The ontogeny of the homing pigeon navigational map: evidence for a sensitive learning period

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Homing pigeons can learn a navigational map by relying on the heterogeneous distribution of atmospheric odours in the environment. To test whether there might be a sensitive period for learning an olfactory-based navigational map, we maintained a group of young pigeons in an aviary screened from the winds until the age of three to four months post-fledging. Subsequently, the screens were removed and the pigeons were exposed to the winds and the environmental odours they carry for three months. One control group of pigeons was held in a similar aviary but exposed to the winds immediately upon fledging, while another control group of pigeons was allowed free-flight. When the pigeons from the three groups were released from two distant release sites at about six months of age post-fledging, the two control groups were found to be equally good at orientating and returning home, while the experimental pigeons held in the shielded aviary for the first three months post-fledging were unable to orientate homeward and they were generally unsuccessful in returning home. This result supports the hypothesis that environmental experience during the first three months post-fledging is critical for some aspect of navigational map learning and that navigational map learning displays sensitive period-like properties.

Keywords: pigeon; homing; navigational map; imprinting

1. INTRODUCTION

Homing pigeons displaced to an unfamiliar location usually fly off in an approximate homeward direction shortly after being released. According to the 'map and compass' model of Kramer (1953, 1961), identifying the home direction from an unfamiliar location, i.e. use of a so-called navigational map, is the first step in the homing process. The navigational map olfactory hypothesis (Papi *et al.* 1971; Papi 1991, 1995; Wallraff 1991, 1996; Roper 1999) proposes that homing pigeons can learn a navigational map by associating environmental odours carried by the winds with the direction from which they come. The outcome of this learning process is a map-like representation of the distribution of salient atmospheric odours in the region around the loft (Wallraff 2000; Wallraff & Andreae 2000). The emergence of a functional navigational map based on atmospheric odours typically occurs during the first two to three months of life post-fledging (Baldaccini *et al.* 1978; Ialè *et al.* 1978, 1990, 2000; Gagliardo *et al.* 1988).

The homing pigeon navigational map provides pigeons with a memory representation of environmental space around the loft. Some early experimental evidence suggests that the homing pigeon navigational map is a plastic or dynamic navigational mechanism, which can be continually modified as a pigeon experiences more of its environment (Baldaccini *et al.* 1978). For example, it has been reported that adult birds, confined for a period of time in a new loft remote from their original home, can learn a second navigational map relative to their new loft (Baldaccini *et al.* 1976; Bingman & Yates 1992). However, it remains to be tested whether older birds are capable of learning a first navigational map, and therefore, the

importance of early experience for navigational map acquisition.

To investigate the importance of early experience for learning a navigational map based on atmospheric odours, young, post-fledging pigeons were initially placed in a screened outdoor aviary that prevented any association between atmospheric odours and wind direction, and therefore olfactory navigational map learning (Wallraff 1966; Papi *et al.* 1973; Baldaccini *et al.* 1974; Ialè & Albonetti 1981). When these pigeons were three months of age post-fledging, an age when young pigeons normally would have already learned a navigational map, the screens were removed from the aviary. The pigeons were then allowed to experience the association between atmospheric odours and the direction of the winds that carry them for the first time, for a period of three months, before they were tested for navigational map learning.

2. MATERIAL AND METHODS

The pigeons used in the experiment were born in Arnino, near Pisa, Italy in 1999. About 30–35 days after hatching, prior to any navigational map learning, each bird was assigned to one of the following treatment groups. (i) Free-flying birds (FF pigeons, $n = 27$). The FF pigeons were housed in a loft from which they could freely leave to perform spontaneous flights, generally beginning in April, until the first experimental release in late August. One pigeon was lost from this group during free-flights. (ii) Prisoner birds (P pigeons, $n = 27$). The P pigeons were housed in an aviary (2.5 m × 2.5 m × 2.2 m), generally beginning in March, open to the winds from all directions. The birds were confined to the aviary until the first experimental release. (iii) Screened prisoner birds (SP pigeons, $n = 28$). The SP pigeons were housed in an aviary identical to the aviary of the P pigeons. However, the walls and two-thirds of the roof

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Table 1. *Results of the experiments*

(Release site: name of the release site, date of the experiment, home direction and distance are indicated; group: as in the text; N , birds released; n , birds for which bearings were recorded; α , mean vector direction; r , mean vector length (Rayleigh test, $^*p < 0.05$, $^{***}p < 0.001$); hc , $\cos(\alpha - \beta)$, where β is the home direction; h (%), percentage of birds that homed after the release.)

release site	group	N	n	α	r	hc	h (%)
Massaciuccoli, 13, 14, 18/8/99, 188°, 19 km	FF	26	26	190°	0.79 ^{***}	0.79	96.2
	P	27	27	170°	0.66 ^{***}	0.63	85.2
	SP	28	28	005°	0.14	-0.14	50
Bolgheri, 25-26/8/99, 336°, 55 km	FF	16	14	291°	0.68 ^{***}	0.49	81.2
	P	16	15	321°	0.69 ^{***}	0.66	100
	SP	13	12	209°	0.56 [*]	-0.34	38.5

were covered with clear polycarbonate transparent panels, which screened the winds. The remaining one-third of the roof was made of a net, which allowed for the free circulation of air and free access to natural sunlight. Polycarbonate screens reflect practically no light and do not interfere with skylight polarization patterns; and they produce no visual artefact as other screens have been reported to do (Phillips & Waldvogel 1982; Waldvogel & Phillips 1991). The birds from this group were generally placed in the aviary in February, and the screens were removed on 1 June. After 1 June, both the P and SP pigeons were exposed to the winds until the experimental releases in late August. The critical difference between the two groups was that the SP pigeons were exposed to the winds, and the atmospheric odours they carry, only after three months of age post-fledging, an age when young pigeons continually exposed to the winds have already learned a navigational map (Gagliardo *et al.* 1988). Twenty days before the first experimental release, all the P and SP pigeons were transferred together to a larger aviary (8 m × 4 m × 3 m) to provide a better opportunity for flight exercise.

The two experimental releases took place when the birds were six to eight months of age post-hatching. The first release was performed in the middle of Lake Massaciuccoli north of home (Bingman *et al.* 1990; Ioalè *et al.* 2000). This was done to discourage the P and SP pigeons from landing (pigeons who have never flown from the home loft tend to land on their first release). Because of the large number of birds released, the Lake Massaciuccoli release occurred over three different days. Subsequently, all the pigeons that returned participated in a second release, which occurred over two days from a second location at Bolgheri, south-east of home (details of the release sites can be found in table 1).

The birds were released singly, alternating between treatment groups, and followed with 10 × 40 binoculars until vanishing. Vanishing times and bearings were recorded at the release site. An observer at the home loft recorded the time of arrival of each pigeon.

For each distribution of vanishing bearings, a mean vector was calculated and the distribution tested for uniformity by means of both the Rayleigh and V -test (Batschelet 1981). For each release, between group differences in the distribution of vanishing bearings were performed by means of the Kruskal–Wallis test (Siegel 1956; see Wallraff 1979) with respect to both the angular difference between the vanishing bearings and the home direction (to test for group differences in orientation), and the angular difference between individual vanishing bearings and the group mean direction (to test for group differences in the dispersion of vanishing bearings). When the Kruskal–Wallis

test identified significant overall group differences, paired-group comparisons were performed with the Dunn's test (Dunn 1964). Group differences in homing performance and vanishing times were also tested using the Kruskal–Wallis test; Dunn's test was used for paired-group comparisons.

3. RESULTS

The vanishing bearings of the three groups from Lake Massaciuccoli are summarized in table 1 and shown in figure 1. The distribution of vanishing bearings of the SP pigeons was not different from uniform (both Rayleigh and V -test, $p > 0.10$). By contrast, both the FF and P pigeons were similarly well orientated in the homeward direction (both Rayleigh and V -test, $p < 0.001$). The distributions of vanishing bearings of the three groups were significantly different with respect to both orientation and dispersion (Kruskal–Wallis, $p < 0.01$ for both). SP birds differed from both FF and P birds in both orientation (Dunn's test, $p < 0.001$ for all comparisons) and dispersion (Dunn's test, SP versus FF, $p < 0.001$ and SP versus P, $p < 0.02$). No significant differences between FF and P birds were found (Dunn's test, $p > 0.5$ for all comparisons).

From Lake Massaciuccoli the homing performance of the three groups was consistent with the vanishing-bearing data. In fact, while most of the FF and P pigeons homed, only 14 out of 28 SP birds returned (table 1 and figure 1). The statistical analysis of the homing performance showed a significant overall difference between groups (Kruskal–Wallis, $p < 0.001$). The homing performance of the SP birds was significantly poorer than the performance of the P and FF birds (Dunn's test, $p < 0.02$ and 0.001 , respectively). The P birds were also significantly slower than the FF birds (Dunn's test, $p < 0.005$).

A significant difference between groups was also found in vanishing times (median vanishing times: FF birds 1 min 59 s, P birds 2 min 30 s, SP birds 4 min 12 s; Kruskal–Wallis, $p < 0.001$). The difference was significant between SP and both P and FF pigeons (Dunn's test, $p < 0.001$ in both comparisons), but not between FF and P birds (Dunn's test, $p > 0.05$).

The results from Bolgheri are generally consistent with the results from the first release. Although the vanishing-bearing distributions from all three groups were different from uniform according to the Rayleigh test (see table 1 and figure 2), and no group difference in the dispersion of

Figure 1. Results of the experimental release from Lake Massaciuccoli. The circular diagrams show the initial orientation of the birds: each symbol on the periphery of each circle identifies the vanishing bearing of one pigeon. Open circles represent FF birds, closed circles P birds, and closed triangles SP birds. Arrows inside each circle represent the mean vector of each group, whose length can be read using the scale shown in the first diagram. The home direction (H) and distance are shown by the arrow outside of each diagram. The linear diagrams below display the homing performance of each group: each symbol over each row identifies the performance of one pigeon (open and closed circles, and closed triangles represent the same pigeon groups as in circular diagrams). For the birds which homed on the day of release (day birds), homing speed is given; following day, pigeons that homed on the day after the release; later, pigeons that homed later than the day after the release; lost, pigeons that never returned home.

vanishing bearings was found (Kruskal–Wallis, $p > 0.05$), the groups did differ with respect to the directions of the vanishing bearings (Kruskal–Wallis, $p < 0.05$). While FF and P pigeons orientated in an approximately homeward direction (V -test, $p < 0.01$ and $p < 0.001$, respectively), the SP pigeons tended to orientate south-south-west (V -test, $p > 0.1$). Paired comparisons revealed a significant difference in orientation only between SP and P pigeons (Dunn's test, SP versus P, $p < 0.005$; SP versus FF, $0.1 > p > 0.05$; P versus FF, $p > 0.5$). Worth noting is that the direction taken by the SP birds (south-south-west) is often displayed by Pisa pigeons from Bolgheri when navigation or initial orientation is impaired by, for example, olfactory deprivation (Benvenuti *et al.* 1992; Benvenuti & Gagliardo 1996) or magnetic disturbance (Ioalè & Teys-sédre 1989; Papi *et al.* 1992).

Homing performance from Bolgheri was significantly different among the three groups (Kruskal–Wallis, $p < 0.001$) and consistent with the initial orientation data (figure 2). Again, most of the FF and P birds homed,

while eight out of 13 SP birds were lost. The SP pigeons displayed impaired homing performance when compared with both P and FF pigeons (Dunn's test, $p < 0.01$ and $p < 0.002$, respectively). No difference between FF and P birds was found (Dunn's test, $p > 0.5$).

Although the SP birds were slower in vanishing than the other two groups (median vanishing times: FF birds 3 min 24 s, P birds 2 min 34 s, SP birds 4 min 4 s) no significant difference was revealed by the Kruskal–Wallis test ($p > 0.05$).

4. DISCUSSION

Young pigeons prevented from learning the spatial relationship between atmospheric odours and wind direction (SP pigeons) during the first three months of life post-fledging were dramatically impaired in their navigational ability. This was true despite the fact that the SP pigeons were exposed to winds and odours for three months after this deprivation period, an amount of time

Figure 2. Results of the experimental release from Bolgheri. Other explanation are as in figure 1.

sufficient for navigational map learning in immediate post-fledging birds (Gagliardo *et al.* 1988). Therefore, the observed impairment in the SP pigeons cannot be attributed to an inadequate amount of time to associate atmospheric odours with wind direction. Collectively, the data suggest the existence of a sensitive period for olfactory-based navigational map learning in homing pigeons. Other examples of sensitive period-like olfactory learning supporting homing behaviour have been reported in some species of salmon (Hasler & Scholz 1983) and sea turtles (Grassmann 1993). Nevertheless, the phenomenon we have observed in homing pigeons seems to be different from the olfactory imprinting in salmon and sea turtles. These species only use odours for site recognition and do not use them to navigate over unfamiliar terrain.

Previous data suggest that pigeons that have already learned a navigational map are able to update it as a consequence of changing environmental experience (Baldaccini *et al.* 1976, 1978; Bingman & Yates 1992). If we assume that adult pigeons can build upon a pre-existing map, or even learn a new map, then the learning deficit in our SP pigeons suggests that the sensitive period is perhaps not specifically related to learning a map, but perhaps preparing or shaping the learning mechanisms and supporting neural architecture necessary for map

learning. This is an exciting possibility that we plan to investigate more thoroughly.

Orientating homeward from a distant, unfamiliar location consists of both determining the direction of displacement by the navigational map and then orientating towards home by use of the sun or some other compass cue (Schmidt-Koenig 1961; Wiltschko & Wiltschko 1988). The SP pigeons were able to see the sun during the entire post-fledging period and it is unlikely that they did not learn a sun compass (Budzynski *et al.* 2000). Nonetheless, in theory, the failure of the SP birds to orientate homeward could be a consequence of not learning a navigational map or not learning to orientate by the sun or some other compass cue. However, although SP pigeons failed to orientate homeward, their vanishing bearings were well orientated from Bolgheri. The orientated vanishing bearings demonstrate that these birds possessed an operational compass mechanism and the failure to navigate homeward was a consequence of not learning a navigational map.

One possible design flaw in our experiment was that we did not place a group of control birds in a screened aviary for three months after an initial three month learning period. However, Papi *et al.* (1973) did raise young pigeons kept alternately for three days in a screened aviary and three days exposed to the environmental

odours for three months, and observed no impairment in homing behaviour. Although these young pigeons were held in a screened aviary for up to 45 days cumulatively, they nonetheless learned a navigational map (Papi *et al.* 1973).

In many cases, research examining the neural correlates of sensitive period-like learning phenomena have highlighted neural plasticity occurring in particular brain regions during a restricted developmental period (e.g. Horn 1986; Bock & Braun 1999). The presence of a sensitive period for some aspect of learning a navigational map based on atmospheric odours is probably associated with a period of developmentally restricted neural plasticity during a pigeon's life. Lesions to the hippocampal formation impair navigational map learning if young pigeons are confined in an outdoor aviary for the first few months of life (Bingman *et al.* 1990; Ioalè *et al.* 2000). However, it has been recently reported that young pigeons subjected to hippocampal ablation and subsequently given training flights from short distances do succeed in learning a navigational map, which they can use to navigate over longer distances and from unfamiliar locations (Ioalè *et al.* 2000). We discuss this hippocampal work not so much to promote the hippocampus as a possible site of neural plasticity necessary for navigational map learning, which is perhaps likely (Clayton 1995; Patel *et al.* 1997) but remains to be investigated, but more to suggest the possibility that flight experience can affect the learning process(es) associated with acquiring a navigational map. One challenge now is to understand whether flight experience might enable young pigeons raised in screened aviaries to learn a map outside the suspected sensitive period for navigational map learning.

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