

SUN-COMPASS ORIENTATION IN HOMING PIGEONS: COMPENSATION FOR DIFFERENT RATES OF CHANGE IN AZIMUTH?

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Accepted 3 November 1999; published on WWW 10 February 2000

Summary

Birds using their sun compass must compensate for the apparent movement of the sun with the help of their internal clock. The movement of the sun is not uniform, being much faster around noon than near sunrise and sunset. If the sun-compass mechanisms are not adjusted to these variations, considerable errors might arise. To learn whether birds are able to take the different rates of sun azimuth change into account, we subjected homing pigeons to a 4 h fast clock-shift. The experiments were performed near Auckland, New Zealand, at a latitude of 37°S, where the expected deflections for a 4 h shift in summer vary from less than 40° to more than 120°, depending on time of day. One group of birds was released just after sunrise or during the corresponding period in the afternoon when the

expected deflections were minimal, the other group during late morning when they were maximal. The different sizes of the observed deflections – between 26° and 51° in the first group, and between 107° and 153° in the second group – clearly show that the birds' compensation mechanisms are closely tuned to the varying rates of change in sun azimuth. The results suggest that pigeons have a rather precise internal representation of the sun curve, which makes the avian sun compass a highly accurate mechanism of direction finding.

Key words: sun compass, internal clock, clock-shifting, sun azimuth, homing, pigeon, *Columba livia* f. *domestica*.

Introduction

When animals use the sun for compass orientation, they must compensate for the apparent movement of the sun with the help of their internal clock. The details of this compensation are not well known. When the sun compass was discovered nearly 50 years ago by Kramer (1950) and von Frisch (1950), it was widely studied, but its accuracy received relatively little attention. Authors traditionally considered an average rate of change in sun azimuth of 15° h⁻¹, expecting a 90° deflection for the standard 6 h clock-shift (e.g. Hoffmann, 1954; Schmidt-Koenig, 1958, 1961; Ferguson et al., 1967; Pardi and Ercolini, 1986; W. Wiltschko and Balda, 1989; and many others). The sun, however, does not follow such a simple rule. The relationship between the sun azimuth, i.e. the direction of the sun over the horizon, and the time of day is far from linear: after sunrise and before sunset, the sun's altitude changes rapidly but the azimuth changes slowly; around noon, the altitude changes slowly but the azimuth changes rapidly. The specific rate of change in sun azimuth depends both on geographic latitude and on season. Especially at lower latitudes, the difference in the rate of change between sunrise/sunset and noon becomes so large that it would seem necessary for any animal to adapt its compensation mechanisms to the varying rates in order to obtain directional information of sufficient accuracy.

Experiments with social Hymenoptera offer some evidence about compensation in insects (e.g. New and New, 1962; Beier and Lindauer, 1970; Gould, 1980; Wehner and Lafranconi, 1981; Wehner and Müller, 1993; Dyer and Dickinson, 1994). In birds, however, the compensation issue has not been addressed previously in studies of the use of the sun compass. The main reasons are that most research has been done at the mid-latitudes of the northern hemisphere by subjecting homing pigeons to a 6 h shift of their internal clock (e.g. Schmidt-Koenig, 1958, 1961, 1972; Graue, 1963; W. Wiltschko et al., 1976, 1984; R. Wiltschko and Wiltschko, 1981; Füller et al., 1983; Neuss and Wallraff, 1988; R. Wiltschko et al., 1994). At these latitudes, the variations in hourly changes of sun azimuth are relatively small; even at summer solstice, the fastest change in azimuth does not exceed 30° h⁻¹. With clock-shifts of 6 h, the difference between objective and subjective time includes periods with slow and with fast progress of the sun. These 6 h clock-shifts, in combination with the scatter normally observed in orientation experiments with pigeons, tend to mask any effect of variations in the hourly changes in sun azimuth. In the tropics, in contrast, the situation is extreme, with the sun crossing the zenith, thus changing azimuth by 180° within minutes. Experimental data seem to indicate that pigeons may

have major problems with their sun compass under these conditions (Schmidt-Koenig et al., 1991).

Recent experiments at Auckland, New Zealand, showed that the sun compass of homing pigeons, a northern hemisphere species, works just as well in the southern hemisphere, even though the sun follows a counterclockwise rather than a clockwise course (R. Wiltschko et al., 1998). Since Auckland, situated at 37°S, has hourly changes in sun azimuth that deviate greatly from the mean rate of 15° h⁻¹, reaching 55° h⁻¹ around noon at summer solstice, this offered a good opportunity to address the question of the accuracy of sun-compass orientation. Here, we report results of 4 h clock-shift experiments with pigeons released at different times of the day.

Materials and methods

The experiments were performed at Auckland, New Zealand, in January when differences in the rate of change in sun azimuth are close to maximal.

The test birds (*Columbia livia* L.) were from a local pigeon breeder's loft near Kumeu (36°48'S, 174°33'E), approximately 25 km northwest of Auckland. The adult pigeons were mostly in their second and third year of life, with single individuals up to 7 years old. The majority of these birds had recently participated in pigeon races over distances of several hundred kilometres and were thus 'directionally trained' to the south.

They were tested at two sites between 30 and 40 km from their loft (see Table 1). The young birds were approximately 6 months old at the time of release; their experience consisted of spontaneous flights at their loft plus two or three flock tosses from up to 20 km from the loft. They were tested at two sites 20–25 km from home (see Table 1). A few of the adult birds were familiar with the Wilson Road site from a homing flight the year before; all other birds were unfamiliar with the release sites.

Clock-shifting took place at the Biology Building of the University of Auckland and followed standard procedures (see Schmidt-Koenig, 1958, 1961): the experimental birds were kept for at least 5 days in a light-tight room and subjected to a photoperiod that began 4 h before sunrise and ended 4 h before sunset (4 h fast shift). The controls were kept during this time in a room that was otherwise identical apart from a large translucent window in the roof that exposed the birds to the natural photoperiod. Each pigeon was subjected to the clock-shifting procedure only once; it may have served as a control in another release.

For the critical tests on sunny days, the experimental birds were pseudo-randomly assigned to two groups that were released in two time windows. (1) ES birds were released during the hour beginning at sunrise (Fig. 1, time window 1a) and during the last hour of the experimental birds' subjective day beginning 5 h and ending 4 h before sunset (Fig. 1, time window 1b). During these intervals, the

Table 1. Results of 4 h clock-shift experiments with homing pigeons near Auckland, New Zealand (37°S)

Test site Date	Age	Treatment	N (n _b)	Mean vector		Difference to		Vanishing interval (min:s)	Home dr (lt)	Homing speed (km h ⁻¹)
				α (degrees)	r	C (degrees)	ES (degrees)			
Howick 290°, 37.5 km 16.1.98	Ad	C	11 (10)	282	0.95***			2:56	11	38.8
		ES	10	333	0.75**	+51**		3:47	8 (1)	45.0
		EL	10	37	0.96***	+115***	+64***	2:59	9 (1)	12.2*
Wilson Road 142°, 32.2 km 26.1.98	Ad	C	14 (12)	147	0.87***			3:09	14	47.1
		ES	14 (11)	173	0.93***	+26***		4:05*	10 (3)	22.5*
		EL	13 (10)	300	0.93***	+153***	+127***	2:34	3 (10)	Day 2**
Kaukapakapa 175°, 23.1 km 21/22.1.98	Yg	C	16 (11)	210	0.81***			3:52	13 (1)	11.8
		ES	11 (10)	252	0.79***	+42*		4:02	5 (6)	Day 2**
		EL	14 (12)	351	0.69**	+141***	+99***	2:32	1 (11)	Day 2***
East Coast Highway 219°, 20.4 km 30/31.1.98	Yg	C	12	194	0.94***			3:09	12	24.5
		ES	10	245	0.97***	+51***		3:01	9	21.9
		EL	14 (11)	301	0.92***	+107***	+56***	3:52	12	9.1*

Under the name of the test site, the direction and distance to home are given.

Age refers to the age of the test birds: Ad, Adults; Yg, young.

C, untreated controls; ES, 4 h fast clock-shifted experimental birds released when the expected deflection was small; EL, 4 h fast clock-shifted experimental birds released when the expected deflection was large.

N (n_b), number of pigeons released and, in parentheses, number of bearings if not identical.

Home dr (lt), number of pigeons that homed on the day of release and, in parentheses, later.

Asterisks next to the vector length r indicate significance (Rayleigh test); asterisks next to difference values indicate significant differences from control or to ES birds as indicated, and asterisks next to vanishing intervals and homing speeds indicate significant differences from controls.

*P<0.05; **P<0.01; ***P<0.001.

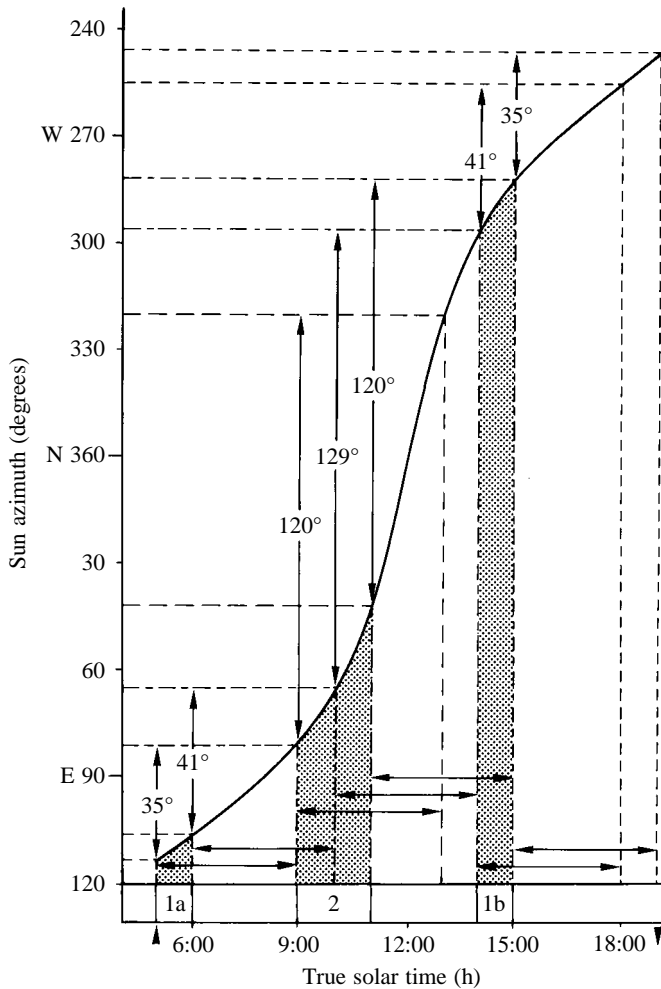


Fig. 1. Sun curve at Auckland, New Zealand (37°S), on 25 January, demonstrating the various deflections expected for a 4h fast clock-shift. The abscissa gives time in true solar time; the shaded areas represent the time windows 1a, 1b and 2 in which the experimental birds were released. Horizontal bars mark the 4h between the true time of day and the experimental birds' subjective time for the beginning and end of each time window. The ordinate gives sun azimuth (sunrise at 114° , sunset at 246°), with the vertical bars indicating the expected deflection for the beginning and end of each time window and the maximum deflection in the middle of time window 2.

difference in sun azimuth between the true time of the day and the subjective time of the birds is smallest. (2) EL birds were released during a 2h period beginning 3h before local noon. During this time, the respective differences in sun azimuth are largest (Fig. 1, time window 2). The untreated control birds were released before time window 2 of the EL birds, after the EL birds and/or before and after ES birds when these were released in time window 1b in the afternoon.

The birds were set free individually and followed by one or two observers using 10×40 binoculars (Zeiss Dialyt) until they disappeared from sight. Their vanishing bearings were measured with a compass to the nearest 5° , and the vanishing

intervals were measured with a stop watch. An observer at the loft recorded returning birds.

From the vanishing bearings of each group, a mean vector was calculated and tested using the Rayleigh test for directional preference. The Watson-Williams test was used to compare the data for the two experimental groups with those of the controls (Batschelet, 1981). The deflections expected as a result of the 4h clock-shift were calculated on the basis of the difference in sun azimuth between the true time of release and the experimental birds' subjective time (Fig. 1; for details, see R. Wiltschko et al., 1994). To determine whether the experimental birds' behaviour coincided with these expectations, the confidence interval was calculated. For vanishing intervals and homing speed, medians were calculated, and the data for the experimental groups and the control birds were compared using the Mann-Whitney U -test.

Results

Fig. 2 shows the vanishing bearings from the four experiments, and Table 1 presents the numerical data. All groups were significantly oriented. The control birds preferred directions close to the home direction. As expected, both experimental groups showed significant clockwise deflections

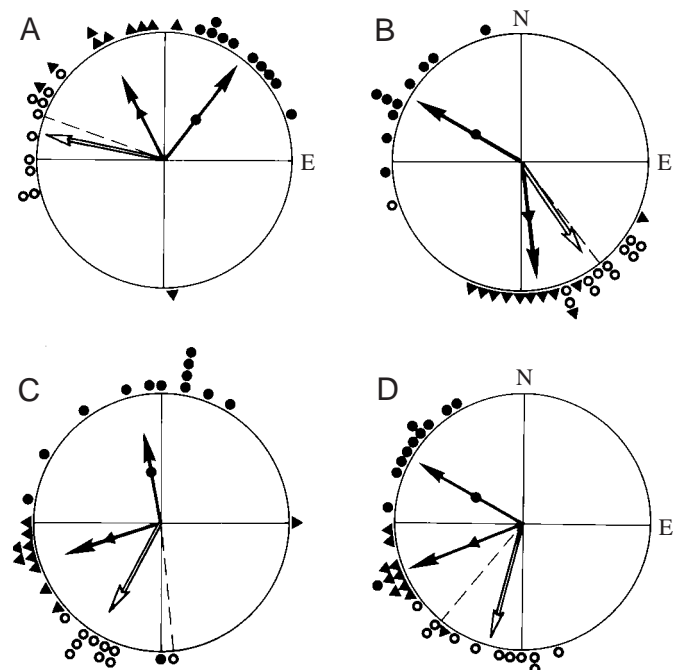


Fig. 2. Vanishing bearings of untreated control birds (open symbols) and 4h clock-shifted pigeons (filled symbols); triangles, ES birds released when the expected deflection was small; circles, EL birds released when the expected deflection was large. (A,B) Releases of adult pigeons at Howick (A) and at Wilson Road (B). (C,D) Releases of young pigeons at Kaukapakapa (C) and at East Coast Highway (D). For numerical data and significant differences between groups, see Table 1. The arrows give the mean bearing and the vector length r of each group; the broken line shows the direction of home.

from the mean of the controls. In our tests, the expected deflections for the 4h clock-shifted experimentals varied between 37° and 40° for the ES birds released in the first time window and between 121° and 123° for the EL birds released in the second time window. The pigeons showed the corresponding behaviour: the ES birds deviated by between 26° and 51° from the mean of the controls, whereas the EL birds deviated by between 107° and 153°. There was no difference between the young and the adult pigeons in this respect. Except in one case, the confidence intervals of the vectors of the experimental birds include the direction resulting from the mean of the controls plus the expected deflection, indicating that the observed deflections are in agreement with expectations; only the EL group in the release at Wilson Road showed a deviation slightly greater than expected ($P < 0.05$, confidence interval). The angular difference between the two 4h clock-shifted groups was significant in all four releases ($P < 0.001$, see Table 1), i.e. the time of day at which the clock-shifted birds were released had a dramatic effect on their bearings.

These differences in initial orientation are borne out by homing performance: the homing speeds of the ES birds were similar to those of the control birds or slightly slower, whereas the EL birds took significantly longer to return (see Table 1), also being slower than the ES birds in all four releases ($P < 0.05$ or $P < 0.01$). These findings indicate that the smaller deflections of the ES birds prolonged homing time only slightly, whereas the larger deflections led the EL birds initially far from home, apparently causing considerable detours before the birds corrected for the error induced by their manipulated sun compass. There was no systematic effect on vanishing intervals.

Discussion

The difference between the two experimental groups, ES and EL, that had received identical treatment clearly shows that the amount of deflection induced by clock-shifting depends on the differences in sun azimuth between the true time of release and the birds' subjective time. This rules out the possibility that pigeons average the sun's progress over the day. Instead, they seem to have a rather precise understanding of the true azimuth of the sun at the various times of day and have tuned their compensation mechanism closely to the varying rates of azimuth change.

Our results have implications for the learning processes establishing the sun compass (W. Wiltschko et al., 1976). Association of sun azimuth with time of day provided by the internal clock and a reference direction provided by the magnetic compass (W. Wiltschko et al., 1983) takes place during a sensitive period when the young pigeons first make spontaneous excursions from their loft, usually during their third month of life (R. Wiltschko and Wiltschko, 1981, 1990). The ability of birds to tune their compensation mechanisms so well to the true changes in sun azimuth suggests that the respective processes of pre-programmed

learning are generating a sun azimuth/time/direction function that reflects the true sun azimuth curve very closely. It suggests that birds record the sun's direction at rather short intervals and store this information together with the information on time in their memory, possibly in a specialized part of the brain, as is often the case when pre-programmed learning is involved. When using their sun compass, the birds then recall this memorized information to interpret the current azimuth of the sun and derive accurate directions. Our adult and young test birds showed identical responses, indicating that the sun compass is fully mature in 6-month-old pigeons.

The accuracy of the compensation mechanisms also implies that these compensation mechanisms are regularly adjusted to the seasonal changes of the sun's arc to maintain this accuracy throughout the year. This interesting question has not yet been studied.

Studies with social Hymenoptera on the accuracy of their compensation mechanisms indicated that desert ants of the genus *Cataglyphis* compensate rather accurately for the varying rates of change in sun azimuth (Wehner and Lafranconi, 1981; Wehner and Müller, 1993). The evidence from honeybees, *Apis mellifera*, is somewhat conflicting: a study by Gould (1980) suggested that bees extrapolate the sun's arc from the last portion they have observed, whereas other studies implied that they compensate for the sun's true movement (New and New, 1962; Beier and Lindauer, 1970; Dyer and Dickinson, 1994). The analysis of the development of the sun compass in ants and bees revealed that it includes substantial innate components because the social insects can derive the sun's course in the morning from one previously observed only in the afternoon and *vice versa* (Lindauer, 1959; Wehner and Müller, 1993; Dyer and Dickinson, 1994). This observation contrasts with the findings from birds, which cannot deduce unknown positions of the sun to the same extent. Birds must observe the sun at various times throughout the day in order to develop a sun compass for the entire day (R. Wiltschko and Wiltschko, 1980; R. Wiltschko et al., 1981). Their sun compass appears to be free of innate components other than a spontaneous tendency to pay attention to the sun (R. Wiltschko et al., 1998).

This difference between birds and social insects may have evolved in accordance with the different life span of the two groups and the availability of alternative compass mechanisms: desert ants and bees, with a foraging life of a few weeks at most, need to acquire a functioning sun compass very quickly. Birds, in contrast, orient their first flights with the help of their magnetic compass (Keeton, 1971). Having this innate compass at their disposal, they can take their time to learn and do not depend on the sun compass in the way that social insects do. Bees may also possess a magnetic compass (DeJong, 1982; Schmitt and Esch, 1993; Frier et al., 1996), yet there are no indications that this mechanism is involved in the orientation of cross-country foraging flights or the dance language, the behaviour patterns in which the sun compass plays its most important roles (Dyer, 1987; Capaldi and Dyer, 1995). In

contrast, learning the sun compass from the start instead of adjusting innate components to the sun's actual arc may be advantageous when dealing with extreme rates of change in sun azimuth, which appear to cause problems for insects, which tend to overestimate the sun's progress when it is slowest and underestimate it when it is fastest (Wehner and Lafranconi, 1981). A completely learned sun compass might enable birds to achieve greater accuracy more easily and it may generally allow more flexibility, which might be helpful when birds adjust their sun compass to the seasonal changes of the sun's arc.

The previously unsuspected fine tuning of the sun compass of pigeons to variations in the hourly rates of change in sun azimuth permits highly accurate directional readings at all times of day. We suggest that the sun azimuth/time/direction function that the birds apparently use to interpret the sun's position will justify further detailed analysis. It is obvious from our present results, however, that the simple rule of thumb often quoted in connection with clock-shift experiments, '15° per hour of shift', is inadequate. Birds know exactly where the sun is at what time of day.

This work was supported by the Deutsche Forschungsgemeinschaft (grant to R.W.), by the Ministry of Research Science and Technology (New Zealand) and the Auckland University Research Committee (grants to M.W). We sincerely thank Jack Longville, Kumeu, for providing the pigeons and for his valuable support, Cordula Haugh for her help with the experiments and Russ Roberts, John Bennett, Tony and Angela Payton, Graham Coghlin and Jaqueline Hamilton for permission to release pigeons from their property. We also gratefully acknowledge the comments of Rüdiger Wehner on an early draft of the manuscript and the suggestions of two anonymous referees.

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