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Hippocampal ablations and the homing behaviour of pigeons

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Etologia. — *Hippocampal ablations and the homing behaviour of pigeons.* Nota di VERNER P. BINGMAN (*), PAOLA BAGNOLI (**), PAOLO IOALÈ (*) e GIOVANNI CASINI (**), presentata (***) dal Corrisp. F. PAPI.

RIASSUNTO. — È stato studiato il comportamento di homing in colombi viaggiatori cui era stata asportata bilateralmente la porzione dorsomediale del telencefalo, corrispondente all'ippocampo di mammiferi. I risultati dimostrano che la struttura asportata gioca un ruolo critico in quello stadio del processo di homing mediante il quale il colombo rientra nella propria voliera una volta giunto nelle sue immediate vicinanze.

INTRODUCTION

Recently completed research has led to an advanced understanding of pigeon homing mechanisms in terms of the cues and learning processes involved (Papi and Wallraff, 1982; Baldaccini, 1983 for references). In contrast, with the exception of a few studies on the role of the pineal body (Semm *et al.*, 1982; Maffei *et al.*, 1983; Papi *et al.*, in press), the neurobiological basis of pigeon homing behaviour remains relatively unknown. The present paper reports the results of some initial experiments designed to examine the neurobiological basis of pigeon homing behaviour.

Pigeon homing behaviour has been conceptualized to consist of a three step process. The map, which enables a pigeon to identify its position in space relative to home, appears to be based on atmospheric odours (Papi, 1982; Wallraff, 1983). The compass, which enables a pigeon to convert map information into an actual direction, seems to be based on the sun and earth magnetism as well as other possible cues (Able, 1980 for references). The third step is the actual location of the loft once a released pigeon returns to its vicinity. This step is probably mediated through visual contact with the home loft and/or surrounding landmarks (Schmidt–Koenig and Wallcott, 1978).

Numerous studies have demonstrated that the mammalian hippocampal system is important for recognition memory processing (Sahgal, 1984 for references). Anatomical evidence suggests a similarity between the mammalian hippocampus and the avian dorsomedial forebrain (Krayniak and Siegel, 1978). Additionally, recent results have shown that bilateral removal of the pigeon hippocampus causes an impairment of recognition memory (Sahgal, 1984). If the avian dorsomedial forebrain subserves a role in spatial behaviour similar

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to that of the mammalian hippocampus (O'Keefe and Nadel, 1979), lesions placed there would be expected to cause a deficit in pigeon homing ability. Consequently, we examined the effect of dorsomedial forebrain lesions on the homing behaviour of pigeons.

Results and Discussion

Experiment I

In these experiments we lesioned the dorsomedial forebrain and studied the homing behaviour of pigeons when released from both a familiar and unfamiliar site.

The 56 pigeons used were one year old and had previously been released up to 40 Km in the cardinal directions. These birds, which were housed in a loft located 30 Km from Pisa, were first given eight training flights from the S. Giusto release site (familiar site, home distance = 31.3 Km, home direction = 111°). After training, lesions were placed bilaterally in the dorsomedial forebrain of 28 pigeons by aspiration through a glass pipette. The lesions involved brain tissue belonging to the hippocampus and area parahippocampalis from anterior 8.00 to anterior 4.00 and from the midline to lateral 4.00 according to the pigeon atlas of Karten and Hodos (1967). Drawings of transverse sections through the brain of a representative pigeon with dorsomedial forebrain ablation are shown in fig. 1 (P 214.510). As can be seen, the lesion involved the hippocampus and the parahippocampus with moderate damage to adjacent structures including the hyperstriatum accessorium (HA), the hyperstriatum ventrale (HV) and the neostriatum (N). The pigeons recovered well from the surgery, their subsequent behaviour showing no qualitative differences when compared to that of unoperated controls.

Eight days after surgery, 15 of the 28 experimentals and 14 controls were examined for their homing ability when released from the familiar site. Two days later, the 13 remaining experimentals and the remaining 14 controls were brought to and released from Torre a Castello (unfamiliar site, home distance = 68.0 Km, home direction = 294°).

Results of the two releases are reported in Table I. It can be noticed that both groups (experimentals and controls) showed good homeward orientation when released either from the familiar or the unfamiliar site. An examination of homing success, however, revealed a striking difference between controls and experimentals. In fact, in contrast to controls who all homed successfully, operated pigeons showed a striking failure to return to the home loft. The lesioned birds failed to return to their home loft despite an intact ability to orient towards home. The dorsomedial forebrain is apparently not involved in the process by which a pigeon identifies its position in space and converts this information into a compass direction. Rather, this structure seems to play a necessary role in the expression of the last step in the homing process.

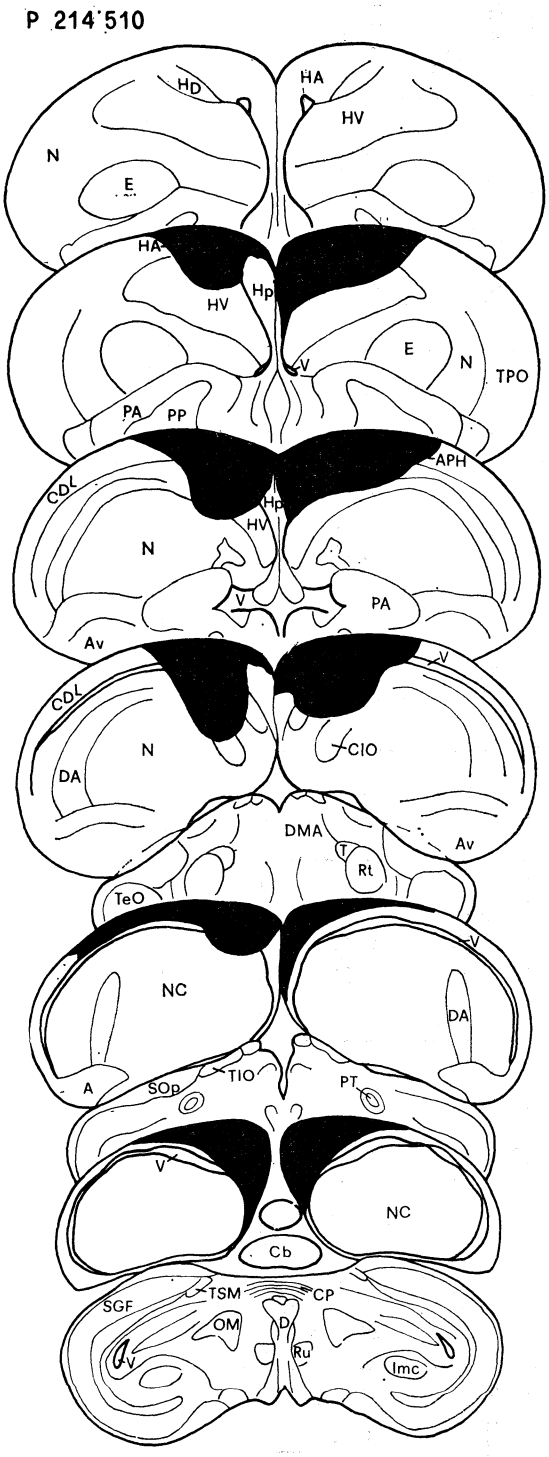

Fig. 1. – Lesion reconstructions for one representative pigeon which belong to the hippocampus ablated group (P 214.510). Drawings of transverse sections and stereotaxis coordinates were derived from the atlas of Karten and Hodos (1967).

Abbreviations: A: Archistriatum; APH: Area parahippocampalis; Av: Archistratum, pars ventralis; Cb: Cerebellum; CDL: Area corticoidea dorsolateralis; CIO: Capsula interna occipitalis; CP: Commissura posterior; D: Nucleus of Darkschewitsch; DA: Tractus archistriatalis dorsalis; DMA: Nucleus dorsomedialis anterior thalami; E: Ectostriatum; HA: Hyperstriatum accessorium; HD: Hyperstriatum dorsale; Hp: Hippocampus; HV: Hyperstriatum ventrale; Imc: Nucleus isthmi, pars magnocellularis; N: Neostriatum; NC: Neostriatum caudale; OM: Tractus occipitomesencephalicus; PA: Paleostriatum augmentatum; PP: Paleostriatum primitivum; PT: Nucleus pretectalis; Rt: Nucleus rotundus; Ru: Nucleus ruber; SGF: Stratum griseum et fibrosum superficiale; SOp: Stratum opticum; T: Nucleus triangularis; TeO: Tectum opticum; TIO: Tractus isthmo-opticus; TPO: Area temporo-parieto-occipitalis; TSM: Tractus septomesencephalicus; V: Ventriculus.

TABLE I

Results of the Experiment I.

Date	Release site	Group	Home direction	Birds released (and bearings recorded)	Mean bearing	Mean vector length	P (V-test)	P (U^2 test)	Number of birds homed	Percent. of returns	Medians of homing times
13–5–1983	S. Giusto (familiar site)	C	111°	14 (14)	120°	0.851	< 0.001	> 0.10	14	100	0^h46^m
		E		15 (14)	102°	0.526	< 0.01		0	0	—
15–5–1983	Torre a Castello (unfamiliar site)	C	294°	14 (14)	291°	0.870	< 0.001	> 0.10	14	100	3^h52^m
		E		13 (10)	292°	0.822	< 0.001		2	15	—

TABLE II

Results of the Experiment II.

	Released	Landed near lofts	Entered lofts	Entered own loft	Entered other lofts	Disappeared	Medians of times landing on the lofts	Medians of times entering into the lofts
Controls (sham perated)	6	6	6	5	1	0	2^m20^s	29^m36^s
Hippocampal ablated pigeons	8	7	2	0	2	6	11^m45^s	—

Experiment II

Since some lesioned pigeons from Experiment I (3 or 4 released from the familiar site and 1 from the unfamiliar site) were observed to return near the loft without re-entering it, Experiment II was designed to remove the actual flight to the home loft from the homing process thereby leaving the birds the sole task of recognizing and entering their respective home lofts.

Summarized in Table II was the homing behaviour of 14 pigeons from two groups (8 pigeons with lesions in the dorsomedial forebrain, and 6 sham-operated controls) when released 800 m away and in full view of their respective home lofts. Although five of six controls returned to their own loft, none of the hippocampus lesioned pigeons homed successfully. After scattering around the loft area, hippocampus lesioned birds were observed to approach individual lofts and explore about, but they failed to enter any loft: in this respect, the hippocampus lesioned pigeons behaved in a manner characteristic of young, inexperienced birds. The results of this experiment suggest that the hippocampus lesioned pigeons were still disposed to associating with a loft, their general failure to do so reflecting an impairment in recognition properties normally involved in the localization of the home loft.

The pigeon dorsomedial forebrain is that part of the brain which is thought to correspond to mammalian hippocampus (Nott, 1980), a structure involved in the organization of spatial behaviour (Olton *et al.*, 1978). Accordingly, it is not surprising that a deficit in a spatial task was found in pigeons as a consequence of lesions placed in this area. Whether information used in the home loft recognition is stored in this structure, however, remains unclear. Our results simply demonstrate that an intact hippocampus is a necessary component of the neural processes involved in the expression of home loft affinity.

Conclusions

The results of this study show that the avian dorsomedial forebrain plays a critical role in that step of the homing process by which pigeon return to its home loft once in its vicinity. The failure to reassociate with the home loft is a likely result of a recognition deficit of the home loft and/or its surrounding area. This evidence supports the hypothesis of a functional correspondence between the mammalian and pigeon hippocampal system, at least to the extent that damage causes a disruption of recognition memory.

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