

# Extremely low-frequency electromagnetic fields disrupt magnetic alignment of ruminants

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**Resting and grazing cattle and deer tend to align their body axes in the geomagnetic North-South direction. The mechanism(s) that underlie this behavior remain unknown. Here, we show that extremely low-frequency magnetic fields (ELFMFs) generated by high-voltage power lines disrupt alignment of the bodies of these animals with the geomagnetic field. Body orientation of cattle and roe deer was random on pastures under or near power lines. Moreover, cattle exposed to various magnetic fields directly beneath or in the vicinity of power lines trending in various magnetic directions exhibited distinct patterns of alignment. The disturbing effect of the ELFMFs on body alignment diminished with the distance from conductors. These findings constitute evidence for magnetic sensation in large mammals as well as evidence of an overt behavioral reaction to weak ELFMFs in vertebrates. The demonstrated reaction to weak ELFMFs implies effects at the cellular and molecular levels.**

cattle | magnetoreception | roe deer | power lines

Diverse animals, including birds, mammals, reptiles, amphibians, fish, crustaceans and insects, use the Earth's magnetic field (EMF) for directional orientation and navigation (1–3). Despite being phylogenetically widespread, magnetic compass orientation has been convincingly demonstrated in only a few species of mammals representing only 2 taxonomic groups: rodents (4–8) and bats (9, 10). Not surprisingly, all these model species are small mammals amenable to experimental manipulation of the ambient magnetic field. Demonstration of magnetic orientation in animals requires well-designed laboratory and/or field experiments combining manipulations of magnetic fields with either spontaneous behavioral reactions (e.g., an innate preference for a certain direction, migration, or homing) or conditioning to magnetic field properties. However, it is technically demanding, if not impossible, to perform such experiments with sufficient numbers of larger mammals. Alternatively, naturally occurring geomagnetic anomalies can be exploited to study the behavior of animals dwelling at these localities. However, this approach has seldom been applied in the study of magnetic orientation of mammals thus far (11).

Recently, we reported that resting and grazing cattle as well as roe deer (*Capreolus capreolus*) and red deer (*Cervus elaphus*) tend to align their body axes in the geomagnetic North-South (N-S) direction (12). Because wind, sunshine, and slope could be excluded as common ubiquitous factors, alignment toward the vector of the magnetic field provides the most likely explanation for the observed behavior. The study thus provided strong but indirect evidence for magnetoreception in ruminants. However, because of the descriptive nature of the original study, alternative explanations (e.g., the sun compass; cf. ref. 13) could not be excluded. We analyzed body orientations of ruminants in localities where the geomagnetic field is disturbed by high-voltage power lines to determine how local variation in magnetic fields may affect the previously described orientation behavior.

Steel pylons deflect the natural geomagnetic field within a radius of up to 30 m (14). Overhead high-voltage power lines

produce an alternating magnetic field (AMF) attributable to the electric current, with a frequency of 50/60 Hz, producing what are known as extremely low-frequency magnetic fields (ELFMFs). Such fields are the strongest (up to about 15  $\mu\text{T}$ /380 kV, 8  $\mu\text{T}$ /220 kV, and 5  $\mu\text{T}$ /110 kV) directly under power lines in the middle of the span between 2 pylons, where the sag of the conductors brings the lines nearest to the ground. Magnetic flux density diminishes with the distance from power lines, such that density reaches the value of 1  $\mu\text{T}$  at about 70 m (380 kV), 45 m (220 kV), and 20 m (110 kV) away from the midline (14–16). According to other measurements, the maximum magnetic field values to which humans and animals are exposed are even lower and increase by about 80% (from 3.4 to 6.2  $\mu\text{T}$  for 380 kV) when changing the position from near the pylon to the flux region (17).

Here, we analyze satellite and aerial images of herds of cattle and field observations of body alignment in grazing roe deer. Assuming that the observed body orientation is attributable to magnetic alignment, we hypothesize that cattle and deer grazing and resting under power lines and near pylons will be disoriented with respect to those outside the influence of local perturbations.

## Results

**ELFMFs Disrupt Alignment.** Cattle and roe deer resting and grazing in open pastures and meadows show very consistent N-S alignment (12). The control cattle recorded in Europe, grazing in localities without overhead high-voltage power lines within a radius of at least 500 m, aligned their bodies significantly along the N-S axis (mean axis = 1.2°/181.2°,  $r = 0.422$ ,  $P < 10^{-8}$ ,  $n = 111$  localities/herds; Fig. 1A). By contrast, cattle grazing under or in the vicinity (<150 m) of high-voltage overhead power lines were randomly distributed (i.e., no preference for orienting their body axes in a certain direction could be revealed) (mean axis = 80.1°/260.1°,  $r = 0.11$ ,  $P = 0.169$ ,  $n = 153$  localities/herds; Fig. 1B).

Similarly, roe deer in locations without overhead high-voltage power lines exhibited roughly N-S alignment (mean axis = 9.1°/189.1°,  $r = 0.83$ ,  $P < 10^{-4}$ ,  $n = 201$  localities/herds; Fig. 1A), whereas those in the vicinity (<50 m) of power lines (mostly in the vicinity of steel pylons) exhibited random body orientation (mean axis = 75.0°/255.0°,  $r = 0.14$ ,  $P = 0.397$ ,  $n = 47$  localities/herds; Fig. 1B).

No alignment with power line direction could be detected when all cattle grazing up to a distance of 150 m from the power lines were taken into account (Fig. 1B). The same was true for roe deer grazing up to 50 m from the power lines (Fig. 1B). The

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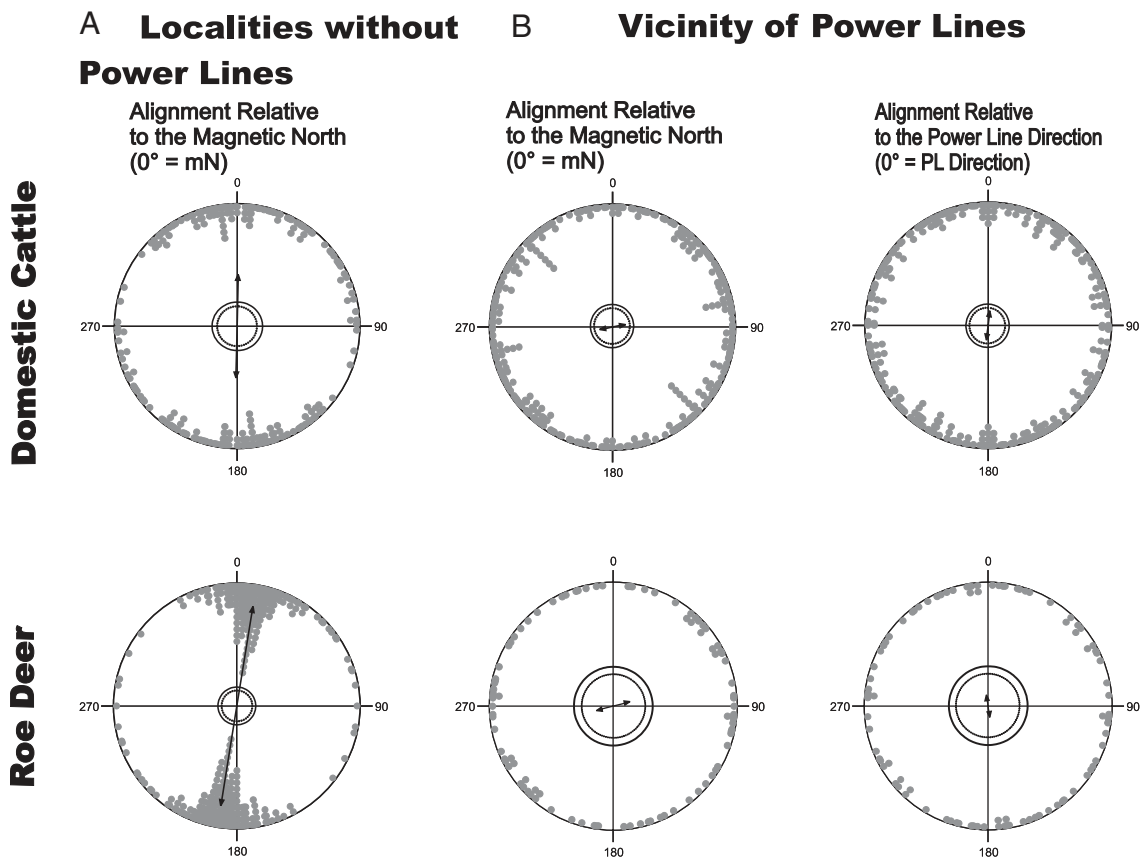
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**Fig. 1.** Axial data revealing body orientation of domestic cattle (*Bos taurus*) (Upper) and roe deer (*Capreolus capreolus*) (Lower). (A, Left) Animals at localities without high-voltage power lines. (B) Animals grazing and resting under or in the vicinity of power lines. (Center) Bearings relative to the geomagnetic N-S axis. (Right) Bearings of body axes relative to power line direction. Each pair of data points (located on opposite sites within the unit circle) represents the direction of the mean axial vector of the herd. The double arrows indicate the length ( $r$ ) and direction of the grand mean axial vectors. The inner circles mark the 5% (dotted) and 1% significance borders of the Rayleigh test. (Copyright 2008, National Academy of Sciences.)

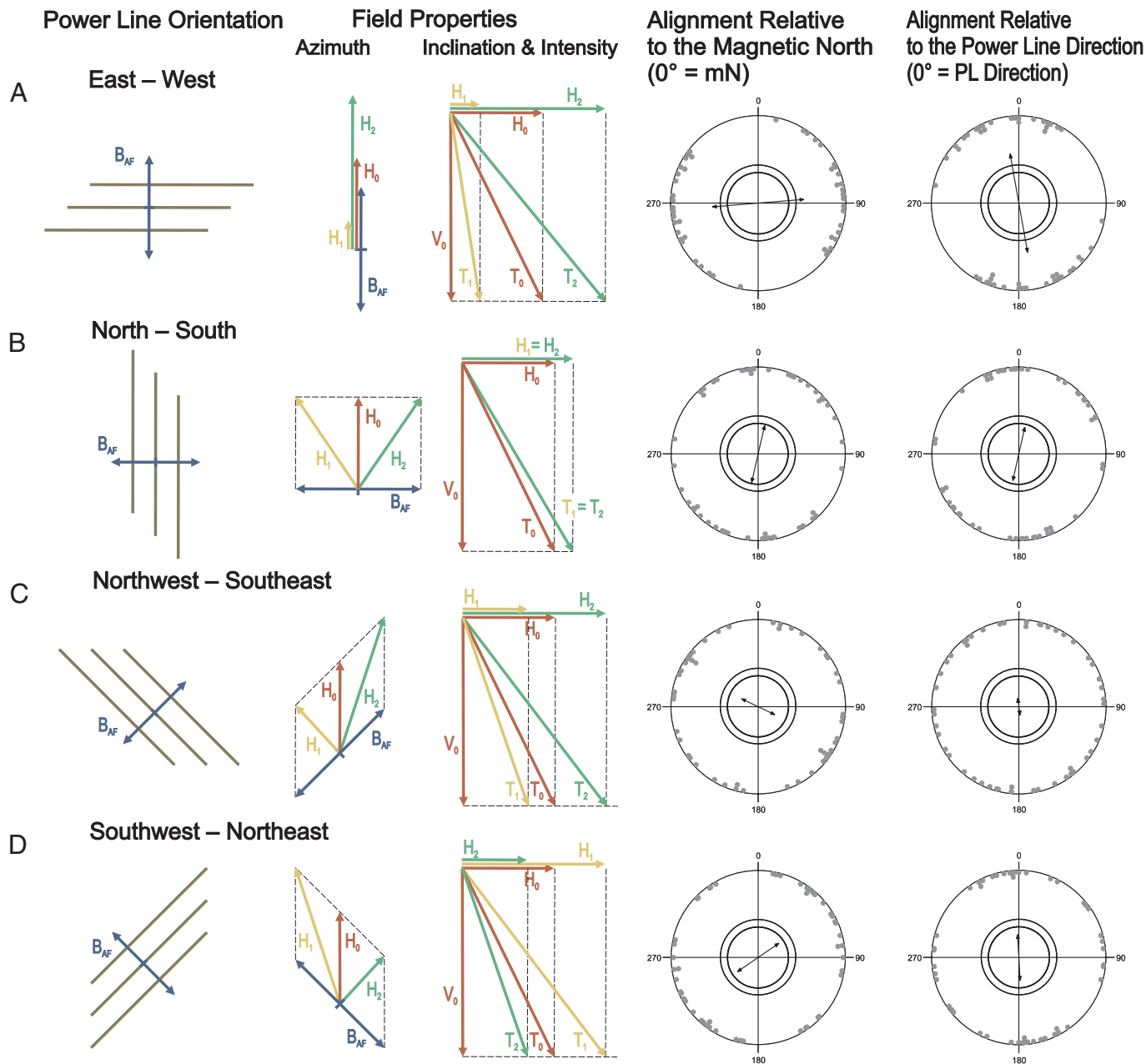
animals' body orientation was random when plotted with respect to the power line direction (cattle: mean axis =  $6.8^\circ/186.8^\circ$ ,  $r = 0.12$ ,  $P = 0.112$ ,  $n = 153$  herds; roe deer: mean axis =  $171.9^\circ/351.9^\circ$ ,  $r = 0.09$ ,  $P = 0.674$ ,  $n = 47$  herds), indicating that the power lines did not serve as a visual orientation cue.

**Magnetoreceptive Nature of Alignment.** The disruptive effect of ELFMEs clearly rules out the effect of the sun's position and implies magnetic alignment cues. Therefore, we tested more specific predictions resulting from the interaction between the AMFs generated by high-voltage power lines and the EMF. First, we analyzed the body orientation of cattle grazing directly under power lines (<5 m from outer conductors) trending in various compass directions [Fig. 2, supporting information (SI) Tables S1 and S2].

Below the power lines, the AMF vector is horizontal and perpendicular to the conductors. Thus, the angle between the AMF and EMF vectors and resultant field characteristics depend on the direction of the power lines (Fig. 2, left 3 columns, and Table S1). In the case of East-West-oriented (E-W) power lines, the AMF vector is parallel to the horizontal component of the EMF lines. Thus, the AMF considerably affects the horizontal intensity but not the azimuth of the EMF. Intensity and inclination of the resultant field oscillate between 2 values as the polarity of the AMF changes (i.e., with a frequency of 50 Hz); the azimuth remains constant. The AMF vector of N-S-oriented power lines is, by contrast, perpendicular to the horizontal component of the EMF lines (i.e., the AMF affects mainly the

azimuth and the horizontal intensity of the EMF much less). The azimuth of the resultant field oscillates symmetrically around magnetic North, although intensity and inclination remain nearly constant. For the Northwest-Southeast-oriented (NW-SE) and Northeast-Southwest-oriented (NE-SW) power lines, the AMF vector is  $45^\circ$  and  $135^\circ$  relative to the horizontal component of the EMF lines, respectively. The AMF affects both the horizontal intensity and the azimuth of the EMF. Intensity, inclination, and azimuth of the resultant field oscillate with a frequency of 50 Hz.

The distribution of body orientation differed significantly among cattle grazing under differently oriented power lines (Mardia-Watson-Wheeler-test:  $W = 22.756$ ,  $P < 0.001$ ; Fig. 2, fourth column, alignment relative to magnetic North). Under E-W power lines, cattle were highly significantly aligned along the power lines/magnetic E-W axis (mean axis =  $85.4^\circ/265.4^\circ$ ,  $r = 0.524$ ,  $P < 0.001$ ,  $n = 25$  herds; Fig. 2A). Their mean alignment axis differed significantly from that of control cattle (Watson-Williams-test:  $F = 62.972$ ,  $P < 10^{-12}$ ) as well as from that of cattle grazing under N-S power lines ( $F = 32.078$ ,  $P < 10^{-6}$ ). Under N-S power lines, cattle tended to align along the N-S axis; the alignment was marginally significant (mean axis =  $13.1^\circ/193.1^\circ$ ,  $r = 0.338$ ,  $P = 0.056$ ,  $n = 25$  herds; Fig. 2B), and the mean alignment axis was not different from that of controls ( $F = 1.446$ ,  $P = 0.231$ ). Interestingly, body axes were distributed almost symmetrically around the N-S axis. Under NW-SE and NE-SW power lines, cattle alignments were indistinguishable from random, with a trend toward bimodal distribution (Fig. 2 C and D and Table S2). Taken together, animals exposed to the fields characterized by maximal oscillations of the horizontal intensity

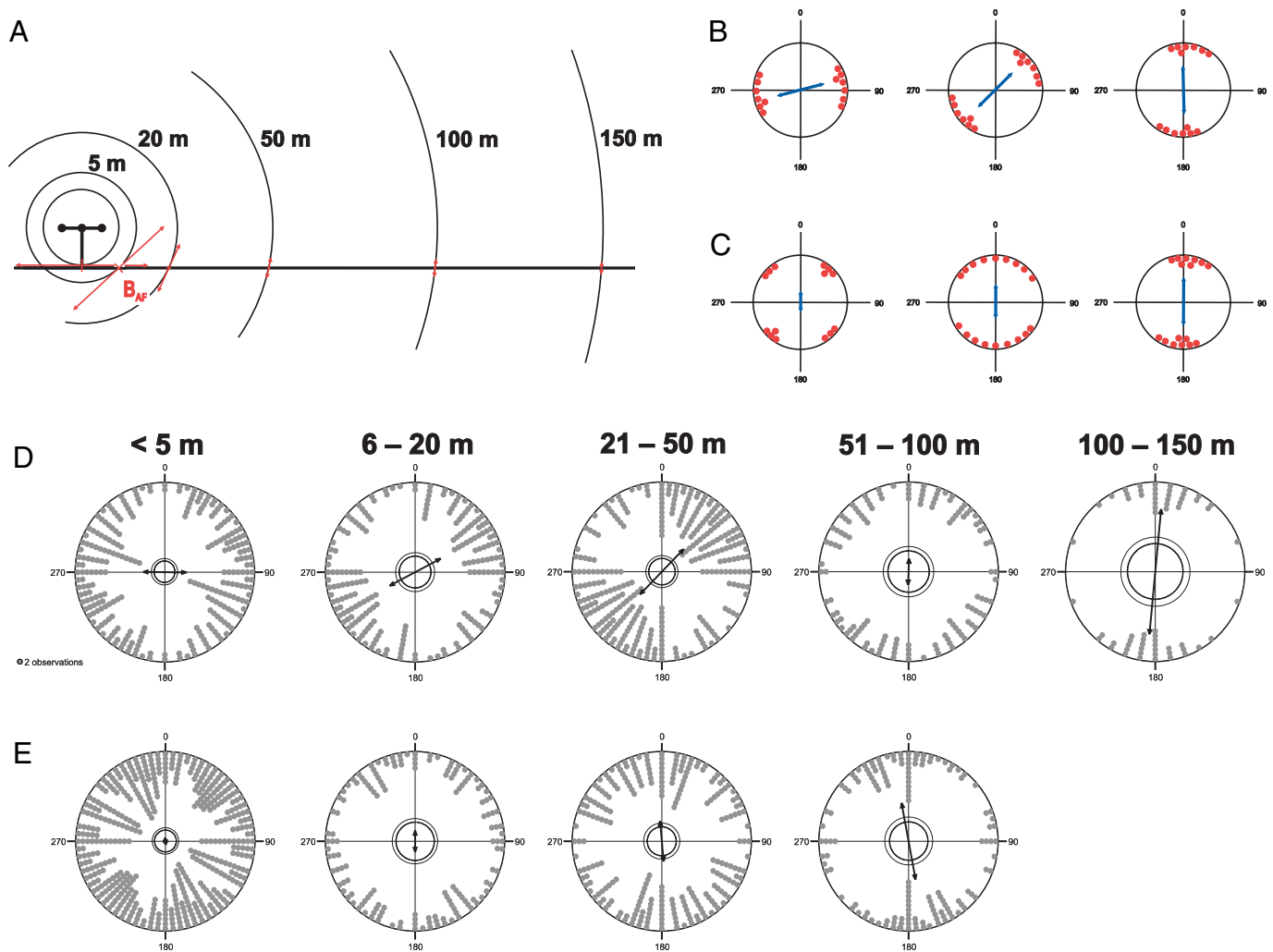


**Fig. 2.** Magnetic field properties and body orientation of cattle directly under power lines. Power lines trending in the ranges of 70°–110°, 340°–20°, 115°–155° and 25°–65° were classified as E-W (A), N-S (B), NW-SE (C), and NE-SW (D), respectively. The total intensity vector of the field (T) can be resolved into 2 vector components: the horizontal field intensity (H) and the vertical field intensity (V). The inclination is a vertical angle between the H (or the Earth's surface) and T. The azimuth is a horizontal angle measured clockwise between the horizontal intensity vector of the EMF ( $H_0$ ) and the horizontal intensity vectors of the fields resulting from summation of the AMF and EMF ( $H_1$  or  $H_2$ ).  $B_{AF}$ , AMF vector;  $H_0$ ,  $V_0$ ,  $T_0$ , vectors of the EMF;  $H_1$ ,  $H_2$ ,  $V_1$ ,  $V_2$ ,  $T_1$ ,  $T_2$ , vectors of the fields resulting from summation of the AMF and the EMF (the actual field oscillates between  $H_1$  and  $H_2$ ,  $V_1$  and  $V_2$ , and  $T_1$  and  $T_2$ , respectively, with a frequency of 50 Hz). Axial alignment data presented as in Fig. 1. See [Tables S1](#) and [S2](#) for numerical values.

and inclination shifted their body alignment by  $\approx 90^\circ$ , animals exposed to the azimuth oscillations increased scatter of their body orientation, and those exposed to the oscillations of all field parameters were disoriented.

To confirm that the observed orientation changes were caused by a direct effect of the oscillating fields on the magnetic alignment and not by nonspecific effects attributable to the utilization of nonmagnetic orientation cues, we analyzed body orientation of individual cows as a function of the distance from the power lines (Fig. 3 and [Table S3](#)). The effect of the ELFMEF should attenuate with the distance from the conductors, and at

a certain distance, animals should be aligned just as on pastures without power lines. Considering the alignment patterns observed directly below lines, predictions differ again when E-W and N-S trending power lines are compared. Cattle should shift their alignment progressively toward the N-S axis with increasing distance from E-W power lines (Fig. 3B), and the scatter in body orientation of cattle near N-S power lines should progressively decrease with increasing distance from power lines (Fig. 3C). Importantly, the prediction is opposite if cattle align themselves visually with the power lines: scatter should increase with increasing distance from N-S power lines.



**Fig. 3.** Body alignment of individual cows as a function of the distance from E-W (*B* and *D*) and N-S power lines (*C* and *E*). (*A*) Decrease of the AMF intensity with the distance from conductors. Predicted (*B* and *C*) and observed (*D* and *E*) alignment patterns. See text and Table S3 for detailed information. Each pair of data points (located on opposite sites within the unit circle) represents the body axis of an individual cow. The double arrows indicate the length ( $r$ ) and direction of the mean axial vector.

The alignment patterns observed at different distances were in very close agreement with the predictions for magnetic alignment (Fig. 3 *D* and *E*). Animals shifted their body orientation progressively from E-W to N-S with increasing distance from E-W trending power lines; with increasing distance from N-S trending power lines, scatter decreased. Cattle were roughly aligned to the magnetic N-S axis (comparable to controls) at a distance of 100–150 m and 50–100 m from E-W and N-S power lines, respectively.

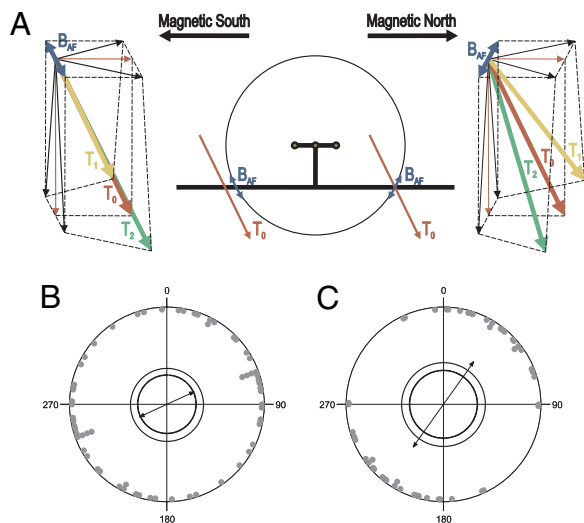
**Functional Properties of Alignment.** Finally, we compared the body orientation of cattle grazing 6–100 m to the south and to the north of E-W trending power lines (Fig. 4). South and north to the E-W power line, the AMF vector is parallel and antiparallel to the EMF vector, respectively (Fig. 4*A*). Consequently, field characteristics are different on the opposite sides of the line (Table S4). At the same distance from the power line, the horizontal intensity and vertical intensity of the EMF are affected equally by the AMF. However, vector addition results in a strong oscillation of the inclination and weaker oscillation of the total intensity on the north side and a weak oscillation of the inclination and a stronger oscillation of the total intensity on the south side. The azimuth remains constant on both sides of the line. The

difference in the intensity oscillation amplitude was accentuated in the analyzed sample, because the mean distance of individual cows being south or north from the power lines was slightly asymmetrical ( $27.9 \pm 1.6$  m SEM and  $32.8 \pm 1.5$  m SEM, respectively).

This complex situation enabled us to identify the magnetic cue that is most decisive for cattle alignment. Because the azimuth of the resultant field remains constant on both sides, an animal using a polarity compass should align likewise north and south of the power line. By contrast, an animal relying on the inclination compass should orient better on the south side. If an unknown physiological mechanism depending on the intensity of the resultant field were to underlie the alignment behavior, animals should orient better on the north side.

The distribution of body orientation as well as the mean alignment axes differed significantly between cattle grazing on the south and north sides of the E-W power lines (distribution:  $W = 6.088$ ,  $P = 0.048$ ; alignment axis:  $F = 7.068$ ,  $P = 0.01$ ; Fig. 4 *B* and *C*). On the south side, animals exhibited a wider spread of body orientation and a larger deflection from the N-S axis (mean axis =  $65.1^\circ/245.1^\circ$ ,  $r = 0.311$ ,  $P = 0.04$ ,  $n = 33$  herds) than animals on the north side (mean axis =  $35.4^\circ/215.4^\circ$ ,  $r = 0.539$ ,  $P < 0.0001$ ,  $n = 25$  herds). Thus, cattle oriented better on the north side of the E-W power lines.





**Fig. 4.** (A) Magnetic field characteristics north and south of E-W power lines, respectively (see Table S4 for numerical values). Alignment of cattle grazing south (B) or north (C) of E-W power lines. Alignment data are given relative to magnetic North (i.e.,  $0^\circ = \text{mN}$ ) and presented as in Fig. 1.  $B_{AF}$ , AMF vector;  $H_0$ ,  $V_0$ ,  $T_0$ , vectors of the EMF;  $H_1$ ,  $H_2$ ,  $V_1$ ,  $V_2$ ,  $T_1$ ,  $T_2$ , vectors of the fields resulting from summation of the AMF and the EMF (the actual field oscillates between  $H_1$  and  $H_2$ ,  $V_1$  and  $V_2$ , and  $T_1$  and  $T_2$ , respectively, with a frequency of 50 Hz).

Because the bird inclination compass works properly only within a narrow range of magnetic intensities ( $\text{EMF} \pm$  approximately 25%; cf. ref. 18), we tested for a possible indirect effect of the total intensity oscillation on the inclination compass. We ran the same analysis but included only cattle being more than 20 m from power lines. At a distance of 20 m from the outer conductors, the intensity certainly remains within the normal functional window of the inclination compass ( $\text{EMF} \pm$  approximately 12%; Table S4). Nonetheless, animals on the north side again oriented better (mean axis =  $31.7^\circ/211.7^\circ$ ,  $r = 0.50$ ,  $P = 0.002$ ,  $n = 24$  herds) than animals on the south side (mean axis =  $54.9^\circ/234.9^\circ$ ,  $r = 0.305$ ,  $P = 0.096$ ,  $n = 25$  herds). The mean distance of individual cows being south or north from the power lines was very similar ( $38.4 \pm 1.95$  m SEM and  $39.0 \pm 1.5$  m SEM, respectively). This finding indicates that the intensity oscillation compromises cattle magnetosensory capacities even when the oscillation amplitude does not exceed the intensity window, in which magnetic compass orientation is functional. These results do not specifically support the polarity compass and are clearly not in line with the inclination compass, but they show that the observed alignment is based on an intensity-dependent mechanism.

## Discussion

**Possible Alignment Mechanisms.** We can only speculate about the physiological mechanisms of the magnetic alignment of ruminants. Of the numerous mechanisms proposed for the direct interaction of electromagnetic fields with the human or animal body, 3 stand out as operating potentially (also) at lower field levels: magnetically sensitive radical pair reactions (19), electric field ion cyclotron resonance interactions (20), and mechanisms based on biogenic magnetite (21–24). Theoretically, each of these mechanisms (separately or in combination) could be responsible for magnetic alignment. For instance, the radical pair hypothesis proposes an intimate coupling of magnetic sensing with vision. According to this hypothesis, magnetic fields are perceived as visual patterns, which are dependent on both field direction and intensity (19). Thus, it is conceivable that the oscillations of the direction and intensity resulting from the EMF

and AMF interaction may blur magnetically modulated visual patterns and, in turn, compromise or disrupt magnetic compass orientation. Likewise, ambient AMF could compromise or disrupt the resonant interactions of the EMF with alternating electric fields occurring in the nervous system. Finally, putative magnetite-based receptors also theoretically could be affected by both the static magnetic field and AMF. Kirschvink (25) and Kirschvink et al. (26) developed a simple biologically plausible biophysical model of the interaction of single-domain magnetosomes in a viscous fluid (cytoplasm) with a mechanically activated transmembrane ion channel. The model shows that motions of magnetosomes induced by an ELFMEF on the order of 0.1 to 1  $\mu\text{T}$  can be large enough to open mechanically sensitive transmembrane ion channels, which, in turn, have the potential to influence a wide range of cellular processes. Depending on where such a channel is located, and whether it is coupled to secondary messenger systems, this process could influence the cell membranes, DNA synthesis, RNA transcription, calcium release, and virtually any ionically mediated cellular processes. Although the applicability of this model has been questioned for ELFMEFs  $< 5 \mu\text{T}$  (27–29), it is apparent that, in any case, the model may be relevant for sites directly beneath and in close proximity to power lines.

Mechanisms of magnetoreception in mammals have been less studied than those of other vertebrates (1, 2, 30, 31). At least for subterranean mole-rats (5, 32–34) and bats (10, 35), there is evidence for the magnetite-based polarity compass. However, whether these properties can be generalized to other mammals remains unclear. The analyses performed in this study are inconclusive with regard to the functional properties of magnetic alignment in ruminants. Theoretically, this behavior might be based on an unknown intensity-dependent mechanism or intensity-dependent polarity compass. Thus, the only safe inference appears to be that the inclination compass does not account for cattle alignment.

**Magnetic Alignment in Ruminants.** Whatever the underlying mechanism, our results provide further evidence that the recently described spontaneous directional preference in grazing and resting cattle and deer represents a case of magnetic alignment. The fact that animals grazing under or near high-voltage power lines were not commonly aligned but exhibited distinct alignment patterns beneath or in the vicinity of power lines trending in various magnetic directions clearly rules out a role of the sun compass in alignment behavior of ruminants. If cattle and deer primarily used the sun compass (i.e., derive directional information from the azimuth of the sun and the internal clock; cf. ref. 13), there should be no effect of the power lines. Furthermore, highly significant alignment in localities without power lines (12) and the fact that the disturbing effect of the ELFMEF attenuates with the distance from power lines clearly show that other factors possibly causing alignment, such as sunshine, wind direction, terrain conditions, herding instinct, or directional plant growth, play only a secondary role.

One can speculate that magnetic alignment may help to synchronize the direction of movement of individuals in herds (e.g., effective grazing, coordinated escape as an effective anti-predatory behavior), and it also may be a manifestation of the magnetic compass orientation or even navigation (being a basic tool for mentally mapping their everyday surroundings and learning new landmarks, J. B. Phillips, personal communication). However, it should be stressed that cattle and deer show magnetic alignment also, particularly when resting (12), such that the role of alignment behavior may be manifold and may also include the regulation of vegetative functions. The disturbing effect of the ELFMEF on body alignment deserves further theoretical and experimental scrutiny.

## Methods

We used the same technique to analyze axial body orientation of domestic cattle as previously described (12). The Google Earth satellite and aerial images used here met the criteria of the former study, but in contrast to the previous study, we were searching for cattle that were located under or near high-voltage power lines and electricity pylons. Although the standards of epidemiological studies (36) consider residences located up to 300 m from 380-kV power lines to be exposed to magnetic fields ( $<0.1 \mu\text{T}$ ), we included only cattle being no more than 150 m away from power lines as “experimental” animals in the analysis to increase the likelihood of a detectable effect. A total of 1,699 cattle in 153 localities in Belgium, Germany, Great Britain, and The Netherlands were analyzed. The number of pastures with different orientations of power lines was balanced [33 pastures with N-S power lines ( $0 \pm 20^\circ$ ), 41 with E-W power lines ( $90 \pm 20^\circ$ ), 39 with NW-SE power lines ( $135 \pm 20^\circ$ ), and 40 with NE-SW power lines ( $45 \pm 20^\circ$ )]. For the analysis of cattle dwelling directly beneath power lines, we evaluated an equal number of randomly chosen pastures ( $n = 25$ ) for each power line direction and analyzed only cattle that were located no more than 5 m lateral to the outer conductors.

Body orientation of roe deer ( $n = 653$  in 47 herds) grazing or resting under high-voltage power lines or no more than 50 m to the side, with the center of the herd being no more than 20 m aside, was studied in the Czech Republic by direct observation during January through December 2008. Because there were almost no recordings of roe deer at the distance of 50–150 m from power lines, we decided to set the distance to 50 m. Typically, in the open countryside with power lines, roe deer prefer the vicinity of electricity pylons. This may be

because the area around a pylon is generally not cultivated and higher grasses and bushes offer more shelter. More than half of the sampled roe deer were observed close to pylons.

Controls for both cattle and roe deer were obtained from our previously published data (cattle:  $n = 1,488$  in 111 localities in Europe; roe deer:  $n = 1,912$  animals at 201 localities in the Czech Republic; cf. ref. 12).

We calculated 1 mean vector per herd to obtain statistically independent data. Only for the analysis of cattle being located at different distances (0–5 m, 6–19 m, 20–49 m, 50–100 m, 101–150 m) from N-S and E-W power lines, respectively, did we use axial data of individuals and not of herds. The distance class of 101–150 m from N-S power lines contained too few data to run the analysis.

The Rayleigh test was used to assess significant deviations from random distribution of the mean vectors of the herds. The Watson-Williams  $F$  test was used to determine whether mean axes of 2 or more samples differed significantly, and the Mardia-Watson-Wheeler test was used for determining whether 2 or more distributions were identical. All circular statistics were calculated with Oriana 2.0 (Kovach Computing).

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1. Wiltschko R, Wiltschko W (1995) *Magnetic Orientation in Animals* (Springer, Berlin).
2. Wiltschko W, Wiltschko R (2005) Magnetic orientation and magnetoreception in birds and other animals. *J Comp Physiol A* 191:675–693.
3. Lohmann KJ, Lohmann CMF, Putman NF (2007) Magnetic maps in animals: Nature's GPS. *J Exp Biol* 210:3697–3705.
4. Burda H, Marhold S, Westenberger T, Wiltschko W, Wiltschko R (1990) Magnetic compass orientation in the subterranean rodent *Cryptomys hottentotus* (Bathyergidae, Rodentia). *Experientia* 46:528–530.
5. Marhold S, Wiltschko W, Burda H (1997) A magnetic polarity compass for direction finding in a subterranean mammal. *Naturwiss* 84:421–423.
6. Kimchi T, Terkel J (2001) Magnetic compass orientation in the blind mole rat *Spalax ehrenbergi*. *J Exp Biol* 204:751–758.
7. Deutschlander ME, et al. (2003) Learned magnetic compass orientation by the Siberian hamster, *Phodopus sungorus*. *Anim Behav* 65:779–786.
8. Muheim R, Edgar NM, Sloan KA, Phillips JB (2006) Magnetic compass orientation in C57BL/6 mice. *Learn Behav* 34:366–373.
9. Holland RA, Thorup K, Vonhof M, Cochran WW, Wikelski M (2006) Bat orientation using Earth's magnetic field. *Nature* 444:653–702.
10. Wang Y, Pan Y, Parsons S, Walker MM, Zhang S (2007) Bats respond to polarity of a magnetic field. *Proc R Soc London Ser B* 274:2901–2905.
11. Kirschvink JL, Dizon AE, Westphal JA (1986) Evidence from strandings for geomagnetic sensitivity in cetaceans. *J Exp Biol* 120:1–24.
12. Begall S, Cervený J, Neef J, Vojtech O, Burda H (2008) Magnetic alignment in grazing and resting cattle and deer. *Proc Natl Acad Sci USA* 105:13451–13455.
13. Schmidt-Koenig K (1990) The sun compass. *Experientia* 46:336–342.
14. Forschungsstelle für Elektropathologie, München (2007) *Electric and Magnetic Fields—Electric Current in Everyday Life*. (VVEW Energieverlag GmbH, Frankfurt am Main) (German, Frankfurt am Main).
15. Hamza A-SH (2005) Evaluation and measurement of magnetic field exposure over human body near EHV transmission lines. *Electric Power Systems Research* 74:105–118.
16. Olsen RG (1993) Electromagnetic fields from power lines. *Proc IEEE International Symposium on Electromagnetic Compatibility* (IEEE, Dallas), pp 138–143.
17. Ozen S (2008) Evaluation and measurement of magnetic field exposure at a typical high-voltage substation and its power-lines. *Radiat Prot Dosimetry* 128:198–205.
18. Wiltschko W (1978) Further analysis of the magnetic compass of migratory birds. *Animal Migration, Navigation, and Homing*, eds Schmidt-Koenig K, Keeton W (Springer, Berlin).
19. Ritz T, Adem S, Schulten K (2000) A model for vision-based magnetoreception in birds. *Biophys J* 78:707–718.
20. Liboff AR, Jenrow KA (2000) New model for the avian magnetic compass. *Bioelectromagnetics* 21:555–565.
21. Kirschvink JL, Gould JL (1981) Biogenetic magnetite as a basis for magnetic field detection in animals. *BioSystems* 13:181–201.
22. Sheherbakov V, Winklhofer M (1999) The osmotic magnetometer: A new model for magnetite-based magnetoreceptors in animals. *Eur Biophys J* 28:380–392.
23. Davila AF, Winklhofer M, Sheherbakov V, Petersen N (2005) Magnetic pulse affects a putative magnetoreceptor mechanism. *Biophys J* 89:56–63.
24. Fleissner G, Stahl G, Thalau P, Falkenberg G, Fleissner G (2007) A novel concept of Fe-mineral-based magnetoreception: Histological and physicochemical data from the upper beak of homing pigeons. *Naturwiss* 94:631–642.
25. Kirschvink JL (1992) Constraints on biological effects of weak extremely-low-frequency electromagnetic fields—comment. Magnetite in human tissues: A mechanism for the biological effects of weak ELF magnetic fields. *Phys Rev A At Mol Opt Phys* 46:2178–2184.
26. Kirschvink JL, Kobayashi-Kirschvink A, Diaz-Ricci JC, Kirschvink SJ (1992) Magnetite in human tissues: A mechanism for the biological effects of weak ELF magnetic fields. *Bioelectromagnetics* 1(Suppl):101–113.
27. Adair RK (1993) Effects of ELF magnetic fields on biological magnetite. *Bioelectromagnetics* 14:1–4.
28. Adair RK (1994) Constraints of thermal noise on the effects of weak 60-Hz magnetic fields acting on biological magnetite. *Proc Natl Acad Sci USA* 91:2925–2929.
29. Polk C (1994) Effects of extremely low-frequency magnetic fields on biological magnetite. *Bioelectromagnetics* 15:261–270.
30. Johnsen S, Lohmann KJ (2005) The physics and neurobiology of magnetoreception. *Nat Rev Neurosci* 6:703–712.
31. Němec P, Burda H, Oelschläger HHA (2005) Towards the neural basis of magnetoreception: A neuroanatomical approach. *Naturwiss* 92:151–157.
32. Němec P, Altmann J, Marhold S, Burda H, Oelschläger HA (2001) Neuroanatomy of magnetoreception: The superior colliculus involved in magnetic orientation in a mammal. *Science* 294:366–368.
33. Thalau P, Ritz T, Burda H, Wegner RE, Wiltschko R (2006) The magnetic compass mechanisms of birds and rodents are based on different physical principles. *Journal of the Royal Society Interface* 3:583–587.
34. Wegner RE, Begall S, Burda H (2006) Magnetic compass in the cornea: Local anaesthesia impairs orientation in a mammal. *J Exp Biol* 209:4747–4750.
35. Holland RA, Kirschvink JL, Doak TG, Wikelski M (2007) Bats use magnetite to detect the Earth's magnetic field. *PLoS One* 3:e1676.
36. van Deventer E (2007) *Environmental Health Criteria* (WHO, Geneva).