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METHODS FOR PRODUCING DISTURBANCES IN PIGEON HOMING BEHAVIOUR BY OSCILLATING MAGNETIC FIELDS

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SUMMARY

Experiments were performed with homing pigeons treated before release with oscillating magnetic fields produced by small Helmholtz coils placed around the neck and on the head of the pigeon or by larger Helmholtz coils surrounding the cage of the birds. In both types of treatment, which both used a single frequency of about 0·14 Hz, the pigeons' initial orientation was strongly affected when the oscillation of the artificial magnetic field was square-shaped, whereas a triangular or sine-shaped variation had no effect.

INTRODUCTION

Viguier (1882) was the first to hypothesize that birds might use magnetic cues to orientate. Merkel and coworkers (1958, 1965), Wiltschko (1972) and Keeton (1971) demonstrated that some species (migratory passerines and homing pigeons) are able to use the earth's magnetic field to orientate when astronomical cues are lacking. The role of magnetic stimuli is less clear under other conditions (for example when the sun is visible). Many researchers have noticed an influence of local magnetic anomalies on the orientation of homing pigeons released under sunny conditions (see Wagner, 1983 for references); Keeton, Larkin & Windsor (1974) discovered that the mean vanishing bearing of pigeons is significantly correlated with the variability of the earth's magnetic field.

Researchers have tried various forms of experimental manipulation to investigate the effect of magnetic information on the navigational mechanism of the homing pigeon. These experiments include magnetic treatments applied to pigeons in the loft, at the release site, during passive transportation and during flight. Kiepenheuer (1978) and Wiltschko, Wiltschko & Keeton (1978) reversed the vertical and horizontal

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components, respectively, of the earth's magnetic field during the transportation of pigeons toward the release site; Papi *et al.* (1978, 1980) transported homing pigeons in iron containers, inside which the earth's magnetic field was strongly reduced. In addition, Benvenuti, Baldaccini & Ioale' (1982) used an experimental device consisting of three pairs of Helmholtz coils, which produced a random oscillation of the magnetic field. If protracted, this treatment is effective, even if performed before and after transportation to the release site (Papi, Meschini & Baldaccini, 1983), and in most cases it led to a change in initial orientation with respect to that of controls, while there was little or no effect on homing performance.

Small magnetic bars applied on the head and the wings of pigeons (Matthews, 1951; Wallraff & Foa', 1982) or only on the neck or head (Keeton, 1971; Walcott, 1980) have been used to produce artificial magnetic stimuli during flight. Walcott & Green (1974), Walcott (1977) and Visalberghi & Alleva (1979) used static magnetic fields of different intensities, produced by small Helmholtz coils, which were placed on the head and around the neck of pigeons. Recently, Lednor & Walcott (1983) employed a similar type of coil, which produced an artificial magnetic field varying in a regular or irregular way; these authors, in fact, wanted to verify the effect of small variations in the magnetic field, in order to test the magnetic navigation hypothesis. These magnetic disturbances during flight generally had little or no effect on initial orientation under sun, while they proved to be very effective under overcast skies (see Walcott, 1982 for a review).

In this paper we report the methods used by us to produce oscillating magnetic fields that interfere with the orientational capabilities of pigeons under sun, and our preliminary results. It was decided to perform all the experiments from a single release site (Bolgheri), because treatments with magnetic stimuli there had had a particularly uniform effect on pigeons belonging to the Arnino lofts, as can be seen in previous experiments (Papi *et al.* 1983) performed from many release places located at various directions and distances from the lofts. They generally produce a strong counterclockwise deviation of bearings without a substantial increase in their scattering, while control birds constantly display a good homeward bearing.

METHODS

The pigeons used in our experiments were housed in lofts at Arnino (Pisa). In experiments A1, A2, B1 and B4 we used pigeons about 5–6 months old at their first experimental release; in experiments B2 and B3 we used pigeons about 1 year old with little homing experience. All the birds were new to the release site.

All the experimental releases were performed from Bolgheri (home direction, 336°; home distance, 54·8 km). The birds were transported in well-ventilated vans and the baskets (which the birds could not see out of) containing the control birds were put on the van roof. Once the experimental treatment had ended, the birds were kept in plastic baskets until release.

Releases were performed in sunny conditions, with little or no wind. Bearings and vanishing times were recorded using standard procedures. We did not check returns to the loft, because these kind of magnetic treatments have very little effect on homing performances (see Papi *et al.* 1978, 1983; Benvenuti *et al.* 1982).

Vanishing bearings were tested for randomness by the Rayleigh test (Batschelet, 1965); clustering around the home direction was tested by the V test (Batschelet, 1981) and comparisons between bearing sets were made using the Watson U^2 test (Batschelet, 1965, 1972).

EXPERIMENTS AND RESULTS

Series A. Experiments with Helmholtz coils applied to the pigeons before release

Experiment A1. 9 August 1982

The experimental device consisted of two Helmholtz coils connected in parallel; one was applied on the top of each pigeon's head and the other around its neck (Fig. 1A), as described by Walcott & Green (1974). Such coils were fed by a wave generator placed inside a waterproof bag applied to the back of the pigeon. Both the head coil and the generator were fastened to the pigeon with tear tape. Each of the two coils consisted of 200 turns of insulated copper wire ($\phi = 0{\cdot}125$ mm); one had a mean diameter of 23 mm and the other of 35 mm. The wave generator was an oscillator based on an Intersil model ICL 7614, low power MAXCMOS operational amplifier, capable of working at supply voltages as low as ±0·5 V, with a power consumption as low as 10 μW. This arrangement was able to ensure a 24-h supply using two 1·5-V 210-mAh Ray-O-Vac model RW 42 mercury batteries. The generated waveform at a frequency of about 0·14 Hz with an amplitude of ±0·65 V is shown in the lower part of Fig. 2B. It is a sine wave with flat sections at the top of the peaks, due to saturation of the amplifier, and near the zero crossing, due to the cut-off in the power section of the circuit. It was considered unnecessary to eliminate these imperfections because the possible advantages would be more than offset by the disadvantage of an increase in the weight and complexity of the system. The upper half of Fig. 2B shows the resultant magnetic flux when the probe of a gaussmeter (model 101 RFL Industries, Inc.) perpendicular to the ground was located between the two coils which were kept at a distance of 40 mm from each other.

It may be inferred from Fig. 2B that the magnetic induction varied between +0·65 and −0·35 G ($1\,\mathrm{G} = 10^{-4}\,\mathrm{T}$), with a positive offset due to the presence of the earth's magnetic field. The slight apparent distortion of the generated field, as shown in the pictures, was entirely due to the differentiating effect of the gaussmeter used in the measurements.

The experimental treatment lasted 2·5 h, and it began when the pigeons left the loft; it was partly given during the journey (lasting about 1·5 h) and partly at the release site. The birds were freed and released after the device had been removed; during the same period of time, the control birds wore inactive coils.

The experimental treatment did not have a statistically significant effect; the initial orientation of both groups is shown in Fig. 3 (upper horizontal series). Both controls and experimentals were homeward orientated (V test, $P < 0{\cdot}001$ and $P < 0{\cdot}01$, respectively). There were no significant differences between the two distributions ($U^2 = 0{\cdot}051, P > 0{\cdot}010$).

Experiment A2. 22 August 1983

For this experiment the wave generator was modified so as to produce a square wave of about 0·14 Hz, with an amplitude of ±0·65 V, as shown in the lower part of Fig. 2C. The upper portion of the picture shows the consequent magnetic flux varying between +0·70 and −0·35 G, measured in the same way, and with the same specifications as in experiment A1. All the other experimental procedures were the same as in A1.

The experimental treatment had a clear effect. Initial orientation is shown in Fig. 3 (lower horizontal series); controls were homeward orientated (V test, $P < 0{\cdot}001$), whereas experimentals were not (V test, $P > 0{\cdot}10$); the two distributions differed significantly ($U^2 = 0{\cdot}380, P < 0{\cdot}001$).

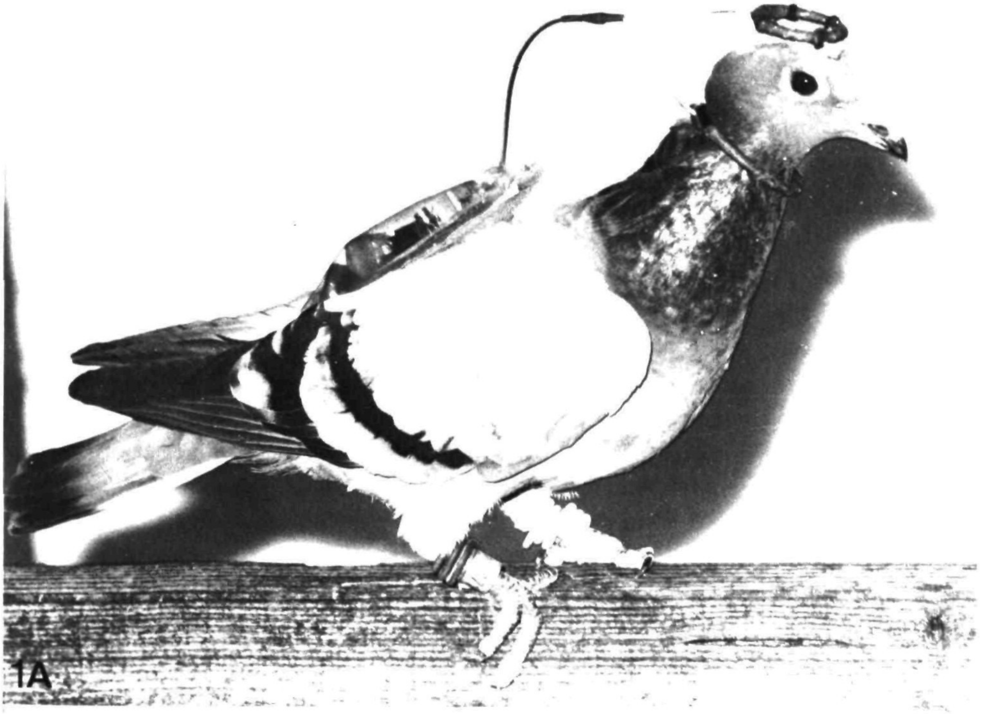


Fig. 1A. Pigeon wearing Helmholtz coils and wave generator.

Series B. Experiments with Helmholtz coils applied around the cage of the pigeons

Experiment B1. 9 August 1982

The experimental device is shown in Fig. 1B; it was carried in a Fiat 127 Fiorino van. The device consisted of three pairs of Helmholtz coils and a wave generator which was fed by means of two 12-V electric batteries connected in series (see also Benvenuti

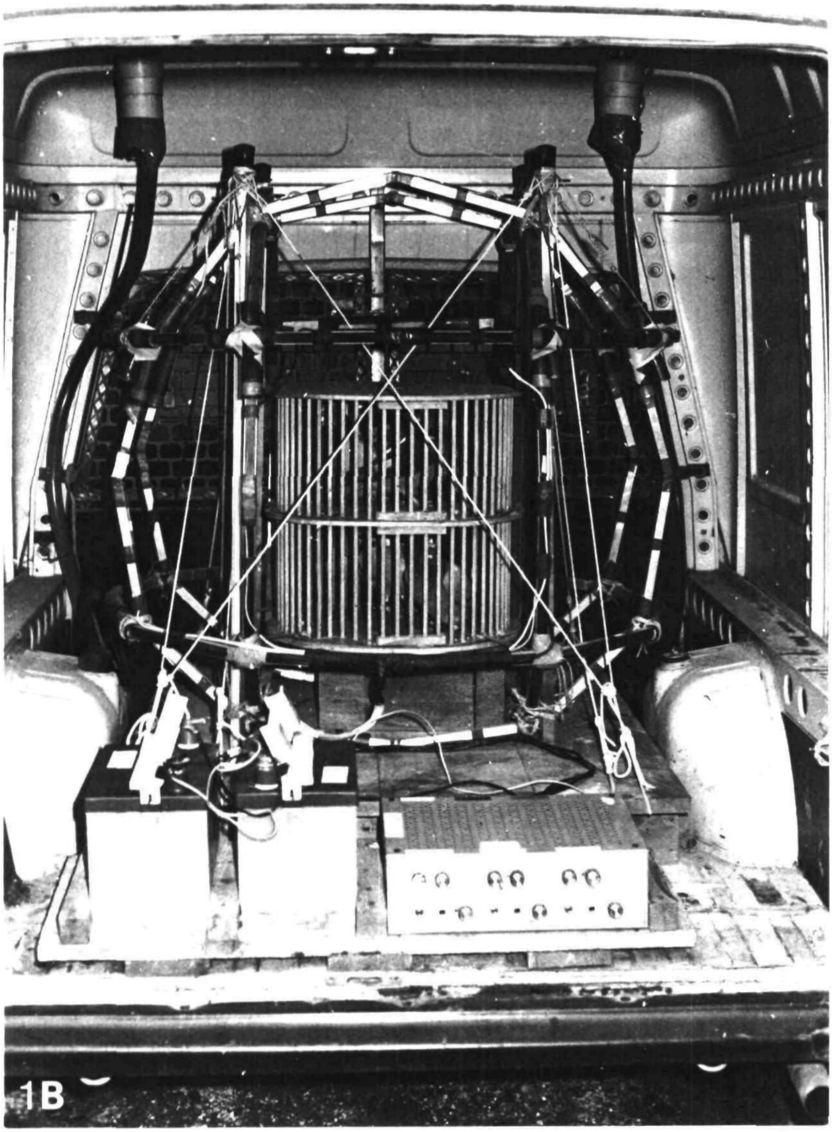


Fig. 1B. A view of the Helmholtz coils surrounding the pigeons' cage, inside the van.

et al. 1982). All coils consisted of 150 turns of insulated copper wire ($\phi = 1$ mm), with a diameter of 95 cm. The two coils in each pair were connected in parallel and each of the three pairs was placed at right angles to the other two. The coils were arranged around two small superimposed wooden cages in which the experimental birds were lodged. In this experiment the three pairs of coils were all fed from the generator with sine waves at a different frequency for every pair – 0·067, 0·043 and 0·026 Hz – where the second frequency refers to the horizontal pair. In this way we obtained a continuous, irregular change in the induced magnetic flux between +0·70 and −0·20 G. These values mainly derive from the magnetic flux induced by the horizontal pair of coils; this was the only one able to produce a magnetic field picked by the probe, when this was kept in the standard position for measurement. The fluxes of the other two pairs of coils produced hardly any appreciable effect on the probe, as they were orientated in the direction to which the probe is least sensitive. The exact value for the intensity of the field induced at each point in the cage and at each moment can be calculated as the resultant of $R = \sqrt{x^2 + y^2 + z^2}$, where x, y and z represent the vectors relative to the field intensity produced by each of the three pairs of coils.

For these measurements, and those of later experiments, we used the same measuring equipment described for experiment A1, setting the gaussmeter probe perpendicular to the ground in the centre of the coil system. In this case too, the experimental treatment lasted 2·5 h, and it began immediately after departure from the loft.

The experimental treatment had a clear effect; initial orientation is shown in Fig. 5 (upper horizontal series). Only the control pigeons were homeward orientated (V test, $P < 0{\cdot}001$) and the two bearing distributions were significantly different ($U^2 = 0{\cdot}353$, $P < 0{\cdot}001$). Note that deflection was the same as in A2.

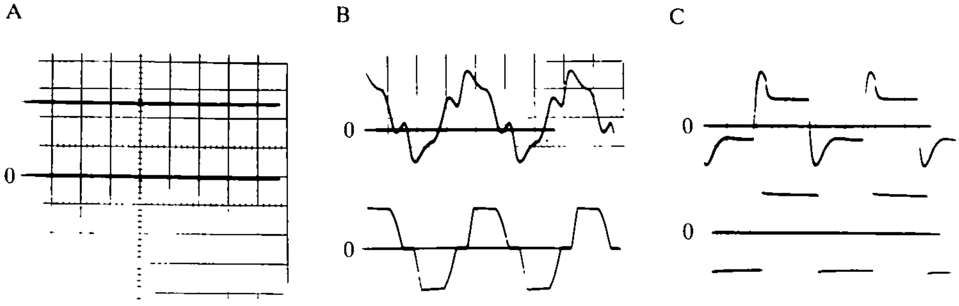


Fig. 2. Voltage feed of the Helmholtz coils worn by pigeons (lower sections) and corresponding magnetic fluxes measured at the centre of coils (upper sections) for: (A) no wave applied, (B) a sine wave, (C) a square wave. Scope parameters: horizontal, 2 s/division; vertical, lower section, 0·5 V/division; upper section, 10 mV/division (corresponding to 0·15 G/division). Note that the traces corresponding to fluxes are not zero-centred because of the earth's magnetic field in Pisa. Traces of voltages and corresponding fluxes are not exactly in phase because of a phase shift in the scope channels. Some apparent distortions of the generated field (particularly in the case of the square wave) are only due to a differentiating effect of the gaussmeter.

Experiment B2. 18 March 1983

In this experiment we used the same device as in B1, but here only one pair of coils – the horizontal one – was supplied with current. The signal, as shown in the lower half of Fig. 4A, took the form of a sine wave with a frequency of 0·14 Hz and an amplitude of ±4 V. In the upper half of Fig. 4A we report the corresponding magnetic flux produced, which has an oscillation between +0·62 and −0·23 G. All the other methods were the same as in B1.

The initial orientation was not influenced by the treatment (Fig. 5, lower horizontal series). Both controls and experimentals were homeward orientated (V test, $P < 0{\cdot}001$

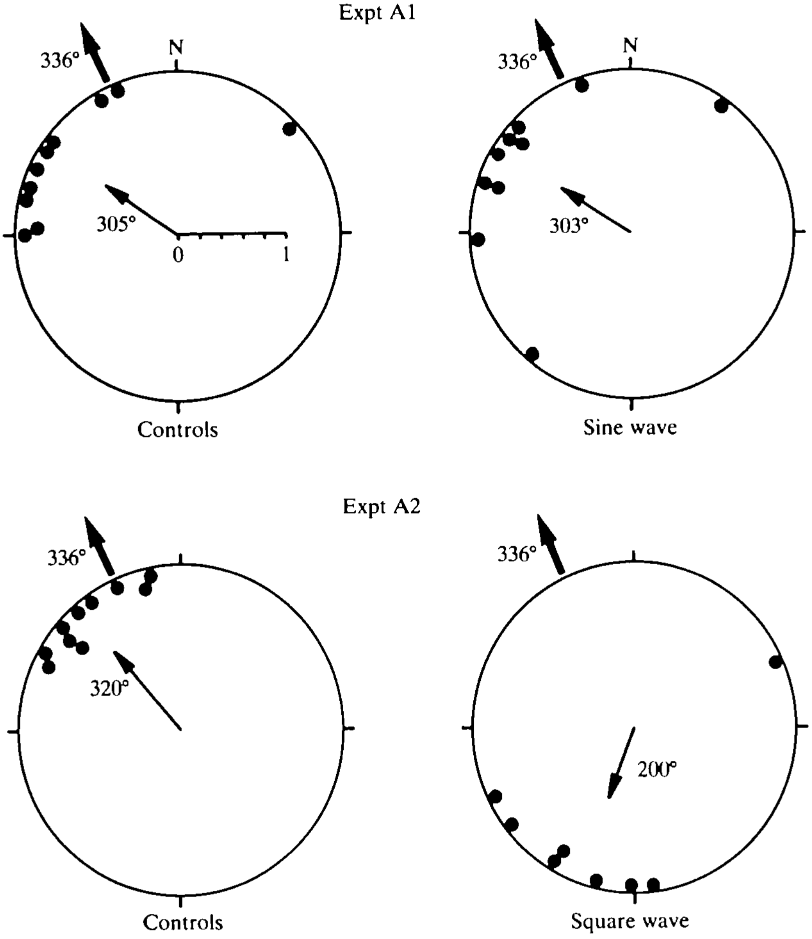


Fig. 3. Initial orientation of pigeons wearing Helmholtz coils before release (Expts A1, A2). The outer arrows indicate the home direction; the inner arrows represent the mean vectors, the length of which can be read according to the scale in the first diagram. Each dot in the periphery of the diagrams represents the vanishing bearing of one bird. The type of treatment given to the birds is reported under each diagram.

and $P < 0.01$, respectively) and no significant differences were found in the initial orientation of the two groups ($U^2 = 0.048$, $P > 0.10$).

Experiment B3. 27 May 1983

In this experiment, in addition to the controls, two groups of experimental pigeons were transported by means of two different vans and were subjected to experimental treatments inside two devices identical to that used in B1. In each device, only the horizontal pair of coils was supplied with current. For the first experimental group the voltage feed was shaped like a triangular wave, as shown in the lower half of Fig. 4B, with a frequency of about 0·14 Hz and an amplitude of ±6·25 V. The upper part of the picture shows the corresponding magnetic flux induced; this oscillated between +0·96 and −0·40 G. For the second experimental group, the voltage feed was shaped like a square wave, as shown in the lower half of Fig. 4C, with a frequency of about 0·14 Hz and an amplitude of ±7·5 V. The upper half of Fig. 4C shows the corresponding magnetic flux induced; this varied from +0·80 to −0·48 G. All the other methods were the same as in experiment B1.

The initial orientation is shown in Fig. 6 (upper horizontal series). Both the controls and the experimentals which were subjected to a magnetic flux shaped like a triangular wave were homeward-orientated (V test, $P < 0.001$ for both groups); the two distributions of bearings did not differ significantly ($U^2 = 0.024$, $P > 0.10$). On the other hand, the experimentals subjected to magnetic flux shaped like a square wave were not homeward-orientated (V test, $P > 0.10$) and the distribution of their bearings was significantly different from those of both other groups ($U^2 = 0.500$, $P < 0.001$ and $U^2 = 0.524$, $P < 0.001$, respectively).

Experiment B4. 22 August 1983

This experiment was similar to the previous one. Our main aim was to see whether the effect on initial orientation, observed in B3, of treatment with a magnetic flux

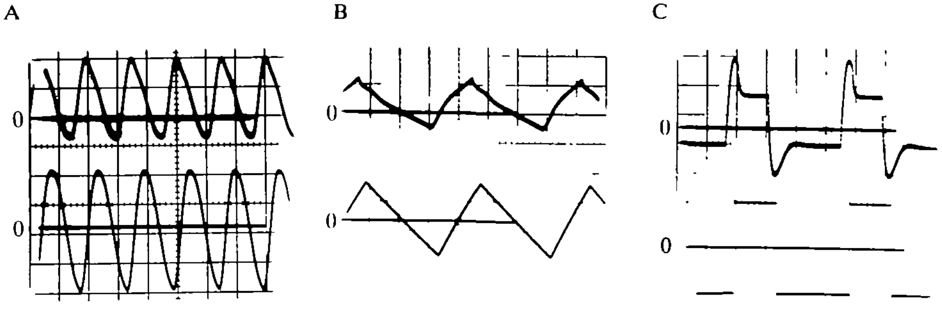


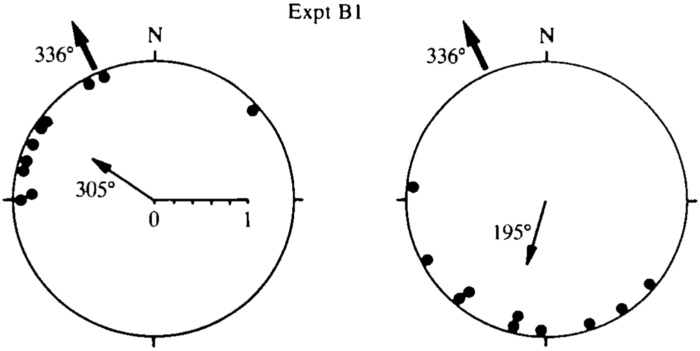
Fig. 4. Voltage feed of the cage coils (lower sections) and corresponding magnetic fluxes measured at the centre of the cage (upper sections) for: (A) a sine wave, (B) a triangular wave, (C) a square wave. Scope parameters: horizontal (A) 5 s/division; (B), (C) 2 s/division; vertical, lower section (A) 2 V/division; (B), (C) 5V/division; upper section (A) 20 mV/division (corresponding to 0·31 G/division); (B), (C) 50 mV/division (corresponding to 0·78 G/division). Other explanations as in Fig. 2.

shaped like a square wave would be confirmed. The methods used were the same as in B3, but one of the two experimental groups was subjected to a sine wave-shaped magnetic flux and, the other, to a square wave-shaped one. The frequencies were again 0·14 Hz for both experimental groups.

The initial orientation is shown in Fig. 6 (lower horizontal series). Both the controls and experimentals subjected to a sine wave-shaped magnetic flux were homeward orientated (V test, $P < 0{\cdot}001$ for both); the two distributions of bearings did not differ significantly ($U^2 = 0{\cdot}079$, $P > 0{\cdot}10$). On the other hand, the experimentals subjected to a square wave-shaped magnetic flux again failed to show homeward bearings (V test, $P > 0{\cdot}10$) and the distribution of their bearings was significantly different from those of both other groups ($U^2 = 0{\cdot}404$, $P < 0{\cdot}001$ and $U^2 = 0{\cdot}361$, $P < 0{\cdot}001$, respectively).

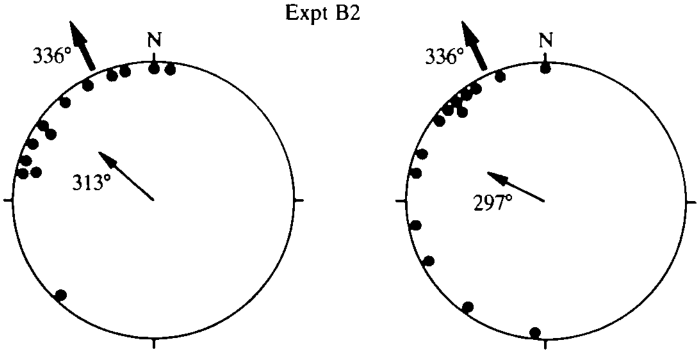
DISCUSSION

The experimental techniques used in the two series differed substantially, in so far as the Helmholtz coils were fixed to the head of each pigeon in series A, while in series



Controls

Sine wave
(3 pairs of coils)



Controls

Sine wave

Fig. 5. Initial orientation of pigeons which had been kept inside a cage surrounded by Helmholtz coils (Expts B1, B2). Other explanations as in Fig. 3.

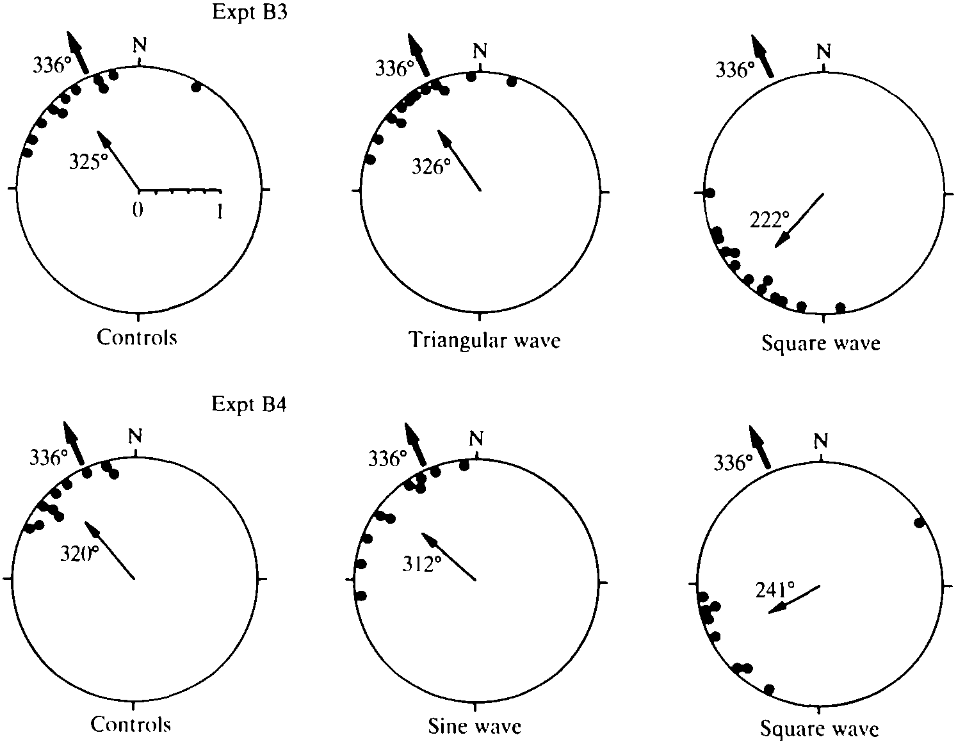


Fig. 6. Initial orientation in Expts B3, B4. Other explanations as in Fig. 3.

B the birds could move in the magnetic field produced by the coils. Using the same type of wave, the experiments gave the same result with the two kinds of treatments; so the question of whether the oscillating field moves with the pigeon or not, seems to be unimportant.

4 Experiment B1 confirms our previous finding (Benvenuti *et al.* 1982; Papi *et al.* 1983) that a magnetic field produced by means of three pairs of coils, each giving a sine wave magnetic flux, has a strong effect on initial orientation. The use of only one pair of coils showed that there is a clear difference between the three kinds of waves. In fact, in spite of the use of similar frequencies, it turned out that only the square wave had a strong effect on initial orientation; this effect is similar to that obtained by means of three pairs of coils producing sine waves simultaneously.

4 Our chief result seems to be the different effects produced by waves of different shapes. It seems likely that frequencies and intensities different from those used by us may produce different results. This fact could explain why Lednor & Walcott (1983) obtained very little or no disorientation when they released homing pigeons with coils which produced a varying magnetic field during flight under sun. This field had parameters very different from ours; its intensity, in fact, was weaker and its frequency was variable or very low. Wiltschko (1978) was the first to use alternating

magnetic fields in the study of bird orientation, but his aim was not to produce magnetic disturbances but to test his hypothesis about the magnetic compass of migratory birds.

The results reported here reflect a preliminary approach to the problem, and further experiments are in progress to try to determine those limits within which magnetic stimuli affect the initial orientation of homing pigeons.

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