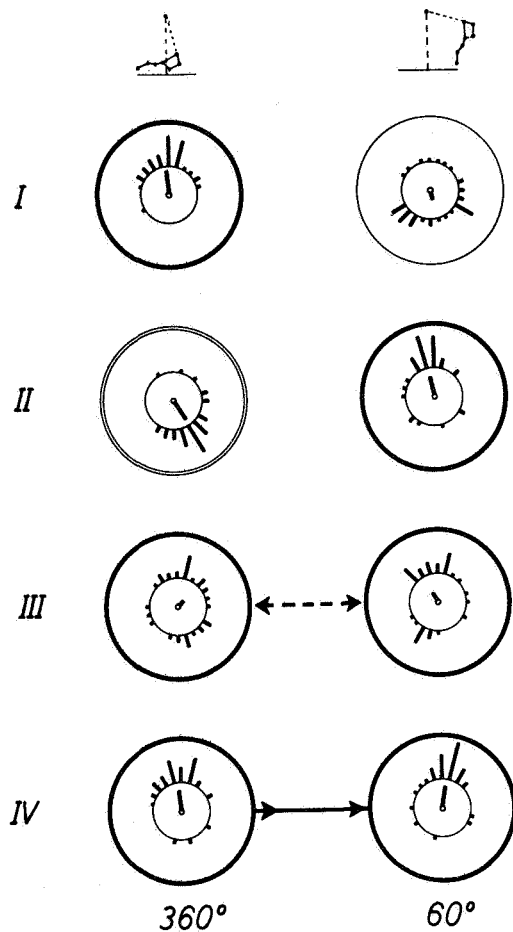


FIGURE 5. Teal A, distributions of the maxima of heart rate and mean vectors derived from them, under two meridian positions of the sphere at simulated latitude 40° N. Training direction (upwards) equals north. Each diagram is based on 40 test cycles. In series I to IV different conditions for training were used.

trained under a motionless starry sky in the first position. The result was as expected; i.e., good orientation with the sky in training position, disorientation under a sky not yet used for training. Thereafter (II) the bird was trained under the other position to the same direction (north). Now it was correctly ori-

ented at 60° , but contrary to my expectation, it had lost its correct orientation under the former training condition at 360° . Nevertheless, it showed an obviously oriented reaction here also, but the maximum heart rate appeared in nearly the opposite direction. Apparently the bird tried to identify the two patterns with each other, and it succeeded at best by identifying the SSE direction under the previous training pattern with North under the current training pattern. The respective planetarium skies are shown in figure 6 in an orientation in which their essential parts obviously looked similar for the bird. For the reader the similarity may not be obvious, nor is it for the writer, but it will be shown below that a mallard reacted in exactly the same way.

During series III the bird was trained alternately under both patterns in intervals of about 30 to 60 min. A bimodal distribution of the responses resulted now, suggesting a conflict situation for the bird. However, the problem was solved by training the teal under a sky continuously moving from the first position to the second one in the natural duration of 4 hr (series IV). Now, after being exposed to all the transitional stages, the bird was able to recognize the training direction under both patterns.

Actually during these experiments the teal was not only tested under positions 360° and 60° as shown in figure 5, but also at intervals of 15° between hour angles 330° and 90° . The complete series is shown in figure 7, together with the reactions of a mallard under the same conditions. The results from these two individuals belonging to different species are remarkably similar, which suggests that both birds evaluated the stellar patterns in a similar manner.

The same two birds also reacted quite similarly in an analogous series under artificial skies not simulating any conditions out-

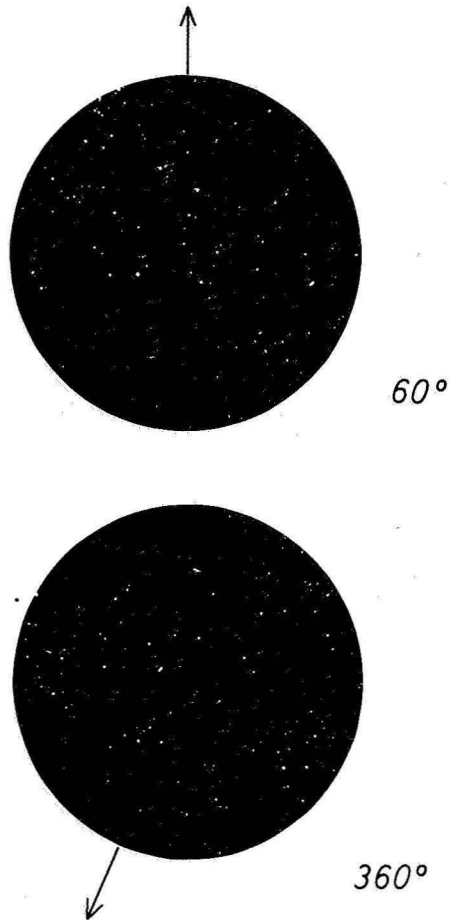


FIGURE 6. Planetarium skies adjusted to hour angles of Aries 60° and 360° at latitude 40° N, photographs of the section visible to the bird, i.e., down to 50° distance from zenith. Sphere is seen "from above" so that compass directions appear "normal," i.e., east is at right of north, and west is at left. The arrows point toward planetarium north.

side. (See fig. 8.) These experiments show that the misinterpretations of the stellar patterns in the former series did not depend in any way on the amount of the angular shift of the sphere. With the same shift but other constellations, the reactions were quite different. No obvious mistakes occurred here. It

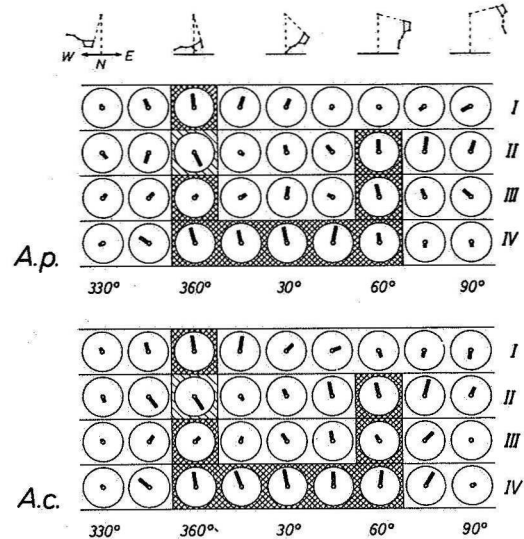


FIGURE 7. Mallard Q (top) and teal A (bottom), series I to IV, under simulated natural skies adjusted to 9 hour angles of Aries with 15° (= 1 hr) intervals (40° N). Current training conditions are marked by cross-hatchings. During training, sphere was motionless in series I to III but rotating in series IV. Training direction = north = uppermost. Each vector represents 40 test cycles.

may be by chance that the birds reacted under both training patterns in about the same way. (It might be suspected that the birds were oriented by other than "stellar" cues in these particular series of experiments. The results at 330° , however, do indeed show dependence on the composition of the stellar sphere. Moreover, half of the tests were conducted under a reversed sky as described in ref. 7.)

A more thorough analysis of the experiments shown in figures 7 and 8 has to take into account the kind of motion of the sphere, i.e., the kind of change of its visible section, as well as the specific contents of the starry skies. Moreover, additional experiments with other variations of the stellar patterns will probably be necessary. Thus, no further

comments will be given here. It may be expected that understanding of these results will be facilitated at later stages of our investigations.

Partial Blocking of the Training Pattern

So far the section of the sphere visible to the bird was considered as a whole. We do not know, however, whether the animal reacts uniformly to all parts of the sky, or whether specific parts are more important than others, either depending on their location within the visual field or on their content of conspicuous stars or configurations of stars.

Our experimental setup allows two methods of blocking portions of the sky from view.

(1) The visual field of the bird can be reduced in size by partially covering the shielding cylinder with opaque disks or rings.

(2) Fields of projected stars can be extinguished by masking individual projectors.

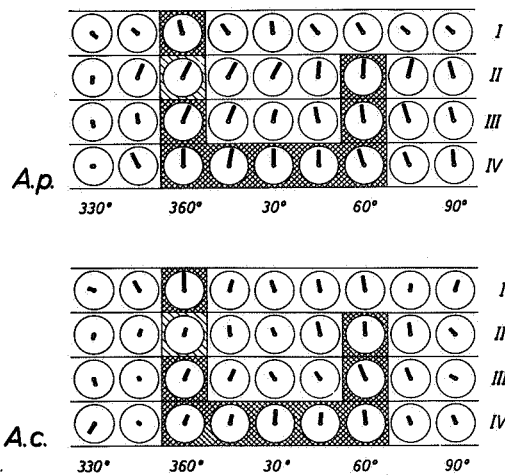


FIGURE 8. Mallard Q (top) and teal A (bottom), series I to IV, under artificial skies. Except for star distribution, procedure was same as in experiments shown in figure 7. (The naming of the hour angles is arbitrary.)

The following series of experiments were all made with teal A and all with the same training condition consisting of a motionless artificial (not simulating) starry sky not yet used for training or testing.

The results with the first kind of blocking are shown in figure 9. Clearly the responses are most concentrated when the test condition is identical with the training condition (A). On the other hand, with the shielding cylinder totally covered, the bird appeared totally disoriented (B). In the four situations with partial blocking, the scatter was in-

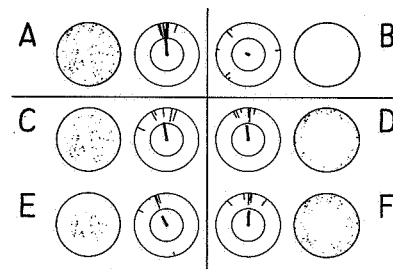


FIGURE 9. Teal A, artificial sky, blocking of the visual field by covering the shielding cylinder with rings and disks. Sphere fixed at a constant position. Star map is based on a photograph, but stars are enlarged in a rather schematic way. The sky is seen "from above" so that left and right is equivalent in both kinds of diagrams. In A, test condition equals training condition with an open view from 0° to 50° distance from zenith. In B, cylinder is completely covered. The open parts (distance from zenith) during the other tests are as follows: C, 0° to 40°; D, 40° to 50°; E, 0° to 30°; F, 30° to 50°. The other diagrams, representing the reactions, do not only show mean vector of total (with maximum length 1 being equivalent to radius of the greater circle), but also mean vectors of the individual tests, each of them consisting of a succession of 10 cycles. For these peripheral vectors, the scale is halved, maximum length being equivalent to distance between the two circles. (For sample size $n = 60$ [six tests] and significance level $P = 0.01$, the critical vector length is $a = 0.28$, i.e., somewhat more than half the radius of the smaller circle.)

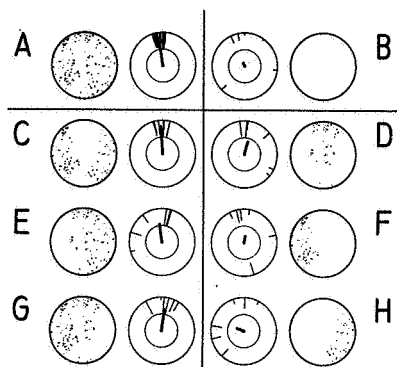


FIGURE 10. Teal A, the same artificial sky as in figure 9, part 1 of blocking experiments conducted by masking various combinations of the 11 individual projectors composing the visual starry sky as shown in A. Figures 10 to 12 refer to same test series. Tests were inserted irregularly into the training program. For further explanation see Figure 9.

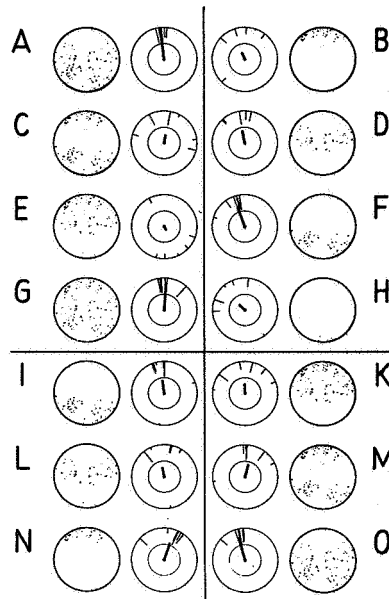


FIGURE 11. Part 2 of blocking experiments.

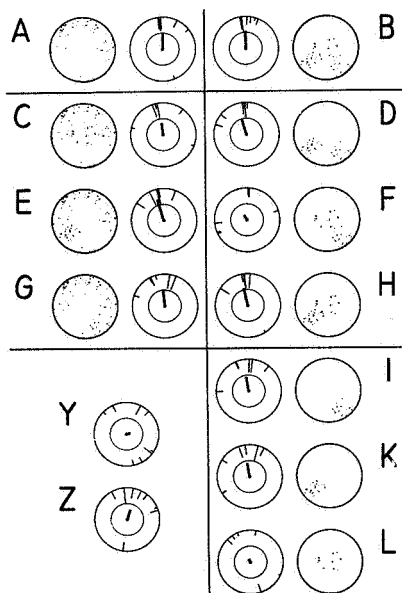


FIGURE 12. Part 3 of blocking experiments. For control in Y and Z no projector was covered, but the whole sphere was shifted around the polar axis by 60° "backward" (Y) or "forward" (Z), respectively, thus showing another section of the sky than during training. ("Latitude" was 30° "N.")

creased, but the maxima of heart rate were still accumulated in the direction of training (C to F). Thus, the bird was able to determine this direction by alternative use of either the periphery or the central part of the original field, though less accurately than with the whole field visible. In case E, a definite deterioration in performance is indicated.

With the second kind of blocking a larger series was conducted (figs. 10 to 12). The results can be used for merely tentative conclusions, for in many cases the reactions obtained during different tests were rather inconsistent, as indicated by the single vectors at the periphery of each diagram. It is unknown whether this inconsistency depends solely on changing states of the general motivation of the duck, or whether it depends in a more specific way on varying modes of recognition of the stellar patterns. With respect to some puzzling results, it should be born in

mind that controls against the bird's using other than stellar cues could not be applied during each individual test. [Control tests with reversed skies (ref. 7) were not conducted in this series in order to avoid creating smaller differences of visible fields by parallax.] Thus, although there is no evidence supporting such a suspicion, it cannot be entirely ruled out. In regard to the series as a whole, clear cases of disorientation demonstrate the dependence on the projected patterns (see, e.g., figs. 10B, 11E, 12L, 12Y).

In the figures the blocking conditions are arranged in pairs, the visible sky in the left column containing the blocked part of the sky in the right column and vice versa. In several cases the bird was obviously oriented under both conditions (see, e.g., figs. 10C and D, 11N and O, 12A and B, 12G and H), demonstrating that it was able to use both parts of the sky alternately, though there were differences either in accuracy (e.g., fig. 10C and D) or in direction (e.g., fig. 11N and O). In other cases, one part of the sky was obviously much more important for the bird's orientation than the other, as shown in figures 10G and H, 11A and B, 11E and F, 12 E and F.

It is not possible to discuss the whole variety of conditions and reactions in detail, but some lines of comparison may be selected. Figure 10 is used as a first example. In C, blocking of considerable parts of the sky—mainly overhead and in the training direction—did not affect the performance at all (compare A). With only the parts blocked in C visible, however, the bird was still oriented (D) though the scatter was increased and a small shift of direction indicated. Exposed to each of the two halves composing condition C, the duck appeared disoriented (F and H). Adding both these parts to D improved the performances as opposed to the results using part D alone (E and G).

Most puzzling are the reactions of the teal under the sky shown in figure 11E. There is not the slightest hint of a training response although huge parts of the sky were visible; more strikingly there were better responses although additional parts of the sky were blocked from view (see fig. 11D, K, L, N). Similarly figure 12I shows better results with a smaller part of the sky visible than figure 12F. If these are not chance results—and the fairly consistent responses in 11E do not support this idea—the only reasonable interpretation might be that under certain conditions the bird is more confused by looking at incomplete configurations than by entirely missing large parts of the starry sky.

Surprisingly good reactions are shown in figure 12I and K with very small parts of the stellar sphere visible. From these and many other cases it becomes clear that the distribution of illuminated parts of the sky or directional differences in brightness do not considerably affect the direction of the response.

DISCUSSION

Regarding the mechanism of pattern recognition, training may be a promising method of analysis because any arbitrary pattern of "stars" can be used. When considering the results, one has to bear in mind, however, that successful training can merely demonstrate what an animal is able to do, i.e., to perceive, to distinguish, etc. But it cannot tell us whether the animal makes use of the respective ability in its natural life. Thus, the experiments reported here cannot lead to a final decision on the mode of stellar orientation in nature. Yet they offer an opportunity for making hypotheses.

It has been shown that birds can learn to distinguish between different patterns composed of more than a thousand star-like spots. They have a remarkable capacity for

memorizing such patterns, and it is unimportant whether the distributions of the spots do simulate natural skies or not. Consequently it has been hypothesized at an earlier stage of these investigations (ref. 7) that migratory birds not only can learn but do learn and have to learn the specific contents of natural starry skies, together with their relation to the coordinates of the Earth. The decision had to come from experiments with birds raised isolated from view of the night sky and then tested with any kind of a "Kramer cage" method recording the spontaneous *Zugunruhe*. Excellent data of this kind were presented by S.T. Emlen at this symposium confirming the hypothesis by clear evidence.

In accordance with these results, my failure in recording oriented *Zugunruhe* in hand-raised European warblers (*Sylvia*) under a planetarium sphere (ref. 15) might be due to their negligible experience with the night sky. However, using birds of the same genus, Sauer (ref. 1) had recorded preferences of the normal fall migration directions—even with two individuals not experienced under the night sky, and with several hand-raised individuals kept indoors with limited possibilities to observe the sky. Thus, there are still incongruities in the results demanding further experimentation.

The question of whether bicoordinate navigation or compensation for displacements (for instance, by wind drift) by using nothing but stellar cues takes place in some species of birds (refs. 1, 11, 16 and 17) is not much affected by the question of whether the "star-map" is learned or inherited, provided a bird is clever enough in "handling" the stars. Only in extreme cases with few or no stars of the experienced constellations available, would a bird necessarily fail to orient when depending on learned patterns.

During its first year of life, a migratory bird might be involved in a continuous learn-

ing process adapting it to the daily, seasonal, and latitudinal changes of the starry skies. Likewise, continuity in change of the appearance of the sky might be a precondition for successfully learning the whole variety of constellations. Once the bird has learned them, however, it does not need actual movement for recognition.

The essential clues by which particular views of the sky are recognized are still obscure. The blocking experiments show that different parts of the sphere can be used alternately. Thus recognition depends neither on the total aspect of the sky nor on a particular key star or constellation. On the other hand, the same experiments show that different parts of the sky are of different importance, as it was indicated in blocking experiments conducted by Emlen (ref. 10). One may hypothesize that the birds search for configurations that are more conspicuous than others and later on concentrate their attention on these selected patterns. This could be a way similar to our method of looking for well-known *Gestalt* stimuli.

At this point, investigation of actual pattern recognition should begin. For this, however, totally self-made "starry skies" allowing any variations would be desired. Since the projector we are using so far does not allow changes within a particular field of stars, further progress has to wait for a completion of our technical facilities.

SUMMARY

A conditioning method was used to investigate the orientational responses of ducks (mallard and European teal) as affected by manipulations of the stellar patterns in a planetarium. Under simulated natural skies, it was possible to train a bird to a particular direction successively under all positions of the rotating sphere at a constant latitude.

The responses were independent of the phase-relationships between local time, season, and appearance of the sky, provided that the bird had been trained under the particular section of the sphere some time before. The longest interval between training and testing was half a year, during which the bird learned to distinguish many additional patterns. No appreciable differences in learning and responding were found under artificial stellar patterns, never occurring anywhere in nature, as compared with simulated natural patterns. A mallard as well as a teal, each of them trained successively under two fixed skies of different appearance, misinterpreted these skies, obviously by trying to identify the two patterns with each other. Both birds were confused in the same way, which suggests that they evaluated these patterns quite similarly. Confusion ceased, however, when the sphere moved continuously from the one appearance to the other.

In another series of tests, parts of a fixed training pattern were blocked from view. It appeared that the bird was able to use different parts of the starry sky alternately to determine the training direction, though in most cases the reactions were less accurate than with the whole training sky visible. Some parts, however, seemed to be more important than others, causing disorientation when blocked from view. These experiments provide some clues to the mechanism of pattern recognition, but many more will be necessary for a real analysis.

DISCUSSION

QUESTION: Have you performed training experiments with rather simple arrangements of lights?

WALLRAFF: Yes, it is much easier to do than with stars.

ENRIGHT: Have you tried experiments with the Moon superimposed on the star pattern?

WALLRAFF: No.

WILLIAMS: In your series of tests, have you taken precautions to guard against day-to-day fluctuations? When you remove part of the sky, do you run that whole part and then go to the other part or do you run section C first and then D and then E?

WALLRAFF: The patterns were shown in irregular sequences, for example C₁, D₁, E₁ and then D₂, C₂, E₂ and then C₃, E₃, D₃ (C, D and E are the blocking conditions; the numbers mean 1st, 2nd, and 3rd test under the respective condition).

REFERENCES

1. SAUER, F.: Die Sternorientierung nachtlich ziehender Grasmucken (*Sylvia atricapilla*, *borin* und *curruca*). Z. Tierpsychol., vol. 14, 1957, pp. 29-70.
2. EMLEN, S. T.: Migratory Orientation in the Indigo Bunting, *Passerina cyanea*. Part I: Evidence for Use of Celestial Cues. Auk, vol. 84, 1967, pp. 309-342.
3. BELLROSE, F.: Radar in Orientation Research. Proc. XIV Int. Ornith. Congr. (Oxford), 1967, pp. 281-309.
4. GRIFFIN, D. R.: The Physiology and Geophysics of Bird Navigation. Quart. Rev. Biol., vol. 44, 1969, pp. 255-276.
5. WILTSCHKO, W.: Uber den Einfluss statischer Magnetfelder auf die Zugorientierung der Rotkehlchen (*Erithacus rubecula*). Z. Tierpsychol., vol. 25, 1968, pp. 537-558.
6. WALLRAFF, H. G.; AND KLEBER, N.: Eine Dressurmethode fur wahrnehmungsphysiologische Untersuchungen und ihre Anwendung in Orientierungsversuchen mit Vogeln. Experientia, vol. 23, 1967, pp. 312-314.
7. WALLRAFF, H. G.: Uber das Orientierungsvermogen von Vogeln unter naturlichen und kunstlichen Sternenmustern. Dressurversuche mit Stockenten. Zool. Anzeiger, Suppl., vol. 32 (Verh. Dtsch. Zool. Ges. Innsbruck 1968), 1969, pp. 348-357.
8. WALLRAFF, H. G.: Direction Training of Birds Under a Planetarium Sky. Naturwissenschaften, vol. 55, 1968, pp. 235-236.
9. MATTHEWS, G. V. T.: The Astronomical Bases of "Nonsense" Orientation. Proc. XIII Int. Ornith. Congr., 1963, pp. 415-429.

10. EMLEN, S. T.: Migratory Orientation in the Indigo Bunting, *Passerina cyanea*. Part II: Mechanism of Celestial Orientation. *Auk*, vol. 84, 1967, pp. 463-489.
11. SAUER, E. G. F.; AND SAUER, E. M.: Star Navigation of Nocturnal Migrating Birds. The 1958 Planetarium Experiments. Cold Spring Harbor Symp. Quant. Biol., vol. 25, 1960, pp. 463-473.
12. HAMILTON, W. J., III: Does the Bobolink Navigate? *Wilson Bull.*, vol. 74, 1962, pp. 357-366.
13. SHUMAKOV, M. E.: An Investigation of the Migratory Orientation of Passerine Birds. *Vestnik Leningradskogo Universiteta, Biol. Ser.*, 1967, pp. 106-118 (in Russian).
14. RABØL, J.: Orientation of Autumn Migrating Garden Warblers (*Sylvia borin*) after Displacement from Western Denmark (Blåvand) to Eastern Sweden (Ottenby). A Preliminary Experiment. *Dansk Ornith. Foren. Tidsskr.*, vol. 63, 1969, pp. 93-104.
15. WALLRAFF, H. G.: Versuche zur Frage der gerichteten Nachtzug-Aktivität von gekäfigten Singvögeln. *Zool. Anzeiger, Suppl.*, vol. 29 (Verh. Dtsch. Zool. Ges. Jena 1965), 1966, pp. 338-356.
16. WALLRAFF, H. G.: Können Grasmücken mit Hilfe des Sternenhimmels navigieren? *Z. Tierpsychol.*, vol. 17, 1960, pp. 165-177.
17. WALLRAFF, H. G.: Does Celestial Navigation Exist in Animals? Cold Spring Harbor Symp. Quant. Biol., vol. 25, 1960, pp. 451-461.