Pigeons combine compass and landmark guidance in familiar route navigation

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How do birds orient over familiar terrain? In the best studied avian species, the homing pigeon (Columbia livia), two apparently independent primary mechanisms are currently debated: either memorized visual landmarks provide homeward guidance directly, or birds rely on a compass to home from familiar locations. Using miniature Global Positioning System tracking technology and clock-shift procedures, we set sun-compass and landmark information in conflict, showing that experienced birds can accurately complete their memorized routes by using landmarks alone. Nevertheless, we also find that route following is often consistent with the shape of the track, but in parallel. Thus, we demonstrate conditions under which compass orientation and landmark guidance must be combined into a system of simultaneous or oscillating dual control.

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Results

Fig. 1. Average anticlockwise deviation in the tracks of clock-shifted birds compared with the same birds' final non-clock-shifted flight, measured as virtual vanishing bearings (20) recorded at 500-m intervals throughout the length of the homing flight. Filled circles show mean deviations of high-familiarity birds; open circles show means of low-familiarity birds. Error bars are circular standard errors of the mean. Dashed lines indicate the expected deviation induced by the clock-shift treatment at each site, based on the magnitude of the shift, date and time of release, and geographical location. (A) Weston Wood. (B) Hinksey Heights. (C) High Cogges. (D) Bladon Heath. At the 2,000-m boundary (the distance at which vanishing bearings are customarily measured), the distributions of angular differences in the low- and high-familiarity groups were significantly different at three of the four sites (Watson's U² test: P < 0.005 at High Cogges; P < 0.05 at Bladon Heath and Weston Wood; P > 0.05 at Hinksey Heights).

Sequential use of a map for position fixing and a compass for onward guidance has long been regarded as the fundamental model characterizing avian navigation (1, 2). Although there continues to be disagreement over the details, it is generally accepted that unfamiliar terrain olfactory signals are used to cue position, and a solar or magnetic compass is used to guide orientation home (reviewed in ref. 1). Curiously, much less is known about what happens when birds reach familiar terrain. Current evidence suggests that pigeons reduce dependence on navigating by atmospheric chemosignals, and instead use the memorized landscape to determine their position with respect to home (1). Nevertheless, there are two competing hypotheses for how homeward orientation is then controlled. The first hypothesis, sometimes called “pilotage” (2, 3), suggests that guidance is compass-independent and involves orienting directly by the pattern of visual landmarks. The second hypothesis, sometimes referred to by the term “mosaic map” (4) by some authors (5), suggests that guidance between familiar locations is compass controlled just as it is from unfamiliar locations (6). Current evidence is equivocal (7, 8). We have previously shown that with extensive local experience homing pigeons come to rely on highly stereotyped, individually distinct flight paths (and that this faithful route-following does not require the magnetic compass; see ref. 9). Birds displaced off route usually return directly to their memorized path, implicating direct attraction to visual landmarks (10). Nevertheless, clock-shift experiments, which attempt to alter the pigeon’s dominant time-compensated sun-compass, indicate that compass orientation may be used even from familiar release sites (8, 11–19). Thus the role of the sun-compass remains substantially unresolved, with inferences largely dependent on classical vanishing data which can only provide partial information on a bird’s navigational decisions. Using miniature precision Global Positioning System (GPS) logging technology, we here test these two hypotheses explicitly by examining the interaction between the sun-compass and the familiar landscape along pigeons’ entire homeward routes.

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Abbreviation: GPS, Global Positioning System.

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to a clock-shift treatment resulting in an ≈90° expected shift in orientation. A final, clock-shifted release was then conducted from the training site, and the experiment was repeated at three further sites directionally balanced around home. A total of 64 clock-shifted releases were thus conducted. Seventeen were incomplete; of these, six (five high-familiarity and one low-familiarity) contained no data, and the other 11 (all low-familiarity birds) did not end at the loft because subjects took longer than the GPS device’s battery life (2.5 h) to return home. These were included in Fig. 1 up to the furthest distance recorded from the subjects, but excluded from any further analyses.

First, we evaluated the impact of clock-shift by using virtual vanishing bearings (20). Subjects’ headings with respect to the release point were determined at 500-m intervals (measured from the release site) in tracks immediately preceding the clock-shift treatment as well as in test releases. Differences in heading at each 500 m boundary for a given bird’s pair of tracks were then taken to represent the effect of the clock-shift treatment on the bird’s orientation. The average deviation

Fig. 2. Nearest-neighbor vector analysis. (A) The calculation of nearest-neighbor vectors is illustrated through an example bird. For each point on the analyzed track (here the “clock-shifted flight”) a vector was drawn to the nearest time-independent neighbor among the points recorded during previous flights by the same bird. Axes show U.K. Ordnance Survey northings and eastings. (B) The nearest-neighbor vectors are plotted for the example bird in A. Each vector is rotated such that the estimated instantaneous trajectory of flight is 0°; the scale for vector lengths is shown by concentric circles. Vectors between non-clock-shifted releases are shown in blue; vectors from the clock-shifted release to nonshifted tracks are shown in red. (C) The distributions of mean vectors for birds in the three groups are examined: non-clock-shifted flights of high-familiarity birds (blue), clock-shifted flights of high-familiarity birds (red), and clock-shifted flights of low-familiarity birds (green). Second-order mean and covariance ellipse are shown for each distribution. The three groups’ distributions are significantly different (two-sample 2D Kolmogorov–Smirnov test, \( n = 133, n = 27, n = 31 \), respectively; \( D > 0.45, P < 0.01 \) for all pairwise comparisons). (D) The mean vectors of high-familiarity birds’ clock-shifted flights are compared with the distribution of their previous, non-clock-shifted flights (blue ellipse). Red dots show mean vectors that are significantly unlikely to have come from the latter distribution (see also Fig. 3); gray dots show mean vectors that cannot be statistically distinguished from non-clock-shifted performance (calculated by using the Mahalanobis distance, with significance threshold at \( P = 0.05 \)). In C and D, Insets magnify the central parts of the plots.
observed across both the high- and low-familiarity groups was in the expected direction for compass control (anticlockwise; see Fig. 1) at each boundary at all four sites, showing that the clock-shift treatment had been effective. However, the magnitude of the deviation varied prominently with release site and level of experience. At three of the four sites, Weston Wood, High Cogges, and Hinksey Heights, high-familiarity birds showed little deviation and most remained very close to their established routes throughout the journey (Fig. 1A–C; individual tracks are shown in Fig. 3). Low-familiarity birds generally showed stronger deviation, although angles were still smaller than predicted for full dependence on sun-compass orientation. At the fourth site, Bladon Heath, average deviations were comparable in the low- and high-familiarity groups and again reduced compared with sun-compass expectations (Fig. 1D).

To investigate further the spatial relationship between tracks on a second-by-second basis, we developed a more detailed analysis of clock-shifted track similarities to each bird’s previous (nonshifted) track or tracks. At every in-flight position the vector to the nearest time-independent neighbor among the same bird’s previous track or tracks was calculated (Fig. 2A). Plotting these vectors for an individual bird’s tracks provides a distribution of intertrack deviation in both distance and trajectory angle, with route recapitulation during training characterized by predominantly short, omnidirectional vectors (blue symbols in Fig. 2B). This result suggests that birds remain faithful to their previous routes and that any displacement is not laterally biased. The short and omnidirectional mean vector distribution across all unshifted high-familiarity tracks (blue ellipse in Fig. 2C) more generally reconfirms this route-recapitulation phenomenon. The mean vector distributions for shifted birds, however, are quite different. Both groups show an anticlockwise deflection, expected if birds remain on the compass-shifted side of their previous route for much of their journey home. But whereas most low-familiarity birds (Fig. 2C, green ellipse) are relatively distantly displaced, most high-familiarity birds (Fig. 2C, red ellipse) are either within the bounds of the unshifted training track distribution or displaced just a short distance. Fig. 2D shows that about a third of the high-familiarity birds’ shifted tracks are no more different from their comparison tracks than are training tracks from each other (gray dots), whereas the remaining two-thirds are significantly displaced, with most of these showing a small anticlockwise bias (red dots).

Fig. 3 shows all high-familiarity clock-shifted birds’ tracks individually in order of decreasing inconsistency between clock-shifted and training tracks, with Fig. 3A plotting those birds showing a track inconsistency too high to be consistent with simple route recapitulation, and Fig. 3B plotting those birds whose clock-shifted and final training tracks are statistically indistinguishable. [For tracks of subjects in the low-familiarity group, see the supporting information (SI) Fig. 5.] Within Fig. 3A, the birds showing the highest track inconsistencies (e.g., tracks 1–4) appeared to respond to clock-shift in the conventional way, albeit with reduced deflection. However, many birds, particularly those with small intertrack inconsistencies, flew routes or segments thereof having the form of their established routes, but in parallel (e.g., tracks 11–18). This parallel route recapitulation is accompanied by a distinct anticlockwise offset. Finally, some birds show this effect, or indeed a conventional clock-shift effect, not at the release site but later on at some point on their recapitulated track (tracks 5, 8–10, 13, 17, and 18). In many cases, response to clock-shift appears after a period of road-following, most clearly seen at the Weston Wood site (Fig. 4).

Discussion

Our previous work has shown that, given sufficient experience, homing pigeons develop individually distinct, stereotyped routes home, which they accurately recapitulate on each subsequent journey (9, 10). However, the exact guidance mechanisms controlling this behavior have remained unclear. The two most obvious possibilities are direct attraction from one familiar landmark to the next or a sequence of compass instructions between familiar landmarks. The present experiments demonstrate that route-recapitulating birds (i.e., our high-familiarity group) are capable of remaining faithful to their established routes even after clock-shifting produces sun-compass information seriously at odds with directional information from the visual landscape. Our findings therefore clearly indicate that memorized visual landmarks can directly provide onward guidance along the entire route home (and not just site recognition cues at release). This is pilotage (2, 3).

Birds less familiar with the release sites showed a much stronger effect of clock-shift than their route-recapitulating counterparts. Nevertheless, consistent with many previous results using familiar release sites (e.g., refs. 15, 16, 18, and 19), deviations in the low-familiarity group were considerably smaller than predicted for full dependence on sun-compass orientation. In addition, a persistent residual influence of the compass along the route appears evident even in some high-familiarity
birds, suggesting a more fundamentally integrated role for the sun-compass even in piloting birds, but one with behavioral effects not easily characterized by using customary summary vanishing-bearing statistics. An unexpected yet prominent phenomenon among high-familiarity birds was the accurate recapitulation of the shape of established routes, but in parallel, offset in the clock-shifted direction. Such parallel route recapitulation must reflect faithful attention to the pattern of memorized landmarks, yet suggests that even piloting birds are attending to onward guidance provided by the shifted sun-compass. The observation that the clock-shift effect can appear not at the release site but at a later point on the recapitulated track (e.g., Fig. 4), implies that some piloting birds may respond to compass instructions at specific points en route.

Rather than constituting two independent mechanisms of guidance within the familiar area, our results therefore show that pilotage and compass orientation may be used in combination: landmark and compass cues may be either perceptually or neurally integrated, or the birds’ attention may shift so rapidly between them that the resulting behavior gives the appearance of simultaneous dual control. Ants (21, 22) are known to correct compass heading inaccuracy by using prominent memorized visual landmarks, and even pigeons in classical clock-shift studies often eventually return home, indicating that at some point something other than pure compass information must provide onward guidance. Although response to sun-compass information en route has not been demonstrated before, it is perhaps not as surprising as the apparently simultaneous combination of the two guidance mechanisms evident in the offset tracks. This is unexpected under conventional theory.

We hypothesize that as familiarity with a route increases, onward guidance from one known place to the next en route is

![Fig. 4. Performance of all high-familiarity birds at the Weston Wood release site, immediately before (blue tracks) and after (red tracks) the clock-shift treatment. Open circle indicates location of the release site; filled circle shows location of home. (Scale bar, 1 km.)](Image)
increasingly controlled by attraction to memorized landscape cues (pilotage), and decreasingly controlled by sun-compass information associated with each known place. Because there is clearly much variation between individuals in the same treatment groups, we suggest that some birds may acquire this familiarity, or switch strategy, quicker than others. Where the two sources of information conflict, the resultant chosen path depends on the strength of pilotage control. Where familiarity is low (or indeed, nonexistent as in true navigation) compass instructions may outweigh any attraction to landmarks and trajectories may break away from the known route. Where familiarity is high, attraction to visual landmarks outweighs compass control, and the established route is recapitulated. Evidence that compass information is not entirely disregarded even in thoroughly familiar birds comes from the offset tracks, in which we hypothesize that a degree of spatial tolerance around the exact memorized route allows birds to accept conflicting information from the two sources without losing sight of the established route. We hypothesize that maintenance of direct visual contact with the route may be what imposes the recapitulating birds’ tolerance limit for attending to competing compass information, and hence is what imposes stability in the parallel route. Thus piloting birds continue to maintain memories of, and attention to, compass information even after they apparently have the sufficient and necessary route-based information for homeward guidance. While it is possible that such compass memories are, and have always been, associated with representations of familiar visual landmarks as hypothesized here, it is also possible that they originate from an initial, and now residual, olfactory navigational map. In addition, a potential role for the magnetic compass acting as a backup to the sun compass when solar and landmark guidance cues are put in conflict (although apparently not otherwise; see ref. 9) still remains to be explicitly investigated. Either way, our results clearly indicate that birds are combining multiple sources of onward guidance information during the local homing task. Both the origin of this compass information and the function of its integration with landmark guidance remain to be elucidated.

Materials and Methods

Subjects and Materials. Thirty-two homing pigeons (*Columba livia*) bred at the Oxford University Field Station at Wytham (51°46’58.34”N, 1°19’01.10”W) served as subjects. All were at least 2 years old, weighed a minimum of 480 g, and had participated in several prior homing experiments. They were familiarized with carrying miniature GPS logging devices attached to the back by a small Velcro strip glued to clipped feathers (20). GPS devices weighed 24–28 g and consisted of an integrated receiver and logger (µ-blox, Thalwil, Switzerland), ceramic patch antenna, and 3.7-V lithium-polymer battery. Data fixes were logged by the device at 1-s intervals, with an accuracy of ±4 m in the latitude/longitudinal plane. On the birds’ return to the home loft, data recorded by the device were downloaded by using the dedicated software µ-logger, and flight tracks were superimposed on Ordnance Survey maps by using Fugawi Mapping software (Northport Systems, Toronto, Canada).

Training and Testing Procedures. Four release sites were chosen for training: Weston Wood (51°51’17.87”N, 2°12’55.46”W; distance and direction from home: 10.6 km, 41.4°), High Cogges (51°46’59.38”N, 1°27’10.41”W; distance and direction from home: 9.4 km, 269.9°), Bladon Heath (51°49’21.62”N, 1°21’12.25”W; distance and direction from home: 5.1 km, 150°), and Hinksey Heights (51°44’03.58”N, 1°16’28.62”W; distance and direction from home: 6.1 km, 331°). Sixteen of the total of 32 subjects were assigned to each release site, 8 of whom were experienced in several prior homing experiments. They were between the high-familiarity group, the remaining 8 the low-familiarity group. None of the birds served as subjects at more than two of the four release sites. Training and testing of all subjects at a particular site were completed before training at the next site began.

In the training phase at each site, birds assigned to the high-familiarity group were released 20 times consecutively, over a period of ~2 weeks. A maximum of three releases per day were conducted, restricted to times when the sun’s disk was clearly visible. Birds carried dummy weights on the first 15 training flights, and GPS devices on the final 5. During the same 2-week period, birds in the low-familiarity group received a comparable number of releases from a variety of sites located in various directions from the home loft, including no more than four releases from the training site, the final one of which was tracked. The final tracks recorded from the training site for each bird were used in subsequent analyses as baseline measures of performance under unshifted conditions.

Once both groups of birds had completed training, subjects were moved into a light-tight chamber. The timing of lights-on and lights-off were adjusted such that they occurred 4 h after true sunrise and sunset times, corresponding to a roughly 90° shift in the sun’s azimuth on the projected dates of release (82.4°, 86.5°, 90.0°, and 90.1° at the four release sites used). Subjects remained in the clock-shift chamber for the duration of a minimum of 5 days (maximum 7), after which they were transported in a light-tight container to the training sites, and released individually. The flights of all subjects during their clock-shifted release were logged by GPS devices.

Track Analysis. All analyses were conducted in Matlab (Mathworks, Natick, MA). Tracks were initially preprocessed by removing any consecutive points where the subject’s position changed by less than 1 m (thus eliminating rest periods). In addition, tracks were terminated once birds had reached to within 50 m of the location of the loft. Tracks were then analyzed by comparing them to one (low-familiarity group) or several (high-familiarity group) previous “comparison” tracks. Vectors were constructed from each point to the nearest neighbor among all points within the set of comparison tracks. For a track with 100 positions, for example, this yielded 100 nearest-neighbor vectors. Positions between consecutive data points on comparison tracks were linearly interpolated to avoid errors due to the discrete nature of the time series. Each vector was then rotated according to the estimated trajectory of the bird at the current point. This trajectory was estimated by using the central difference of the position five steps (seconds) ahead and five steps (seconds) before the current position (the line that passed through these points was the estimated trajectory). Thus, a nearest neighbor that lay directly ahead of the subject would have had a vector angle of 0° (resulting in a dot positioned along the 0° line in Fig. 2B, with distance from center corresponding to the length of the vector).

For high-familiarity subjects, nearest-neighbor analysis was conducted among the final five non-clock-shifted flights (taking each flight in turn and comparing it to the other four), and then between the clock-shifted flight and the five non-clock-shifted flights. For low-familiarity subjects, the clock-shifted flight was compared with the lone previous non-clock-shifted flight.

Comparison of Mean Vector Distributions. Comparisons between the three distributions shown in Fig. 2C were conducted by using a two-sample 2D Kolmogorov–Smirnov test (23). This nonparametric test was preferred because of the heavy skew seen in the three distributions. Because 12 tracks in the dataset containing the low-familiarity birds’ clock-shifted flights were either missing or incomplete (did not end at the loft), we performed the analysis both with and without these data to explore their influence on the results.
The conclusions of the statistical tests were unchanged. To determine whether the mean nearest-neighbor vectors from the clock-shifted flights of high-familiarity birds were significantly outside of the mean vector distribution of non-clock-shifted flights, the Mahalanobis distance (24) was used. Each clock-shifted mean vector was compared with the distribution of mean vectors obtained from non-clock-shifted flights. In normal distributions the Mahalanobis distance follows the $\chi^2$ distribution with $n - 1$ degrees of freedom. Therefore any vectors with a Mahalanobis distance of more than 5.99 lie significantly ($P < 0.05$) outside the distribution.

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