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Commentaries

Does familiarity with the release site reduce the deflection induced by clock-shifting?

A comment to the paper by Gagliardo et al. (2005)

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When homing pigeons are subjected to a shift of their internal clock, their vanishing bearings are deflected with respect to untreated controls, indicating the use of the sun compass. However, the induced deflection is often smaller than the difference in sun azimuth between the birds' subjective time and the real time of day (e.g. Schmidt-Koenig, 1961). This phenomenon is most pronounced in old, experienced pigeons, which, on average, show only about 50–60% of the expected deflection (Wiltschko et al., 1994; Wiltschko and Wiltschko, 2001). Wallraff et al. (1999), as well as Kamil and Cheng (2001), hypothesized that the reduced deflection was caused by these pigeons' greater experience, in particular their familiarity with local landmarks. Gagliardo et al. (2005) recently published a paper claiming that familiarity with the release site is indeed one of the factors reducing the deflection induced by clock-shifting.

This claim, however, is not justified. An analysis of the response to clock-shifting must be based on the behavior of normal, otherwise untreated pigeons, i.e. the data of the control group C in Series I and the data of Series II (tables 3 and 4 in Gagliardo et al., 2005). Unfortunately, the pigeons familiar and unfamiliar with the release sites were from different groups, with possible differences in pre-experience, and were released in different years. More importantly, however, the pigeons familiar with the release sites were released as clock-shifted birds at all three sites used, whereas the pigeons unfamiliar with the sites were released only once under clock-shifted conditions. This is a serious flaw in test design, making any comparison problematic. The familiar pigeons undertook their second and third flights as clock-shifted birds after they had just experienced that their sun compass provided them with false information and that they had to ignore this false information to return home. This affects the sun compass: repeated releases alter the sun compass readings and eventually lead to a recalibration, as has been convincingly demonstrated in two experimental series transferring pigeons to a 'permanent' clock-shift (Wiltschko et al., 1976, 1984). The test design of Gagliardo et al. (2005), by repeatedly releasing the familiar birds under clock-shifted conditions, thus tends to reduce the deflection of this group.

The authors claim that this is not the case, referring to Foà and Albonetti (1980), who released clock-shifted birds several times and observed larger shifts at two unfamiliar sites. However, deflections induced by clock-shifting always show considerable variation. Foà and Albonetti (1980) failed to do the critical test indicating whether the sun compass was still intact, namely to record the orientation of the formerly clock-shifted birds immediately after their sun compass was set back to normal. This was done in the two studies by Wiltschko et al. (1976, 1984), with a pronounced deflection in the reverse direction indicating a recalibration of the sun compass.

The familiar birds of Gagliardo et al. (2005) indeed showed their largest deviation, 98°, on their first clock-shift release, a deflection that lies clearly within the range of the deflections observed in the unfamiliar birds – 127°, 116° and 68°. The later deflections of the familiar birds, 78° and 31°, are smaller and can no longer be assumed to reflect an intact sun compass.

Yet even so, the claim that familiarity with the release site reduces the deflection is not justified. A statistic based on matched pairs of data cannot be applied on just three releases, and a test such as the *t*-test does not show a significant difference (t=1.334, P>0.05). Hence, although the test design leads to a decrease in deflections of the familiar birds, one might say that, at best, the case is open.

To answer the question requires more data obtained under equal conditions for the familiar and unfamiliar birds. We have just completed a series of six such tests, with birds of equal pre-experience released on the same days at sites that were familiar to some of the birds but unfamiliar to the others, with controls and 6 h fast-shifted birds of both groups. Our data clearly contradict the claim of Gagliardo et al. (2005): the deflections vary considerably, but those of the familiar birds range from 39° to 169° (median, 81°) and those of the birds unfamiliar with the site range from 27° to 124° (median, 68°) (Wiltschko et al., 2005). That is, the size of the deflection induced by clock-shifting is not affected by familiarity with the release site.

To answer the question of what factor reduces the clock-shift-induced deflection, we may point out that clock-shifted pigeons show the expected deviation when their magnetic compass is temporarily disrupted by magnets (Wiltschko and Wiltschko, 2001): old pigeons seem to fly a compromise between the directions indicated by their sun compass and their magnetic compass.

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Response to 'Does familiarity with the release site reduce the deflection induced by clock-shifting?'

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The central issue of the paper by Gagliardo et al. (2005) is that three factors are relevant in reducing the expected deflection in the initial orientation of clock-shifted pigeons: (1) familiarity with the release site; (2) anosmia and (3) the release site features. However, in their comments to our paper, Wiltschko et al. (2005a) did not consider either anosmia or the site effects and disputed that familiarity can affect the size of the deflection, so determining a correction of the initial orientation towards the home direction.

In their comments, they state that the size of the deflection is smaller in aged and experienced birds. It is worth noting that the more homing experience a pigeon acquires, the higher the level of familiarity with a geographical area surrounding the release sites and that very often older birds turn out to be more experienced in terms of homing flights. In the protocol adopted in the cited experiments (Wiltschko and Wiltschko, 2001; Wiltschko et al., 1994), familiarity with the release site area, age and homing experience was interdependent or uncontrolled, making it impossible to unravel the role of each factor. To the best of our knowledge, no evidence demonstrating that the age *per se* reduces the deflection after clock-shift has been reported. Also, the protocol adopted by Wiltscko et al. (2005b) does not help in clarifying the debated question. All the pigeons used in this experiment were very familiar with an area extending 40 km from home in the cardinal compass direction, and the 'unfamiliar locations' chosen as test sites were either within or 2–15 km outside of this area. Therefore, the authors ended up comparing the behaviour of pigeons surely familiar with the release site with the behaviour of pigeons probably familiar with the release site. Not surprisingly, both groups behaved in the same way.

The main criticism regarding our paper raised by Wiltschko et al. (2005a) concerns the possibility that the observed reduction in the size of the deflection is due to a recalibration of the sun compass mechanism in permanently clock-shifted birds (Wiltschko et al., 1984). We do not agree with this criticism for the following reasons. (1) The results reported in Gagliardo et al. (2005) are not consistent with the recalibration hypothesis. In fact, the size of the deflection does not decrease progressively from the first to the third release (Series I, birds familiar with the release site). Actually, the deviations of the control shifted pigeons at familiar sites with respect to their orientation in the unshifted condition were as follows: first release, 98°; second release, 31°; third release 75°. However, by also comparing only the first release of Series I (Arnaccio), in which the sun compass recalibration can surely be excluded, with the corresponding test of Series II (birds unfamiliar with the sites), a clear difference in the size of deflection emerged, most likely attributable to the familiarity factor: when the birds were familiar with the release site, the observed deflection was 92.4% of the expected size; when the birds were unfamiliar with the site the observed deflection was 126% of the expected size. (2) Foà and Albonetti (1980) provided convincing evidence against the recalibration hypothesis, showing that the size of the deflection in permanently clock-shifted birds diminished progressively in the subsequent tests at the familiar site, but it increased again at the unfamiliar location. (3) A critical experiment to test the recalibration hypothesis would consist of performing subsequent releases of permanently clock-shifted birds from several unfamiliar locations. So far, such a test has never been done and no convincing evidence of recalibration of the sun compass is available. In fact, the data reported in Wiltschko et al. (1984) can be interpreted differently than in terms of a recalibration of the sun compass, even supposing that their pigeons used a site-specific compass orientation (site recognition and compass orientation): permanently phase-shifted birds, released many times within a familiar area, might update the association between the familiar site and the home direction according to the route experienced during the numerous training flights from the same locations. Therefore, according to this view, the association 'release site–compass direction', rather than the association 'time of the day–sun azimuth', is actually recalibrated.

Another criticism raised by Wiltschko et al. (2005a) concerns the comparison between the data Series I (birds familiar with the release sites) and Series II (birds unfamiliar with the release sites). We are aware that an optimal experimental plan would have provided for the test of birds familiar and unfamiliar with the sites in the same day and we stated in our paper that this comparison must be considered with caution. On the other hand, Wiltschko et al. (2005a) based their hypothesis on meta-analysis in which they compared orientation of birds released not only in different years but also from different sites (Wiltschko et al., 1984). In any case, the orientation shown by the pigeons unfamiliar with the release sites reported in Gagliardo et al. (2005) can constitute an indicative baseline, it being an example of the initial orientation of clock-shifted birds unfamiliar with the same sites used in Series I.

Wiltschko et al. (2005a) proposed that older birds deviated less because they tend to rely more on the magnetic compass than the young pigeons do. It is worth noting that Wiltschko and Wiltschko (1980, 1985) have proposed that very young pigeons possess only the magnetic compass and use it for a route-reversal mechanism for homing, learning a sun compass mechanism only later on. To conciliate the two hypotheses, we should acknowledge that very young pigeons exclusively use the magnetic compass and, once adult, rely predominantly on the sun compass. However, when they are older than two years, their attention to magnetic cues increases again. This certainly does not seem to be the simplest explanation of the data set on compass orientation in homing pigeons.

Although a role of the magnetic compass information in correcting the initial orientation of the shifted birds is plausible, the hypothesis that a decrease in the size of the deflection after clock-shift occurs is always and solely due to the contemporary use of the sun and the magnetic compass is unrealistic and not based on experimental evidence. The hypothesis of a role of the magnetic compass in reducing the expected deflection explains neither the behaviour of our anosmic pigeons released from familiar sites nor that of the birds released from unfamiliar locations. Why should the use of the magnetic compass be more important for the anosmic pigeons than for the intact birds? Why should our adult pigeons released from unfamiliar locations totally ignore the magnetic compass information?

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