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Bursts of magnetic fields induce jumps of misdirection in bees by a mechanism of magnetic resonance*

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Summary. Magnetic field (MF) bursts at a frequency of 250 Hz oriented parallel to the field-lines of the EMF induce unequivocal 'jumps' of misdirection of up to +10°. The regression of burst intensity (BI in γ; for a range of 10–1400 γ) and the size of the induced jumps of misdirection (DMID in angular degrees) follow the equation: DMID = −1 + ln BI. Compensation (< 5% of the total intensity) of the EMF, continuous 250 Hz fields and bursts perpendicular to the static MF have no effect. The effects described are discussed from the point of view of magnetic resonance.

Introduction

The natural earth's magnetic field (EMF) as well as artificial magnetic fields (MF) are known to affect the misdirection of the waggle-dance of honeybees (Lindauer 1976; Lindauer and Martin 1968; Martin and Lindauer 1973, 1977). Misdirection tends towards zero (zero point) if the sagittal plane of the dancing bee coincides with the direction of the field-lines of the EMF or if there is a compensation of the total intensity of the EMF (< 5% of total) (Martin and Lindauer 1973, 1977). The variation (ΔF) of the EMF is described as the component which affects the waggle-run. Latencies of 20–40 min are observed before the effects of MF appear.

Abbreviations: *BI* burst intensity in γ; *DMID* difference (jump) of misdirection in angular degrees; *EMF* earth's magnetic field; ΔF MF variation of the total component; *g* stands for γ in figures; *H* magnetic field force in Oersteds; *MF* magnetic field; *NAT* natural magnetic field in Tables (=EMF); *Oe* Oersted, unit of the magnetic field force; $\gamma = 10^{-5}$Oe; *g* gyromagnetic ratio (a nuclear specific constant) in Hertz/Gauss; μ_N nuclear magneton; ω_L Larmor frequency

* Dedicated to Prof. Dr. Drs. h.c. H. Autrum on the occasion of his 80th birthday

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In this paper, we examine the effects of these slow, dynamic MF-variations when there is a superimposed higher frequency burst in the physiological range. The frequency of 250 Hz was chosen in collaboration with the physicists Landwehr and Hönlein (Department of Physics, University of Würzburg, FRG) because that is the frequency of the buzzing sounds of bees during the waggle-run. This sound signal was used as a basis for the conception of a MF-producing burst generator to study a possible magnetic resonance effect. The frequency, duration and pulse sequence of sounds generated during the waggle-dance are correlated with the daily variation of the EMF (Kilbert 1979). This study attempts to determine how the application of such an artificial MF signal affects the waggle-dance of the honeybee.

Material and methods

The direction of the waggle-dances of individually marked bees was recorded 'by hand' with a protractor according to von Frisch (1965). Further experimental conditions for the recording of the dance angle are described in Lindauer and Martin (1968). The expected direction of the waggle-line and the 'misdirection' were calculated from the the local azimuth of the sun on the respective experimental day.

The observation hive was adjusted in magnetic N-S direction; the dances were read from the east side of the combs. The feeding place was located at a distance of 600 m and in a direction 4° east of geographic N.

As for the generated MF bursts (see Fig. 1), the following parameters could be varied independently: pulse repetition frequency, pulse number, duration of the intervals between two successive bursts, and amplitude.

The electrical signal produced by the generator fed a pair of Helmholtz coils 2 m in diameter and thus generated the corresponding MF oscillations. The axis of the Helmholtz coils was oriented in the magnetic N-S direction unless otherwise noted and adjusted to be parallel to the local inclination of the EMF, which was 65.4°. A second pair of Helmholtz coils was used for compensation (< 5% of the EMF's total intensity) or amplification of the EMF.

The extent of MF compensation, the field intensity and the time course of the bursts was controlled by a Hall detector

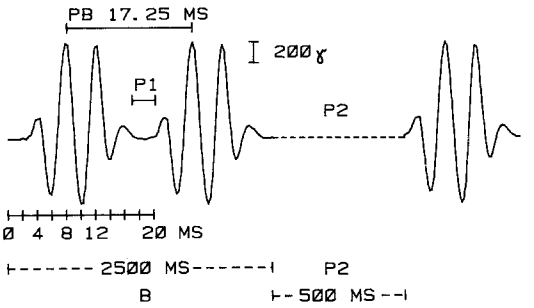


Fig. 1. Timing and intensity characteristics of the MF bursts, e.g. signal of 250 Hz, 1400 γ. Abscissa, time; ordinate, field intensity; *PB* period between two successive MF bursts; *B* complete interval of 2500 ms from a group of 145 subsequent bursts (only two bursts are shown); P_1, P_2 pauses of 4 and 500 ms between single bursts and a group of 145 bursts

(Bell Inc., Florida, USA). The artificial MF conditions were operated by a remote control. The duration of the artificial MF can be seen in the figures.

Results

The following results are based on 128 experimental days with a total of more than 80000 recorded dances.

In the test series described below the daily variation of misdirection is shown for a series of measurements lasting 3–4 h each, including the zero point (no misdirection). As regards the adjustment of the hive used in the experiments, the zero point is located at an angular direction of 204.6° under

Table 1. Relation between burst intensity and misdirection

Year	cond	$\bar{x}$	SD	*n*	nd	diff	Nb bN	DIFFNN
1983	NAT	0.66	4.25	145	3		5.20	
	1400 γ	5.23	3.17	135	3	4.56	−5.40	10.60
	NAT	0.64	3.45	98	2		6.27	
	700 γ	6.34	2.66	95	2	5.70	−6.03	12.30
	NAT	−0.90	2.49	88	2		4.58	
	350 γ	3.66	2.28	83	2	4.55	−4.94	9.52
	NAT	−1.93	4.18	221	4		5.10	
	200 γ	2.89	3.65	205	4	4.82	−5.78	10.88
	NAT	−1.47	2.83	91	2		4.21	
	80 γ	2.68	2.39	87	2	4.16	−4.08	8.29
	NAT	−1.47	2.70	120	2		1.83	
	40 γ	1.21	2.75	123	2	2.68	−3.33	5.16
	NAT	−1.32	2.80	253	4		2.14	
	20 γ	1.28	2.49	254	4	2.60	−2.79	4.93
	NAT	1.27	2.05	162	4		0.97	
	10 γ	2.79	2.67	190	4	1.52	−1.35	2.32
1984	NAT	−1.56	4.99	265	5		3.16	
	1400 γ	1.70	4.04	233	5	3.26	−4.01	7.17
	NAT	−1.92	5.76	71	2		0.84	
	1000 γ	0.25	6.56	67	2	2.17	−2.18	3.02
	NAT	−5.98	6.35	66	1		0.72	
	250 γ	−4.77	7.11	83	1	1.22	−3.08	3.80
1985	NAT	−3.63	4.67	341	6		3.17	
	1400 γ	−0.23	4.38	301	6	3.41	−3.66	6.83
	NAT	−3.10	3.70	146	2		1.29	
	700 γ	−1.58	4.02	146	2	1.52	−2.38	3.67

Definition of abbreviations from left to right: year of tests; *cond* MF conditions indicating NAT (EMF), and burst intensities in γ; $\bar{x}$, *SD*, *n* the usual statistical terms for averaged EMF and burst MFs; *nd* number of test days; *diff* $\bar{x}_{\text{burst}}-\bar{x}_{\text{NAT}}$; *Nb* difference of the means of the last three misdirection values before switching from EMF to burst conditions and the first three after; *bN* adequate jumps switching from burst to EMF; *DIFFNN* bN–Nb. All figures except those for *n* and *nd* indicate the misdirection in angular degrees. – These data indicate positive jumps of misdirection switching from NAT to burst conditions and inversed (negative) jumps switching from burst to NAT conditions. The regression between burst intensity (BI in γ) and jumps of misdirection (DMID in angular degrees) in the range from 10 to 1400 γ is described by DMID $= -1 + \ln$ BI; the correlation is 0.92 with $P<0.001$. The regression curve is shown in Fig. 8

EMF conditions. Since dances are almost faultless in this range, the zero point is very suitable for controlling the proper adjustment of the experimental set-up in the EMF. The slope of a misdirection curve under EMF conditions depends on the preceding magnetic variation ΔF. This slope may start with a substantial deviation from the predicted dance-angle and passes through the zero point with nearly no deviation. Subsequently the deviation again depends on ΔF. The variation in misdirection throughout the day in its form of an-hysteresis and hysteresis is determined by ΔF (Martin and Lindauer 1977). Therefore, the daily misdirection curves vary from day to day, with the exception of the zero point which remains constant, i.e. independent of ΔF provided there is no change of the positions of hive and feeding place. For this reason the zero point is emphasized as a reference point (marked by ∅ in the figures).

As a criterion for the efficiency of the bursts the summed average values between dances in the EMF (NAT) and under MF burst conditions are compared. Since the burst-induced misdirection overlaps the misdirection caused by ΔF, the artificially induced misdirection may easily be leveled. Therefore, an unequivocal characterization of the initial difference of misdirection (DMID in degrees), i.e. those occurring immediately after the start of the MF burst, is necessary. The differences of the last three dances before and the first three dances after switching of the field are calculated (see Nb in legend to Table 1) as well as the corresponding total differences.

Bursts in the direction of inclination of the EMF

Application of 250 Hz MF bursts of an intensity of 1400 γ in the direction of the inclination of the EMF results in immediate positive jumps of misdirection of up to 10° (Figs. 2–4). This responsiveness is spontaneous, and of such a type that a continuous change of the dance angle can be directly observed in a single bee if it starts dancing in the EMF and continues in the burst field. Bursts of the same intensity mostly induce larger jumps of misdirection after the zero point than before.

With an intensity of 20 γ the stimulus threshold lies far below the EMF intensity of 42000 γ at the location of the experiments. Pulse intensities of more than 20000 γ have no effect, indicating a 'window' of stimulus efficacy well below the intensity of the EMF. When switching from EMF to artificial MF conditions the magnitude of the misdirection jumps (DMID) is proportional to the burst intensity (BI) in the range from 10–1400 γ

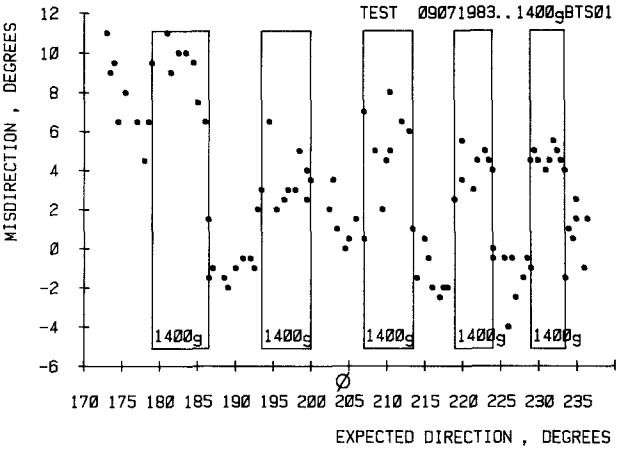


Fig. 2. 250-Hz MF bursts of intensity 1400 γ oriented parallel to the field vector of the EMF cause distinct positive jumps of misdirection; g stands for γ. Abscissa, the predicted angle, in angular degrees; ordinate, the misdirection in angular degrees. The points outside the frames were obtained in the EMF (=NAT). Inside the frames, bursts of the intensity shown have been applied. The first 8 figures in the test code give the date of the experiment

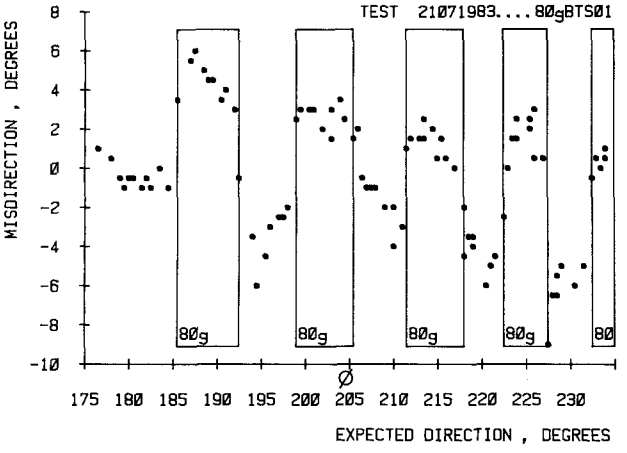


Fig. 3. 250-Hz MF bursts of intensity 80 γ. See Fig. 2 for details

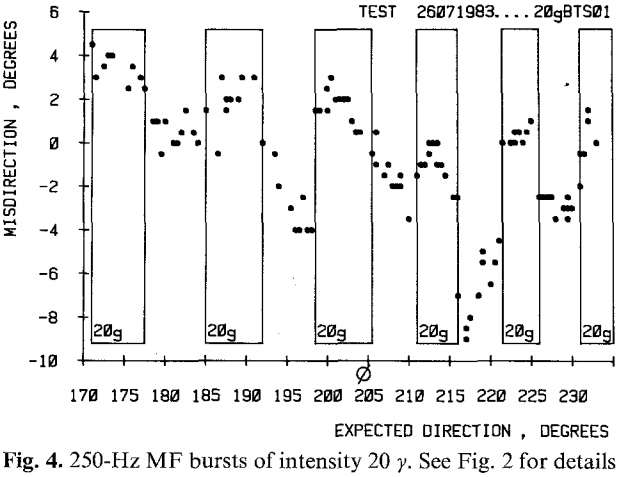


Fig. 4. 250-Hz MF bursts of intensity 20 γ. See Fig. 2 for details

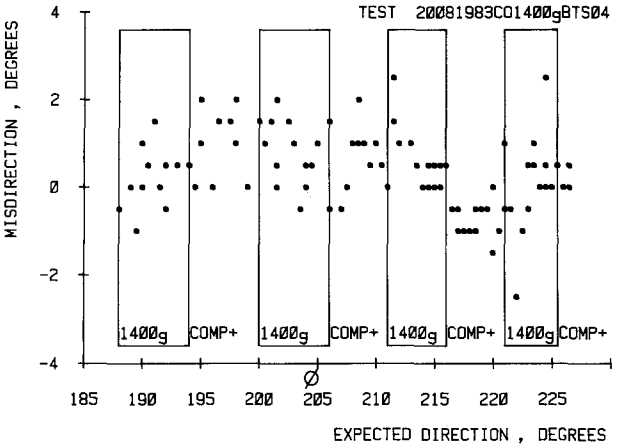


Fig. 5. In the compensated EMF (<5%, COMP+) with no static MF component, 1400 γ MF bursts have no effect on misdirection. See Fig. 2 for details

and follows the equation DMID = −1 + ln BI (Fig. 8).

The different bee colonies used in successive years varied in their sensitivity to bursts of equal intensity. Thus, the jumps of misdirection in Table 1 are listed separately for each swarm and year.

Bursts in the compensated EMF

If the EMF is compensated to less than 5% of total intensity no jumps of misdirection can be observed (Lindauer and Martin 1968; Martin and Lindauer 1977). In addition to an application of MF bursts of 1400 γ no jumps of misdirection appeared (Fig. 5, Table 2B). The daily slopes of direction indication are similar to those found by Lindauer and Martin (1968) and Martin and Lindauer (1977).

Continuous 250 Hz field

Application of a continuous 250 Hz field, i.e., one without the pauses characteristic of the bursts (see P1 and P2 in Fig. 1), does not lead to any jumps of misdirection (Table 2A). These results also correspond to those from earlier experiments with MFs of frequencies 5, 15, 250 and 770 Hz (Martin and Lindauer 1977).

Table 2. Some special burst conditions and their influences on misdirection

	cond	$\bar{x}$	SD	n	nd	diff	Nb bN	DIFFNN
A	NAT	0.13	1.75	50	1		−0.70	
	CONT 1400 γ	0.55	3.55	51	1	0.42	−0.37	−0.33
B	COMP+	0.13	0.94	137	3		0.20	
	40, 350, 1400 γ	0.54	1.60	148	3	0.42	−0.22	0.42
C	NAT	2.05	2.04	145	3		0.03	
	10, 140, 1400 γ	2.28	2.06	154	3	0.23	−0.09	0.12
D	NAT	−0.59	5.03	66	1		0.08	
	−65° 1400 γ	−0.41	3.41	68	1	0.18	−0.17	0.25
	NAT	−1.11	5.09	63	1		0.37	
	−40° 1400 γ	−1.30	3.88	61	1	−0.19	−2.04	2.41
	NAT	−0.89	6.05	59	1		−0.17	
	−15° 1400 γ	−0.16	4.99	74	1	0.73	−2.67	2.50
	NAT	1.91	4.76	66	1		0.67	
	+ 5° 1400 γ	2.60	4.03	67	1	0.70	−1.42	2.09
	NAT	0.16	3.97	184	3		0.40	
	+25° 1400 γ	0.90	4.11	196	3	0.74	−1.08	1.48

Definition of abbreviations from left to right: *cond* MF conditions indicating NAT (EMF) and burst intensities in γ; *angle* angular deviation of burst direction from geomagnetic inclination in degrees; *COMP+* compensation of the EMF to <5% of the total intensity; *CONT* continuous 250 Hz oscillation; $\bar{x}$, *SD*, n the usual statistical terms for averaged EMF and burst MFs; *nd* number of test days; *diff* $\bar{x}_{burst}-\bar{x}_{NAT}$; *Nb* difference of the means of the last three misdirection values before switching from EMF to burst conditions and the first three after; *bN* adequate jumps switching from burst to EMF; *DIFFNN* bN–Nb. All figures except those for n and *nd* indicate the misdirection in angular degrees. Special test conditions: *A CONT*, continuous 250 Hz oscillations under EMF conditions (NAT) do not affect misdirection; *B COMP+*, compensated EMF and applying 40, 350, 1400 γ bursts in the direction of the previous EMF does not lead to any jumps of misdirection; *C*, burst intensities of 10, 140, 1400 γ at right angles to the total component of the EMF do not affect misdirection; *D*, 1400 γ bursts, whose angles gradually differ from the direction of the total component of EMF (angular values of burst direction positive or negative, based on the geomagnetic inclination of 65.4°) lead to a decrease of misdirection jumps

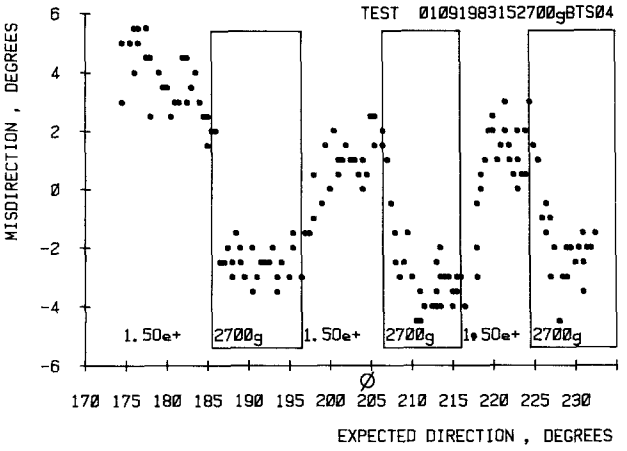


Fig. 6. Under conditions where the static component of the EMF is amplified from 42000 γ to 150000 γ, 2700-γ MF bursts bring about negative jumps of misdirection with a latency of 2–4 min. See Fig. 2 for details

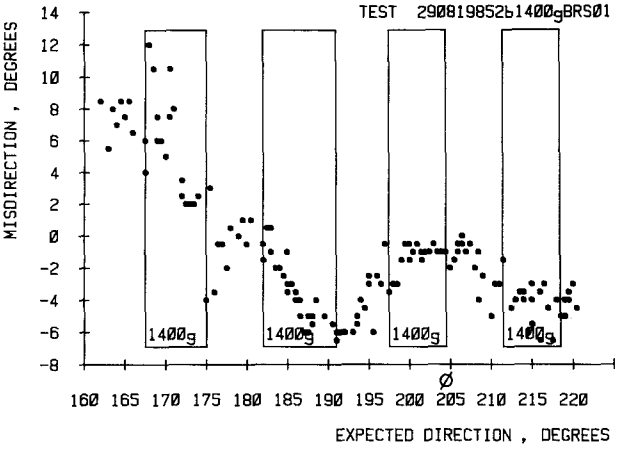


Fig. 7. 250-Hz MF bursts with an intensity of 1400 γ, applied at right angles to the static MF component, are not effective. The misdirection depends on ΔF and shows a normal daily pattern with zero misdirection at 204.6°. See Fig. 2 for details

Bursts in the amplified static MF

Since compensation of the EMF results in suppression of burst-induced jumps of misdirection, the simultaneous influence of an amplified static MF and bursts, both aligned parallel to the inclination of the EMF, was examined. In the amplified static field (1.5 Oe in contrast to 0.42 Oe of the EMF), jumps of misdirection are delayed by 2–4 min; they have, in general, a lower amplitude. At a burst intensity of 2000 γ the sign of the misdirection inverts: bursts below 2000 γ cause (see above) a positive deviation and above this intensity a negative deviation from the predicted dance angle (Fig. 6).

Different angles between static and oscillating MF

If the direction of the bursts differs from the inclination of the EMF or an artificial static MF, jumps of misdirection get smaller with increasing angular differences (0°–90°). Differences between the direction of the bursts and of the static component of only a few degrees result in reduced jumps of misdirection. The dependence of positive deviations of the dances on the angular difference between both MFs is shown in Table 2C, D. Bursts perpendicular to the plane of inclination yield the same results as in the compensated MF: no jumps of misdirection can be observed (Fig. 7). In contrast to the experiments in the compensated field, the daily slope of the misdirection curve depends upon ΔF; no misdirection is observed at the zero point.

Discussion

The sensory basis of MF perception in animals is still obscure. On the basis of behavioural and

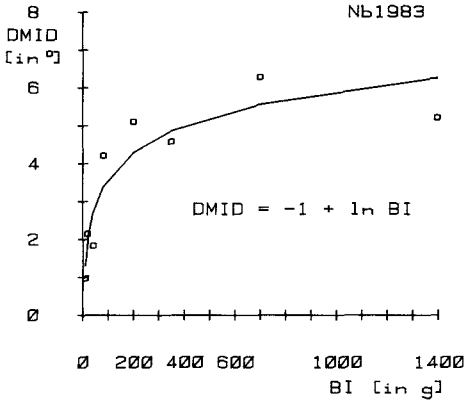


Fig. 8. Regression line of burst intensity (BI in γ) and the size of the jumps of misdirection (DMID in angular degrees), showing the variation in the moment of switching from EMF to MF burst; data are taken from column Nb of the year 1983 (see Table 1); $n=8$, $r=0.92$, with $P<0.001$

physiological data several models have been proposed, including the involvement of radical reactions (Schulten and Windemuth 1986) and single-domain magnetite (Kirschvink and Gould 1981). However, for the ferrimagnetic theory it is difficult to understand the high sensitivity of bees and pigeons to the daily magnetic variation in the γ-range, superimposed to the basic intensity of the EMF with 42000 γ, even when there is no change of direction of the EMF. Furthermore, the changes in membrane permeability necessary on the basis of this model cannot be explained. Our results add another obstacle: single-domain magnetite should realign itself to a change of MF direction after 30 ms (Kirschvink 1981), a velocity far below the 250 Hz bursts that produce the effects described above.

The results presented here add new aspects to the discussion on the mechanisms involved in the perception of magnetic fields.

We favour the following hypothesis of the vectorial relations and the relations of field strengths between static and oscillating MFs. The unequivocal directional relation between bursts and the static MF points to an interpretation of MF action on the basis of molecular resonance phenomena, i.e. nuclear or electron spin resonance. Even though only parallel fields are effective in our experiments, which is in contrast to classical resonance experiments where high-frequency fields are applied at right angles to the static component, a common basis of interpretation cannot be excluded. During the dance, the bee passes all possible angles of divergence with respect to the static and oscillating components. The static MF could offer a chance to adjust to as yet unknown structures in specific cellular compartments. The magnetization of oriented biological material could be preserved by remanence and be excited by the oscillating MF when the proper angle of divergence is reached.

This assumption is supported by the absence of misdirection jumps when the static MF is compensated and by the narrow effective 'intensity window' of the bursts, between 80 and 2000 γ. Resonance can only be achieved with MF-oscillations if a static MF is simultaneously present. Additionally, resonance only occurs at a given ratio of intensity between the static and oscillating MFs (described by the Larmour equation $\omega_L = g \cdot H$), i.e. the lower the intensity of the static MF, the lower the frequency necessary to induce resonance (Korall and Martin 1987). The magnetic dipole moment of the electron is much greater than that of the proton, i.e. 2.79 fold of the nuclear magneton, μ_N. In this context the base 2.72 of the natural logarithm used in the equation $\mathrm{DMID} = -1 + \ln \mathrm{BI}$ is of interest. The equation describes the modulation of a complex biological system by distinct MF conditions. This relation should be pointed out, even if it depends on the use of an arbitrary, relative scale system.

In the experimental series the MFs used were characterized by burst-pause duration of 2 s:1 s and 2.5 s:0.5 s. Continuously oscillating fields of equal intensity did not lead to misdirection jumps. The pause length is in the range of proton relaxation times, which are between 0.2 and 0.8 s (Roth and Gronenborn 1982). There is a certain flexibility in this range because the frequency of precession of an atomic species depends on the chemical shift evoked by the molecular composition of the surrounding (Dwek 1973; Knowles et al. 1976). The induction of resonance in phosphatidylcholine membranes depends strongly on the direction of the applied MF (McLaughlin et al. 1977).

The parallels with respect to resonance phenomena can be summarized as follows. There is a strong dependence on the angle between the bursts and the static MF component, a small range of effective intensity with higher field intensities leading to saturation effects and causing the modulated, biological output signal to disappear, and there must be defined periods of relaxation between the bursts. These parallels make the theoretical considerations discussed above plausible.

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