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Mathematical analysis of the navigational process in homing pigeons ☆

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ABSTRACT

In a novel approach based on the principles of dynamic systems theory, we analyzed the tracks of pigeons recorded with the help of miniaturized GPS recorders. Using the method of time lag embedding, we calculated the largest Lyapunov exponent to determine the system's predictability and the correlation dimension to estimate the number of factors involved. A low Lyapunov exponent around 0.02, which proved to be rather constant over all calculations, indicates that the navigational process is almost deterministic. In the distribution of the correlation dimension estimates we found three distinctive peaks, at 3.3, 3.7 and 4.2, indicating that avian navigation is a complex multi-dimensional process, involving at least four or five independent factors. Additional factors, as indicated by an increase in the correlation dimension, seem to be included as the pigeons approach their home loft. This increase in correlation dimension and its fractal nature suggest that the various navigational factors can be included as required and weighted independently. Neither the correlation dimension nor the Lyapunov exponent is affected by increasing familiarity of the pigeons with the terrain. This suggests that the navigational strategy is stable with the same process controlling the flight across familiar as well as unfamiliar terrain.

1. Introduction

GPS receivers for tracking pigeons have been available for 10 years (von Hünerbein et al., 2000; Steiner et al., 2000). Meanwhile they have been applied in numerous studies (e.g. Biro et al., 2002; Lipp et al., 2004; Meade et al., 2005; Wiltschko et al., 2007), but so far, GPS data have mostly provided supporting evidence for already existing theories, and have not yet resulted in a deeper understanding of the processes involved in the pigeons' homing flight. Hence, we felt the need to develop a method that would pay tribute to this new type of data, analyzing them in a way that provides insight into the nature of the navigational processes themselves. We used an approach based on dynamic systems theory, the method of time lag embedding (Takens, 1981), which allows us to reconstruct the underlying navigational process from a one dimensional time series provided by the tracks recorded during the homing flight of the pigeons. This allows us to analyze the process without any a priori knowledge about the number of factors involved and their specific interactions. The parameters we focused on are the *largest Lyapunov exponent*, a measure of the system's predictability (see Sano and Sawada, 1985; Wolf et al., 1985; Rosenstein et al., 1993; Kaplan and Glass, 1995), and the *correlation dimension* (see Grassberger and Procaccia, 1983a, 1983b), a measure of the system's degrees of freedom, reflecting the number of factors involved in the navigational process.

2. Theoretical considerations

Current assumptions about navigation in pigeons evolve around different navigational strategies applied in different situations. When pigeons are still young and inexperienced, they use directional information gathered during the outward journey to find their way home (Schmidt-König, 1970; Wiltschko and Wiltschko, 1978). This initial mechanism is based on route information; it is replaced by site information as soon as a navigational 'map' becomes available (Wiltschko and Wiltschko, 1985). This 'map' is based on experience, being a mental representation of the spatial distribution of available navigational factors of various kinds.

Basically, there are two types of site-specific information a pigeon could use and include in such a 'map': (1) point-like information tied to a specific location, like e.g. familiar landmarks that characterize a site, and (2) information based on extended geophysical gradients (see Wallraff, 1974; Wiltschko and Wiltschko, 2003 for review), like e.g. the geomagnetic field. Point-like information could be used in two ways, namely as a direct means of navigation, with the path

☆ This study is dedicated to Ulrich Nehmzow (1961–2010), who inspired this work.

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towards home defined by a series of successive landmarks, a strategy called 'piloting' (Griffin, 1952; Mann et al., 2011); it could also be used as component of a 'mosaic map' (Wallraff, 1974; Graue, 1963) where each familiar landmark is associated with a compass course indicating the direction from the respective location towards the home loft. Information on the direction and the steepness of geophysical gradients is learned and represented in the navigational 'map', thus allowing pigeons to interpret local values of these gradients in reference to a home value. Here multiple gradients of different nature could be used simultaneously to increase reliability and precision of that 'map'. Unlike point-like information, information based on gradients is not tied to a specific location and can, by extrapolation, provide pigeons with a means to determine the home course even from distant, unfamiliar sites.

The type of information used, i.e. route information, point-like information or geophysical gradients, and how this information is used, i.e. landmarks for piloting or as elements of a mosaic map, has direct consequences on the degrees of freedom of the underlying navigational process, which should be reflected by the correlation dimension. If pigeons e.g. use landmarks for piloting, then the underlying process is rather simple: the information provided is merely the path towards the next landmark—this type of information offers only one degree of freedom.

Navigation based on a mosaic map, in comparison, requires the involvement of at least one additional factor, a compass. Hence it can be assumed that navigation based on a mosaic map would result in a higher dimensional process with a correlation dimension of at least 2. As the mosaic map is assumed to consist of static cues, each cue within the mosaic map is equivalent to every other, basically providing the same information. Multiple cues of the same type thus may increase certainty and allow pigeons to uniquely identify a specific cue, but essentially do not provide more information than a single cue alone.

If pigeons use different environmental gradients simultaneously as navigational cues, the degrees of freedom of the navigational process depend on the number of gradients involved, leading to a corresponding increase in the correlation dimension. Two different factors, one providing an equivalent to longitudinal and one providing an equivalent to latitudinal information, as well as one compass cue would suffice to allow pigeons to find their way home, hence the correlation dimension should be at least 3.

The correlation dimension could thus indicate the type of strategy applied: low correlation dimensions throughout the entire flight would thus suggest simpler forms of navigation, like navigation based on point-like information, while higher correlation dimensions would suggest navigation based on multiple environmental gradients. A marked change in the correlation dimension would then indicate a change in the navigational strategy.

3. Material and methods

3.1. Recording tracks

The experimental birds were adult pigeons from the loft at the Goethe-University Frankfurt (50°08′N, 8°40′E). They were released from the six sites whose positions are listed in Table 1. At two of the sites, N30 and S30, we conducted a series of repeated releases—not every flight was recorded (for additional details on the test birds, GPS receivers and the release procedure, see Electronic Supplemental Material Section 1).

3.2. Analysis of tracks

All calculations are based on the headings of the pigeons determined as the direction between two consecutive positional fixes in relation to the current home direction. We used two different approaches:

(1) a conservative approach, based on distinctive phases defined by the so-called 'Points of Decisions' (see Schiffner and Wiltschko, 2011, 2009 and Electronic Supplemental Material Section 2 for details), to determine the largest Lyapunov exponent and the correlation dimension and
(2) a dynamic approach to identify changes during the pigeon's flight based on the correlation dimension for single segments of the track.

Table 1
Names and location of release sites and correlation between correlation dimension and distance from the loft. N, sample size, i.e. the number of 500 m distance steps analyzed; r_{sp}, correlation coefficient for Spearman's rank correlation, with asterisks *** indicating significance at $p<0.001$.

Site	Longitude	Latitude	Direction	Distance (km)	N	r_{sp}
N30	50°24′N	8°43′E	189°	30.7	57	−0.919***
N60	50°36′N	8°51′E	194°	54.5	60	−0.894***
S30	49°52′N	8°34′E	13°	28.8	57	−0.202
S60	49°36′N	8°28′E	14°	58.9	60	−0.637***
NE40	50°24′N	9°06′E	225°	44.8	89	−0.786***
SW40	49°47′N	8°08′E	61°	42.2	84	−0.590***

3.2.1. Conservative approach

We determined the so-called 'Points of Decisions' (Schiffner and Wiltschko, 2011, 2009) dividing the tracks into distinctive phases. Each of these phases was then treated as an independent time series for the calculation of the largest Lyapunov exponent and the correlation dimension. All calculations were performed for the original time series and for the first and second half of each time series separately to identify non-stationary and noise contaminated time series, where application of time lag embedding would not yield meaningful results. For details on implementation of the algorithms, selection of the variables and filtering of the data, see Section 3 in the Electronic Supplemental Material.

3.2.2. Dynamic approach

For the dynamic approach, we determined the correlation dimension and the steadiness of the flight, with steadiness defined as the vector length resulting from consecutive headings. Both variables were calculated as sliding means over 180 s in fixed intervals of 30 s. Due to the reduced number of data points in this specific approach, the resulting estimate of the correlation dimension can no longer be considered to be exact. However, as previous studies (Ramsey and Yuan, 1990; Stefanovska et al., 1997) on the effect of reduced number of data points indicate, they may still serve as a rough estimate allowing us to determine changes in the correlation dimension.

3.3. Statistical analysis

Histograms illustrate the range of estimates observed for both variables. We tested the data for difference from random, using the Chi-Squared test, and for normal distribution, using the Anderson–Darling test (Anderson and Darling, 1952). We also tested both variables for interdependence using the Chi-Squared test; for this purpose we formed categories of equal range over the area where estimates were above chance level, resulting in three categories for the largest Lyapunov exponent and five for the correlation dimension. The Mann Whitney U-Test was used to compare the largest Lyapunov exponent and the correlation dimension between the single releases and to compare the different release sites (Sachs, 1978). As pigeons never flew along