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Authors: Čapek, František, Průcha, Jaroslav, Socha, Vladimír, Hart, Vlastimil, and Burda, Hynek

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Directional orientation of pheasant chicks at the drinking dish and its potential for research on avian magnetoreception

František ČAPEK[1], Jaroslav PRŮCHA[2], Vladimír SOCHA[2], Vlastimil HART[1] and Hynek BURDA[1,3]*

[1] *Department of Game Management and Wildlife Biology, Faculty of Forestry and Wood Sciences, Czech University of Life Sciences, 165 21 Praha 6, Czech Republic; e-mail: hynek.burda@uni-due.de*
[2] *Faculty of Biomedical Engineering, Czech Technical University in Prague, 166 36 Praha 6, Czech Republic*
[3] *Department of General Zoology, Faculty of Biology, University Duisburg-Essen, 451 17 Essen, Germany*

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Abstract. Magnetoreception has been widely studied in birds mainly through the paradigm of homing or seasonally appropriate migratory direction. It was found that in total darkness or under selected light regimes (differing in colour and/or intensities), migratory birds display orientation towards certain "fixed" directions which do not correspond to the migratory or homing direction. This "fixed orientation" might correspond to the so-called magnetic alignment recorded in animals of different non-avian taxa. Here we demonstrate that also "common", non-migratory birds, pheasants, adopt a preferred position and body orientation when drinking at a circular dish. We recorded these parameters by means of camera traps in a pheasantry under control conditions and under experimental exposure to bright blue light. We identified three types of orientation at the edge of drinking dish: standing radially or tangentially with left or right eye to the dish. The position of tangentially drinking chicks was significantly non-random. While the position of radially drinking chicks was random under control conditions, it became significantly non-random, concentrated at about the north and south pole of the dish, under bright blue light. Our results show that this alignment has some similarities with the "fixed orientation". We suggest that the preference towards a "fixed" direction serves to calibration, organization and reading of the mental (cognitive) map of the space and as a direction indicator. We discuss heuristic potential of the presented research (experimental and evaluation) design for further study on magnetoreception.

Key words: pheasants, magnetic alignment, fixed orientation, spatial orientation, mental map

Introduction

Magnetoreception, the ability to sense the Earth's magnetic field, has been most intensively and in depth studied in birds, notably in migratory birds and homing pigeons (for recent reviews see e.g. Mouritsen 2014, Kishkinev & Chernetsov 2015, Wiltschko & Wiltschko 2015). The established research paradigm is observation of vanishing directions after release in the field, tracking of flight routes using telemetry, or observation of preferred escape direction in the Emlen's funnel. The studies of magnetoreception using other bird species in other behavioural contexts but migration or homing are still rare. Such studies involve e.g. conditioning on magnetic cues in domestic chicken (Denzau et al. 2011), domestic ducks (Freire et al. 2012), domestic pigeons (Bookman 1977, Mora et al. 2014, Mora & Bingman 2014), or zebra finches (Voss et al. 2007, Muheim et al. 2016). Generally, however, there is consensus that conditioning of birds to magnetic stimuli is an extremely challenging task (Wiltschko & Wiltschko 1996, 2007, Kishkinev et al. 2012).

Another observational and experimental approach to the research of biomagnetism is the study of magnetic alignment, a spontaneous tendency of animals to align their body in a predictable respect to the magnetic field lines (reviewed in e.g. Wiltschko & Wiltschko 1995, Begall et al. 2013). Contrary to the studies of magnetic alignment in some invertebrates (reviewed in Vácha 2015), fish (e.g. Hart et al. 2012), "reptiles" (Landler et al. 2015, Diego-Rasilla et al. 2017), and mammals (Begall et al. 2008, 2011, Burda et al. 2009, Červený et al. 2011, 2017, Hart et al. 2013a, b, Slabý et al. 2013, Obleser et al. 2016), this paradigm has been rarely employed in birds. We reported magnetic alignment-like responses in water birds landing on water surface (Hart et al. 2013), in resting flamingos (Nováková et al. 2017), and in foraging corvids

* *Corresponding Author*

(Pleskač et al. 2017) and we suggested that magnetic alignment plays a role as "direction (heading) indicator" in navigational mapping.

We suggest that the so-called orientation towards "fixed" direction, henceforth called "fixed orientation", described in two migratory passerines, the European robin (*Erithacus rubecula*) and the Australian silvereye (*Zosterops lateralis*), in darkness, might represent a behavioural display similar in some aspects to magnetic alignment in other animals. The fixed orientation represents directional response which does not correspond either to homing or to migratory direction. Whereas a westerly directional preference was displayed by birds in darkness or under dim red light (Muheim et al. 2002, Stapput et al. 2008, Wiltschko et al. 2008), fixed orientation in other directions was recorded under exposure to high intensities of full-spectrum and monochromatic lights of various wavelengths, including bi-coloured lights (Wiltschko & Wiltschko 2009). The fixed orientation is characterized by following features – it depends on the ambient magnetic field, it represents a polar response, and thus does not involve the inclination compass, it is not displayed in the context of migratory orientation, it probably involves magnetite-based magnetoreception, yet the fixed orientation is dependent, in a still unclear way, on the specific light regime.

Wiltschko & Wiltschko (2009) already suggested that the fixed orientation might have some similarity to magnetic alignment, yet they also pointed out that fixed orientation does not occur under natural conditions and that it was observed only in the laboratory under light conditions that seem to drive the normal compass mechanism beyond its limits. Furthermore, the authors suggested that possibly, the directional input underlying the "fixed direction" – responses is some kind of phylogenetic relict. With all the respect to the authors, we want to argue that actually no one has thus far studied occurrence of "fixed orientation" under natural conditions and no one has studied it in non-migratory bird species.

Under assumption that birds might display, in certain behavioural contexts, magnetic alignment like other animals (see above), we carried out numerous surveys for existence of magnetic alignment in non-migratory birds. In the present study we address following questions: does the common pheasant, i.e. a common non-migratory, non-passerine game bird species display alignment, i.e. spontaneous preference for a certain compass direction? The ultimate goal of the study we present here was to test whether the displayed alignment represents a magnetic alignment and can thus be employed as a research paradigm to investigate presence and properties of the magnetic sense. Is there any homology or analogy between the "fixed direction-response" and magnetic alignment in birds? Is magnetic alignment responsive to changes in some parameters of the light-regime which were used as diagnostic tools in the studies of magnetic sense in migratory birds?

Material and Methods

The study was conducted in a pheasantry in Hluboká, 49°02′50.8″ N, 14°24′35.3″ E, in six neighbouring, identically constructed aviaries, each of them 6.5 m wide (oriented north-south) × 30 m long (west-east). The western part (in the length of 6.5 m) of the aviary was roofed, the western wall was closed by wooden partition with an entrance door. All other walls and the ceiling of the unroofed part of the aviary were made of wire mesh. The two marginal aviaries at the north and south of the complex were not studied. The six central aviaries were used as five control and one interspaced experimental enclosure. In each aviary there were 200 chicks of the common pheasant (*Phasianus colchicus*). The study was performed for 100 days, from 30.05.2015 until 08.09.2015 (from the age of chicks of two weeks). Total intensity of the Earth's magnetic field at the place and in time of the study was 49 μT, inclination 65° down, declination 3°.

One automatic drinking dish (diameter 37 cm) was placed in the centre of the roofed part in each aviary. Above each drinking dish a camera was fixed, making snapshots of the dish and its surroundings in a radius of about 65 cm from the centre of the dish every five minutes. From photos from each aviary a subsample of 1000 snapshots was selected by a computer random integer set generator. On each snapshot, on average 3-4 chicks were recorded. The chicks were on photos "manually" identified as "drinking", "looking around", and of "undetermined activity". Centre of the dish, occiput (atlas) and the pygostyle (region of the caudal vertebrae) were manually marked on a computer screen of each chick on each photograph. From these marks a custom-made computer program calculated automatically position of the head with respect to the centre of the dish and caudo-cranial medial compass body axis. Furthermore, it was distinguished between chicks standing radially to the dish (the caudo-cranial body axis and the axis between the centre of the dish and occiput of the chick did not diverge for more than +/– 0°-45°, i.e. the divergence angle ranged between 136° and 224°) and tangentially to the dish (both axes diverged in an angle < 45° or

> 45°, i.e. the divergence angle ranged between 90° and 135° or between 225° and 270°). This means that a "perfectly" radially oriented chick was aligned at 180°, a "perfectly" tangentially oriented chick was aligned at 90° (with right eye turned to the dish) or at 270° (with left eye looking on the dish).

We analysed body alignment and position of the chicks at the drinking dish separately for all the three behavioural categories: drinking, looking around, and undefined activity. Since only drinking chicks were non-randomly distributed and non-randomly aligned under control and experimental conditions, we focus here only on this category. Moreover, chicks standing tangentially to the dish when drinking were differently oriented than chicks standing radially to the dish so that it proved to be meaningful to distinguish between both subsamples. For the sake of comparability of different experimental and control conditions and testing the differences between them, random subsamples of the same size (n = 40) of drinking chicks in each situation were generated. Besides that, random subsamples of equal sizes were taken for comparisons between different categories (radially, tangentially with left eye or with right eye turned to the dish) and conditions (control aviaries, experimental conditions). The random subsamples were found to be representative of the respective samples from which they originated.

In one experimental (randomly selected) aviary, a discharge tube was hung 1.5 m above the drinking dish, producing intensive blue light, 6 × LED 450 nm + 6 × LED 470 nm, with a quantal flux of 2.361×10^{19} quanta $s^{-1}m^{-2}$ (i.e. 39.2 µE $s^{-1}m^{-2}$). A circle with a diameter of about 1.1 m under the lamp was homogenously

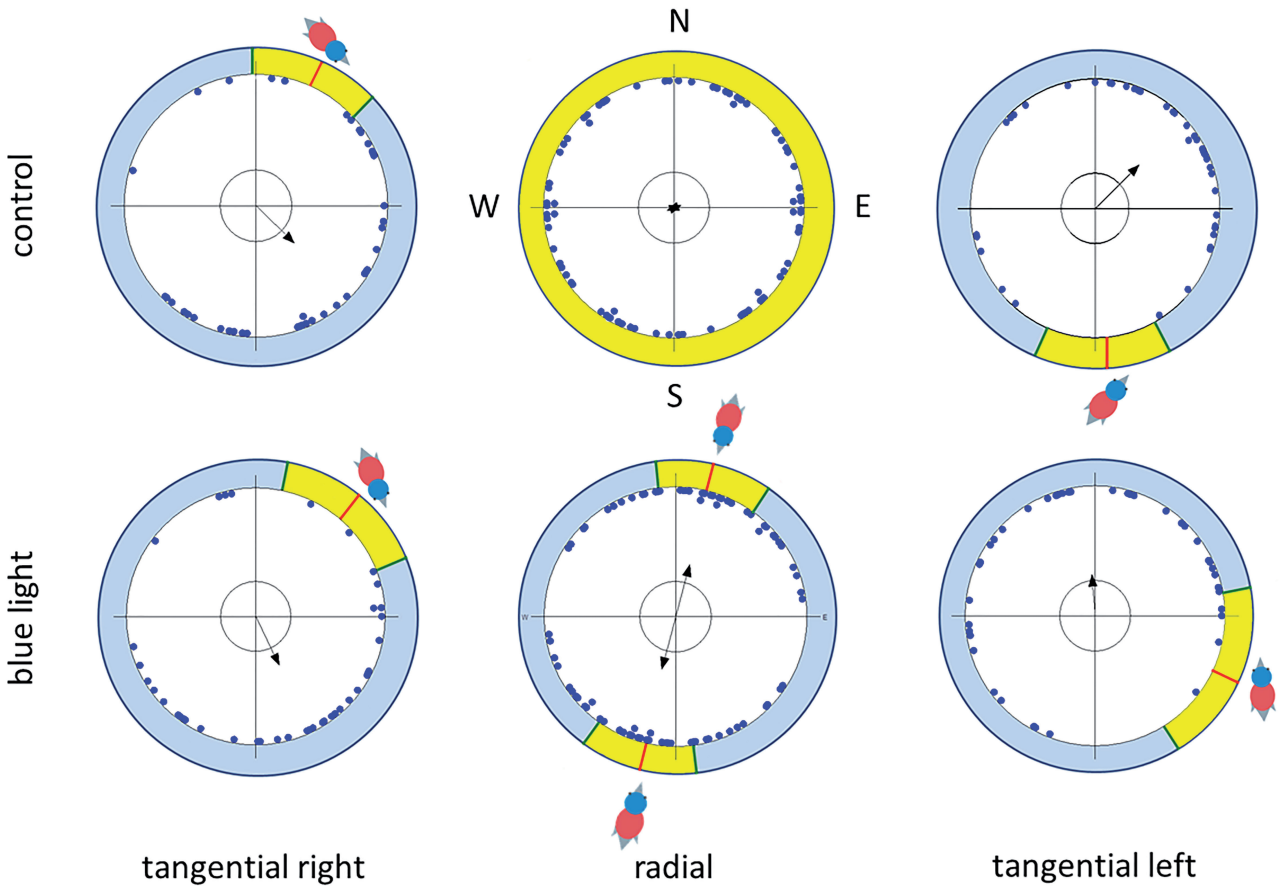

Fig. 1. Preferred heading of drinking pheasant chicks at the edge of the drinking dish. The samples have size of n = 40 and represent random subsamples created from larger samples. Upper row: control conditions, lower row: exposure to intensive blue light. First (left) column: chicks oriented tangentially with their right eye (right body side) turned to the dish were those with their caudo-cranial body axis being within the range of 90°-135° with respect to the radial (the radial being 180°). Second column: radially oriented chicks had their body axis within the range of 136°-224°. Third column: chicks oriented tangentially with their left eye (left body side) turned to the dish are those with their body axis being within the range of 225°-270° with respect to the radial. Each dot represents a measured angular position of a drinking chick at the edge of the drinking dish in the respective subsample. The arrow (in tangentially oriented chicks) and the double-headed arrow (in radially oriented chicks) indicate the mean angular or axial vector (µ), respectively. The length of the mean vector (r) provides a measure of the degree of clustering in the distribution of measured positions. The inner circle marks the 0.05 level of significance border of the Rayleigh test. The yellow segment coloured segment in the outer ring marks the 95 % confidence interval for the mean vector (marked by the red line) of the preferred position of chicks at the dish. Cf. Table 1-2 for statistics.

Table 1. Statistical analysis of the compass position of drinking chicks at the edge of the drinking dish. In the upper part of the table values for whole samples, in the lower part values for random subsamples of respective categories are given. Watson's U^2 test is performed pairwise with reference to the control. Chicks oriented tangentially with their right eye (right body side) turned to the dish were those with their caudo-cranial body axis being within the range of 90°-135° with respect to the radial (the radial being 180°). Radially oriented chicks had their body axis within the range of 136°-224°. Chicks oriented tangentially with their left eye (left body side) turned to the dish are those with their body axis being within the range of 225°-270° with respect to the radial. Unreliable values (because of low concentration, i.e. uniform, random distribution) are not given.

Position of drinking chicks	Tangential right		Radial		Tangential left		Radial	
	Angular		Angular		Angular		Axial	
	Control	Blue light	Control	Blue light	Control	Blue light	Control	Blue light
Sample size (n)	143	41	808	538	120	43	808	538
Mean vector (μ)	14°	41°	99°	54°	170°	113°	115°/295°	5°/185°
Length of mean vector (r)	0.514	0.431	0.133	0.010	0.597	0.344	0.065	0.107
Circular standard deviation	66°	61°	115°	174°	65°	84°	67°	61°
95 % Confidence interval (–/+) for μ	2°-26°	12°-69°	78°-120°	-	157°-183°	79°-148°	94°-137°	349°-21°
Rayleigh test (p)	$< 1 \times 10^{-12}$	3.69×10^{-4}	5.72×10^{-7}	0.951	$< 1 \times 10^{-12}$	0.006	0.032	0.002
Random subsample size (n)	40	40	40	40	40	40	40	40
Mean vector (μ)	23°	40°	66°	96°	177°	112°	74°	14°
Length of mean vector (r)	0.485	0.418	0.201	0.129	0.459	0.346	0.116	0.294
Circular standard deviation	69°	76°	103°	116°	71°	83°	59°	45°
95 % Confidence interval (–/+) for μ	359°-47°	11°-68°	-	-	151°-203°	77°-147°	-	353°-35°
Rayleigh test (p)	4.92×10^{-5}	7.33×10^{-4}	0.198	0.517	1.48×10^{-4}	0.008	0.587	0.03
Watson's U^2 test (p)	-	> 0.5	-	$0.5 > p > 0.2$	-	$0.1 > p > 0.05$	-	< 0.05

Table 2. Statistical analysis of the heading (caudo-cranial body alignment) of drinking chicks. In the upper part of the table values for whole samples, in the lower part values for random subsamples of respective categories are given. Watson's U^2 test is performed pairwise with reference to the control. Chicks oriented tangentially with their right eye (right body side) turned to the dish were those with their caudo-cranial body axis being within the range of 90°-135° with respect to the radial (the radial being 180°). Radially oriented chicks had their body axis within the range of 136°-224°. Chicks oriented tangentially with their left eye (left body side) turned to the dish are those with their body axis being within the range of 225°-270° with respect to the radial. Unreliable values (because of low concentration, i.e. uniform, random distribution) are not given.

Heading of drinking chicks	Tangential right		Radial		Tangential left		Radial	
	Angular		Angular		Angular		Axial	
	Control	Blue light	Control	Blue light	Control	Blue light	Control	Blue light
Sample size (n)	143	41	808	538	120	43	808	538
Mean vector (μ)	125°	156°	269°	96°	53°	358°	112°/292°	174°/354°
Length of mean vector (r)	0.483	0.431	0.051	0.024	0.498	0.315	0.068	0.145
Circular standard deviation	69°	61°	140°	156°	67°	66°	66°	56°
95 % Confidence interval (–/+) for μ	113°-138°	127°-185°	-	-	39°-66°	320°-36°	91°-132°	162°-186°
Rayleigh test (p)	$< 1 \times 10^{-12}$	3.74×10^{-4}	0.126	0.728	$< 1 \times 10^{-12}$	0.015	0.024	1.14×10^{-5}
Random subsample size (n)	40	40	40	40	40	40	40	40
Mean vector (μ)	134°	154°	220°	309°	46°	357°	71°	15°
Length of mean vector (r)	0.405	0.421	0.227	0.036	0.468	0.320	0.057	0.416
Circular standard deviation	77°	75°	99°	148°	69°	86°	69°	38°
95 % Confidence interval (–/+) for μ	105°-164°	126°-183°	-	-	22°-70°	317°-34°	-	29°-356°
Rayleigh test (p)	0.001	6.61×10^{-4}	0.127	0.950	4.82×10^{-5}	0.016	0.88	7.71×10^{-4}
Watson's U^2 test (p)	-	> 0.5	-	$0.5 > p > 0.2$	-	$0.2 > p > 0.1$	-	< 0.05

illuminated. It should be acknowledged that resulting illumination was not purely monochromatic as it was partly "polluted" by ambient natural light.

Circular statistics were carried out with Oriana 4.02 (Kovach Computing Services, Pentraeth, Wales, U.K.). For body alignment and position of chicks at the edge of the drinking dish we calculated a mean vector for each control aviary and each experimental situation. First-order (Rayleigh and Rao test) statistics were employed to test the headings for significant deviations from random distribution. Differences between mean headings and distributions between groups were tested for significance by means of the Watson U^2 test.

Results

All the pheasant chicks we observed in aviaries of the pheasantry Hluboká were habituated on presence of humans, even if attempts were made to interact with the chicks as little as possible and water and food were provided automatically ad libitum. The chicks did not show any alert and escape reactions if a human appeared in the (neighbouring) aviary. A drinking chick may spend several seconds or minutes in the vicinity of the drinking dish, though each drinking act lasts just a few seconds. Since water was available all the time, there were usually only 1-3 chicks drinking at the same time. About 25 % of all the chicks photographed in each aviary were categorized as drinking. Under all the conditions, the majority (about 80 %) of drinking chicks were drinking in a radial, the minority (about 20 %) in a tangential orientation with respect to the drinking dish. Of the tangentially oriented chicks about one half was drinking with their left side (called "left-sided" chicks here), the other half with their right side of the body being turned to the dish ("right-sided" chicks). Under all the tested conditions, the "right-sided" chicks preferred the north-eastern sector of the dish and headed preferentially about south-eastwards. The "left-sided" chicks gathered preferentially in the south-eastern sector and headed mainly north-eastwards (Fig. 1). The radially oriented drinking chicks used to be more randomly distributed around the drinking dish and under the control conditions there was no significantly preferred position. This distributional pattern differed in detail between control and the blue light exposure conditions.

Control conditions

Drinking chicks (n = 1071) concentrated mainly at the eastern semicircle of the dish and were heading southwards or south-westwards respectively. Of most of the chicks, 75 %, were drinking in a radial orientation, 11.5 % were "tangential left-sided", 13.5 % were "tangential right-sided". The non-random distribution was highly significant for "tangential" chicks: whereas "right-sided" chicks preferred NNE and headed southwestwards, "left-sided" chicks preferred south of the dish and headed north-eastwards. The distribution was non-random and highly significant (Table 1-2, Fig. 1). The same pattern was observed in all the five control aviaries and the differences between aviaries were not significant (Watson's U^2: $p > 0.5$).

Blue light conditions

Pheasant chicks (n = 622) drinking at the dish illuminated by blue light displayed partly similar, yet significantly different distribution and alignment at the drinking dish than chicks under control conditions. Markedly more chicks (86 %) were radially oriented, only 6 and 7 % were tangentially oriented ("right-sided" and "left-sided", respectively). This difference to the control was highly significant (chi-square 43.861, $p < 0.0001$). Generally, the sector at the edge of the dish where birds were drinking was narrower, the concentration of "radial" birds was less apparent, i.e. the scatter was higher, "tangential" chicks gathered more at the eastern edge of the dish (Table 1-2, Fig. 1). Heading of all the drinking birds showed a significant axial north-south pattern ($\mu = 174°/354°$, $r = 0.126$, $SD = 58°$, Rayleigh $Z = 9.869$, Rayleigh $p = 5.17 \times 10^{-5}$, $n = 622$). The radial chicks under blue light were markedly (and highly significantly) oriented along the roughly NNE-SSW axis (Tables 1-2, Fig. 1).

Discussion

Technical considerations

The pheasantry is located in placid country area with no high voltage power lines, no radio transmitters, and no accumulation of electric and electronic devices in surroundings. The main building is built of bricks and wood. No disturbances of the Earth's magnetic field were measured at the site. We are aware that it would be advantageous to monitor control and experimental situation in an alternate manner in one and the same aviary and with the same birds. This was, however, because of technical and logistic reasons not possible. However, measurements in all the control aviaries provided identical results and there is no reason to assume why the birds in the interspaced experimental aviary should, under control conditions, behave differently. Ambient conditions were semi-natural, not controlled for, but the conditions in all the aviaries

were the same. The ambient effects might thus have contributed to noise and increased scatter of values but since all the measurements were taken in parallel, all the aviaries were subject to the same effects.

Geometry and topographic orientation of aviaries with the drinking dish being placed in the western (roofed) part of the facility, and the open enclosure encompassing the eastern part were putatively decisive for organization of the cognitive map and visual cues (landmarks, light gradient) could therefore be used for topographic orientation. On the other hand, no frightening behaviour leading to escape to and hiding in certain parts of the aviary were observed. Also random overall orientation of most of the chicks under control conditions do not indicate existence of any preferred direction.

Noteworthy, random subsamples were representative of the respective whole samples (cf. vector values for the whole samples and for the subsamples, Table 1-2).

Findings

Under blue light exposure, chicks might still have oriented according to visual landmarks but orientation with respect to light gradient was surely disturbed. Orientation became more axial along the north-south axis. Apparently relatively less chicks drank in the tangential orientation and instead became "radial". The effect is reflected in higher scatter (i.e. rather "disorientation") in tangential "left-sided" chicks. In radial and "right-sided" chicks the exposure results not in disorientation but rather in (clockwise) shifted orientation. The axial alignment in radially oriented chicks is conspicuous and highly significant (Fig. 1, Tables 1-2). Interestingly, a similar response was shown under exposure to intensive blue and green light in migratory birds (Wiltschko & Wiltschko 2009).

It is unclear which factor is biologically (more) significant – whether the position or the alignment. Nevertheless it should be noted that both parameters are interconnected. For example, once a tangential chick changes its heading (alignment) for more than 45° in one direction, it falls into the category of "radial" chicks; once it changes its heading in an opposite direction it will be no more considered as a "drinking" chick. Of interest is, however, the fact that the tangential chicks (both, "left- and right-sided") preferred to drink with their right eye looking about southwards and left eye looking about northwards. This preference was highly significant. One could imagine also the existence of a category of "tangential left-sided" chicks (at the northern edge of the dish) turned with right side northwards and "right-sided" chicks (at the southern edge of the dish) turned with left side southwards. Yet such chicks were significantly underrepresented in our sample. Generally, the question is about the biological significance and relevance of tangential versus radial posture during drinking. Since tangential posture is more seldom, yet its position and heading are highly significant and since its heading in both semicircles of the dish is one-directional, i.e. in the northern semicircle the chicks are "right-sided", in the southern semicircle they are "left-sided", we may speculate that tangential orientation is somehow relevant for compass orientation, e.g. calibrating of the compass, organization of cognitive map, keeping oriented, whereas the category of "radial chicks" includes chicks which are differently motivated – they just came from a given direction to drink. Some of the "radially-oriented" chicks are actually occupying either the "right" position or heading in the "right" direction as the "tangentially-oriented" chicks.

Interpretation and conclusions

Our experimental design (observing and manipulating freely moving birds in large aviaries) and technical possibilities did not allow us to perform classical tests in behavioural magnetobiology research: changing the magnetic field polarity and inclination by means of Helmholtz (or similar) coils. Although we do not exclude orientation according to topographic cues, we show that the pheasants show well-defined highly significant directional and positional preferences. Furthermore, we show that these preferences can be affected by exposure to blue light.

Fixed orientation-responses in different directions were observed also under abnormal light regimes. It is speculated that this type of orientation response depends on magnetite-based mechanism (and not on the radical pair mechanism) combined with a specific light regime. Specifically, under bright blue light, robins changed their seasonally appropriate angular migratory direction to axial north-south preference (Munro et al. 1997, Wiltschko et al. 2007, Wiltschko & Wiltschko 2009).

Although we tend to compare magnetic alignment with the "fixed direction-response", it should be acknowledged that the aforementioned authors considered the latter to be an "artefact observed only in the laboratory under light conditions that seem to drive the normal compass mechanism beyond its limits" (Wiltschko et al. 2007). It should be nevertheless pointed out that "fixed-direction response"/magnetic alignment was, according to our knowledge, not systematically studied (surveyed)

in birds under natural conditions. We suggest that magnetic alignment in birds might (as in mammals) serve the calibration, arranging and reading of the cognitive map of space (Hart et al. 2013a, b). (In analogy: it is easier to rotate the body than to perform a mental rotation of the spatial map – similarly we turn our paper map so that the north points upwards or forwards and we align accordingly.)

Last but not least it should be pointed out that magnetoreception was evidenced also in domestic chicken (Freire et al. 2005, Denzau et al. 2011) and showing it also in the genetically relative pheasant thus indicates that it might be widely distributed also among non-migratory, "common", birds.

We consider our research (experimental and evaluation) design to have heuristic potential and capacity for further development and usage in the studies on biomagnetism. In a simple, non-invasive, objective and blind way, data can be quickly sampled on common, non-protected bird species, also out of the migratory context, and thus seasonally restricted, context. Moreover the ambient magnetic field and light regime surrounding the drinking dish can be manipulated in future experiments. However, also the role of the topographic orientation due to specific geometry of enclosures should be addressed in future studies and the behaviour of drinking birds should be videotaped and analyzed with respect to distinguished behavioural categories of tangentially and radially oriented birds.

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