

RESEARCH ARTICLE

Development of the navigational system in homing pigeons: increase in complexity of the navigational map

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SUMMARY

In the present study we analysed GPS-recorded tracks from pigeons of different ages from 11 sites between 3.6 and 22.1 km from the home loft, which revealed changes in the navigational system as the birds grew older and became more experienced. The efficiency of juveniles in their first year of life, at only 0.27, was rather low, indicating that the young birds covered more than three times the direct distance home. In the second year, after a standard training programme, the efficiency of the same birds increased to 0.80 and was no longer different from that of older pigeons. The short-term correlation dimension, a variable that reflects the number of factors involved in the navigational process, also increased with age. In juveniles, it was markedly lower than in the other two groups, but even in yearlings it was still significantly lower than that of old pigeons, indicating that the navigational map of yearlings is still developing. Our results indicate that the map system, although functional in the first year of life, continues to become more complex – older pigeons seem to either consider more navigational factors than younger ones or at least weigh the same factors differently.

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INTRODUCTION

Kramer's Map-and-Compass model describes pigeon navigation as a two-step process: pigeons first establish their position relative to their loft and determine the compass course leading home, then they use their compass to locate this course (Kramer, 1957). The second step, the compass step, is very well understood and so is its development. The magnetic compass is innate; it is based on direct sensory input; the sun compass, in contrast, is established by experience (see Wiltschko, 1983). The magnetic compass serves as a directional reference when the sun compass is being established (Wiltschko and Wiltschko, 1990). The sun compass becomes functional in the third month of life, but this process can be accelerated by early flying experience (Wiltschko, 1983).

The map step, however, is not yet completely understood. When pigeons begin to fly, they appear to apply a simple strategy to obtain their home direction, namely route reversal (Schmidt-König, 1970) based on recording the direction of the outward journey with their magnetic compass (Wiltschko and Wiltschko, 1978). Yet, with increasing experience, pigeons no longer rely on outward journey information alone but increasingly base their navigation on local information obtained at the release sites (Wiltschko and Wiltschko, 1985). They establish a 'navigational map', a mental representation of the distribution of navigational factors within their home range. This requires detailed knowledge of the surrounding area, which the young pigeons presumably acquire by exploration.

It has been suggested (e.g. Graue, 1963; Wallraff, 1974; Wiltschko and Wiltschko, 1982) that pigeons rely on two types of 'map' that supplement each other. One of them, used for long-range navigation, is assumed to be based on at least two environmental

gradients; it allows pigeons to extrapolate information acquired in the home range and hence determine their home course at distant, unfamiliar sites. A multitude of factors have been proposed to be an integral part of this so-called 'gradient map'; these include magnetic cues (Viguer, 1882; Wagner, 1976; Walcott, 1978; Dennis et al., 2007; Wiltschko et al., 2010), Coriolis force (Yeagley, 1947), olfactory cues (e.g. Papi et al., 1971; Papi, 1986; Gagliardo et al., 2009) (but see Jorge et al., 2009; Jorge et al., 2010; Gagliardo et al., 2011), infrasound (Quine, 1982; Hagstrum, 2000; Hagstrum, 2013), gravity (Lednor and Walcott, 1985) and landscape features (Baker, 1984), but to date only a few are actually supported by experimental evidence. A mathematical analysis of tracks from pigeons recorded with GPS-based flight recorders suggests that at least four factors are involved in the navigational process, which means that, aside from the compass, three or more factors are included in the pigeons' 'map' (Schiffner et al., 2011a).

This 'gradient map' is supplemented by an additional map for short-range navigation, assumed to consist of a multitude of prominent landmarks in the area around the home loft and their directional relationship to home (Graue, 1963; Wallraff, 1974; Biro et al., 2007). The range of this so called 'mosaic map' would theoretically be limited by the amount of detailed information it requires; the studies by Michener and Walcott, and Braithwaite (Michener and Walcott, 1967; Braithwaite, 1993) suggest an expansion of up to 10 km around the loft. The two types of map appear to overlap, with a gradual transition.

It has long been known that increasing experience, e.g. by training flights, improves the homing performance of pigeons considerably; here, general knowledge of the region appears to play a much more

important role than local familiarity with a specific site (e.g. Wallraff, 1959; Schiffner et al., 2011a). However, it is not yet clear how experience affects the underlying navigational process. The navigational processes in pigeons of different ages, corresponding with increasing general experience, have never been investigated in detail. In the present study, we applied the method of time lag embedding (Schiffner et al., 2011a) and determined the correlation dimension, an indicator of the complexity of the system and the number of factors involved, to find out whether there are systematic differences in the navigational process and long-term changes in the homing behaviour as pigeons become older and more experienced.

MATERIALS AND METHODS

The experiments were conducted in the years 2005, 2006 and 2007 in sunny weather with no or little wind. The experiments were performed according to the rules and regulations of animal protection in Germany.

Experimental pigeons

The experimental birds were homing pigeons, *Columba livia* f. *domestica* Gmelin 1789, from our Frankfurt loft (50°08'N, 8°40'E). The juvenile pigeons in their first year of life were between 6 and 7 months old and had little flying experience aside from a few training flights with GPS recorders. The majority of releases involved yearling pigeons, the same pigeons in their second year of life, and older pigeons that had completed at least their second year. These birds had participated in a training programme with flights of up to 40 km in the cardinal compass directions in their first year of life. They had similar experience flying with a GPS recorder, the older pigeons because they had homed as adult birds in previous experiments and the yearlings because they had participated in the study as juveniles.

Release sites

Releases were performed at 11 sites at distances ranging from 3.2 to 23.5 km (distance and home directions are included in Table 1); thus, all sites lay within an area that can be considered as generally familiar to the pigeons. The juveniles were released from the four sites CP, EP, GT and HO for the first time; the data analysed here are the same as those analysed in a different way in a previous paper (Schiffner et al., 2011b). The yearlings were also new to the release sites, except for the four sites mentioned above, from which they had homed as juveniles. The older pigeons were released at all sites

for the first time except for EP, from which they had homed once before in flocks of five pigeons.

Experimental procedure

We used the same GPS recorders as in previous studies (Schiffner et al., 2011a; Schiffner et al., 2011b) with a mass of ca. 23 g including the battery. They were set to take a positional fix every second and had an operation limit of 3 h. The GPS recorder was wrapped in plastic foil and was attached to the pigeon's back by means of a harness made of Teflon tape. Once equipped, the birds were released singly by hand. In order to assure pigeons had left the release site, pigeons were released in 5 min intervals (see Schiffner et al., 2011a; Schiffner et al., 2011b).

The releases at a specific site took place over several days to minimize any potential influence of variability in the availability of navigational factors on any given day. With the exception of the site HO, yearlings and old pigeons were released on the same days in alternating order.

Mathematical and statistical analysis of tracks

The tracks of the pigeons were analysed to determine: (1) the overall efficiency, which is the beeline distance divided by the actual length of the track; it was calculated only for complete tracks with less than 10% signal loss (for a further traditional analysis of the tracks, see Appendix, 'Determining the points of decision' and 'Analysis of headings, steadiness and flying speed'); and (2) the short-term correlation dimension by means of time-lag embedding (Schiffner et al., 2011a) (see Appendix, 'Mathematical analysis: implementation of algorithms' for a brief summary). In contrast to the true correlation dimension of a track based on all data points, it was calculated as sliding mean over only 180 s and averaged for each 500 m step from the home loft. As a consequence, it is lower than the true correlation dimension, but can be used for comparisons.

From the efficiencies, we calculated the medians and compared the data of the yearlings and old birds in a second-order analysis using the Wilcoxon signed rank test for paired samples; the Mann–Whitney *U*-test was used to compare variables of yearlings at familiar and unfamiliar sites. The short-term correlation dimensions of the tracks were compared on the first-order level for each site individually by a two-way ANOVA with repeated measures using a factorial design, with the independent factors being the distance from the release site at which the short-term correlation estimates were taken and the age groups of the pigeons released at a given site. When the ANOVA indicated significance, we used the

Table 1. Location of the release sites with respect to the home loft, and efficiencies of the three groups of birds

Site	Distance	Home direction	Juveniles		Yearlings		Old pigeons	
	(km)	(deg)	<i>N</i>	Median	<i>N</i>	Median	<i>N</i>	Median
CP	3.6	261	21	0.26	4	0.87	12	0.88
GT	5.3	313	6	0.28	6	0.82	12	0.80
EP	6.3	120	14	0.24	7	0.79	11	0.82
NI	9.0	336			4	0.80	10	0.86
MT	11.6	263			4	0.82	7	0.82
OB	12.5	297			5	0.80	11	0.88
HO	13.6	247	11	0.41	4	0.79	17	0.85
HOF	13.8	83			3	0.89	10	0.81
AH	14.6	105			5	0.87	8	0.89
RB	19.0	195			2	0.90	5	0.92
RAV	22.1	251			3	0.91	6	0.81
Median				(0.27)		0.80		0.85

Distance refers to distance from the loft; *N*, number of tracks.

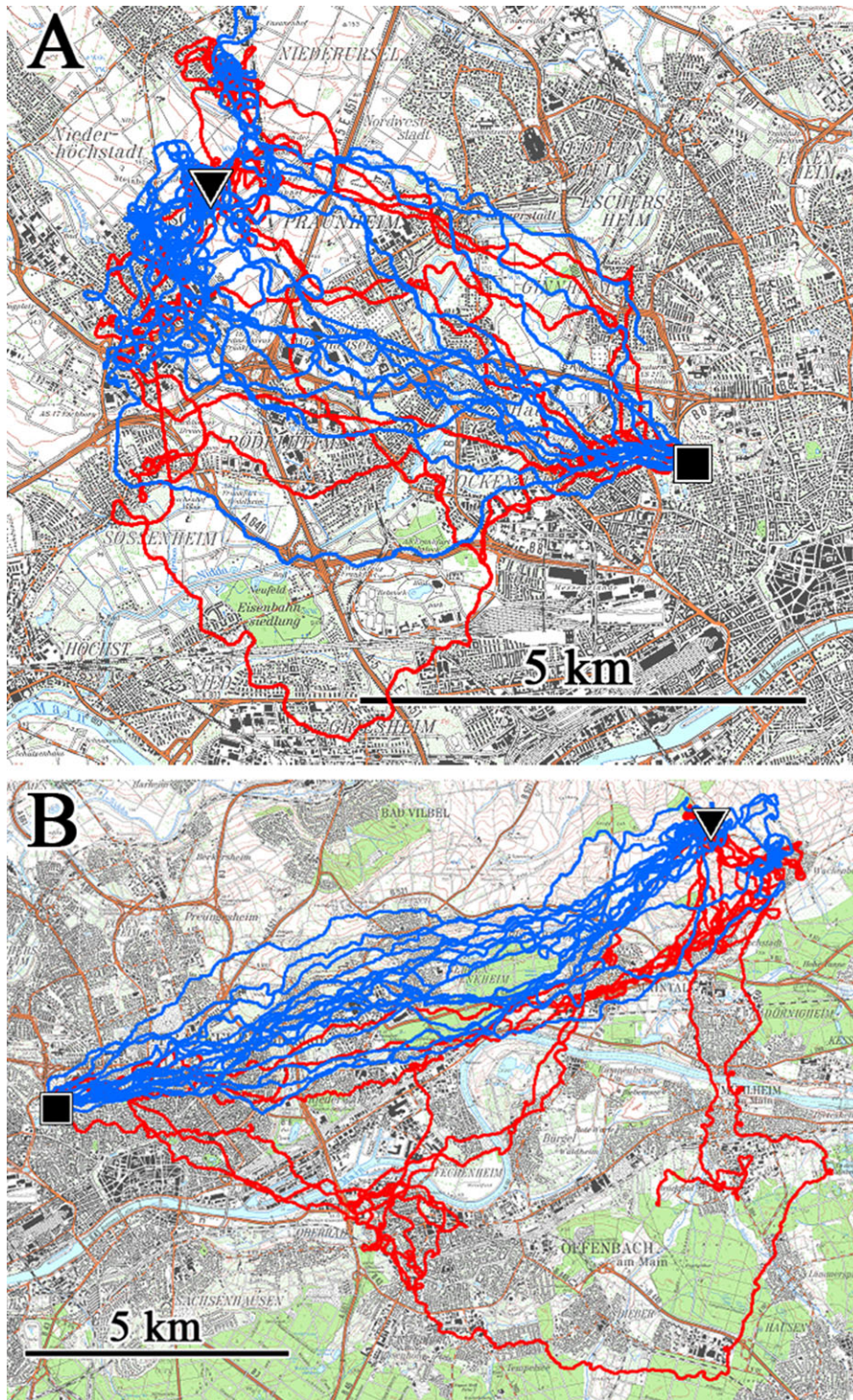


Fig. 1. Tracks of yearlings (red) and older pigeons (blue) from (A) EP (6.3 km; home direction 120 deg) and (B) HO (13.6 km; home direction 247 deg). The release sites are marked with a black triangle and the home loft with a black square.

Tukey HSD test to look for a difference between yearlings and old pigeons. Additionally we compared the data of the two older groups of pigeons on a second-order level using the median short-term correlation dimension over 5 km segments from home by the Wilcoxon signed rank test. The data of yearlings released at familiar sites and those from unfamiliar sites were compared with the Mann–Whitney *U*-test.

RESULTS

The analysis was based on 117 tracks from juvenile birds, 68 tracks from yearlings and 130 tracks from old pigeons. Fig. 1 gives, as

examples, the tracks for the yearlings and old birds from the sites EP and HO; the tracks of the juvenile birds in their first year of life are presented in Schiffner et al. (Schiffner et al., 2011b).

Table 1 lists the efficiencies of the three age groups returning from the release sites. With a median of 0.27, the juveniles are much less efficient than the two other groups, flying on average more than three times the direct distance, while the yearlings and the older birds, with median efficiencies of 0.80 and 0.85, respectively, do not differ significantly (Wilcoxon signed rank test, $T=20.5$, n.s.). The other traditional variables are essentially the same for the two older groups, except that the yearlings tend

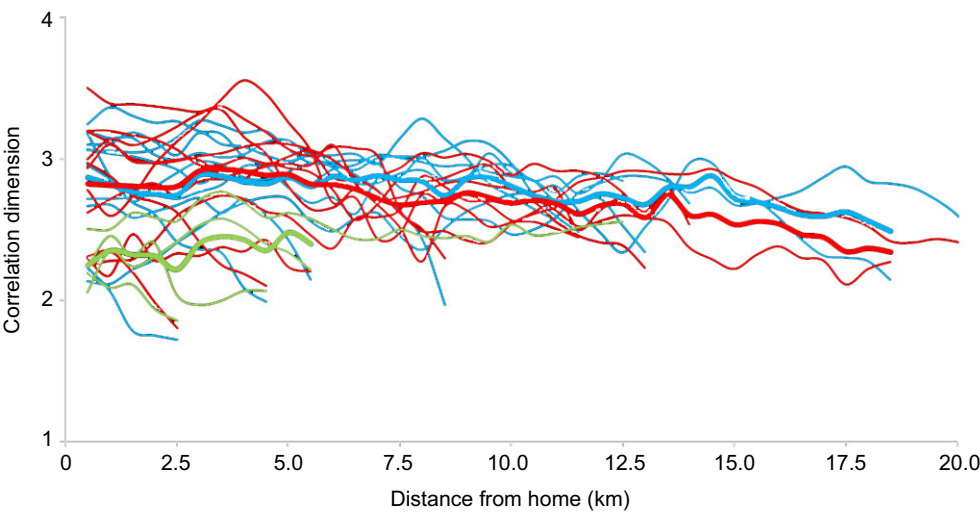


Fig. 2. Average short-term correlation dimension for all releases for juveniles (green), yearlings (red) and old pigeons (blue). The thin lines indicate the means of the single sites; the thick line gives the average.

to fly at higher speeds and deviate further from the home course during the final homing phase (see supplementary material TableS1).

The short-term correlation dimensions are given in Fig. 2, their medians are listed in Table2 and a more detailed representation of the medians over 5 km distance intervals is given in Table 3. Those from the younger birds are mostly lower than those of the older birds. This is most pronounced in the juveniles, where the correlation dimensions, never exceeding 2.51, are significantly lower than those of the two older groups. Yet, as the pooled data from all sites in Fig. 2 show, the average short-term correlation dimension estimate for yearlings is still mostly lower than that for the old pigeons. This difference is most pronounced at distances of 10–15 km from the loft; at the two sites at greater distances, there are no significant differences (see Table3). While there appears to be a general trend for higher short-term correlation dimensions in the old birds, there are at least indications that this may not hold for releases in the south. From the two release sites GT and NI, the correlation dimension is actually higher in yearlings, although this difference is only significant in the release from NI.

The fact that they had homed from a site the year before did not affect the efficiency or the median correlation dimension of the yearlings (Mann–Whitney *U*-test, both *U*=5, n.s.).

The short-term correlation dimensions show a typical trend: they are generally markedly lower at the beginning of the flight, but soon reach a higher level of the normal homing flight. At all sites, we observed a clear correlation with distance, with the short-term correlation dimension increasing as the pigeons approached their loft (Table3; see supplementary material TableS2 for the *F*-values of the ANOVA). This trend is significant for releases with yearlings and old birds, but it is not so pronounced in juveniles, where only tracks from four sites are available; here we even found a slight decrease when the juveniles returned from the farther sites (see Fig. 2).

In summary, we found the following differences between the age groups: (1) the efficiency increased considerably as the pigeons completed a training programme and reached their second year of life; and (2) the short-term correlation dimension also increased, and continued to do so as the birds grew older and more experienced, at least in the range between 10 and 15 km, reflecting the fact that the navigational system becomes increasingly complex.

DISCUSSION

Our data reveal a marked development in the navigational system between the first and second year of life, reflected by a considerable increase in efficiency and in short-term correlation dimension. In

Table2. Median short-term correlation dimension of the three groups of pigeons

Site	Distance (km)	Juveniles		Yearlings		Old pigeons		Difference
		<i>N</i>	Median	<i>N</i>	Median	<i>N</i>	Median	
CP	3.6	41	1.94	6	1.98	12	1.75	n.s.
GT	5.3	11	2.07	10	2.42	14	2.36	n.s.
EP	6.3	35	2.34	9	2.30	15	2.62	***
NI	9.0			5	3.09	11	2.75	***
MT	11.6			6	2.90	11	3.03	*
OB	12.5			5	2.73	12	3.03	***
HO	13.6	30	2.51	8	2.79	17	2.90	*
HOF	13.8			6	2.59	11	2.87	***
AH	14.6			6	2.93	10	2.95	***
RB	19.0			4	2.69	9	2.52	n.s.
RAV	22.1			3	2.72	8	2.80	n.s.
Median			2.21		2.71		2.80	

Distance refers to distance from the loft; *N*, number of tracks.
The last column indicates the significance of the difference between yearlings and old pigeons by the Tukey HSD test. ****P*<0.001, **P*<0.05; n.s., not significant.

Table 3. Median short-term correlation dimension of the two older groups of pigeons at 5 km distance intervals

Site	Distance (km)	<5 km		5–10 km		10–15 km	
		Yearlings	Old pigeons	Yearlings	Old pigeons	Yearlings	Old pigeons
CP	3.6	1.98	1.81	–	–	–	–
GT	5.3	2.50	2.43	2.05	2.06	–	–
EP	6.3	2.33	2.64	1.95	1.90	–	–
NI	9.0	3.33	2.81	2.59	2.48	–	–
MT	11.6	3.07	3.10	2.68	3.02	2.36	2.43
OB	12.5	3.10	3.13	2.63	3.00	2.11	2.37
HO	13.6	2.77	2.90	2.82	2.94	2.63	2.78
HOF	13.8	2.52	3.16	2.64	2.84	2.38	2.45
AH	14.6	2.98	3.08	2.96	2.91	2.65	2.78
RB	19.0	3.11	2.45	2.80	2.57	2.51	2.70
RAV	22.1	3.06	2.84	2.67	2.71	2.85	2.79
Median		2.98	2.84	2.66	2.77	2.51	2.70
Difference			n.s. (30)		n.s. (20)		* (1)

Distance refers to distance from the loft.

The last row indicates the difference between yearlings and older pigeons by the Wilcoxon signed rank test, with the test statistic *T* in parentheses. **P* < 0.05; n.s. not significant.

our previous study on the routes chosen by young pigeons during the period in which they establish their map system (Schiffner et al., 2011b), we interpreted the long, seemingly inefficient homing flights as representing exploratory behaviour. At the age of 6 months, the developing map had probably become functional but was still rather crude and inexact. The lower short-term correlation dimensions indicate that the juveniles rely on fewer navigational factors than the other two groups. The young pigeons continued to explore in order to become more familiar with the distribution of navigational factors within their home range. Interestingly, their behaviour appears to include strategies to avoid getting lost, such as limiting the flights to a semicircle and not going further away from the release point than the direct distance, using the release site as an anchor point, etc. (see Schiffner et al., 2011b). With a value of 0.41, the efficiency of the last flight as juveniles was already greater than that of the three previous flights, probably as a result of increasing experience from spontaneous exploration.

The increase in efficiency from juveniles to yearlings appears to reflect a great step in the maturation of the navigational system. The training programme, with flights of up to 40 km in the cardinal compass directions at the end of the first year of life, had familiarized them with a larger area of their home region. With this additional knowledge, their homing flights became considerably more efficient. On the one hand, their 'map' had become a more realistic representation of the distribution of the navigational factors and their possible irregularities; on the other hand, their tendency to explore during their homing flights probably decreased as they became more and more familiar with their home region. Single long tracks as shown in Fig. 1, however, suggest that individual birds still explored.

While the efficiency of homing in yearling birds appears to have reached the level of older pigeons, at least within a radius of about 25 km from the loft, where this study took place, the short-term correlation dimension still generally increased as the birds grow older and more experienced. Systematic differences in the navigational maps of yearlings and older pigeons are apparent, particularly in the range between 10 and 15 km. This may mean that older pigeons include more factors in their navigational process. However, as the differences are not very large, it could also mean that although the birds are using the same navigational factors, the older pigeons weigh these factors differently because of their more extensive experience. This may represent a parallel case to the use

of the sun compass, where slight differences in the weighing of the sun and the magnetic field between young and older birds has also been observed (Wiltschko et al., 1994).

The changes of the short-term correlation dimension with distance are interesting. The short-term correlation dimension when homing from the closest site, CP, just 3.6 km from the loft, is below 2.0 in all three groups, suggesting a strategy based mainly on landmarks (Schiffner et al., 2011a). At the two furthest sites, about 20 km away, the observed differences in the short-term correlation dimension between yearlings and old birds are not significant, while they are most pronounced between 7 and 15 km, that is, at distances where, according to previous estimates (Michener and Walcott, 1967; Braithwaite, 1993), navigation by the grid map changes into navigation by the mosaic map of landmarks. The lower short-term correlation dimension of the yearlings may thus reflect a still limited knowledge of landmarks in this range. Or it could mean certain problems with detecting the differences between the local values of the environmental gradients and the home values, which must be expected to become increasingly more difficult the closer the pigeons get to their home – older, more experienced pigeons are perhaps better able to cope with this situation. At greater distances, the environmental gradients are probably easier to use – this is in agreement with the observation that the difference in short-term correlation dimension between yearlings and older birds disappears at greater distances.

A pronounced gap in short-term correlation dimension, as the pigeons enter the 7–15 km range around their loft, was not observed, suggesting a gradual transition between the two types of 'map'. The continuously high values near home, which have also been observed in another study (Schiffner et al., 2011a) suggest that the environmental gradients are still involved in the vicinity of the loft. This interpretation is in agreement with earlier observations (Schlichte, 1973) that pigeons deprived of object vision managed to approach the Frankfurt loft very closely. The tracks of pigeons very familiar with the area between the release site and the loft (Wiltschko et al., 2007; Schiffner et al., 2011a) showed that these birds chose slightly different routes from day to day, which argues against merely following familiar landmarks, as proposed for pigeons studied in the Oxford region (e.g. Biro et al., 2004; Meade et al., 2005). The increase in correlation dimension as the pigeons approach their loft, observed here (see Table 3) and previously

(Schiffner et al., 2011a), however, points to an additional use of familiar landmarks in the mosaic map near the home loft. While an increase in experience would not lead to increased short-term correlation dimension if navigation was based solely on the mosaic map (Schiffner et al., 2011a), the range of the mosaic map may have increased, allowing pigeons to use the two maps in parallel over larger distances. Yet, it is also possible that the increase in short-term correlation dimension observed with increasing experience is mainly due to the integration of additional factors or a change in the weighting of factors in the grid map.

Our findings suggest that the formation of the navigational map system is a longer lasting process. The experience during the first year of life may form a framework for the map system, including obvious landmarks near the loft and the directions of the most prominent gradients. Pigeons continue to improve their maps by including new information such as more landmarks and perhaps additional local factors in order to develop their map system into a realistic representation of all suitable navigational factors in their home region. Even for an area within a 15 km radius around the loft, the map proved not yet complete in the second year of life – new factors and/or better interpretations of factors already included were still being added, as indicated by the mostly higher short-term correlation dimension of the older pigeons. Old, experienced pigeons are still able to learn the navigational factors and update their ideas on the distribution of the ‘map’ factors in distant regions later in life (Grüter and Wiltschko, 1990). Improvements to the navigational ‘map’ appear to continue as long as the pigeons live.

APPENDIX

Determining the points of decision

For the traditional analysis, we divided the tracks in several phases separated by ‘points of decision’ (PoD) (see Schiffner and Wiltschko, 2009). PoD were identified with the help of the following two variables and the changes in these variables over time: (1) cumulative velocity, defined as the current distance from the release point divided by the time passed since release, and (2) steadiness, here defined as the vector length of headings over a period of 60 s, calculated as a sliding mean every 15 s.

The greatest increase in steadiness immediately before or during a period of increasing cumulative velocity marks a PoD. The first one, usually close to the release point, indicates the moment when a pigeon decides to leave and head home (see Schiffner and Wiltschko, 2009). When released at greater distances and/or when they are younger, as many birds in the present study were, pigeons often do not fly home in one rush. Their tracks include more periods of increasing and decreasing cumulative velocity and steadiness so that additional PoD can be determined in the same way, namely as the momentary highest increase in steadiness immediately before or during a period of increasing cumulative velocity that follows a period of decreasing cumulative velocity (see Schiffner et al., 2011b).

The PoD thus divide the tracks into several phases: the first one marks the end of the ‘initial’ phase, where the pigeon flies around the release point, and the beginning of the ‘departure’ phase where it leaves the site. If there is only one PoD, this departure phase is identical to the ‘final homing’ phase that ends at the loft. If there are more PoD, we can define a separate final homing phase and occasionally intermittent phases between the departure phase and the final homing phase.

Analysis of headings, steadiness and flying speed

Supplementary material Table S1 compares data from the various phases of the homing flight for juvenile birds, yearlings and old

pigeons, based on the median of the median of all release sites. The data include the total number of PoD, the median time passed until the first PoD, that is until the pigeons decided to leave, and the median distance of the first PoD from the release point. For the initial phase, the departure phase and the final homing phase, the median deviations of the headings from the home direction, the median vector length indicating the agreement among birds, the median steadiness of flight (determined over the entire phase) and the median flying speed of the pigeons are indicated. When there is only one PoD, the first 300 s of the phase following this PoD are analysed as the departure phase.

Juveniles were released at only four sites so their data cannot be compared with those of the yearlings and the old pigeons. Hence, the last column in supplementary material Table S1 gives the test statistics of the Wilcoxon signed rank test for paired samples and significance levels for the comparison between yearlings and old birds only.

Mathematical analysis: implementation of algorithms

Time lag embedding (Takens, 1981), a method derived from dynamic systems theory, allows the reconstruction of an underlying process from a one-dimensional time series. In this particular case, we were interested in the navigational process of the pigeon and the one-dimensional time series is provided by the tracks recorded during the homing flight. The use of time-lag embedding requires no *a priori* knowledge about the number of factors involved and their specific interactions; instead the methods used here allow us to create a physical model of the process using only the recorded data. From this model we can calculate several parameters. In the current study we focused solely on the so-called correlation dimension, a measurement reflecting a system’s degrees of freedom, i.e. in this particular case the number of factors involved in the navigational process. The calculation, with some minor enhancements, as listed below, was based on the original algorithm proposed by Grassberger and Procaccia (Grassberger and Procaccia, 1983).

(1) In order to ensure ‘optimal embedding’, we determined the embedding lag for each individual time series. We used the first minimum of the mutual information to determine an appropriate embedding lag (Fraser and Swinney, 1986) and a fixed range of embedding dimensions – from 3 to 5 – in order to avoid spurious effects from using different embeddings. For calculation of the ‘mutual information’ we decided to implement a new non-parametric approach in order to circumvent problems with unevenly distributed data. To ascertain that data were always evenly distributed, we divided the data into $\log_2 N$ (with N being the number of data points in the time series) partitions and assigned a fixed number of elements to each partition. This new approach allowed us to get much better convergence and well-defined minima and maxima.

(2) In addition, we implemented an algorithm for ‘automatic selection of a proper scaling region’, thus ensuring that all values would be selected on objective criteria. This was achieved by embedding the time series three times, with successively increasing embedding dimensions. We then chose the scaling region defined by the minimum standard deviation over all three embeddings. As the standard deviation tends to decrease as we approach the size of the attractor, the so-called depopulation region, we added some restrictions: (i) the first minimum in standard deviation was used to define an initial estimate; other potential scaling regions with lower standard deviation were ignored, if the resulting correlation dimension would fall below this initial estimate (\pm s.d.); and (ii) the size of the scaling region was fixed to 1/4 of the length of the attractor. Although the latter restriction seems to be a rather coarse

solution, it ensures that the scaling region will never lie within the depopulation region and allows for better comparison of estimates from different time series.

Test statistics of the ANOVA for the short-term correlation dimension

Supplementary material TableS2 gives details on the two-way ANOVA for the short-term correlation dimensions calculated as a sliding means and averaged for each 500 m segment relative to the home loft for each site. Factors analysed were (1) the age of the pigeons and (2) the distance from the home loft.

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AUTHOR CONTRIBUTIONS

I.S. and R.W. conceived and designed the experiments. I.S. performed the experiments and analyzed the data. I.S. and R.W. wrote the paper.

COMPETING INTERESTS

No competing interests declared.

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Supplemental Material

Development of the Navigational Map in Homing Pigeons: Differences between Pigeons of different Age

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Table S1. Comparing the behavior of the three age groups during the homing flight

Variable	Juveniles median	Yearlings median	Old birds median	Difference Yearlings/Old significant?
Sites involved	4	11	11	
Number PoDs.	2.2	1.5	1.7	25.0
Time to 1 st PoD (s)	240	142.5	105	26.5
Distance (m)	299	491	552	6.31
<i>Initial Phase</i>				
Δ home	18°	30°	33°	26.5
Vector length	0.33	0.66	0.63	26.0
Steadiness	0.21	0.30	0.33	26.0
Flying speed (km/h)	50	53	51	5.0**
<i>Departure Phase</i>				
Δ home	-15°	71°	27°	16.0
Vector length	0.62	0.70	0.90	15.0
Steadiness	0.66	0.80	0.85	14.5
Flying speed (km/h)	57	62	57	3.5**
<i>Final Homing Phase</i>				
Δ home	19°	13°	3°	0.0**
Vector length	0.81	0.98	0.99	17.5
Steadiness	0.70	0.82	0.85	16.5
Flying speed (km/h)	57	61	56	5.5

PoD, Point of decision; Δ home, angular deviation of the mean heading from the home direction; vector length, length of the mean vector based on the headings. **, $P < 0.01$

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Table S2. Results of two way ANOVA for the short-term correlation dimension

Site	Age of pigeons			Distance from home			Interactions		
	Df	F-Values	Sign?	Df	F-Values	Sign?	Df	F-Values	Sign?
CP	2	0.909	n.s.	11	12.702	***	13	0.963	n.s.
GT	2	21.143	***	18	6.460	***	22	0.473	n.s.
EP	2	7.895	***	35	9.765	***	29	1.298	n.s.
NI	1	21.916	***	26	10.911	***	18	0.428	n.s.
MT	1	4.577	*	28	3.842	***	24	0.590	n.s.
OB	1	10.762	**	25	4.606	***	24	0.285	n.s.
HO	2	5.866	***	56	5.136	***	60	1.016	n.s.
HOF	1	34.719	***	33	4.062	***	28	0.616	n.s.
AH	1	7.620	**	30	2.277	***	30	0.123	n.s.
RB	1	2.548	n.s.	39	2.517	***	38	0.749	n.s.
RAV	1	0.241	n.s.	49	5.254	***	48	0.486	n.s.

Df, degrees of freedom; significance levels: n.s, not significant; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.