Robins have a magnetic compass in both eyes

ARISING FROM W. Wiltschko *et al.* *Nature* **419,** 467–470 (2002)

The magnetic compass of migratory birds is embedded in the visual system[1–3] and it has been reported by Wiltschko *et al.*[1] that European Robins, *Erithacus rubecula*, cannot show magnetic compass orientation using their left eye only. This has led to the notion that the magnetic compass should be located only in the right eye of birds[1,3–5]. However, a complete right lateralization of the magnetic compass would be very surprising, and functional neuroanatomical data have questioned this notion[2,6–8]. Here we show that the results of Wiltschko *et al.*[1] could not be independently confirmed using double-blind protocols. European Robins can perform magnetic compass orientation with both eyes open, with the left eye open only, and with the right eye open only. No clear lateralization is observed.

More or less pronounced lateralization is a common feature of the avian brain[9], but an all-or-nothing lateralization like the one reported by Wiltschko *et al.* in European Robins[1] and Silvereyes[4], *Zosterops lateralis*, would be highly unusual for any sensory system and seems evolutionarily counterproductive. A bird having a magnetic compass located exclusively in its right eye would be more easily affected by eye infection or monocular damage than a bird having functional magnetic compasses in both eyes.

We therefore tested 27 European Robins during autumn migration, when they use simple compass orientation[10], and equipped them with light tight[8,11] hoods enabling them to see with both eyes, their right eye only, or their left eye only. In all three conditions, the birds oriented in their expected autumn migratory direction towards the South-West in the unchanged geomagnetic field (normal magnetic field, NMF; both eyes open: $236^\circ \pm 20^\circ$ (95% confidence intervals), $r = 0.69$, $N = 27$, $P < 0.001$, Fig. 1a; left eye open: $217^\circ \pm 27^\circ$, $r = 0.57$, $N = 27$, $P = 0.001$, Fig. 1c; right eye open: $192^\circ \pm 24^\circ$, $r = 0.65$, $N = 26$, $P < 0.001$, Fig. 1e) and towards the East in a magnetic field turned 120° counter-clockwise (changed magnetic field, CMF; both eyes open: $78^\circ \pm 20^\circ$, $r = 0.72$, $N = 27$, $P < 0.001$, Fig. 1b; left eye open: $47^\circ \pm 45^\circ$, $r = 0.38$, $N = 26$, $P < 0.03$, Fig. 1d; right eye open: $112^\circ \pm 30^\circ$, $r = 0.52$, $N = 27$, $P = 0.001$, Fig. 1f). In all cases, the CMF direction is significantly (no 95% confidence intervals overlap) turned in the expected direction compared to the NMF direction.

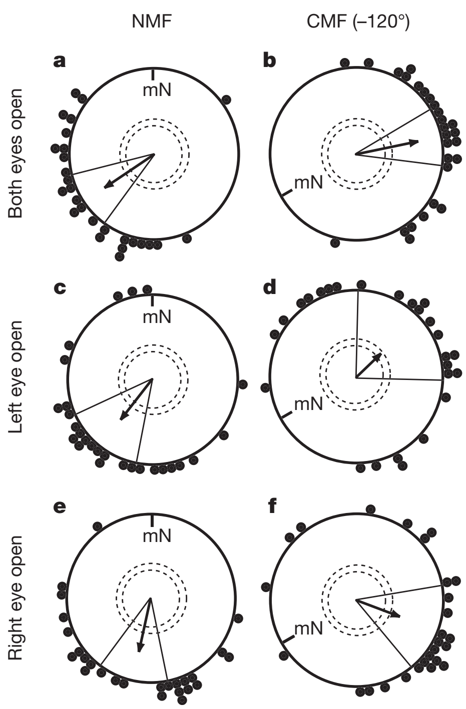

Figure 1 | European Robins wearing eye covers can use their magnetic compass if light and/or visual input reaches any one eye. a–f, Each dot at the circle periphery represents the mean orientation of one individual bird tested several times with the given type of hood. mN, magnetic North. The arrows indicate the group mean vectors. The inner and outer dashed circles indicate the radius of the group mean vector needed for significance according to the Rayleigh Test ($P < 0.05$ and $P < 0.01$, respectively). The lines flanking the group mean vector indicate the 95% confidence intervals for the group mean direction.

Our results showing that European Robins have a magnetic compass in both eyes are in line with other recent findings, which otherwise would be difficult to explain: (1) garden warblers have a magnetic compass in both eyes[11]; (2) the putative magnetoreceptive cryptochromes are located in both eyes[6]; (3) Cluster N[7,8], the brain area recently shown to be necessary for magnetic compass orientation in European Robins[2], shows similar activation in both brain hemispheres during magnetic compass orientation[7,12]. In fact, Cluster N activation in European Robins shows a slight but significant dominance of the left eye and right brain hemisphere[8], that is, lateralization in the opposite direction to that suggested by Wiltschko *et al.*[1,4]; (4) the neuronal pathways between the eye and Cluster N seem to be symmetrical[13]; (5) magnetic compass orientation is only weakly lateralized in pigeons[14,15]. We suggest that the Wiltschko *et al.*[1] data may have been artefacts of the unnatural green light conditions under which their birds were tested or of the non-blinded procedures. Alternatively, they might have resulted from the more complicated interaction of map and compass information potentially occurring in spring.

In conclusion, it is very possible that some smaller degree of lateralization of magnetic information processing exists in birds[8,14,15]. However, our data show that the magnetic compass of night-migratory songbirds is not strongly lateralized and certainly not located in only one of the birds' eyes.

METHODS

We tested the birds' magnetic compass orientation capabilities under broad spectrum white light[2] in the normal geomagnetic field (NMF) and in a changed geomagnetic field with magnetic North turned 120° counter-clockwise (CMF). We used a double-blind protocol and large, three-dimensional, double-wrapped, Merritt 4-coils to produce highly homogenous magnetic fields (for details see ref. 2). The same current ran through the coils in both magnetic field conditions. We tested all birds inside aluminium-lined wooden huts, where no cues other than the geomagnetic field were available. The mean directions are based on 4.11 ± 2.76 (s.d.) active and oriented tests per condition (six conditions).

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Received 29 June 2010; accepted 11 January 2011.

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Competing financial interests: declared none.

doi:10.1038/nature09875

Wiltschko *et al.* reply

REPLYING TO C. M. Hein, S. Engels, D. Kishkinev & H. Mouritsen *Nature* **471,** doi:10.1038/nature09875 (2011)

Hein and colleagues[1] challenge our 2002 paper[2], claiming that they cannot replicate our findings. The paper had two conclusions: (1) magnetic compass information is mediated by the eyes, as had been proposed by Ritz and colleagues[3], and (2) the magnetic compass is lateralized in favour of the right eye. The new data do not contradict the first conclusion; in fact, this has been supported by a recent paper from the authors[4]. It is only the second conclusion they question, although it has been demonstrated not only in two species of migrants[2,5], but also in domestic chickens[6] and is the basis of a new paper indicating an interaction between contour vision and magnetoreception[7].

These obvious differences in findings require explanations, and offhand, three possibilities come to mind:

(1) The authors do not observe migratory orientation, but a 'fixed direction' response. 'Fixed direction' responses do not involve the inclination compass based on the radical pair mechanism, but are polar responses originating in the magnetite-based receptors in the beak[8]; they are not lateralized[9]. The observed scatter is in agreement with this interpretation, as 'fixed directions' are often more scattered than compass responses[8]. Critical tests to distinguish between the two types of responses, like inverting the vertical component of the magnetic field, are missing.

(2) The studies by Hein *et al.*[10] were autumn experiments, where young birds fly innate compass courses[11], whereas ours[2,5,7,8] involved spring experiments, where birds can use true navigation to head back to the familiar breeding regions[12]. There are indications that the navigational 'map' is lateralized in favour of the right eye/left brain system[13], which, in turn, could have led to a lateralized response.

(3) Another difference between the studies is the number of tests per bird. Whereas we tested the birds two[2,5] or three[7,9] times, the authors' means are based "on 4.11 ± 2.76 (s.d.) active and oriented tests per condition", which implies that the individual birds have been tested more often. Hence the total time the birds had their right eye covered was considerably longer than in our studies. In certain tasks acquired unihemispherically, an interhemispheric transfer is observed in animals that have to rely on the naive eye; in some cases, this takes just a few hours[14]. A similar transfer may have occurred when the right eye was covered for a longer period. The observation that the vectors of the birds with the right eye covered are the shortest in both magnetic conditions is in agreement with this interpretation. This could also explain the weaker lateralization observed in pigeons[15], where the total time of covering the right eye was also much longer. It would mean that although the avian magnetic compass is normally mediated by the right eye only, left-eye input is able to substitute the process after a critical amount of time.

In summary, there are considerable differences between the studies. Which of them or which possible combination of them caused the difference in findings cannot be decided at present, but will be determined by future experiments.

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Received 16 July 2010; accepted 11 January 2011.

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Competing financial interests: declared none.

doi:10.1038/nature09876