

Hippocampus and homing in pigeons: left and right hemispheric differences in navigational map learning

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Abstract

One-month-old, inexperienced homing pigeons, prior to any opportunity to learn a navigational map, were subjected to either right or left unilateral ablation of the hippocampal formation (HF). These pigeons were then held together with a group of age-matched control birds in an outdoor aviary, where they were kept for about 3 months with the opportunity to learn a navigational map. When subsequently tested for navigational map learning at about 4 months of age posthatching, control and right HF-ablated pigeons were equally good at orienting homeward from distant, unfamiliar locations, indicating successful navigational map learning. By contrast, left HF-ablated pigeons were impaired in orienting homeward, indicating a failure to learn a navigational map. Interestingly, both right and left HF-ablated pigeons displayed impaired homing performance relative to controls. These results suggest that different aspects of homing pigeon navigation may be lateralized to different hemispheres, and in particular, the HF of the different hemispheres. The left HF appears critical for navigational map learning, i.e. determining an approximate direction home from distant, unfamiliar locations. The right HF, and possibly the left HF as well, appear to play an important role in local navigation near the loft, which is likely based on familiar landmarks.

Introduction

On the basis of similarity in development, connectivity and neurochemistry (see Casini *et al.*, 1997 for a review), the avian dorsomedial forebrain (hippocampal formation, HF) is believed to be homologous with the mammalian hippocampus. In both rodents (Morris *et al.*, 1982; Eichenbaum *et al.*, 1994) and birds (Sherry & Vaccarino, 1989; Hampton & Shettleworth, 1996; Strasser & Bingman, 1997), lesioning the hippocampus results in impaired landmark navigation in laboratory tasks of spatial memory. Similar results have been obtained from observations and experiments carried out in naturalistic settings. Food-storing birds have a relatively larger HF compared with nonstoring birds (e.g. Krebs *et al.*, 1989; Sherry *et al.*, 1989), and there is considerable evidence identifying an important role for HF in homing pigeon navigation (see Bingman *et al.*, 1998 for review). In particular, the homing pigeon HF is critical for learning a navigational map under some training conditions (Bingman *et al.*, 1990; Ialè *et al.*, 2000), and navigation by familiar landmarks, either in the vicinity of the loft (Bingman & Mench, 1990) or over distant, familiar areas (Gagliardo *et al.*, 1999).

Homing pigeons are thought to navigate from distant, unfamiliar locations by means of 'map and compass' mechanisms (Kramer, 1953), which allow an approximate determination of the direction of displacement with respect to home (map) and subsequent orientation

towards home, both at the release site and 'en route' (compass). Numerous experiments have shown that a young pigeon can learn a navigational map by associating environmental odours carried by the winds with the direction from which they come (see Papi, 1990; Wallraff, 1990, 1996; Roper, 1999). Indeed, birds held in an outdoor aviary exposed to the winds can successfully learn a navigational map even if prevented from making spontaneous flights outside the aviary (Wallraff, 1966; Papi *et al.*, 1973; Baldaccini *et al.*, 1974; Ialè, 1982; Bingman *et al.*, 1990; Ialè *et al.*, 2000). The hippocampal formation plays a critical role in olfactory navigational map learning when pigeons are kept in an outdoor aviary without any opportunity to fly outside (Bingman *et al.*, 1990; Ialè *et al.*, 2000).

Functional specialization of the left and right sides of the brain ('lateralization'), once thought to be a uniquely human characteristic, has now been well documented in birds (see Rogers, 1996; Güntürkün, 1997; Vallortigara *et al.*, 1999; for recent reviews). In birds, considerable evidence has accumulated suggesting a major role of the right hemisphere in topographical spatial learning in highly familiar environments (chicks: Rashid & Andrew, 1989; Vallortigara *et al.*, 1996; parids: Clayton & Krebs, 1994). However, these studies did not explicitly attempt to identify which particular brain structures, e.g. hippocampus, may be important for the lateralization phenomena. Using navigational map learning in homing pigeons as our behavioural model system, we present evidence in support of the hypothesis that different navigational mechanisms lateralize to different brain hemispheres and that the hippocampal formation is one structure that displays functional lateralization.

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TABLE 1. Release parameters for homing pigeons released from three separate locations

	Treatment	Number of birds tossed (<i>N</i>)	Vanishing bearings recorded (<i>n</i>)	Mean vector direction (α)	Mean vector length (<i>r</i>)	Mean homeward component (<i>hc</i>)	Median homing time
Massaciuccoli Lake	C	30	30	161°	0.55**	+0.49	1 day
4–12/8/1999	RHF	29	29	144°	0.37*	+0.27	Lost
188°, 19.0 km	LHF	27	26	21°	0.31 ^{NS}	-0.31	> 1 day
Saline di Volterra	C	16	13	298°	0.77**	+0.76	4 h 08 min
24/8/1999	RHF	12	11	287°	0.60*	+0.57	9 h 00 min
306°, 50.0 km	LHF	14	12	249°	0.42 ^{NS}	+0.23	1 day
Agliaiana	C	14	12	239°	0.75**	+0.75	4 h 07 min
31/8/1999	RHF	11	9	220°	0.83**	+0.76	6 h 02 min
243°, 59.6 km	LHF	11	9	194°	0.17 ^{NS}	+0.11	1 day

Birds were control (C), left (LHF) or right hippocampus lesioned (RHF). * $P < 0.02$; ** $P < 0.001$, NS $P > 0.05$, Rayleigh test.

Materials and methods

The research was authorized by the Comitato di Ateneo per la Sperimentazione Animale (CASA) of the University of Pisa. Ninety-four homing pigeons housed in the Arnino Field Station (Pisa, Italy) were used in the experiment. About 1 month posthatching, the birds were assigned to three different experimental groups: control pigeons (C, $n = 30$), right HF-lesioned pigeons (RHF, $n = 35$) and left HF-lesioned pigeons (LHF, $n = 33$). After completion of the lesion surgery, the three groups were placed together in an outdoor aviary exposed to the winds from all directions. They were not allowed to fly outside the aviary until the first experimental release. A bilateral HF lesion group was not used because two experiments investigating navigational map learning in pigeons with bilateral HF lesions have already been carried out and published (Bingman *et al.*, 1990; Ialò *et al.*, 2000).

The RHF and LHF pigeons underwent lesion surgery at about 1 month posthatching; before they had any opportunity to learn a navigational map. During surgery, the pigeons were anaesthetized with an intramuscular injection of 20% chloral hydrate (2 mL/kg body weight). The lesion target coordinates were stereotaxically identified according to the atlas of Karten & Hodós (1967). Unilateral aspiration lesions were targeted to the hippocampal formation (hippocampus and parahippocampus of Karten & Hodós, 1967). Prior to the experimental releases, six pigeons from each lesion group were chosen randomly to provide an unbiased sample of the extent of lesion damage. Histological and lesion reconstruction procedures are described elsewhere (Bingman *et al.*, 1984).

The first experimental release took place about 3 months after the birds were placed in the outdoor aviary. The first experimental release took place from the middle of Lake Massaciuccoli. This was done to discourage the birds, which had never flown outside the aviary, from landing. In total, three experimental releases from three different locations were performed (see Table 1 for details). The first release took place over 3 days because of the large number of birds released and a change in weather. During all releases, the sun was visible and wind speed was lower than 5 m/s. The birds were released singly, alternating between treatment groups, and followed by an experimenter with 10 × 40 magnification binoculars until vanishing from sight. Data recorded for each bird during the experimental releases were vanishing bearing, homing speed and success, and vanishing time.

For each distribution of vanishing bearings, a mean vector and homeward component were calculated; the latter measure ranges from -1.0 to +1.0 and gives an indication of the strength of homeward orientation. The Rayleigh test was applied to determine whether a distribution of vanishing bearings deviated from uniform (Batschelet,

1981). Comparisons among the three experimental groups were carried out by applying an analysis of variance to: (i) the absolute angular difference (0–180°) between the vanishing bearing of each subject and the mean direction of its group to test for group differences in dispersion, and (ii) the angular difference (0–180°) between the vanishing bearing of each subject and the home direction to test for group differences in orientation with respect to the homeward direction (Wallraff, 1979). For data distributed normally, an ANOVA was used; when the data were not normally distributed a Kruskal–Wallis analysis of variance (Siegel, 1956) was used. Group comparisons for homing performance and vanishing times were compared with a Kruskal–Wallis analysis of variance and Dunn's test for multisample comparisons (Dunn, 1964).

Results

Behaviour

Both the intact, control pigeons and the right hippocampal-damaged (RHF) pigeons, although never flying outside the aviary until the experimental releases, successfully learned a navigational map. Both groups orientated close to the homeward direction with mean vectors significantly different from uniform for all the experimental releases (Rayleigh test, see Fig. 1 and Table 1). By contrast, the pigeons subjected to left hippocampal lesion (LHF) failed to give any indication of learning a navigational map. They displayed vanishing bearings that were not different from uniform for all three experimental releases (Rayleigh test, see Fig. 1 and Table 1). The Kruskal–Wallis test revealed no significant between-group difference in the dispersion of the groups' vanishing bearings for all three releases ($P > 0.1$ for all releases). However, a significant between-group difference in orientation was found in all three releases (ANOVA; Massaciuccoli, $P < 0.001$; Saline di Volterra, $P < 0.05$; Agliana, $P < 0.005$). The LHF pigeons were always significantly different from the C birds (Dunn's test; Massaciuccoli, $P < 0.001$; Saline di Volterra, $P < 0.025$; Agliana, $P < 0.01$). The LHF pigeons were also different from RHF birds from Massaciuccoli ($P < 0.005$) and Agliana ($P < 0.01$). No difference was ever observed between the C and RHF pigeons.

During the experimental release from Lake Massaciuccoli, the three groups displayed significantly different vanishing times (median vanishing times, C = 2'33"; RHF = 4'10"; LHF = 5'08"; Kruskal–Wallis $P < 0.0001$). Dunn's test revealed that the control birds were significantly faster in vanishing than both lesioned groups (Dunn's test, $P < 0.05$), but no significant difference between the RHF and LHF pigeons was found. During the other two experimental releases, there was no significant difference in vanishing times among the

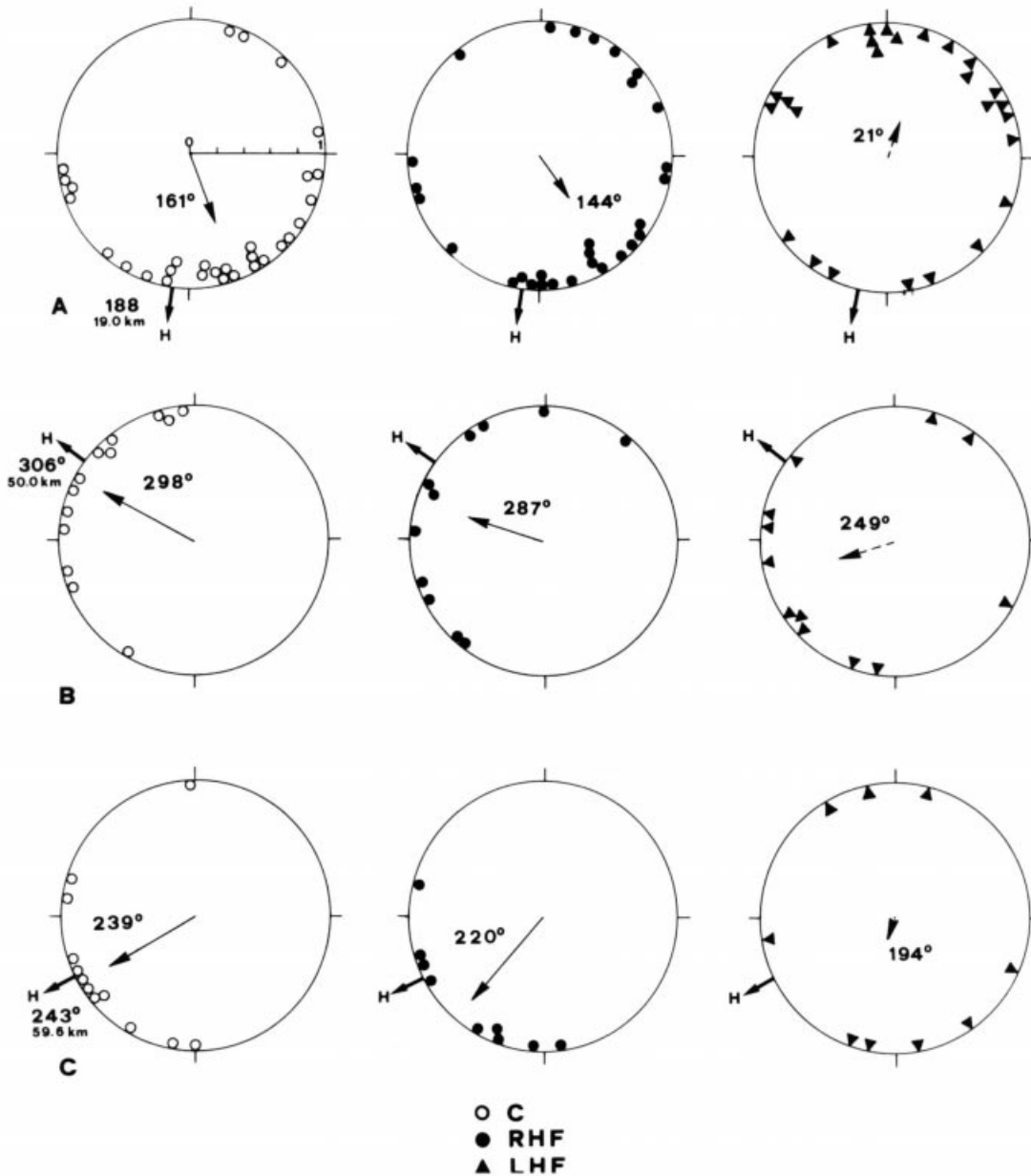


FIG. 1. Vanishing bearing diagrams. (A) Lake Massaciucoli; (B) Saline di Volterra; (C) Agliana (see also Table 1). Inner arrows identify vanishing bearing mean vectors; a dotted line means that the distribution did not differ from uniform. The length of the mean vector can be read from the scale in the first diagram. Outer arrows represent the home direction. Each symbol represents the vanishing bearing of a single pigeon. (○) Control pigeons, C; (●) right hippocampal formation damaged pigeons, RHF; (▲) left hippocampal formation damaged pigeons, LHF.

groups, although a pattern of increasing median vanishing time across C, RHF and LHF pigeons persisted (median vanishing times: Saline di Volterra, C = 3'01", RHF = 3'48", LHF = 6'12"; Agliana, C = 2'10", RHF = 2'32", LHF = 3'12").

The homing performance recorded during the three experimental releases is shown in Fig. 2. A comparison of homing performance among the groups revealed a significant difference for two out of the three experimental releases, and the difference approached significance in the third (Kruskal–Wallis, Massaciucoli, $P < 0.002$; Saline di Volterra, $P = 0.053$; Agliana, $P < 0.05$). Multisample comparisons showed that the control group was significantly faster (Dunn's test, $P < 0.001$) than both unilateral lesion groups from Massaciucoli, but only the LHF group from Agliana ($P < 0.05$). In general, looking at

the group median homing times (Table 1), the intact pigeons were always faster than the two lesion groups. Of interest, the homing performance of the RHF pigeons was surprisingly poor considering their good homeward orientation. Finally, while homing speed from Lake Massaciucoli (the first release) was poor for all groups, the control and RHF pigeons tended to home faster during subsequent releases. By contrast, the LHF pigeons were consistently slow in homing, although the number of LHF birds lost during the second and third releases was negligible.

Histology

The lesion damage sustained by the sampled birds is summarized in Fig. 3. For the lesion groups, damage was confined to the left or right

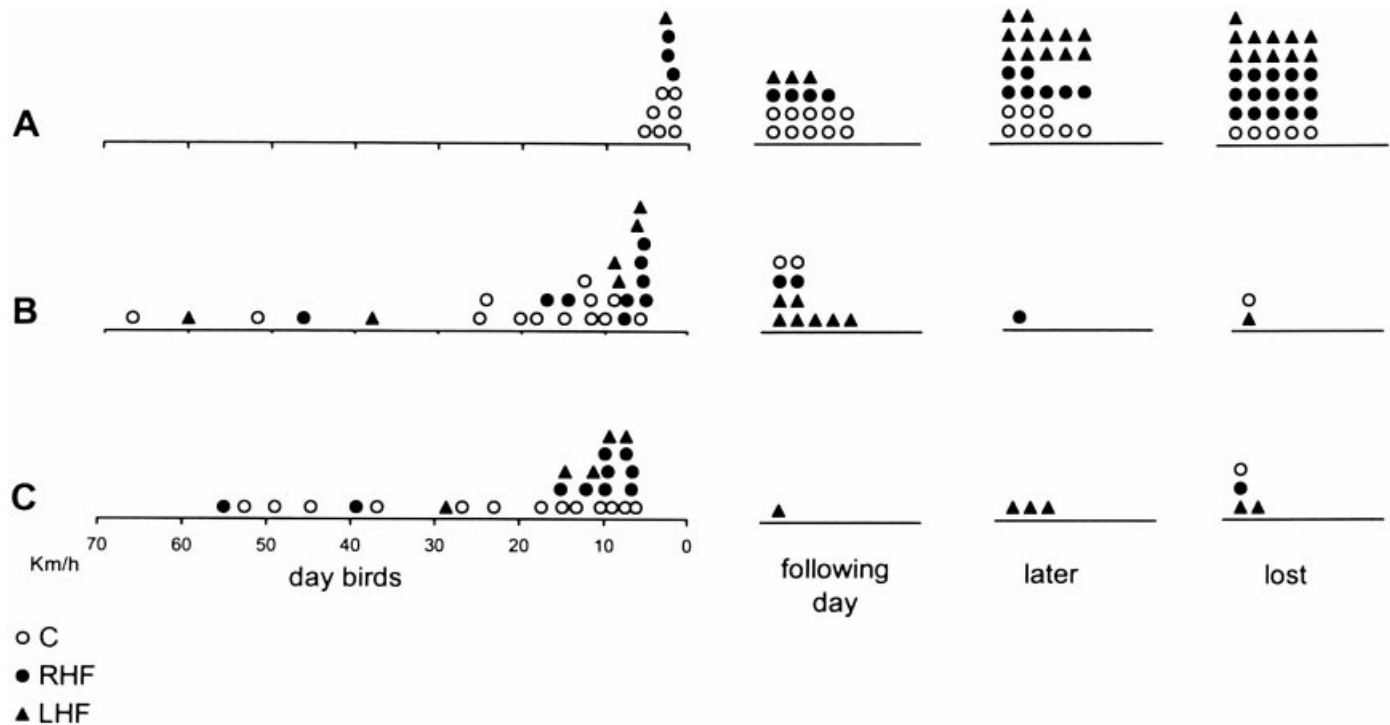


FIG. 2. Homing performance diagrams. (A) Lake Massaciuccoli; (B) Saline di Volterra; (C) Agliana. Each symbol represents one subject. (○) Control pigeons; (●) right hippocampal formation damaged pigeons, RHF; (▲) left hippocampal formation damaged pigeons, LHF. For pigeons that homed on the day of release, symbols are ordered according to homing speed.

hemisphere. Hippocampal damage was substantial in the parahippocampal region, while considerable sparing of the hippocampus was observed. Some birds experienced damage to neighbouring structures: the hyperstriatum ventrale, hyperstriatum accessorium and neostriatum. RHF pigeons generally sustained more damage to these neighbouring areas than the LHF birds.

Examination of whole brains following perfusion often revealed striking hemispheric asymmetry in telencephalic volume outside the HF (see Fig. 4). In an attempt to quantify this difference, we measured non-HF telencephalic area at two anterior coordinates (A): 9.0 and 7.5 (Karten & Hodos, 1967). [When lesion damage extended to the dorsomedial areas of the non-HF telencephalon near HF, area values were computed by visually filling in the damaged area to match the shape of the telencephalon at that anterior coordinate, as seen in the atlas of Karten & Hodos (1967)]. For the six LHF pigeons, mean non-HF telencephalic area at A 9.0 was 41.76 mm² (SE = 1.91) for the right hemisphere and 32.96 mm² (SE = 1.63) for the left hemisphere. At A 7.5 it was 39.13 mm² (SE = 1.53) for the right hemisphere and 26.12 mm² (SE = 1.55) for the left hemisphere. For the five RHF pigeons analysed (one RHF-lesioned bird was excluded from this analysis because the quality of the tissue precluded an accurate measure of area), mean non-HF telencephalic area at A 9.0 was 35.31 mm² (SE = 1.29) for the right hemisphere and 39.36 mm² (SE = 1.68) for the left hemisphere. At A 7.5, it was 29.58 mm² (SE = 1.56) for the right hemisphere and 38.12 mm² (SE = 1.64) for the left hemisphere. Paired *t*-tests revealed significant differences in telencephalic area between the hemispheres ipsilateral and contralateral to the lesion site at both anterior coordinates 9.0 ($P < 0.02$ for both RHF and LHF pigeons) and 7.5 ($P < 0.005$ for both RHF and LHF pigeons). In summary, in addition to damaging HF, the lesions also resulted in a notable reduction in non-HF telencephalic volume ipsilateral to the lesion site.

A closer examination of the telencephalon ipsilateral to the lesion site revealed, for most of the lesion subjects, a disruption in the laminar boundaries that normally separate various telencephalic subdivisions. Figure 4 shows that whereas contralateral to the lesion site all appropriate telencephalic subdivision were readily discernible with clear laminar boundaries, the telencephalon ipsilateral to the lesion site was strikingly undifferentiated with vague and distorted laminar boundaries. The absence of clear separation between telencephalic subdivisions renders it practically impossible to specify which subdivisions may have been particularly impacted. However, in more anterior portions of the telencephalon away from the lesion site, laminar boundaries were more easily seen ipsilateral to the lesion site, and it was apparent that a reduction in the size of the ipsilateral lobe paraolfactorious as present. By contrast, no obvious differences could be found among the layers of the wulst (the avian telencephalic visual area) either ipsilateral or contralateral to the lesion site.

Discussion

The results reveal a striking asymmetry between left and right hippocampal-damaged young pigeons in their success at orienting homeward from three distant, unfamiliar locations, i.e. navigational map learning. The RHF pigeons, like the control pigeons, appeared to have acquired a navigational map whereas the homeward orientation of LHF pigeons was consistently impaired, suggesting that they failed to learn a navigational map.

However, the homing performance results indicated that the right HF is not without a role in navigation. Despite their good homeward orientation, RHF-lesioned pigeons consistently took more time to return home, perhaps reflecting impaired local navigation near the loft (Bingman *et al.*, 1988). Noteworthy is that the homing

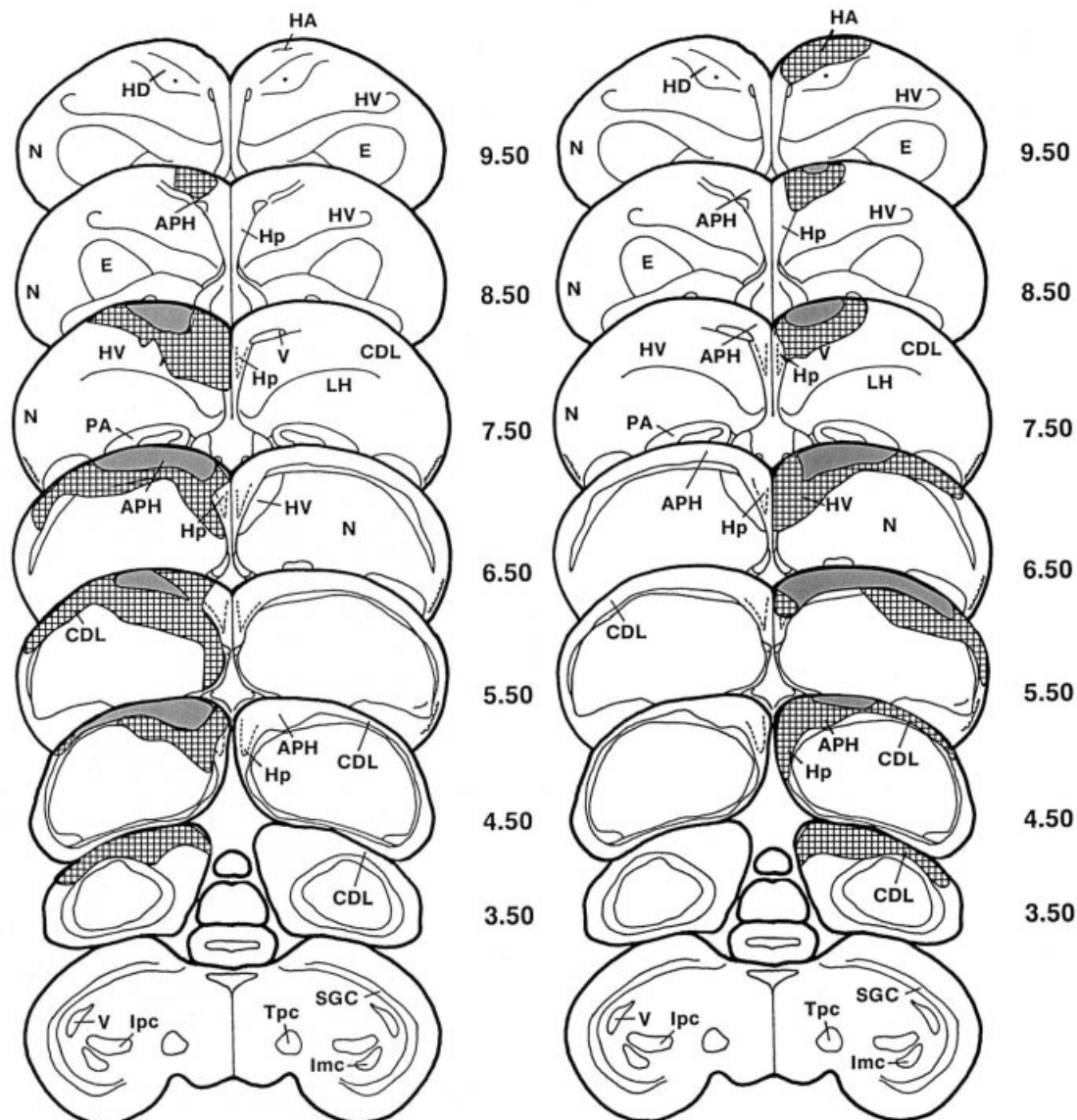


FIG. 3. Summary lesion reconstructions of the six LHF and six RHF sampled pigeons. Stippled areas represent ablated areas common to at least five of six pigeons. Cross-hatched areas represent lesioned areas common to at least two of six pigeons. APH, area parahippocampalis; CDL, area corticoidea dorsolateralis; E, ectostriatum; HA, hyperstriatum accessorium; HD, hyperstriatum dorsalis; Hp, hippocampus; HV, hyperstriatum ventrale; Imc, nucleus isthmi, pars magnocellularis; Ipc, nucleus isthmi, pars parvicellularis; LH, lamina hyperstriatica; N, neostriatum; PA, palaeostriatum augmentatum; SGC, stratum griseum centrale; Tpc, nucleus tegmenti pedunculo-pontinus, pars compacta; V, ventriculus.

performance in both lesioned groups seemed to improve during the second and third experimental releases. This finding can be explained in part by releasing birds on the second and third releases that returned home from Lake Massaciucoli and the homing experience associated with that return. For example, if, as we believe, LHF pigeons are impaired in navigational map learning more than landmark navigation, the LHF birds that homed from Massaciucoli after 1 or more days likely gained considerable experience with the distribution of landmarks around the loft. This learning may have enabled them to return more quickly during the subsequent releases.

The most parsimonious explanation of the results is that the left HF plays a dominant role in navigational map learning. In two previous studies (Bingman *et al.*, 1990; Ioalè *et al.*, 2000), young homing pigeons subjected to bilateral HF lesions and held in an outdoor aviary during the time of learning failed to acquire a navigational

map. The present results suggest that the bilateral lesion results can be explained entirely by damage to the left HF. In fact, the performance of the LHF pigeons in the present study is remarkably similar to the behaviour of bilaterally lesioned birds.

The histological analysis identified a number of interesting findings that warrant discussion. First, the hippocampus subdivision of HF was substantially spared. However, Bingman & Mench (1990) have already shown that lesion damage limited to either the hippocampus or parahippocampus has the same deleterious effect on navigational performance. Because of the anatomical organization of the avian HF, lesioning the parahippocampus effectively disrupts hippocampus function as well (Casini *et al.*, 1986). Second, there was more damage to neighbouring structures than usually observed in our previous aspiration lesion studies (e.g. Gagliardo *et al.*, 1999; Ioalè *et al.*, 2000). However, the additional damage was seen overwhelmingly in

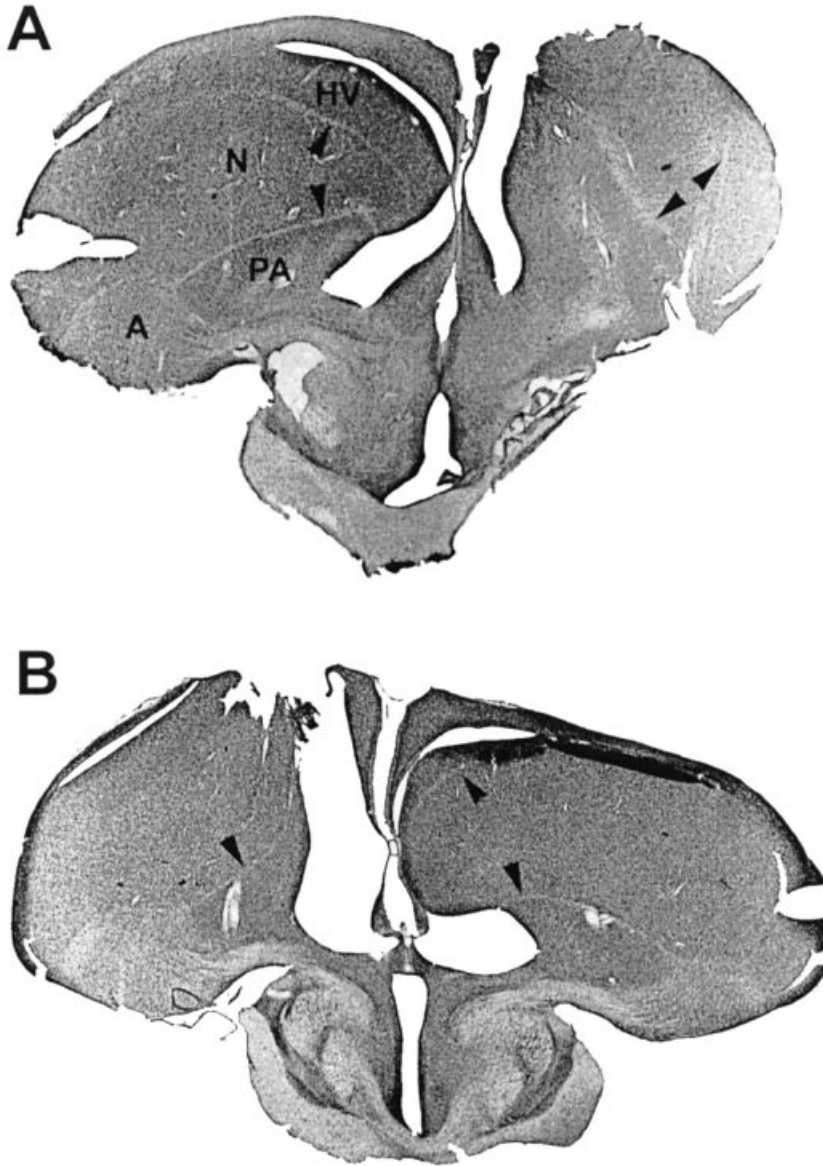


FIG. 4. Photomicrographs of two brain sections, one taken from a pigeon with left HF lesion (A) and one taken from a pigeon with right HF lesion (B). The sections correspond approximately to anterior coordinate 7.5 (A) and 7.0 (B) according to the atlas of Karten & Hodós (1967). Arrows highlight laminar boundaries between telencephalic subdivisions. A, archistriatum, see Fig. 3 for the remaining abbreviations. Note the striking asymmetry in telencephalic area and the clear and appropriate laminar boundaries contralateral to the lesion site with either absent or distorted boundaries ipsilateral.

the RHF-lesioned pigeons; pigeons that successfully learned a navigational map. The lesions of the LHF birds were relatively limited to HF, and were similar to the lesions reported in our previous work.

Of potentially more interest was the unexpected asymmetry in telencephalic volume, i.e. the smaller volume ipsilateral to the lesion site. Visual inspection of the brains clearly revealed that the telencephalon ipsilateral to the lesion site was smaller compared with the contralateral hemisphere, as if portions of the telencephalon had failed to develop normally or atrophied. The effects of the unilateral HF lesions appear to extend beyond HF and influence the organization and/or development of at least a portion of the remaining telencephalon (recall that the birds were still relatively young at the time of lesion). This is of considerable interest from developmental and anatomical perspectives, and the focus of further work. Although it is reasonable to conclude that the left HF damage sustained by the LHF birds was a critical element in failing to learn a navigational map (Bingman *et al.*, 1990; Ioalè *et al.*, 2000), we cannot exclude the possibility that the failure of these pigeons to learn was also in part

attributable to changes in telencephalon development or organization outside the HF.

Evidence that the left hemisphere of the brain, not just HF, is implicated in navigation based on visual cues has been recently reported by Ulrich *et al.* (1999). These authors found that pigeons who had binocularly learned the homeward route from remote, but familiar, release sites subsequently displayed better homing performance when released with only the right eye (effectively left hemisphere) rather than the left eye (effectively right hemisphere) available (they used eye patches to cover either the left or right eye). Any comparison between our study and theirs is difficult because they examined navigational performance from familiar sites. Moreover, lateralization revealed by monocular tests may reflect neural asymmetries at any level in the nervous system and cannot be interpreted as asymmetry in HF or even telencephalic function. Nonetheless, their results suggest that the left HF may be involved not just in navigational map but other kinds of spatial learning as well.

A number of laboratory studies in birds have suggested that the *right* hemisphere may play a dominant role in structuring topo-

graphical spatial representations (Rashid & Andrew, 1989; Clayton & Krebs, 1994; Vallortigara *et al.*, 1996). Similarly, although our RHF pigeons learned a navigational map, their good homeward orientation coupled with poor homing performance hints at a role of the right HF in familiar landmark navigation near the home loft. For example, at least during the first release, the RHF pigeons that returned home were challenged to recognize the local familiar environment around the loft from a novel spatial perspective, i.e. from outside and above rather than from inside the aviary. It could be entirely coincidental, but nonetheless worth mentioning, that difficulties in the recognition of familiar objects from novel perspectives is typically associated with right-hemispheric (parietal) lesions in humans (Warrington & Taylor, 1973). It has been suggested that Warrington and Taylor's 'unconventional' perspectives would actually correspond to views in which an important natural axis in shape is foreshortened in the image (Marr, 1982). This is what our pigeons would experience during their first flight outside the loft.

It is impossible to determine whether the left hemisphere might also take part in landmark navigation near the loft because the LHF-lesioned pigeons orientated poorly to begin with. It is conceivable, therefore, that the HF of both hemispheres may participate in familiar landmark navigation near the loft, but perhaps in different ways. For example, it might be that the right HF is important for representing landmarks in a relational or map-like fashion whereas the left HF uses landmarks more as recognition or guidance cues (Eichenbaum *et al.*, 1994; Gagliardo *et al.*, 1999). Such an interpretation would be in agreement with data demonstrating hemispheric asymmetry in relational or map-like representations of space (e.g. mammals: Crowne *et al.*, 1992; Abrahams *et al.*, 1997; Cowell *et al.*, 1997; Bohbot *et al.*, 1998; birds: Rashid & Andrew, 1989; Clayton & Krebs, 1994; Vallortigara *et al.*, 1996; Vallortigara, 2000). Clearly these thoughts on the relationship between the left and right HFs and familiar landmark navigation are highly speculative, but are useful nonetheless in shaping future research designed to better understand hemispheric specialization in the representation of space.

Neuroethological research, such as the present study, may have important implications for neuropsychological research in humans. The use of natural and seminatural research settings to investigate real-world topographical spatial representations in humans has benefited from recent advances in brain imaging. For example, right hippocampal activation has been documented in taxi drivers asked to mentally navigate the streets of London (Maguire *et al.*, 1997); a condition of highly familiar routes possibly resembling navigation near the loft in our pigeons. Our study suggests that the traditional notion of asymmetry in hemispheric superiority for 'spatial' cognition needs to be reconsidered in terms of task characteristics, the nature of spatial information processing and their possible pattern of lateralization. From such a perspective, functional asymmetry in mammalian and avian brains can prove to be a powerful instrument to anatomically dissect the different cognitive processes involved in real-world spatial navigation.

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Abbreviations

A, anterior coordinate; HF, hippocampal formation; LHF, left hippocampal formation lesioned; RHF, right hippocampal formation lesioned.

References

- Abrahams, S., Pickering, A., Polkey, C.E. & Morris, R.G. (1997) Spatial memory deficits in patients with unilateral damage to the right hippocampal formation. *Neuropsychologia*, **35**, 11–24.
- Baldaccini, N.E., Benvenuti, S., Fiaschi, V., Ioalè, P. & Papi, F. (1974) Pigeon homing: effects of manipulation of sensory experience at home site. *J. Comp. Physiol.*, **94**, 85–96.
- Batschelet, E. (1981) *Circular Statistics in Biology*. Academic Press, London.
- Bingman, V.P., Bagnoli, P., Ioalè, P. & Casini, G. (1984) Homing behavior of pigeons after telencephalic ablations. *Brain Behav. Evol.*, **24**, 94–108.
- Bingman, V.P., Ioalè, P., Casini, G. & Bagnoli, P. (1988) Hippocampal ablated homing pigeons show a persistent impairment in the time taken to return home. *J. Comp. Physiol. A*, **163**, 559–563.
- Bingman, V.P., Ioalè, P., Casini, G. & Bagnoli, P. (1990) The avian hippocampus: evidence for a role in the development of the homing pigeon navigational map. *Behav. Neurosci.*, **104**, 906–911.
- Bingman, V.P. & Mench, J.A. (1990) Homing behavior of hippocampus and parahippocampus lesioned pigeons following short-distance releases. *Behav. Brain Res.*, **40**, 227–238.
- Bingman, V.P., Ritters, L.V., Strasser, R. & Gagliardo, A. (1998) Neuroethology of avian navigation. In Balda, R.P., Pepperberg, I.M., Kamil, A.C. (eds), *Animal Cognition in Nature*. Academic Press, London, pp. 201–226.
- Bohbot, V.D., Kalina, M., Stepankova, K., Spackova, N., Petrides, M. & Nadel, L. (1998) Spatial memory deficits in patients with lesions to the right hippocampus and to the right parahippocampal cortex. *Neuropsychologia*, **36**, 1217–1238.
- Casini, G., Bingman, V.P. & Bagnoli, P. (1986) Connections of the pigeons dorsomedial forebrain studied with WGA-HRP and 3H proline. *J. Comp. Neurol.*, **245**, 454–470.
- Casini, G., Fontanesi, G., Bingman, V.P., Jones, T.J., Gagliardo, A., Ioalè, P. & Bagnoli, P. (1997) The neuroethology of cognitive maps: contributions from research on the hippocampus and homing pigeon navigation. *Arch. Ital. Biol.*, **135**, 73–92.
- Clayton, N.S. & Krebs, J.R. (1994) Memory for spatial and object-specific cues in food storing and non-storing birds. *J. Comp. Physiol. A*, **174**, 371–379.
- Cowell, P.E., Waters, N.S. & Denenberg, V.H. (1997) The effects of early environment on the development of functional laterality in Morris maze performance. *Laterality*, **2**, 221–232.
- Crowne, D.P., Novotny, M.F., Mier, S.E. & Vitols, R.W. (1992) Spatial deficits and their lateralization following unilateral parietal cortex lesions in the rat. *Behav. Neurosci.*, **106**, 808–819.
- Dunn, O.J. (1964) Multiple contrasts using ranks sums. *Technometrics*, **6**, 241–252.
- Eichenbaum, H., Otto, T. & Cohen, N.J. (1994) Two functional components of the hippocampal memory system. *Behav. Brain Sci.*, **17**, 449–517.
- Gagliardo, A., Ioalè, P. & Bingman, V.P. (1999) Homing in pigeons: the role of the hippocampal formation in the representation of landmarks used for navigation. *J. Neurosci.*, **19**, 311–315.
- Güntürkün, O. (1997) Avian visual lateralization: a review. *Neuroreport*, **8**, 3–11.
- Hampton, R.R. & Shettleworth, S.J. (1996) Hippocampal lesions impair memory for location but not color in passerine birds. *Behav. Neurosci.*, **110**, 831–835.
- Ioalè, P. (1982) Pigeon homing: effects of differential shielding of home cages. In Papi, F., Wallraff, H.G. (eds), *Avian Navigation*. Springer-Verlag, Berlin, pp. 170–178.
- Ioalè, P., Gagliardo, A. & Bingman, V.P. (2000) Hippocampal participation in navigational map learning in young homing pigeons is dependent on training experience. *Eur. J. Neuroscience*, **12**, 1–9.
- Karten, H. & Hodos, W. (1967) *A Stereotaxic Atlas of the Brain of the Pigeon *Columba livia**. Johns Hopkins, Baltimore, MD.
- Kramer, G. (1953) Wird die Sonnenhöhe bei der Heimfindorientierung verwertet? *J. Ornithologie*, **94**, 201–219.
- Krebs, J.R., Sherry, D.F., Healy, S.D., Perry, V.H. & Vaccarino, A.L. (1989) Hippocampal specialisation in food-storing birds. *Proc. Natl. Acad. Sci. USA*, **86**, 1388–1392.
- Maguire, E.A., Frackowiack, R.S.J. & Frith, C.D. (1997) Recalling routes around London: activation of the right hippocampus in taxi drivers. *J. Neurosci.*, **17**, 7103–7110.
- Marr, D. (1982) *Vision*. Freeman, San Francisco, CA.
- Morris, R.G.M., Garrud, P., Rawlins, J.N.P. & O'Keefe, J. (1982) Place navigation impaired in rats with hippocampal lesions. *Nature*, **297**, 681–683.

- Papi, F. (1990) Olfactory navigation in birds. *Experientia*, **46**, 352–363.
- Papi, F., Fiore, L., Fiaschi, V. & Benvenuti, S. (1973) An experiment for testing the hypothesis of olfactory navigation of homing pigeons. *J. Comp. Physiol.*, **83**, 93–102.
- Rashid, N. & Andrew, R.J. (1989) Right hemisphere advantages for topographical orientation in the domestic chick. *Neuropsychologia*, **27**, 937–948.
- Rogers, L.J. (1996) Behavioural, structural and neurochemical asymmetries in the avian brain: a model system for studying visual development and processing. *Neurosci. Biobehav. Rev.*, **20**, 487–503.
- Roper, T.J. (1999) Olfaction in Birds. In Slater, P.J.B., Rosenblatt, J.S., Snowden, C.T., Roper, T.J. (eds), *Advances in the Study of Behavior*. Academic Press, London, pp. 247–320.
- Sherry, D.F. & Vaccarino, A.L. (1989) Hippocampus and memory for food caches in black-capped chickadees. *Behav. Neurosci.*, **103**, 308–318.
- Sherry, D.F., Vaccarino, A.L., Buckenham, K. & Herz, R.S. (1989) The hippocampal complex of food-storing birds. *Brain Behav. Evol.*, **34**, 308–317.
- Siegel, S. (1956) *Nonparametrics Statistics for Behavioral Sciences*. McGraw-Hill, New York, NY.
- Strasser, R. & Bingman, V.P. (1997) Goal recognition and hippocampal formation in the homing pigeon (*Columba livia*). *Behav. Neurosci.*, **111**, 1245–1256.
- Ulrich, C., Prior, H., Duka, T., Leschchins'ka, I., Valenti, P., Güntürkün, O. & Lipp, H.-P. (1999) Left-hemispheric superiority for visuospatial orientation in homing pigeons. *Behav. Brain Res.*, **104**, 169–178.
- Vallortigara, G. (2000) Comparative neuropsychology of the dual brain: a stroll through left and right animals' perceptual worlds. *Brain Lang.*, **73**, 189–219.
- Vallortigara, G., Regolin, L., Bortolomiol, G. & Tommasi, L. (1996) Lateral asymmetries due to preferences in eye use during visual discrimination learning in chicks. *Behav. Brain Res.*, **74**, 135–143.
- Vallortigara, G., Rogers, L.J. & Bisazza, A. (1999) Possible evolutionary origins of cognitive brain lateralization. *Brain Res. Reviews*, **30**, 164–175.
- Wallraff, H.G. (1966) Über die Heimfindeleistung von Brieftauben nach Haltung in verschiedenartig obgeschrämten Volieren. *Z. Vgl. Physiol.*, **52**, 215–259.
- Wallraff, H.G. (1979) Goal-oriented and compass-oriented movements of displaced homing pigeons after confinement in differentially shielded aviaries. *Behav. Ecol. Sociobiol.*, **5**, 201–225.
- Wallraff, H.G. (1990) Navigation by homing pigeons. *Ethology, Ecol. Evol.*, **2**, 81–115.
- Wallraff, H.G. (1996) Seven theses on pigeon homing deduced from empirical findings. *J. Exp. Biol.*, **199**, 105–111.
- Warrington, E.K. & Taylor, A.M. (1973) The contribution of the right parietal lobe to object recognition. *Cortex*, **9**, 152–164.