Computer Simulation of Long-Range Bird Navigation*

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Abstract

This paper presents a numerical simulation of the homing behaviour of carrier pigeons, using Kramer's "map and compass" model (Kramer, 1959) and the concept of the "navigational map" (Wallraff, 1974, Wiltschko and Wiltschko, 1998).

The simulations show that homing is indeed possible, using the model. Furthermore, they make predictions about the homing efficiency of carrier pigeons, which appear to be compatible with behavioural findings.

1. Introduction

The design of adaptive systems and research into autonomous mobile robotics takes much inspiration from biology, especially ethology. Often, however, the mechanisms underlying the behaviour of a biological agent are unknown, and hypotheses have to be formed.

One method of investigating such hypotheses would be to use numerical simulation: A numerical model, based on the hypothesis in question, is used to make predictions that are then evaluated against observations of the animal being modelled. Any discrepancies can then be used to refine the model. An example of such an approach is Nepomnyashchikh's and Gremyatchikh's modelling of the carp's exploratory behaviour (Nepomnyashchikh and Gremyatchikh, 1996). Observing the number of turns per time interval of an individual carp in a circular, narrow tank, they model this behaviour by a one-dimensional map: observation of the animal in question leads to a mathematical model that can subsequently be used to make predictions about the mechanisms used by the animal, or the animal's responses to certain stimuli.

This paper presents a numerical simulation of long-range pigeon navigation, using Kramer's "Map and Compass" model (Kramer, 1959). This model postulates that pigeons use naturally occurring gradients to determine the course to the loft, and a compass sense to establish and maintain this direction. The objective of the simulations here was to investigate whether homing *is* possible, using this model, and to determine the influence of various parameters upon homing performance.

The question of how to simulate behaving agents — alive or machines — is obviously relevant to autonomous mobile robotics, too. The example of bird navigation presented in this paper provides a case study of how a model can be derived through experimental observation of the agent, and how predictions made by the model can be verified through subsequent experiments. It is, therefore, a case study investigating the value of simulation in understanding animal behaviour.

2. The Grid-Map Model of Bird Navigation

2.1 Experimental Observations in Pigeons

Birds are able to return home from distant, unfamiliar sites. This is not only true when they have actively performed the outward journey, but also when they have been passively displaced. The question is how this is accomplished.

Experiments analysing the avian navigational system are normally conducted by releasing homing pigeons at the distant site, observing their initial flight directions and recording their homing times. At distant sites, pigeons normally depart roughly in the home direction. At some sites, however, they show deviations from the true home course. These deviation are mostly small, rarely exceeding 60°; they are site-specific in the sense that they are regularly observed in *all* pigeons from a loft released at that particular site. The birds return from such sites just as well as from sites where they depart directly in the home direction. Pigeons are heading in their home direction or future vanishing direction within less than a minute after release, which indicates that they are aware of their home course right from the beginning, thus excluding a necessity for searching flights. For more details, see (Wiltschko, 1992, Wiltschko and Wiltschko, 1999).

Neither initial orientation nor homing performance are markedly impaired when adult pigeons are transported

*Proc. Simulation of Adaptive Behavior 2000, MIT Press.

to the release site under conditions that prevent their access to any kind of known navigational information.

Pigeons have been carried to the release site on irregularly rotating turntables (Matthews, 1951, Keeton, 1974), they have been subjected to distorted magnetic fields (Kiepenheuer, 1978, Wiltschko and Wiltschko, 1985), they have been subjected to both treatments and an additional olfactory deprivation (Wallraff, 1980) — they have even been carried to the release site under complete anaesthesia (Walcott and Schmidt-Koenig, 1973). But despite all these treatments, they were able to return home successfully.

These observations rule out that birds rely on route-specific information obtained during the outward journey and dead reckoning. They suggest that instead pigeons must be able to make use of navigational information obtained at the release site. The observation that this applies also for sites where the birds have never been before excludes the use of familiar landmarks.

Clock-shifting, i.e. manipulating of the birds' sense of time, leads to misjudging of the position of the sun, which, in turn, alters the reading of the birds' sun compass. When released, clock-shifted birds fly in directions that are deflected from those of untreated birds in a characteristic way, with the size of the deflection roughly corresponding to the difference in sun azimuth between the true and the bird's subjective time of day. Such deflections are observed at familiar and unfamiliar sites alike (e.g. (Schmidt-Koenig, 1961), for a summary, see (Wiltschko et al., 1994)). The effect of clock-shifting again excludes that homing is achieved by either dead reckoning or by following sequences of familiar landmarks. Additionally, it indicates a very important aspect of the avian navigational system, namely, that birds determine their home direction as a compass course.

These above-mentioned observations led to the Map-and-Compass model first proposed in (Kramer, 1959) that is described below.

2.2 The Map and Compass Model

Kramer's map and compass model (Kramer, 1959) postulates that avian navigation is a two step process. In a first step, the home direction is determined as a compass course, equivalent to our human concept of North, East etc. In a second step, this course is established and transformed into a direction of flight with the help of a compass.

2.2.1 The Navigational Map

While the *additional* use of familiar landmarks and dead reckoning under normal conditions cannot be excluded, the experimental evidence mentioned above suggests that *another* mechanism of homing exists, based on site-specific information that is accessible also at distant, unfamiliar sites. This points to factors that can be extrapolated beyond the range of direct experience. Therefore, the present model of avian navigation postulates that birds determine their homeward course using gradient fields.

For this method to be practical, there must be at least two, possibly more environmental gradients, which must cover a large enough area to be useful for navigation, and that intersect at not too acute an angle. The exact physical nature of these gradients is still under dispute. The factors proposed include magnetic and gravitational cues, odours, infra-sound, and the view of landscape features (see (Wallraff, 1974, Baker, 1984, Wiltschko and Wiltschko, 1998) for details). These gradients, in particular their directions, are represented in the bird's "navigational map" or "grid map", which is established by experience during the first months after fledging. From direct observations during spontaneous flights at their home loft, young pigeons become familiar with the local landmarks, landscape features, and, more importantly for this study, with the local gradient values and the course of these gradients in their home region. The latter information is memorised to constitute the grid map, which thus consist of a directionally orientated mental representation of the gradient distribution within the home region. This means that adult birds are aware of the course of gradients, and, by extrapolating this knowledge, can use their map to interpret local gradient values also at distant, *unfamiliar* sites.

The process of determining the homeward course from the release site is postulated to take place as follows: The birds measure the local scalar values at the release site and compare them with the remembered home values. The sign and the size of the differences indicate the relationship of their present position to the home site and allow them to determine their home course. For example, if they know that gradient X increases towards the east (see figure 1), encountering scalar values of X greater than the home values will tell them that they are east of home, and hence have to head westward. The greater the increase, the farther east they are, and the stronger the westward component of their course becomes. Once the home course is determined this way, the compass is used to establish it and maintain course during the homing flight. In other words: gradients are used to determine the required course, the compass is used to maintain that course.

The model described above offers an explanation for the frequently observed deviations from the true home course, the so-called release site biases (Keeton, 1973). They are attributed to local deviations from gradient fields that are otherwise changing monotonically across the terrain. The right part of figure 1 shows such a situ-

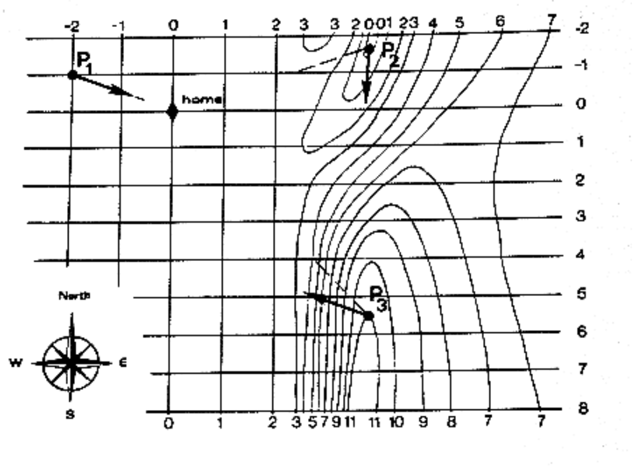

Figure 1: Release site bias due to local fluctuations in the gradient (after (Wiltschko and Wiltschko, 1999). Lines shown are isometric lines of equal gradient value in $x-$ and $y-$directions resp.

ation. The pigeons, expecting the gradients to change as they do within the vicinity of their home site, misjudge their position and consequently determine a course that differs from the true home course. However, birds repeat the navigational step in regular intervals, re-determine their course and thus correct their initial error. This explains why the homing performance from those sites is little affected.

Close to home where the difference between the local values and the home values of the gradients can no longer be measured, the birds switch to another system, using local landmarks of their immediate home range to indicate position. These landmarks are incorporated in the "mosaic map", an analogue to the grid map, which is a mental representation of the spatial distribution of familiar *landmarks* in the vicinity of the home loft. It allows birds to home on a direct route once the area covered by the mosaic map is reached.

2.2.2 The Birds' Compass Sense

Adult pigeons possess two compass mechanisms, both of which they use for establishing course. On the one hand, there is a magnetic compass sense that derives direction from the inclination of the magnetic field lines with respect to the earth's surface. In other words, this compass does not distinguish northward and southward, but polewards and equatorwards. This magnetic compass is present in pigeons from birth. Secondly, there is a sun compass which is a mechanism based on experience. After fledging, during the first twelve weeks of their lives, young pigeons learn to correlate the sun's apparent motion at their local site with time of day and with their magnetic compass sense. Once established, pigeons prefer to use the sun compass, but can switch over to the magnetic compass without apparent loss of navigational capability if necessary, for example on overcast days.

Both sun compass and magnetic compass give the birds equivalent information. In the simulations presented here, we have therefore assumed a generic compass sense, giving the simulated bird its current heading within a definable error margin, without specifically modelling either sun compass or magnetic compass.

3. Computer Modelling of the Grid-Map Model

3.1 Numerical Representation of the Grid Map

In the numerical model, the underlying x- and y- gradients are represented as grey-level images in *gif* format. In these gradient images, grey-level values represent gradient values, i.e. the simulated bird experiences the same gradient value along a line of identical grey-level, as does the living bird when moving such that its perception of the gradient field does not change, for example when moving parallel to one of the two gradient fields.

Figure 2 shows a simulation environment with regular monotonic gradients at about 90°, figure 3 shows a second simulation environment, which is a representation of the distorted gradient field of figure 1. Both simulation environments measure 1000 arbitrary units in each direction.

3.2 Basic Assumptions About the Simulated Bird

Simulating the navigation of experienced birds, we assume that the birds posses a grid map that represents regular gradients as in figure 2 and judge the gradient differences accordingly. Two simulation parameters have been arbitrarily fixed and were kept constant during all simulations. These are the maximum segment length and size of the immediate home range.

A maximum segment length was introduced to model the assumption that pigeons do not compute the required heading to the loft continuously, but only in regular intervals. It indicates the distance the simulated bird will travel before it computes the course to the home loft anew. In all simulations, the maximum segment length was set to 10 arbitrary distance units.

The size of the immediate home range represents the area around the home loft covered by the mosaic map of familiar landmarks. The bird's route is controlled by the gradient values until the simulated bird crosses the boundary of the immediate home range. There, this type of navigation ends, and the birds returns to the home loft on a direct route. For all simulations presented here, the size of this area was set to 30 arbitrary units.

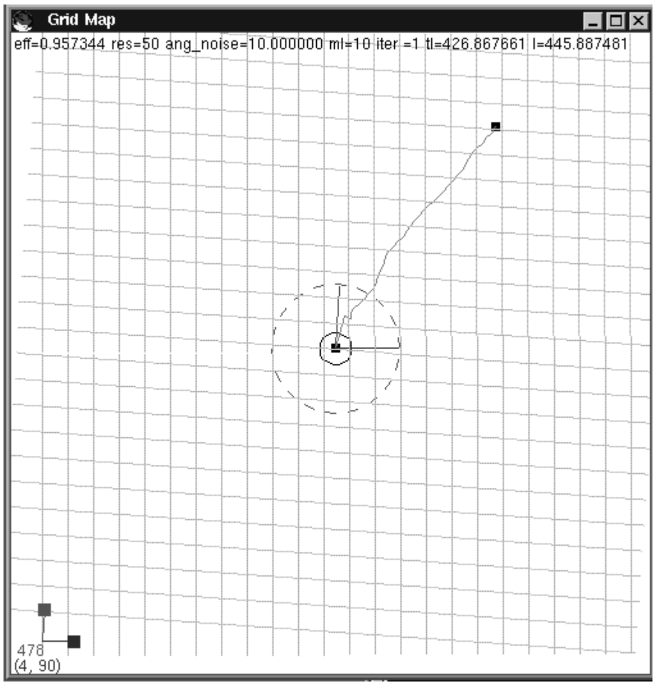

Figure 2: Simulation environment with gradients changing monotonically across the terrain. The two gradients are at 90° angles. The release site is indicated by a black square. The lines shown are isometric lines of equal gradient value in $x-$ and $y-$direction respectively.

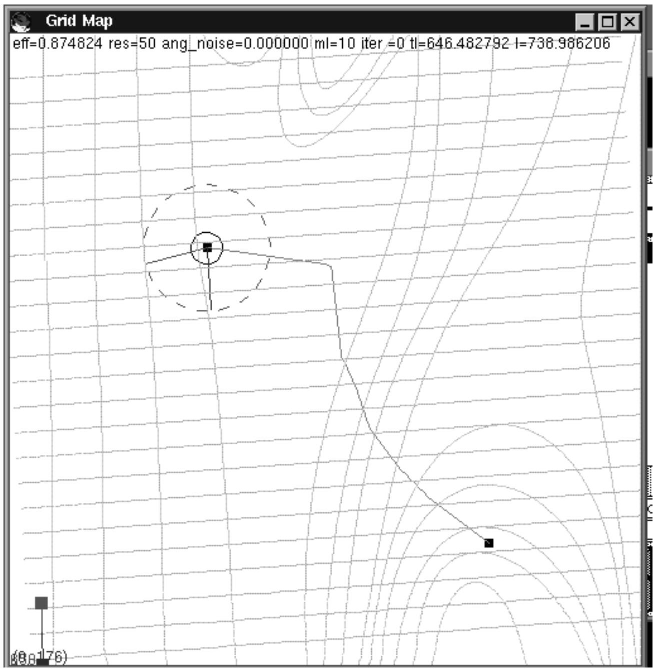

Figure 3: Simulation environment with locally distorted gradients. Again, the release site is indicated by a black square. The solid circle surrounding the loft indicates the range within which the loft is visible to the simulated bird.

3.3 Simulation Mechanism

The fundamental element of our simulation is a "run", which is the completion of one trip from a randomly chosen release site to a randomly chosen loft, under specified simulation conditions (see section 3.4 for a description of these conditions).

At the beginning of a run, the simulated bird determines the current gradient values by consulting the *gif* image, and determines from this the required heading for the loft, as well as an estimated of the distance between release site and loft. This is repeated at regular intervals throughout the run. The course is maintained using the generic compass, which gives the simulated bird its current heading within a definable error margin.

A run is either terminated when the simulated bird gets within 30 units of the loft, at which point we assume familiar landmarks allow the use of the mosaic map to approach the loft directly, or when the simulated bird has completed 110% of the shortest distance between release site and loft. This latter condition is an approximation of the birds' use of the mosaic map: birds switch over to the mosaic map once familiar landmarks appear.

However, in simulation environments with grossly distorted gradients it can happen that the simulated bird is nowhere near the loft after 110% travel, and it is unrealistic in those cases to assume that the bird would be able to fly straight home. We intend to modify this aspect of the simulator for future work, but results presented here are slightly distorted by this approximation.

Once the simulated bird has reached the loft, the efficiency of the homing behaviour is determined according to equation 1. Another run is then performed in the same manner.

Before starting the simulation, the user can specify over how many runs efficiency is to be averaged, before simulation parameters are modified. All results presented in this paper are averaged over 50 runs.

3.4 Variable Simulation Parameters

The numerical simulation of the pigeon's map-and-compass model allows for independent modification of the following parameters:

- **Angle between gradients**. Ideally, gradients should be at right angles, however it is unlikely that this situation occurs in nature. The angle between gradients can therefore be modified, either by the user prior to a simulation, or by the simulator itself to obtain data such as the curves shown in figures 4 and 7.

- **Angle noise (AN)**. This is the maximum difference in degrees between the simulated bird's *true* heading and *perceived* heading, induced by a normally distributed noise term (i.e. the accuracy to which the simulated bird is able to determine its heading, using the compass).

- **Resolution (Res).** This is the smallest detectable change in gradient value, and was included in the model to simulate the effects of diminished sensor acuity in a living bird. A larger value for *resolution* (see figure 6) indicates a larger required change in gradient for detection by the simulated bird, i.e. a lower sensing acuity.

4. Simulation Results

All simulations were carried out by modifying one of the above-mentioned parameters only, and determining the homing efficiency E as defined below:

$$E = \frac{d_{min}}{d_{act}}, \qquad (1)$$

with d_{min} being the shortest distance between the release site and the loft, and d_{act} being the actual distance travelled by the simulated bird.

For each simulation run (i.e. for each completion of one journey between release site and loft), release site and loft position are randomly chosen within the simulated environment, and obviously kept constant for that run. The simulated bird then navigates home, influenced by the parameters defined for the respective simulation. After having completed the entire trip, the efficiency is computed using equation 1. The efficiency given in the graphs in the following sections is the average efficiency over fifty runs under identical simulation parameters (but using fifty different release site - loft pairs).

4.1 Simulations in Environments with "Perfect" Gradients

A first set of simulations was carried out assuming "perfect" (i.e. straight-line) gradients (i.e. the simulation environment shown in figure 2), with the exception of the first experiment. Here, the angle between the two gradients was changeable.

In all other simulations the best case of a 90° angle between gradients was used.

4.1.1 Changing the Angle Between Gradients

If navigation using the grid map model of two intersecting gradients is to work at all, the angle between gradients must not be too acute. Optimal performance, obviously, is expected for a 90° angle between gradients, and worst performance for an angle of 0°

The way different angles between gradients was simulated is as follows. The picture file (*gif* format) that represents a gradient distribution — be it straight or distorted — is used twice to represent the gradient distribution in x and in y direction. For a 90° angle, for instance, these two images are at right angles to each other, for a 0° angle they are parallel to each other. In this way, even two distorted gradients can be at "right angles" for simulation purposes.

Figure 4 confirms our hypothesis that performance is best if gradients are at right angles, showing how efficiency decreases as the angle between the gradients becomes smaller.

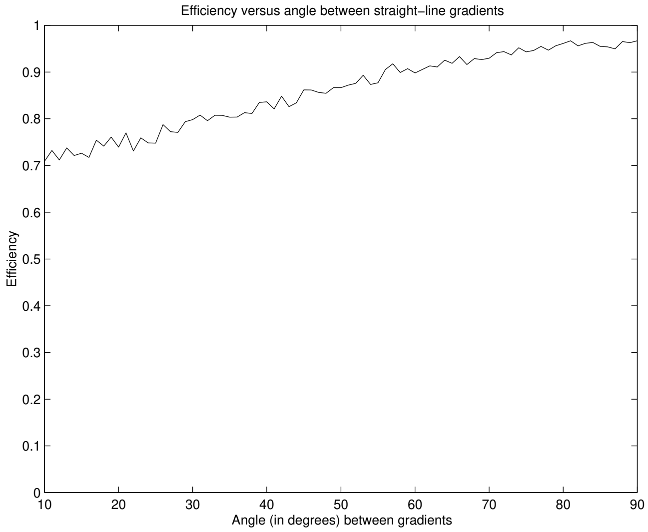

Figure 4: Efficiency versus angle between two straight-line gradients. Simulation parameters: $AN = 10°$, $Res = 10$.

For all subsequent simulations in this section it was assumed that the angle between gradients is constant, at 90°.

4.1.2 Changing the Angle Measuring Acuity by Adding Noise

The simulated bird uses the two gradients to determine the required compass heading for home. It then uses its compass sense (in the living bird the sun compass or the magnetic compass) to establish and maintain the required course.

Like any measurement, the bird's compass sense is subject to noise. We have simulated this by adding or subtracting a noise component to the simulated bird's *true* heading. Figure 5 shows the effects of angle noise on homing efficiency.

It is interesting to note that homing efficiency drops more sharply once the noise exceeds ±25°, indicating that there is a band of compass noise tolerance before homing performance is affected.

As would be expected from theoretical considerations, the simulated bird is able to home even for noise values

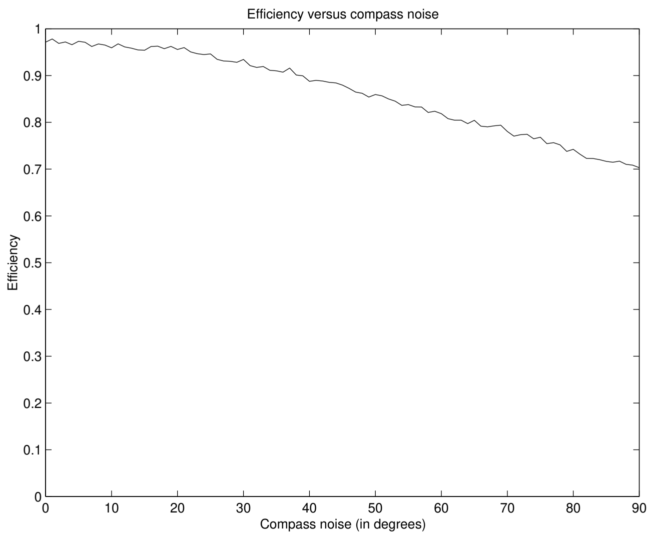

Figure 5: Efficiency versus compass noise in a simulated environment with perfect gradients at 90°. Simulation parameters: $Res = 10$.

approaching ±90°, but efficiency becomes much lower.

4.1.3 Changing Resolution

A further simulation parameter that influences the simulated bird's ability to home is the smallest detectable gradient change (i.e. acuity of gradient perception) within the navigational map, referred to as "resolution" here. Figure 6 shows how homing efficiency decreases as resolution decreases.

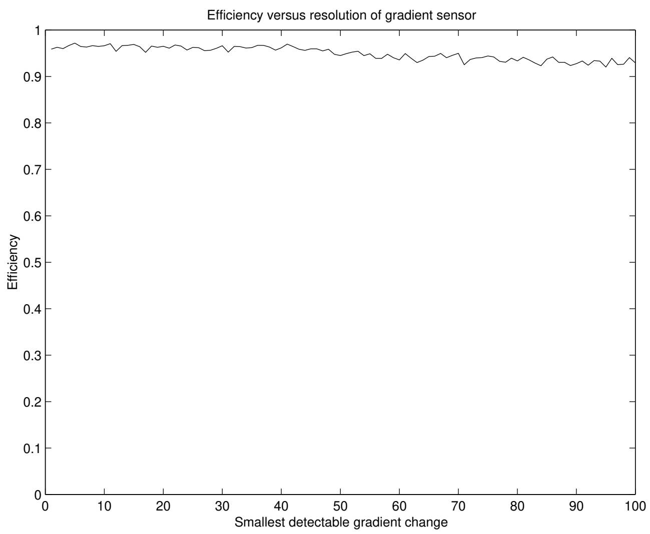

Figure 6: Efficiency versus gradient resolution acuity in a simulated environment with perfect gradients at 90°. Simulation parameters: $AN = 10°$.

Figure 6 shows that homing performance is very little affected by the simulated bird's gradient sensor resolution: the curve is very flat, and the *resolution* parameter proves to be the least critical in the simulations. This is clearly demonstrated by comparing figures 4, 5 and 6.

4.2 Simulations in Environments with "Realistic" Gradients

It is very unlikely that gradients used by birds look like straight lines intersecting at 90°. Rather, observations like release-site bias indicate that there are local fluctuations to naturally occurring gradients, as shown in figures 1 and 3.

The simulations shown in the following sections are identical to the ones discussed above, with the difference that one of the gradients was distorted, as shown in figure 3.

4.2.1 Changing the Angle Between Gradients

To determine the sensitivity to the angle between gradients, the same simulation as in section 4.1.1 was carried out. The results are shown in figure 7.

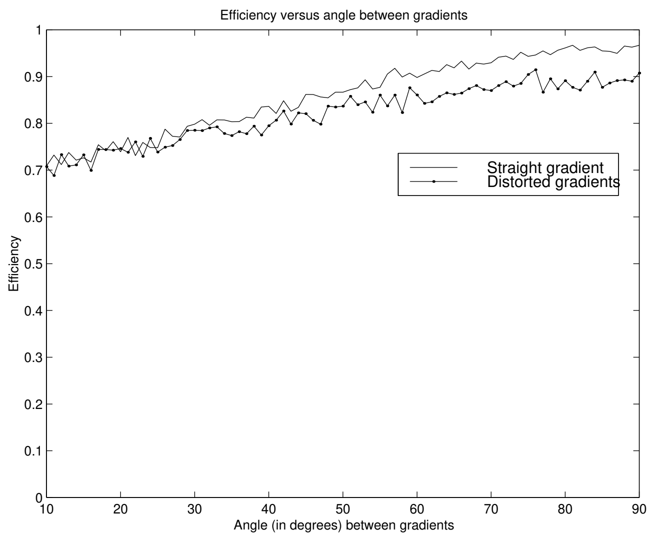

Figure 7: Efficiency versus angle between a straight-line and a distorted gradient (lower graph). Performance using two straight-line gradients is shown for comparison (upper graph). Simulation parameters: $AN = 10°$, $Res = 10$.

One would expect that performance with a distorted gradient is inferior to that with straight-line gradients, which is confirmed by the results shown in figure 7. However, once the angle between gradients falls below 20°, there is no noticeable difference in efficiency any more.

Furthermore, the efficiency curve in the "distorted" environment is shallower, meaning that homing performance is less affected by a decreasing angle between gradients than in the "perfect" environment.

4.2.2 Changing Angle Measuring Acuity by Adding Noise

The next simulation investigated the influence of compass noise on homing efficiency. As in the previous simulation (section 4.1.2), performance under distorted gradients is worse than under straight-line gradients (figure 8).

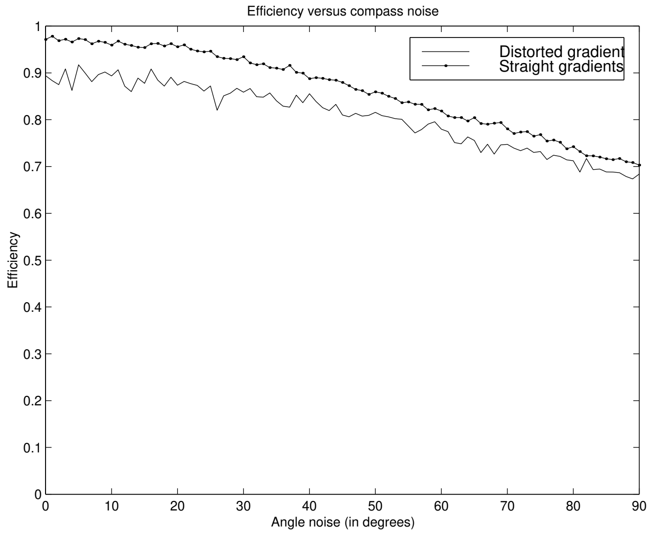

Figure 8: Efficiency versus compass noise in a simulated environment with one distorted and one straight gradient (lower graph). Performance in an environment with perfect gradients is shown for comparison (upper graph). Simulation parameters: $Res = 10$.

However, the performance curve for the distorted gradient again is shallower, meaning that angle measuring noise affects efficiency less than in an environment with straight-line gradients.

4.2.3 Changing Resolution

In a third simulation under realistic conditions the effects of diminishing gradient sensor acuity were investigated. As in the simulations in a "perfect" environment discussed above (section 4.1.3), performance under distorted gradients is worse, in comparison with straight-line gradients (figure 9).

As before, Res is shown to be less critical for homing performance than compass noise or angle between gradients, both in the "perfect" and the "distorted" environment homing performance is very little affected by decreasing resolution.

5. Discussion and Conclusions

The current hypothesis regarding avian navigation assumes that carrier pigeons and other birds use a global map based on environmental gradients that intersect at

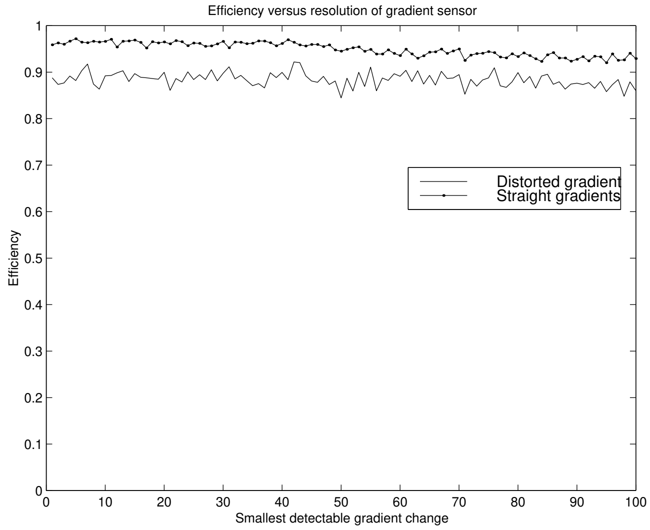

Figure 9: Efficiency versus gradient resolution acuity in a simulated environment with one distorted and one straight gradient (lower graph). Performance in an environment with perfect gradients is shown for comparison (upper graph). Simulation parameters: $AN = 10°$.

large angles to determine their home course and a compass to locate and maintain that course (Wallraff, 1974, Wiltschko and Wiltschko, 1998, Papi, 1990). Our numerical simulation of this "map and compass" model allows us to observe the behaviour of a simulated bird in a controlled environment and to modify parameters such as angles between gradients, resolution of the bird's compass sensor and the resolution of the bird's gradient sensor in a controlled way.

The most important observation is obviously that the simulated bird is indeed able to return home, using the gradients and its compass sense alone. The second crucial observation is that the simulated bird is also able to return home in environments whose gradients are distorted, a case we must assume in many natural environments. Although the overall performance is, of course, better in a "perfect" environment with straight-line gradients, it is interesting to note that the system is less sensitive to angle between gradients, compass noise and changes in gradient sensor resolution in a distorted environment.

Being a model of bird navigation, our simulator makes certain predictions regarding the homing performance of carrier pigeons, and it is important to compare these predictions with actual data on pigeon homing.

Unfortunately, this is not easily done. Return routes of pigeons, as simulated in our test environment, can at present be recorded only with an enormous expenditure of money and/or man power and are not available over greater distances. And yet, it is *long-distance* navigation that is being simulated here!

To obtain at least some measure of plausibility of our simulation results, the customarily recorded homing speeds of pigeons can be used as a criterion for homing efficiency (see equation 1). In our simulation, homing efficiency is solely dependent on the straightness of the path home. In birds, straightness of path is *not* the only criterion for homing speed. Instead, homing speeds depend also on trivial factors such as wind conditions, frequency of rests during the homing flight, or temporarily joining other pigeons. In some cases, median homing speed cannot even be determined at all, because the birds rest over night and only arrive on the next day!

One further complication in estimating the "efficiency" of pigeon homing is that any previous experience of the pigeons plays a vital role in the ability to return to the loft. The birds are able to return much faster from an area they have visited (even only once) before (Grüter and Wiltschko, 1990).

Bearing all these caveats in mind, the median return speeds of pigeons released at unfamiliar sites more than 100 km from their loft, although being very variable, are commonly observed to be about 45 kmh^{-1}. Assuming a flying speed of about 60 kmh^{-1} of an adult pigeon, this means a homing efficiency of 0.75. To compare this with our simulation results, the simulated birds achieved an average efficiency of 0.75 when the angle between gradients was about 30° (both in the "perfect" and the "distorted" environment — see figure 7), having a resolution of 10 distance units and a compass noise of $\pm 10°$. Comparing with pigeons, these values seem plausible.

For future research, the median or average homing speed of releases of several birds from the same site may prove to be even more useful. If releases from sites in certain regions consistently produce slower homing speeds than releases from similar distances in other directions, this might reflect problems with navigation in the respective regions. This, in turn, could indicate that the gradients in that region are more difficult to read for the birds, maybe because they are flatter or more distorted than elsewhere.

In conclusion, the scant behavioural data available suggests that the simulation parameters we have chosen here, which have led to a homing efficiency of between 0.7 and 0.9, appear to be biologically plausible, as there is some experimental evidence that pigeons have a homing efficiency of roundabout 0.75.

The usefulness of this simulator as a tool of synthetic ethology is that it facilitates the controlled and isolated manipulation of bird-specific parameters such as compass accuracy and gradient resolution, and environmental factors such as gradient shape and angles between gradients, and to observe their influence on overall homing efficiency — something that is extremely hard, if not impossible with carrier pigeons.

Acknowledgements

John Sear wrote the simulation software used for this research. We acknowledge his valuable contribution.

We thank Claudia Nehmzow for helpful comments on earlier versions of this paper.

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