

Importance of the hippocampus for the learning of route fidelity in homing pigeons

Anna Gagliardo¹, Enrica Pollonara¹, Giovanni Casini¹, Maria Grazia Rossino¹, Martin Wikelski^{2,3} and Verner P. Bingman^{4,5}


¹Department of Biology, University of Pisa, Via Volta 6, I-56126 Pisa, Italy

²Department of Migration, Max Planck Institute of Animal Behaviour, Am Obstberg 1, 78315 Radolfzell, Germany

³Centre for the Advanced Study of Collective Behaviour, University of Konstanz, 78457 Konstanz, Germany

⁴Department of Psychology, Bowling Green State University, Bowling Green, OH 43403, USA

⁵J.P. Scott Center for Neuroscience, Mind and Behavior, Bowling Green, OH 43403, USA

 AG, 0000-0003-0214-3817; VPB, 0000-0002-5295-7096

The avian hippocampal formation (HF) is thought to regulate map-like memory representations of visual landmarks/landscape features and has more recently been suggested to be similarly important for the perceptual integration of landmarks/landscapes. Aspects of spatial memory and perception likely combine to support the now well-documented ability of homing pigeons to learn to retrace the same route when homing from familiar locations, leading to the prediction that damage to the HF would result in a diminished ability to repeatedly fly a similar route home. HF-lesioned homing pigeons were repeatedly released from three sites to assess the importance of the hippocampus as pigeons gradually learn a familiar route home guided by familiar landmark and landscape features. As expected, control pigeons displayed increasing fidelity to a familiar route home, and by inference, successful perceptual and memory processing of familiar landmarks/landscape features. By contrast, the impoverished route fidelity of the HF-lesioned pigeons indicated an impaired sensitivity to the same landmark/landscape features.

Keywords:

hippocampal formation, homing pigeons, route fidelity, GPS tracking

Author for correspondence:

Anna Gagliardo

e-mail: anna.gagliardo@unipi.it

1. Introduction

The functional profile of the avian hippocampal formation (HF) bears a striking resemblance to the properties of the 'cognitive map' proposed by O'Keefe and Nadel [1] as a functional characterization of the mammalian hippocampus (see [2,3]). The avian HF is critically important for a variety of spatial cognitive processes adapted to the natural history of birds including songbirds, pigeons and chicks [4–9]. In the context of navigation, the avian HF has been hypothesized to be necessary for learning and recalling familiar, landmark/landscape-based maps as homing pigeons with HF-damage have difficulty navigating familiar spaces [10–12]. Beyond memory, recent evidence has suggested an additional role of the avian HF in the perception of environmental space and/or spatial attentional processes as pigeons learn about and navigate space [13,14]. One example of homing behaviour that highlights the interaction between perceptual and memory aspects of space is the ability of pigeons to acquire fidelity to a route home when repeatedly released from the same location [15–18]. Following from the hypothesis that the avian HF is critical for memory-based navigation by familiar landmarks/landscape features and the perceptual binding of landscape/landmark elements, we predicted that HF-lesioned pigeons would be impaired in learning to fly a similar, faithful route home when repeatedly released from the same location.

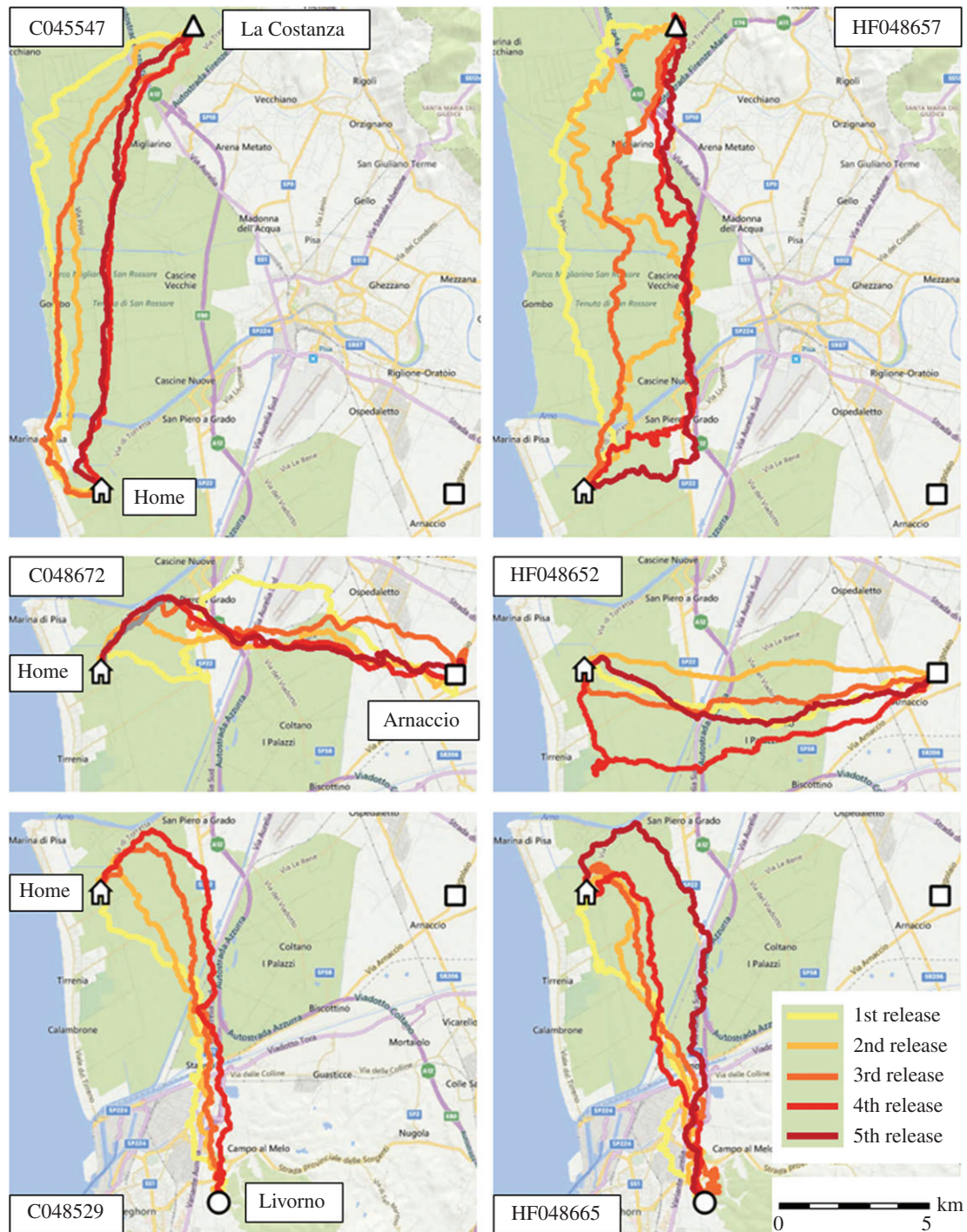


Figure 1. Representative tracks (near-median-group fidelity fixes (FF) scores) of C- and HF-pigeons repeatedly released from the same site.

2. Material and methods

(a) General procedure

Thirty-four, 1-year-old homing pigeons (*Columba livia*) with previous homing experience (one or two homing flights), hatched and kept at the Arnino field station (43°39'26" N, 10°18'14" E; Pisa, Italy), were used. Prior to the experiment, the pigeons could perform spontaneous flights around the loft and were treated according to Italian law on animal welfare (permit number 524/2018-PR). In order to accustom the birds to carrying a device, two weeks before the first release PVC dummies were attached by means of a Velcro® strip glued to the trimmed feathers of the pigeons' backs.

Nineteen pigeons were subjected to bilateral ablation of the hippocampal formation (HF-group) following procedures described in [5], while 15 birds were assigned to the unmanipulated control group (C-group). About ten days after surgery, the experimental releases began under sunny conditions with no or light wind.

For the experimental releases, birds carried a GPS logger (Mobile Action IgotU; 20 g) recording 1 position fix/second. The GPS-tracks were visualized with QGIS (<http://www.qgis.org/>). All the GPS data are available at the data archive www.movebank.org (doi:10.5441/001/1.6v5c77t3). The pigeons were released singly, five times from each of three sites (figures 1 and 2, table 1). The order of the first releases was Arnaccio, La Costanza and Livorno, which were then unfamiliar; subsequent releases varied across birds.

(b) Quantitative analyses and statistical procedures

GPS-recorded positional fixes with a speed greater than 5 km h⁻¹ were used in the analysis. Fixes closer than 0.5 km from the release site (soon after release) and those closer than 0.5 km from home (at the end of the flight home) were excluded from the analysis. We considered 'joined' all fixes of a pigeon closer than 80 m to

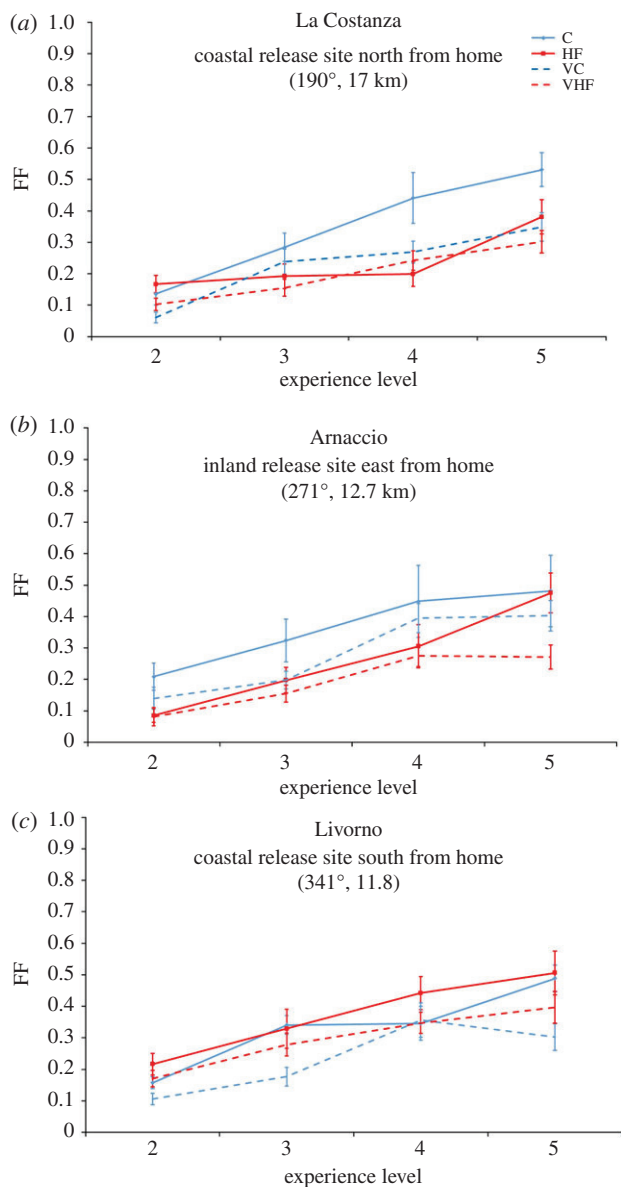


Figure 2. Mean FF scores, \pm s.e., from the second to the fifth release (experience level). FF, fidelity fixes; VC and VHF, virtual C and virtual HF, respectively.

another pigeon during a 5 s window [18]. If less than 30% of the fixes of a pigeon's track home were joined with another bird and provided that most of the solo fixes were beyond 2 km from the release site, the position fixes when the bird was flying alone were included in the route fidelity analysis. The portions of a pigeon's track during which they joined in flight with another bird were not analysed to assess the fidelity of that flight.

(c) Route fidelity and path efficiency

For each bird's track from the second to the fifth release, the percentage of fixes when flying alone closer than 100 m to a fix from any of its previous flight paths, regardless of release site and including fixes when joined by another pigeon, was computed (FF, fidelity fixes, which served as our dependent measure of the tendency to retrace a familiar path home; see electronic supplementary material for the rationale for the use of FF). Analyses on FF computed using different thresholds (50 and 200 m) and on Fidelity Index [19], which is not dependent on thresholds, are reported in the electronic supplementary material. To control for inflated FF scores as more comparison tracks were accumulated across the series of releases, FF were also computed for 'virtual pigeons', groups VC (virtual C) and VHF (virtual HF), obtained

by comparing sequential tracks of blindly selected, different C- and HF-subjects, respectively (see electronic supplementary material for details). The test distributions were subjected to angular transformation. A Kolmogorov–Smirnov and Levene's test applied to residuals of the test distributions were used to assess normality and homoscedasticity, respectively. Using SPSS 20, we applied a linear mixed model (LMM) to the FF distributions to assess the effect of HF-lesion and release site on fidelity to a position occupied on a previous flight (random factor: subject; fixed factors: treatment, release site, experience level, treatment \times release site, treatment \times experience level). We applied LMM to the Efficiency Index distributions (EI = beeline distance 'release site-home' / track length, random factor: subject; fixed factors: treatment, experience level, experience level \times treatment; interrupted tracks were excluded from this analysis). Least-Squared Difference (LSD) was used for *post-hoc* analyses.

(d) Histology

The extent of HF-lesion damage was assessed for a subsample ($n = 9$) of birds. Histological procedures were the same as those described in [14] and lesion reconstructions were based on the pigeon brain atlas [20].

3. Results

During the releases 5 C- and 9 HF-pigeons were lost. However, for 12 C- and 12 HF-birds enough tracks suitable for the analyses were available (see table 1 for details).

(a) Route fidelity and path efficiency

The residuals of both the FF and EI distributions were normally distributed (Kolmogorov–Smirnov, FF $D = 0.034$, $p > 0.6$; EI $D = 0.044$, $p > 0.6$) and homoscedastic (Levene's test, $p > 0.09$ for both FF and EI). Figure 1 displays representative tracks of C- and HF-lesioned pigeons. Figure 2 reports the mean percentage of fixes closer than 100 m to any positional fix of a previous track (FF) at increasing experience levels. The FF significantly increased across training stages ($F_{3,480} = 98.434$, $p < 0.001$), but more importantly, the increasing FF scores differed among the comparison groups. A significant difference was found between treatments ($F_{3,480} = 6.901$, $p < 0.001$) and release sites ($F_{2,480} = 7.393$, $p = 0.001$), with a higher degree of fidelity from Livorno compared to La Costanza (LSD, $t = 3.805$, $p < 0.001$) and Arnaccio ($t = 2.420$, $p < 0.05$). No difference was found between La Costanza and Arnaccio. A significant interaction between treatment and release site was found ($F_{6,480} = 5.123$, $p < 0.001$), but no significant interaction between treatment and experience level emerged ($F_{9,480} = 1.473$, $p > 0.1$). *Post-hoc* analyses revealed a difference between C- and all the other groups (LSD, C versus HF $t = 2.033$, $p < 0.05$; C versus VC $t = 3.588$, $p < 0.001$; C versus VHF $t = 4.184$, $p < 0.001$). HF-pigeons displayed a FF distribution significantly greater than their virtual group (HF versus VHF $t = 2.183$, $p < 0.05$) but comparable to the VC-pigeons (HF versus VC $t = 1.573$, $p > 0.1$). This suggests that both C- and HF-tracks from later releases became increasingly likely to overlap a previous route taken, but to different extents. Interestingly, both virtual groups' distributions were comparable (VC versus VHF $t = 0.617$, $p > 0.5$). The level of route fidelity of the C-birds was greater than its comparison, virtual group across all release sites (C versus VC Arnaccio $t = 2.553$, $p = 0.011$; La Costanza $t = 3.146$, $p = 0.002$; Livorno $t = 2.210$, $p = 0.028$), while the HF-pigeons never differed from their virtual group (HF versus VHF

Table 1. FF values; *n*: number of tracks (from the second to the fifth release) for each site; *j*: bird flew joined with another pigeon; *l*: pigeon lost; *na*: track not available.

pigeon	Arnaccio					La Costanza					Livorno				
	2	3	4	5	<i>n</i>	2	3	4	5	<i>n</i>	2	3	4	5	<i>n</i>
C045547	0.06	0.16	0.31	0.21	4	0.22	0.42	0.16	0.42	4	0.40	<i>j</i>	0.05	0.52	3
C048468	<i>j</i>	0.11	<i>j</i>	0.64	2	0.10	0.23	<i>j</i>	0.50	3	<i>j</i>	<i>j</i>	<i>j</i>	<i>j</i>	0
C048483	<i>j</i>	0.52	<i>j</i>	<i>j</i>	1	<i>j</i>	<i>j</i>	<i>j</i>	0.50	1	<i>j</i>	<i>j</i>	0.28	0.67	2
C048505	0.29	<i>j</i>	<i>j</i>	<i>j</i>	1	0.07	0.24	0.64	<i>l</i>	3	0.12	0.36	0.55	<i>na</i>	3
C048529	0.29	0.29	0.50	<i>na</i>	3	0.16	0.48	0.11	<i>na</i>	3	0.19	0.49	0.41	<i>l</i>	3
C048547	0.32	0.43	0.85	<i>j</i>	3	<i>j</i>	0.26	<i>j</i>	0.25	2	0.10	0.46	0.23	0.34	4
C048548	0.13	0.13	0.08	0.25	4	0.00	0.12	0.32	0.47	4	0.00	0.29	0.37	0.07	4
C048585	0.18	0.61	<i>j</i>	0.32	3	0.01	0.09	<i>j</i>	0.62	3	<i>j</i>	<i>j</i>	0.41	0.66	2
C048672	0.20	0.21	0.44	0.73	4	0.36	<i>j</i>	0.47	0.82	3	<i>na</i>	0.13	0.19	0.53	3
C048679	<i>j</i>	0.57	0.21	0.21	3	0.23	0.32	0.59	0.56	4	0.06	<i>j</i>	0.38	0.53	3
C271720	<i>j</i>	<i>j</i>	0.76	0.95	2	0.14	0.41	0.49	0.77	4	0.28	<i>j</i>	0.57	0.62	3
C271721	<i>j</i>	0.21	<i>j</i>	0.55	2	0.07	<i>j</i>	0.75	0.40	3	0.12	0.32	<i>j</i>	0.46	3
HF045530	<i>j</i>	<i>j</i>	0.17	0.17	2	0.04	0.18	0.00	0.12	4	0.07	0.41	0.22	0.71	4
HF045535	0.06	0.06	0.32	0.22	4	0.17	0.13	0.36	0.41	4	0.19	0.46	0.38	<i>na</i>	3
HF045536	0.10	0.30	0.72	0.61	4	0.19	<i>j</i>	0.34	0.25	3	0.20	<i>j</i>	<i>j</i>	0.13	2
HF048462	0.22	0.04	0.44	0.47	4	0.17	0.21	0.07	<i>l</i>	3	0.25	0.25	0.80	<i>na</i>	3
HF048533	0.20	0.38	0.66	0.90	4	0.37	0.55	0.14	0.69	4	0.09	0.32	0.53	0.39	4
HF048593	0.02	<i>j</i>	0.03	<i>j</i>	2	0.11	0.18	0.08	0.29	4	0.23	0.21	0.20	<i>j</i>	3
HF048613	0.08	0.16	0.42	0.48	4	0.14	0.18	0.08	0.18	4	0.54	0.67	0.40	0.66	4
HF048629	<i>j</i>	<i>j</i>	<i>j</i>	<i>j</i>	0	0.20	0.04	<i>j</i>	0.48	3	0.22	<i>na</i>	0.58	0.52	3
HF048652	0.03	0.14	0.13	0.48	4	0.05	0.14	0.22	0.48	4	0.16	0.05	0.59	0.79	4
HF048657	0.03	0.22	0.13	0.53	4	0.10	0.15	0.21	0.37	4	0.16	<i>j</i>	0.42	0.60	3
HF048663	0.08	0.14	0.14	0.46	4	0.29	0.15	0.36	0.51	4	0.27	0.18	0.35	0.42	4
HF048665	0.07	0.35	0.21	0.43	4	0.17	0.21	0.31	<i>l</i>	3	0.20	0.41	0.39	0.33	4

Arnaccio $t = 1.830$, $p \geq 0.05$; La Costanza $t = 1.098$, $p > 0.2$; Livorno $t = 1.943$, $p = 0.053$). Importantly, the level of route fidelity was significantly poorer for the HF-pigeons compared to the C-birds from the northern coastal site La Costanza ($t = 2.693$, $p = 0.007$) and the inland site Arnaccio ($t = 3.069$, $p = 0.002$), while no difference was found from the southern coastal site Livorno ($t = 1.292$, $p > 0.1$), where the HF-group displayed significantly greater FF scores compared to VC ($t = 3.687$, $p < 0.001$). The same pattern of results was also observed with FF-threshold differences of 50 and 200 m as well as the fidelity Index (FI) analysis (see electronic supplementary material).

Control and HF-pigeons displayed comparable EI scores (table 2, $F_{1,282} = 0.174$, $p > 0.6$), with differences among experience levels ($F_{4,282} = 11.731$, $p < 0.001$). In fact, the EI on the first release was significantly smaller than the subsequent releases ($p < 0.001$ in all comparisons), while no other differences emerged ($p = 1$ for all other comparisons). Therefore, the increase in FF across the training releases is not attributable to the pigeons simply flying an increasingly straighter path home.

(b) Histology

Brain lesion damage included substantial, bilateral portions of the hippocampus and parahippocampus similar to previous studies [13,14]. On average, 73.8% (± 18.5) of the HF was

damaged across the nine sampled pigeons (see electronic supplementary material, figure S1) with sparing limited to its most anterior parts. Small, irregular damage also occurred in the hyperpallium apicale and mesopallium. No detectable change was observed in motor ability (flight and walking behaviour) following lesion.

4. Discussion

The HF plays a critical role supporting avian spatial cognition [4–9]. For homing pigeons, the HF's role in the map-like, memory representation of space [10–12], and its suspected role in supporting perceptual aspects of environmental space [11–14], enable navigation by familiar landmarks and landscape features. We thus hypothesized that the HF is necessary for learning a faithful route home, predicting that hippocampal lesions would impair progressively increasing route fidelity as pigeons repeatedly fly home from the same locations [15–18]. Consistent with the prediction, the FF scores were significantly higher in the C- compared to HF-pigeons, especially from La Costanza and Arnaccio. Additionally, the flight paths of the C-pigeons from all release sites became increasingly faithful as training progressed, clearly outpacing their virtual controls (VC). Although HF-pigeons

Table 2. Efficiency indexes of each track from the first to the fifth. *j*, tracks interrupted. *i*, bird flew joined with another pigeon; *l*, pigeon lost; *na*, track not available.

pigeon	Arnaccio					La Costanza					Livorno				
	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
C045547	0.73	0.33	0.59	0.66	0.66	0.67	0.74	0.78	0.83	0.83	0.75	0.84	<i>j</i>	0.91	0.89
C048468	0.50	<i>j</i>	0.33	<i>j</i>	0.55	0.26	0.42	0.75	<i>j</i>	0.44	<i>j</i>	<i>j</i>	<i>j</i>	<i>j</i>	<i>j</i>
C048483	0.67	<i>j</i>	<i>i</i>	<i>j</i>	<i>j</i>	0.35	<i>j</i>	<i>j</i>	<i>j</i>	0.53	0.26	<i>j</i>	<i>j</i>	0.44	0.56
C048505	0.43	0.58	<i>j</i>	<i>j</i>	<i>j</i>	0.80	0.53	0.59	0.61	<i>l</i>	0.22	0.77	0.61	0.66	<i>na</i>
C048529	0.40	0.52	0.55	0.49	<i>na</i>	0.72	0.76	0.84	0.72	<i>na</i>	0.69	0.64	0.60	0.57	<i>l</i>
C048547	0.75	0.52	0.52	0.62	<i>j</i>	0.53	<i>j</i>	0.64	<i>j</i>	0.60	0.63	0.64	<i>i</i>	0.64	0.83
C048548	0.77	0.58	0.46	0.34	0.74	0.34	0.74	0.65	0.65	0.62	0.83	0.71	0.63	0.70	0.95
C048585	0.75	0.81	0.68	<i>j</i>	0.67	0.61	0.71	0.75	<i>j</i>	0.85	0.63	<i>j</i>	<i>j</i>	0.75	0.89
C048672	0.55	0.77	0.54	0.74	0.70	0.68	0.72	<i>j</i>	0.51	0.72	0.31	<i>na</i>	0.73	0.54	0.48
C048679	0.73	<i>j</i>	0.69	0.54	0.65	0.68	0.80	0.77	0.51	0.81	0.38	0.76	<i>j</i>	0.54	0.48
C271720	0.54	<i>j</i>	<i>j</i>	0.54	0.61	0.77	0.76	0.88	0.87	0.75	0.63	0.62	<i>j</i>	0.83	0.82
C271721	0.69	<i>j</i>	0.72	<i>j</i>	0.67	0.35	0.81	<i>j</i>	0.58	0.70	0.25	0.67	0.65	<i>j</i>	0.53
mean sd	0.63 0.13	0.59 0.16	0.56 0.12	0.62 0.11	0.64 0.04	0.58 0.17	0.71 0.09	0.74 0.10	0.66 0.14	0.72 0.09	0.51 0.23	0.71 0.08	0.64 0.05	0.66 0.14	0.71 0.20
HF045530	0.55	<i>j</i>	<i>j</i>	0.66	0.37	0.53	0.63	0.68	0.52	0.63	0.70	0.74	0.71	0.58	0.82
HF045535	0.71	0.80	0.80	0.77	0.86	0.64	0.72	0.61	0.83	0.86	0.14	0.68	0.72	0.84	<i>na</i>
HF045536	0.73	0.83	0.77	0.68	0.81	0.50	0.69	<i>j</i>	0.85	0.76	0.31	0.64	<i>j</i>	<i>j</i>	0.87
HF048462	0.68	0.66	0.70	0.51	0.65	0.64	0.73	0.61	0.67	<i>l</i>	0.68	0.77	0.81	0.87	<i>na</i>
HF048533	0.15	0.43	0.40	0.71	0.67	0.35	0.46	0.66	0.67	0.65	0.13	0.56	0.55	0.80	0.75
HF048593	0.45	0.57	<i>j</i>	0.36	<i>j</i>	0.45	<i>i</i>	0.62	0.76	0.52	<i>j</i>	0.52	0.51	0.58	<i>j</i>
HF048613	0.30	0.57	0.45	0.55	0.58	0.82	0.72	0.66	0.72	0.47	0.20	0.77	0.77	0.78	0.74
HF048629	0.51	<i>j</i>	<i>j</i>	<i>j</i>	<i>j</i>	0.63	0.41	0.66	<i>j</i>	0.69	0.52	0.60	<i>na</i>	0.79	0.82
HF048652	0.80	0.94	0.85	0.61	0.83	0.81	0.79	0.84	0.83	0.76	0.17	0.70	0.91	0.83	0.91
HF048657	0.38	0.79	0.60	0.64	0.56	0.59	0.51	0.70	0.60	0.61	<i>j</i>	<i>i</i>	<i>j</i>	0.66	0.82
HF048663	0.31	0.42	0.44	0.23	0.56	0.48	0.46	0.51	0.48	0.47	0.54	0.56	0.58	0.36	0.38
HF048665	0.61	0.52	0.48	0.67	0.74	0.47	0.61	0.70	0.56	<i>na</i>	0.59	0.62	0.40	0.69	0.54
mean sd	0.52 0.20	0.65 0.18	0.61 0.17	0.59 0.17	0.66 0.15	0.58 0.14	0.61 0.13	0.66 0.08	0.68 0.13	0.64 0.13	0.41 0.22	0.65 0.09	0.66 0.17	0.70 0.15	0.73 0.17

generally displayed increased fidelity compared to their virtual controls, at none of the release sites did the HF-pigeon FF scores outpace the VHF-baseline group. Taken together, the data support the hypothesis of compromised spatial cognitive and perceptual abilities in the HF-lesioned pigeons, and the importance of these HF-mediated abilities for the learning of a familiar route.

One curious finding was that from Livorno little difference was found between the C- and HF-pigeons in their increasing route fidelity. A GPS-tracking study on monocular occluded pigeons conducted in the same area reported that the acquisition of route fidelity is facilitated when pigeons flying north view the leading line of the coast principally with the left eye/right brain hemisphere system, which would apply to releases from Livorno [18]. Could coastal, left-eye viewing have favoured familiar landmark/landscape-based route fidelity in the HF-pigeons, or might the observed fidelity from Livorno be a simpler consequence of holding a more consistent direction home derived from the interaction among the pigeon navigational map, compass cues and topographical guidance cues? In our view, the similar FF scores of HF-lesioned and their virtual control (VHF) pigeons support the latter interpretation. Relevant here is that the HF-pigeons during their homing flights seemed able to follow leading-line, landscape features running approximately in the direction of home (examples of HF-pigeons following roads are depicted in figure 1). For instance, from Arnaccio, it is notable that across the repeated releases, 4 out of 12 HF-birds followed the leading line of the same road for short (HF045536 and HF048613) or longer (HF048533 and HF048629) tracts. The general tendency of pigeons to follow linear, leading-line landscape features, such as coastlines and roads, is well known [21–23]. However, this ability is not necessarily related to familiar landmark/landscape-based navigation [13,24]; it is often observed the first time a pigeon homes from an area with leading-line features. The advantage of following a leading line would allow a pigeon to maintain a compass direction, or compensate for wind drift without continually relying on the sun azimuth. Notably, although HF-lesioned pigeons can be directionally guided by a coastline, they are less able to incorporate this landscape feature into a map-like representation needed for re-orienting home following a navigational error [13]. In fact, it has been reported that while a view of a coastline facilitates map-like, landmark/landscape-based corrective re-orientation in phase-shifted, *intact* pigeons, phase-shifted HF-lesioned birds more enduringly rely on their sun-compass [24], even when able to view the coast, and so much so that they often continue to fly out over the open sea for several kilometres [13].

Most of the HF-lesioned pigeons were able to home during the first release from each site, confirming that HF does not

participate in the odour-based navigational map used by pigeons to home from unfamiliar sites [14,25]. The operational navigational map available to all the pigeons during the current study also explains the unimpaired flight path efficiency (EI) of the HF-birds. During the subsequent releases, both intact and lesioned pigeons could have used both olfactory and familiar visual cues to take up a homeward bearing [26,27]. Distinct visual feature recognition is also unaffected by HF-lesions [6,28,29], as HF-lesioned pigeons can recall a compass direction home by visually recognizing a release site location [13,24,30,31]. We propose that the increasing route fidelity displayed by the HF-lesioned pigeons from Livorno was, at least in part, more aligned with HF-independent, object-like recognition of specific landscape features, e.g. go north when viewing some local, recognizable feature of the Livorno release site, and maintaining a consistent northerly bearing by viewing the coastline with the left eye.

Finally, if the impaired route fidelity of the HF-pigeons was in part owing to a spatial perceptual neglect or attentional deficit, then it would suggest that HF-lesioned pigeons are impaired at perceiving an integrated spatial representation of a landscape/landmark panorama. If true, then part of the functional profile of the avian HF would resemble functional properties typically associated with visual regions of the mammalian parietal lobe and its interactions with retrosplenial cortex, which would act on inputs from the hippocampus [32,33]. However, the data we present are not intended to prove that the functional profile of the avian HF includes a role in the perception of space, but rather, advance the conversation that such a possibility is worthy of further investigation.

Ethics. The pigeons were kept and treated according to Italian law on animal welfare. This research was authorized by the Italian Ministry of Health (permit number 524/2018-PR).

Authors' contributions. The experiment was conceived by A.G., V.P.B. and M.W.; the surgery was performed by A.G. and G.C.; releases were performed by A.G., E.P. and V.P.B.; histology was performed by G.C. and M.G.R.; the analysis of the data was performed by A.G. and E.P.; A.G., V.P.B., M.W., E.P., M.G.R. and G.C. contributed to writing the manuscript. All authors agree to be held accountable for the content of the manuscript; the revised version of the manuscript was approved by all authors.

Competing interests. We declare we have no competing interests.

Funding. M.W. was funded by DFG EXC2117-422037984; V.P.B. was funded by NSF grant no. IOS-1457304.

Acknowledgements. Thanks to Lorenzo Vanni and Andrea Guidi for pigeons' care, Daniele Santerini for the figures and Dimitri Giunchi and Alessandro Massolo for useful suggestions.

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