

New Experiments on the Effect of Clock Shifts on Homing in Pigeons

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THIS SYMPOSIUM may be considered a successor to the Cold Spring Harbor Symposium of 1960. I, therefore, decided to report on experiments that are extensions of those reported at the previous symposium (ref. 1) even though I have not yet completed them (these data were also included in a preliminary report with limited circulation).¹ More experiments are being carried out at the present time.

Clock shifts have, so far, been the only experimental tools to predictably interfere with homing. Clock shifts introduce specific errors in the birds' Sun azimuth compass (refs. 1 to 3) resulting in corresponding errors during initial orientation and, probably, also during orientation enroute.

In previous experiments, the effect of shifts of 6 hr and of 12 hr has been investigated in releases from 2 km up to 170 km distance, mostly from distances between 12 km and 70 km (refs. 1, 3, and 4). Upon 6-hr

clock shifts, the initial orientation of experimental birds deviated roughly 90° from that of the controls and roughly 180° upon 12-hr clock shifts, as would be expected theoretically. However, this was true only on the average: There were considerable and unexplained deviations from the expected values at various individual release sites.

During the past 8 years we have extended these investigations in Germany and the U.S. with particular emphasis on the following questions:

(1) Is the deviation accomplished by the clock shift influenced by the distance of release?

(2) Would smaller degrees of clock shift produce correspondingly smaller deviations? The same methods were used as previously (e.g., ref. 4) with one major exception: Only well-experienced pigeons (as, e.g., in refs. 5 and 6) participated in these releases. About one-half of the planned total of releases has been carried out to date. A successful shifting experiment involving 6 or more hr of shift, unfortunately, means partial or complete loss of the experimental birds, a

¹SCHMIDT-KOENIG, K.: Weitere Versuche, durch Verstellen der inneren Uhr in den Heimkehrprozess der Brieftaube einzugreifen. *Verh. Dt. Zool. Ges. Würzburg*: 1970, pp. 243-245.

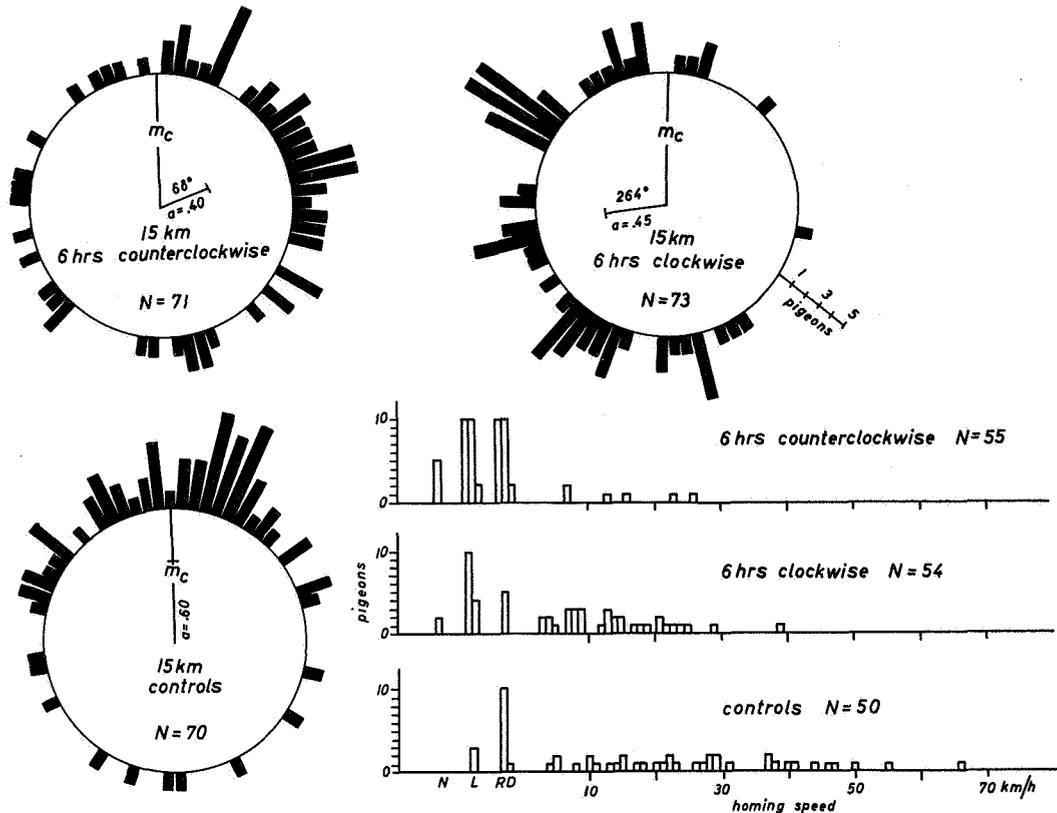


FIGURE 1. Initial orientation (circular diagrams) and homing performance of control and experimental birds from 6-hr shifts clockwise and counterclockwise from 15 km N, E, S, and W at Durham, N.C. From each site, controls and both groups of experimentals were released on the same day. Lengths of bars indicate number of birds according to scale given. Initial orientation of experimentals is plotted with reference to combined mean of controls (m_c). Direction (in deg) and length (a) of mean vectors are given along with sample size (N). N of initial orientation and of homing performance is different because homing performance was not recorded in one of the four experiments.

group of well trained "veterans." Experiments of this kind are, therefore, extremely expensive and time consuming.

DISTANCE OF RELEASE

According to recent findings from North Carolina and Germany (refs. 5 and 6) supported by the results of other investigations (ref. 7)² the accuracy of initial orientation of normal pigeons is a function of their dis-

tance from home. One possible interpretation of these results is the assumption of the operation of two navigation mechanisms one operating over short distances (up to about 20 km) and the other over long distances (beyond about 100 km). Therefore, we

² Also, SONNBERG, A., AND SCHMIDT-KOENIG, K.: Zur Auslese qualifizierter Brieftauben durch Übungsflüge. *Z. Tierpsychol.*, vol. 27, 1970, pp. 622-625.

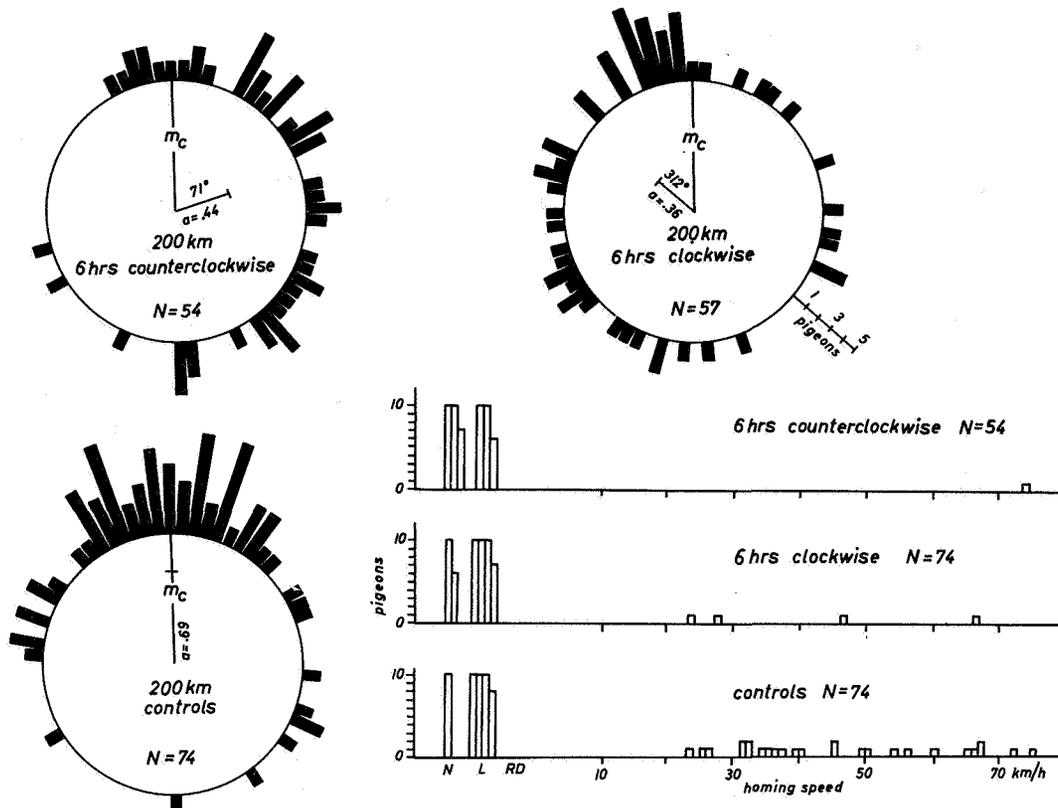


FIGURE 2. As figure 1; however, from 200 km N, E, S, W to Durham, N.C.

sought to discover whether clock shifts would act differently on short-distance and on long-distance releases. In other words, we wanted to find out whether the two hypothetical navigation mechanisms may differ in operating with or without clock and compass. Clock shifts of 6 hr clockwise and counterclockwise (imposed for at least 4 days) were used in a series of releases from 15 km and from 200 km from the cardinal compass directions.

Figures 1 and 2 give the data for initial orientation and homing performance so far accumulated. The following preliminary results may be taken from figures 1 and 2.

(1) The observed deviation confirms pre-

vious evidence: the initial orientation was shifted by roughly 90° clockwise or counterclockwise depending upon the sign of the clock shift. Homing performance of the shifted birds was clearly inferior to that of the controls. All differences are significant ($p < 0.01$; Watson test, refs 8 and 9; and Mann-Whitney U-test, e.g. ref. 10).

(2) There was no significant difference between the results from 15 km and 200 km.

These data give a preliminary indication that the Sun compass is in fact utilized in short-distance releases as well as in long-distance releases. Thus, if there were, indeed, two navigation mechanisms, they do not seem to differ in this respect.

SMALL CLOCK SHIFTS

Shifts of 2 hr and of 30 min counterclockwise (imposed for at least 4 days) were chosen in another series of experiments. If the Sun is used as a compass, a 2-hr shift can be expected to produce a deviation of about 30° in initial orientation and, perhaps, slightly inferior homing performance (especially on long distances) as compared with controls. In view of the large scatter usually encountered in experiments of this kind, small differences like these cannot be expected to reach significance, certainly not in small samples. Correspondingly, a 30-min shift should produce a deviation of about 8° in initial orientation, thus a measurable difference in initial orientation and homing performance cannot be expected. If, however, the Sun were used for navigation as, for example, suggested by Matthews (ref. 11), a 2-hr clock shift should be

interpreted by the bird as a longitudinal displacement of roughly 2000 km (depending upon latitude) and a 30-min clock shift should be interpreted as a longitudinal displacement of roughly 700 km (depending upon latitude). The shifted bird consequently should head east upon a counterclockwise clock shift. Thus, we may expect clearcut results: Little or no appreciable differences should occur in the case of Sun compass orientation, but drastic differences in initial orientation and homing performance in the case of Sun navigation, especially if the direction of displacement is E or S as was the case here.

Figure 3 gives the data of initial orientation and homing performance so far accumulated upon clock shifts of 2 hr counterclockwise. There is no significant difference between the initial orientation of experimentals and controls (Watson test). Homing per-

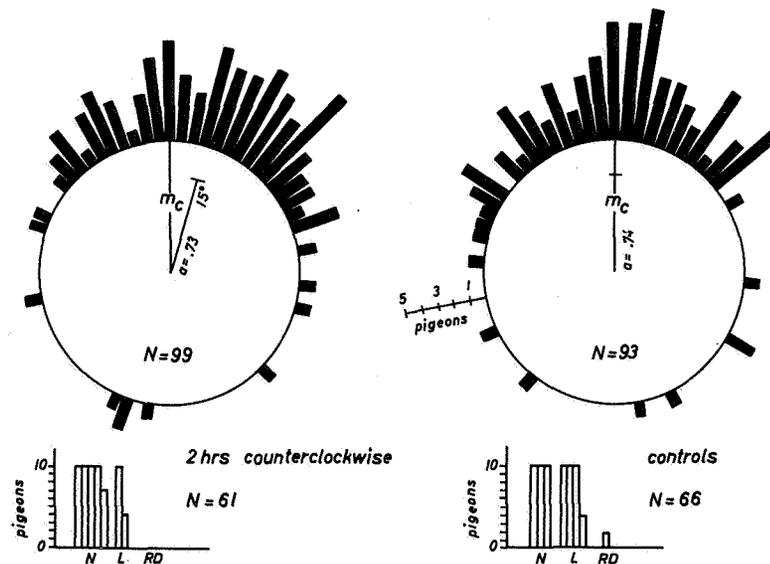


FIGURE 3. Initial orientation (circular diagrams) and homing performance (rectangular diagrams) of control birds and of experimental birds upon 2-hr shifts counterclockwise from 460 and 320 km S and from 280 km E to Wilhelmshaven, Osnabrück, Germany, and Durham, N. C. Symbols as in figure 1.

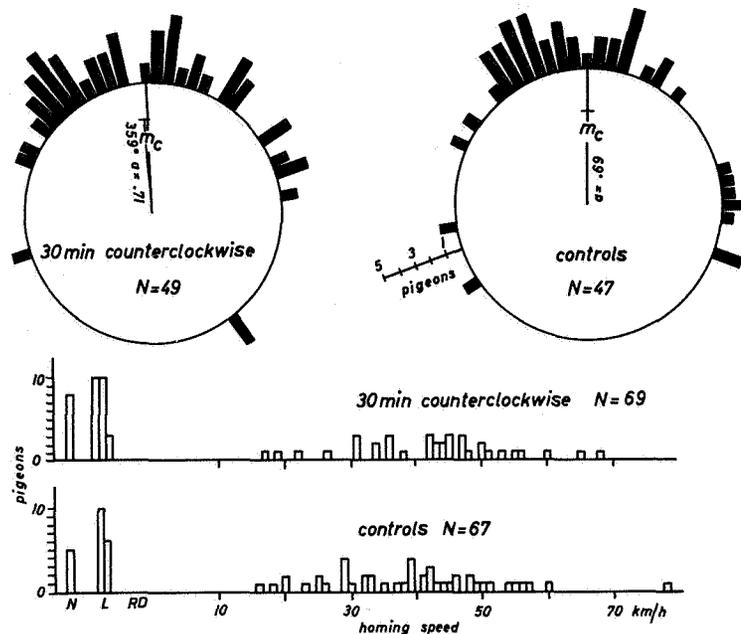


FIGURE 4. Initial orientation (circular diagrams) and homing performance (rectangular diagrams) of control birds and of experimental birds upon 30-min shifts counterclockwise from 130 km S, W, N and 200 km E to Durham, N.C. Symbols as in figure 1. Initial orientation of controls and experimentals at 130 km W was at random; these data had, therefore, to be omitted from the circular diagrams.

formance of controls and experimentals was, however, significantly different ($p < 0.01$; χ^2 test).

Figure 4 presents the corresponding data upon clock shifts 30 min counterclockwise. There was no significant difference in either initial orientation or homing performance.

These results clearly support and considerably strengthen previous evidence that the Sun is used for compass orientation and not for navigation. This holds for short distances as well as for long distances. The results from 15 km demonstrate once more that even very experienced birds are easily misled not very far from the loft, indicating that possible knowledge of local factors cannot be very essential to homing.

ACKNOWLEDGMENTS

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DISCUSSION

GRIFFIN: How well were the controls oriented toward home?

SCHMIDT-KOENIG: After we knew that initial orientation is a function of the distance of release, those distances were selected which gave rather

well homewardly directed initial orientation, 15 km and 130 or more km. Thus, the controls were rather well homewardly directed.

QUESTION: Can you conceive of a clock flexible enough to be used as a compass clock and also being stiff enough to be used as a longitude clock?

SCHMIDT-KOENIG: No. A clock for navigation would have to be rather rigid.

WILLIAMS: Was there any methodological rationale for not using similar release points in your various shifts? You took 2-hr shifts between 200 and 450 km and a 30-min shift between 130 and 200 km. This might introduce a new variable.

SCHMIDT-KOENIG: That's correct. These experiments extended over eight years. In Germany the only long distance is to the south. These experiments were done in 1961. Since then, we have become much more sophisticated. We are now using the same release sites for all experiments. However, if you want to generalize these results, they must work at any release site.

ENRIGHT: Are these symmetrical release sites? Were the numbers of releases then balanced in all directions?

SCHMIDT-KOENIG: The 2-hr shifts were not balanced but the others were. The 2-hr shifts were from the south and from the east. There were no north releases and none from the west. Since you would expect the birds to head east, releases from the south and from the east should give you a very clear-cut result if the Sun is used for navigation.

EVANS: In the 2-hr shift experiments, some birds seemed to go off in the same direction as the controls. Did these (experimental) birds have faster homing speeds than those which showed a shift of initial orientation?

SCHMIDT-KOENIG: It is a matter of argument whether or not there is a general correlation between the direction of initial orientation related to homing and homing speed. The long distance releases were very long distances and I don't think that you can get a correlation.

BALDWIN: Can you describe the method of time shifting that you used?

SCHMIDT-KOENIG: The birds are placed in a closed room which is well ventilated and operated automatically on timers. You just reset the timer by as many hours as you want. Since a 6-hr shift takes four days to be completed, all birds were subjected to four days of shifting, even the 30-min birds. The controls are locked up in artificial conditions with no shift. Thus, the only difference is the phase difference in the illumination of the birds.

COCHRAN: In your experiments involving 30-min and 2-hr clock shifts to test navigation, did you have a program where you released the birds at sunrise, at noon and in the evening?

SCHMIDT-KOENIG: The time of day in which you have to release your experimental birds is determined by the clock shift. You have to have the light period which is common for the experimentals and the controls. For birds shifted 6 hr clockwise it is the forenoon; for birds shifted 6 hr counterclockwise it is the afternoon, and for birds shifted 12 hr it is a few hours early in the morning and a few hours late in the evening, in which the artificial day and the natural day overlap. Thus, you are restricted to a certain time of day for the release. Otherwise, you would release your experimental birds in the real day but their personal night. This poses problems of a different sort.

ENRIGHT: What happens when you do release them at night?

SCHMIDT-KOENIG: You get a large scatter. There is some indication that the pigeons (as was demonstrated in stationary training experiments) unlike bees, "think" that the Sun goes counterclockwise at night. We roughly got the corresponding departure directions. We discontinued these experiments because they don't lead very far.

KEETON: We have not yet tracked birds by airplane when they have been clock-shifted, but we have tracked them by radio from the ground. The birds in a 6-hr shift head off roughly 90° wrong. They are still going in that wrong direction when we lose them at about 16 km.

SCHMIDT-KOENIG: We have one more point of evidence. In Germany we have a contrast to the situation in North Carolina. We get many reports of birds that do not home; the direction of the reports roughly agrees with the takeoff direction of shifted birds only for those reports made during the release day or the next day. If more days had elapsed between release and report, then the relation deteriorates very rapidly.

ADLER: You released your birds close to the distances you had previously identified as the "dead belt" (ref. 5). Did you do anything more on exploring whether this effect is true or not?

SCHMIDT-KOENIG: I repeated the North Carolina experiment in Germany. The results from Durham were confirmed in Western Germany with one major or minor exception, the reason for which I don't yet know. The initial orientation again deteriorates beyond 200 km; at 300 km it is particularly bad. I don't know how regular this is going to con-

tinue if you extend releasing to 400, 500 and 600 km.

KEETON: We have now completed nearly 175 releases involving approximately 2550 birds and do not find a distance effect. We have also done clock-shift tests at 32, 48, 64, and 80 km and obtain precisely the same kind of results as at longer distances. We have also done a series of tests at even shorter distances of about 2 km. As long as they cannot see the loft directly the birds appear to be still going off in the wrong direction. If they can see the loft they head straight for it, as Graue has also found.

SCHMIDT-KOENIG: I have done a number of releases in Wilhelmshaven, Germany about 2 km away from the loft. Although they could see the loft very well many experimentals headed away from the loft. Some were recaptured in Ruhrgebiet which is 250 km away.

KEETON: Wondering what information the birds might be getting from the Sun, we conducted this summer a series of tests in which birds being shifted were permitted to go out into an aviary and see the Sun during the overlap period between their shifted day and the true day. When those birds were tested at the end of about five days, they were just as well shifted as ones that had been in a completely light-tight room. Apparently as long as they are just sitting in the aviary it doesn't matter whether they can see the Sun; the only information they appear to obtain from the Sun under such circumstances is whether the lights are on or off.

SCHMIDT-KOENIG: Right. Our evidence is not as sophisticated but if we kept the birds uncovered before the release at the release site for, let us say 2 hr or so, there was absolutely no impact on the shifting effect.

KEETON: I might mention a more confusing thing, although it may not hold up when more tests are conducted. During the overlap period between the true day and the shifted day some birds were permitted to go out and exercise, that is, fly over the loft. When these birds were tested at the end of the proper number of days, they went random (in three tests so far). In other words, if they just sit in the aviary and see the Sun, pigeons are shifted effectively and go non-randomly at the predicted wrong angle from home when tested, but if they are permitted to fly during the overlap periods while being reset, they appear to become confused and do not orient when tested. I emphasize again, however, that these are very preliminary results.

SCHMIDT-KOENIG: That all agrees quite well

with what we have found, but there is a disagreement between your finding and my finding of this initial orientation and distance relation. I am very curious what the basis for this may be.

You also find an effect of overcast on shifting. We did not find it with rather small samples, however. I understand that Ithaca, N. Y., has a long period of solid overcast, which we don't have, even if the well-known bad climate of Germany is considered. If you look for solid overcast you just don't find it. That may be the reason for the difference.

KEETON: We find, just as you do, that if we test birds without previous experience under overcast they go random. If, however, the birds have been given a series of 4.8 to 16 km training flights under overcast, they can then be jumped to 160 or 240 km and will orient under overcast. It is essential for the birds to have had some prior short-distance experience under overcast before they are tested at these longer distances. It is certainly true that in Ithaca our birds experience solid overcast much of the time during the autumn months.

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