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REPORT

The magnetic compass mechanisms of birds and rodents are based on different physical principles

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Recently, oscillating magnetic fields in the MHz-range were introduced as a useful diagnostic tool to identify the mechanism underlying magnetoreception. The effect of very weak high-frequency fields on the orientation of migratory birds indicates that the avian magnetic compass is based on a radical pair mechanism. To analyse the nature of the magnetic compass of mammals, we tested rodents, Ansell's mole-rats, using their tendency to build their nests in the southern part of the arena as a criterion whether or not they could orient. In contrast to birds, their orientation was not disrupted when a broad-band field of 0.1–10 MHz of 85 nT or a 1.315 MHz field of 480 nT was added to the static geomagnetic field of 46 000 nT. Even increasing the intensity of the 1.315 MHz field (Zeeman frequency in the local geomagnetic field) to 4800 nT, more than a tenth of the static field, the mole-rats remained unaffected and continued to build their nests in the south. These results indicate that in contrast to that of birds, their magnetic compass does not involve radical pair processes; it seems to be based on a fundamentally different principle, which probably involves magnetite.

Keywords: magnetic compass; magnetoreception; high-frequency fields; radical pair mechanism; magnetite; *Cryptomys anselli*

1. INTRODUCTION

Magnetic compass orientation is widespread among animals (Wiltschko & Wiltschko 1995). However, the physical principles underlying the reception processes that mediate magnetic compass information have so far been analysed in detail only in birds, where a radical pair mechanism has been identified (Ritz *et al.* 2004). In such a mechanism (Schulten *et al.* 1978; Ritz *et al.* 2000), light absorption by specialized photopigments creates a radical pair that decays into spin-selective, i.e. singlet or triplet, products. Internal (hyperfine interactions) and external magnetic fields change the spin states of the radical pair and thereby influence the relative yield of singlet and triplet products. Most radical pairs contain at least some anisotropic hyperfine interactions and, hence, the product yield is influenced by the strength of an external magnetic field as well as by the alignment of the molecules forming the radical pair with external field. Assuming that the radical pairs within a cell are sufficiently ordered, the sensitivity of radical reactions on the direction of an external magnetic field can provide the basis for a magnetic compass sense (for details of the model see Ritz *et al.* 2000). Weak intensity high-frequency (HF) fields in the MHz-range interfere with the singlet–triplet interconversion and thus provide a diagnostic tool to identify radical pair processes: the pattern of HF effects in birds indicates that the avian magnetic compass is indeed based on radical pair processes (Ritz *et al.* 2004; Thalau *et al.* 2005; Wiltschko *et al.* 2005).

These findings raise the question about the nature of the primary processes underlying magnetic compass mechanisms of other vertebrates. Of particular interest are groups whose magnetic compass was found to differ from that of birds, like marine turtles and mammals (Wiltschko & Wiltschko 1995, 2005). The present study analyses the magnetic compass mechanism of a mammalian species, Ansell's mole-rats (*Cryptomys anselli*, Bathyergidae). In captivity, these subterranean rodents tend to build their nests preferably in the southern sector of a round arena, a reliable spontaneous behaviour that had been used before to analyse the functional mode of their magnetic compass (Marhold *et al.* 1997*a*).

2. METHODS

Ansell's mole-rats are eusocial and live in underground tunnels. Our test animals were eight pairs of Zambian origin or the descendents of mole-rats caught in Zambia, derived from the breeding stock at the University of Duisburg-Essen, Germany. The experiments were performed in spring 2004 and 2005, from 8 March to 3 May 2004 and from 4 March to 25 April 2005, using the same groups of mole-rats except for one group that had to be replaced (see table 1). The animals were transported to Frankfurt two weeks prior to testing for habituation. They were housed in animal housing facilities under a 12 : 12 light regime at 21–23 °C and provided with food *ad libitum*. The test groups consisted of two animals each. Six of the groups came from two colonies consisting of six animals; here, the two animals of the test group were rejoined with their colony directly after testing.

Testing took place in darkness in four wooden huts in the garden of the Zoological Institute, Frankfurt am Main, where the local geomagnetic field of 46 000 nT, 66° inclination was undisturbed. For producing

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Table 1. Orientation of nest building in mole-rats under the various test conditions. (The control tests were performed in the local geomagnetic field; the 'control before high-frequency (HF) tests' in 2004 were all performed before the individual group of mole-rats had been tested in the HF field for the first time to document their normal behaviour; the 'control during HF testing' were interspaced with the tests in the HF fields. There is no difference between the two datasets indicating that the treatment with HF fields had no after-effects. For the other test conditions, the respective HF field was added to the geomagnetic field in a vertical alignment, so that the HF vector was at a 24° angle with the geomagnetic vector. The table shows, under N, the number of groups tested and, under n_g, the number of tests per group. med. r_g gives the median of the vector lengths based on the directions of the nests of each group, indicating the intra-group variance of the directional choices; α_N, r_N give the grand mean vectors based on mean directions of the eight groups indicating the inter-group variance, with the asterisks indicating the significance of these vectors by the Rayleigh test (Batschelet 1981). ΔC shows the differences to the mean of the respective control tests (marked C in this column), with the last column indicating whether the difference between the two distributions is significant by the Mardia–Watson–Wheeler test and the Watson's U^2-test (Batschelet 1981). Significance levels: $^{*}p<0.05$; $^{**}p>0.01$; $^{***}p<0.001$; n.s., not significant.)

year	test conditions	N	n_g	med. r_g	α_N (deg.)	r_N	ΔC	sign.?
2004	control before tests in HF fields	8	6–9	0.37	169	0.92^{***}	C	
	control during tests in HF fields	8	5–7	0.42	178	0.88^{***}	+9°	n.s.
	broad-band 0.1–10 MHz field, 85 nT	8	5	0.43	162	0.77^{**}	−7°	n.s.
2005	control (before and during HF tests)	8	5–6	0.58	192	0.67^{*}	C	
	1.315 MHz field, 480 nT intensity	8	5–6	0.41	174	0.65^{*}	−18°	n.s.
	1.315 MHz field, 4800 nT intensity	8	5–6	0.66	179	0.72^{*}	−13°	n.s.

the broad-band HF field and the 1.315 MHz field of 480 nT, we used the same equipment that we had used in the corresponding experiments with birds (Ritz *et al.* 2004; Thalau *et al.* 2005): a coil antenna of a single winding of coaxial cable with 2 cm screening removed opposite the feed was mounted horizontally on a wooden frame surrounding the test arena. Oscillating currents from a HF generator were amplified by a HF amplifier and were fed into the coil through a resistance of 51 Ω. For the 1.315 MHz field of 4800 nT, the arena was surrounded by a double winding of coaxial cable also with 2 cm of the screening removed. The HF fields were measured before each test session with a spectrum analyser (for details on the equipment used see Ritz *et al.* 2004). In 2004, we performed a series of control tests in the geomagnetic field before we started the tests in the HF fields and another series interspaced with the HF tests. Since there was no difference between the mole-rats' behaviour (see table 1), the control tests in 2005 were performed before and between the HF tests.

For testing, the pair of mole-rats was moved in closed opaque plastic buckets to the round test arena in the wooden huts. This plastic arena had a diameter of 80 cm and a wall 30 cm high. A plastic bucket of 17 cm diameter was placed in the centre to ensure analysable nest positions. The ground of the arena was covered with peat; a sufficient amount of stripes of tissue paper was homogeneously scattered to provide nesting material, and food items (potatoes and carrots) were radially supplied (for details see Burda *et al.* 1990). When the test began, the animals were left in the middle of the arena in their transport bucket for a 30 min habituation; then they were released into the arena. The arena was closed with an opaque plastic lid, resulting in a light level of less than 0.001 mW m^{-2} inside the arena.

The animals were tested once per day, in the morning or in the afternoon, mostly with a day between tests. The time until a nest was constructed varied between 30 min and about 6 h, with great differences between individual groups, as some animals regularly built faster than others. The outside temperature also had a certain influence, with nest building usually being faster at low temperatures. When the animals had not build a nest within 6 h, they were normally removed to their housing cages; in exceptional cases, they were left in the arena and built a nest after up to 9 h. After each test session, the peat was removed and the arena cleaned and washed with 10% acetic acid. Each group of animals was tested with its individual peat.

3. RESULTS

Table 1 summarizes the data of the various test conditions and table 2 gives the vectors of the individual groups of mole-rats.

In control tests in the local geomagnetic field of 46 000 nT, the mole-rats preferred to build their nests in the southern part of the arena (figure 1, left diagrams). To find out whether or not a radical pair mechanism was underlying their magnetic compass, we exposed the mole-rats to a broad-band HF field with frequencies ranging from 0.1 to 10 MHz (intensity of 85 nT) and to a 1.315 MHz field of 480 nT intensity, both presented vertically, i.e. with the HF field vectors at a 24° angle to the vector of the static geomagnetic field. In previous studies, these HF fields had completely disrupted the orientation of birds (Ritz *et al.* 2004; Thalau *et al.* 2005). The mole-rats, however, continued to build their nests in the southern part of the arena. Even increasing the intensity of the 1.315 MHz field 10-fold to 4800 nT did not disrupt their orientation: their nests were still preferably situated in the south (figure 1). The vectors of the individual pairs of mole-rats in each test condition are given in table 2. The distribution of nests in the various experimental conditions does not test different from each other ($p>0.05$, Mardia–Watson–Wheeler test and Watson's U^2-test; Batschelet 1981).

Table 2. Mean vectors of the individual groups of two mole-rats. (Control tests were performed in the local geomagnetic field; in the other test conditions, the respective HF field was added (see table 1 for the various two control conditions in 2004). n_g, number of tests per group; α_g, r_g, direction and length of the group's mean vectors.)

2004 experiments

	control before HF tests			control during HF testing			broad-band HF field, 85 nT		
group	n_g	α_g (deg.)	r_g	n_g	α_g (deg.)	r_g	n_g	α_g (deg.)	r_g
M 1	6	148	0.65	6	162	0.50	5	114	0.26
M 2	9	181	0.28	6	131	0.26	5	151	0.21
M 3	7	165	0.40	6	217	0.34	5	136	0.60
M 4	7	187	0.14	5	184	0.72	5	131	0.82
M 5	8	187	0.16	6	169	0.95	5	238	0.28
M 6	7	186	0.53	6	219	0.12	5	186	0.59
M 7	6	115	0.33	7	150	0.03	5	214	0.57
M 8	6	173	0.63	6	192	0.69	5	145	0.24

2005 experiments

	control			1.315 MHz, 480 nT			1.315 MHz, 4800 nT		
group	n_g	α_g (deg.)	r_g	n_g	α_g (deg.)	r_g	n_g	α_g (deg.)	r_g
M 1	6	286	0.17	6	242	0.34	6	131	0.56
M 2	6	172	0.82	5	157	0.94	5	161	0.67
M 3	6	152	0.68	5	159	0.41	5	127	0.82
M 4	6	206	0.59	5	164	0.86	5	158	0.66
M 5	6	130	0.35	5	157	0.19	5	268	0.27
M 6	6	224	0.60	6	151	0.22	5	180	0.71
M 7	6	240	0.20	6	339	0.42	6	224	0.32
M 9	5	155	0.58	5	187	0.52	6	205	0.78

4. DISCUSSION

None of the HF fields did affect the magnetic orientation in mole-rats. This differs greatly from the responses of European robins, *Erithacus rubecula*, in similar experiments: their orientation behaviour was strongly affected by weak HF fields, with a marked effect being observed at the frequency of 1.315 MHz that matches the energetic splitting induced by the local geomagnetic field (Thalau *et al.* 2005). These contrasting results clearly show that the magnetic compass of mole-rats is based on a receptor different from that of birds. Since one would generally expect that HF fields at strength of more than one-tenth of the static geomagnetic field's intensity affect radical pair processes, it is very unlikely that the magnetic compass of mole-rats is based on a radical pair mechanism.

This conclusion is in agreement with earlier experimental findings on the functional characteristics of the mole-rats' magnetic compass, which differs from that of birds in two important aspects (Marhold *et al.* 1997*a*): (i) it is not light-dependent like that of birds, and (ii) it is a 'polarity compass' distinguishing between magnetic North and South and not an 'inclination compass' like the avian compass that detects only the axis of the magnetic field lines (see Wiltschko & Wiltschko 1995, 2005 for details). These characteristics of the mole-rats' compass are at variance with a radical pair mechanism, in which photons are postulated to be involved in forming the radical pairs, and because radical pair processes are not sensitive to the polarity of magnetic fields and, hence, would result in axial rather than polar responses (Ritz *et al.* 2000). These theoretical considerations predict the absence of a radical pair mechanism in mole-rats, a prediction that is now confirmed by the use of HF magnetic fields as a novel diagnostic tool.

Recently, a second type of directional response to magnetic fields has been described in birds, so-called 'non-compass responses', which become evident under specific light regimes as headings in 'fixed' directions; they are fundamentally different from the normal avian magnetic compass as they do not involve the inclination compass and are not based on radical pair processes (Wiltschko *et al.* 2005). The mechanism underlying these responses is not yet known; whether it is related to the mole-rats' magnetic mechanism remains to be determined.

An alternative hypothesis for mechanisms underlying magnetoreception (e.g. Yorke 1979; Kirschvink & Gould 1981; Davila *et al.* 2003) proposes a mechanism based on magnetite (Fe_3O_4), a ferromagnetic material of biogenic origin that has been demonstrated in a wide range of animal species (Kirschvink *et al.* 1985). A magnetite-based mechanism seems to be indeed an option for the mole-rats' magnetic compass, since a magnetite-based sensor would not be affected by the weak HF magnetic fields applied in the present study. Magnetite has not yet been reported in mole-rats; behavioural evidence, however, indicates an involvement of magnetite in the

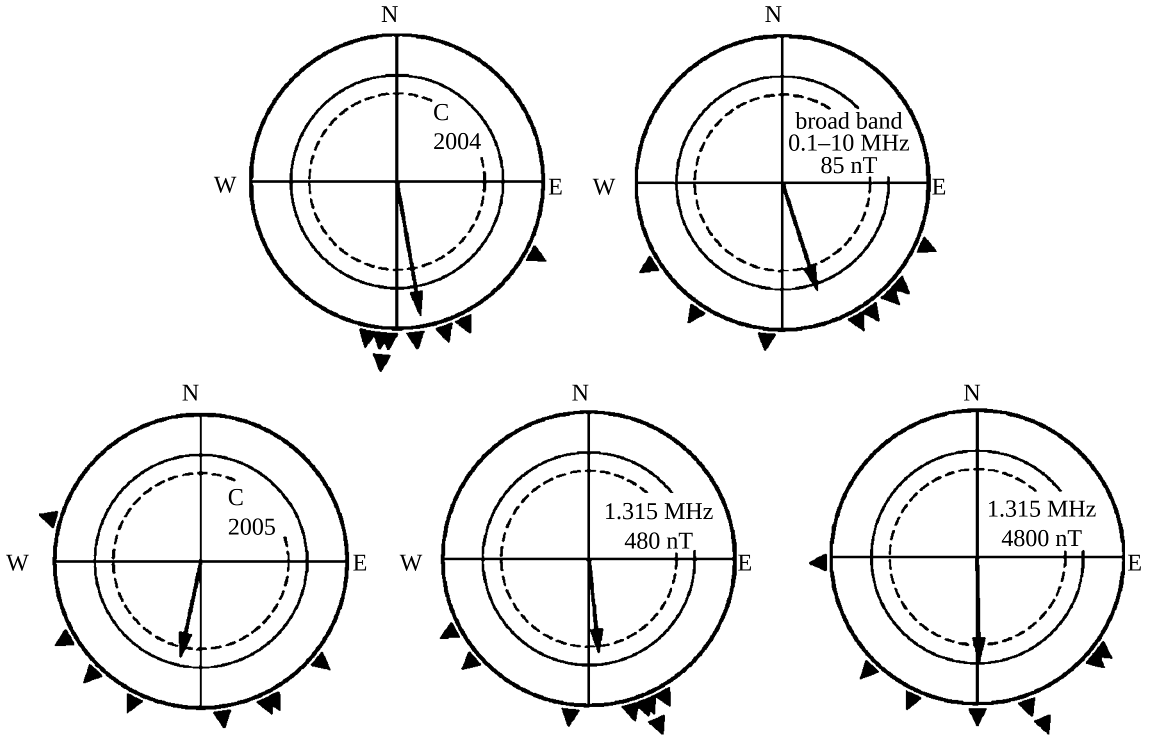

Figure 1. Orientation of the nests built by mole-rats in the local geomagnetic field (C), combining the two sets of control data from 2004, and with various high-frequency fields added (frequency and intensity indicated). The symbols at the periphery of the circle marks the means of the nests of the eight groups; the arrows represent the grand mean vectors based on these means, drawn proportional to the radius of the circle = 1. The two inner circles represent the 5% (dashed circle) and 1% (solid circle) significance border of the Rayleigh test (Batschelet 1981). For numerical data, see tables 1 and 2.

orientation processes of this species: a brief, strong magnetic pulse designed to alter the magnetization of magnetite particles caused the mole-rats to markedly shift the direction of their nests, a tendency that was stable for more than three months after pulse treatment (Marhold *et al.* 1997*b*). In view of these findings and the absence of HF effects in the present study, a magnetite-based compass in mole-rats appears most likely.

It is not yet clear, however, to what extent our findings with mole-rats are characteristic for mammals in general. In birds, a magnetic compass has now been demonstrated in more than 20 species from four different orders. So far, the European robin is the only species where a radical pair mechanism has been identified; yet the functional mode as an inclination compass, which is to be expected if radical pair processes are involved, has been found in all avian species tested for it. In mammals, a magnetic compass was first indicated in woodmice, *Apodemus sylvaticus* (Mather & Baker 1981); in the following years, magnetic compass orientation was reported in other species of rodents (Mather 1985; August *et al.* 1989; Burda *et al.* 1990, 1991), horses (Baker 1989*a*) and humans (Baker 1989*b*). However, mole-rats are the only species where the functional mode has been analysed and where the underlying physical processes are indicated (Marhold *et al.* 1997*a*,*b*; this study). Mole-rats live in underground tunnels, and their visual system is reduced (Němec *et al.* 2004); hence it cannot be excluded that their magnetic compass is a special development adapted to their subterranean lifestyle. On the other hand, many mammalian species are nocturnal or live in habitats with little light. This is also reflected by their sensory systems, with their optic sense inferior to that of day-active animals like birds, yet their auditory sense and in particular their sense of smell highly developed. In view of this, it would also seem possible that mammals generally have a magnetic compass based on a non-light-dependent mechanism and that this helped them to adapt to a subterranean lifestyle—an interesting topic for future research.

Among vertebrates, birds and rodents thus seem to have developed different reception mechanisms to obtain magnetic compass information. Amphibians seem to have a light-dependent inclination compass like birds (Phillips 1986; Phillips & Borland 1992), so that a radical pair mechanism is to be expected. Another group of vertebrates where the magnetic compass has so far been analysed in some detail are marine turtles: their magnetic compass is an inclination compass (Light *et al.* 1993) like that of birds, but at the same time, it is independent of light (Lohmann & Lohmann 1993) like that of rodents. It will be most interesting to identify the underlying reception mechanisms.

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REFERENCES

August, P. V., Ayvazian, S. G. & Anderson, J. T. G. 1989 Magnetic orientation in a small mammal, *Peromyscus leucopus*. *J. Mammal.* **70**, 1–9.

Baker, R. R. 1989*a* Navigation and magnetoreception by horses and other non-human animals. In *Orientation and navigation—birds, humans and other animals*, paper 12. Cardiff: Royal Institute of Navigation.

Baker, R. R. 1989*b* *Human navigation and magnetoreception*. Manchester: Manchester University Press.

Batschelet, E. 1981 *Circular statistics in biology*. London: Academic Press.

Burda, H., Marhold, S., Westenberger, T., Wiltschko, R. & Wiltschko, W. 1990 Evidence for magnetic compass orientation in the subterranean rodent *Cryptomys hottentotus* (Bathyergidae). *Experientia* **46**, 528–530. (doi:10.1007/BF01954256)

Burda, H., Marhold, S., Wiltschko, W., Beiles, A., Nevo, E. & Simon, S. 1991 Spontane magnetische Richtungspräferenzen bei Blindmäusen, *Spalax ehrenbergi* superspecies (Rodentia, Mammalia). *Verh. Dtsch. Zool. Ges.* **84**, 339.

Davila, A. F., Fleissner, G., Winklhofer, M. & Petersen, N. 2003 A new model for a magnetoreceptor in homing pigeons based on interacting clusters of superparamagnetic magnetite. *Phys. Chem. Earth* **28**, 647–652.

Kirschvink, J. L. & Gould, J. L. 1981 Biomagnetic magnetite as a basis for magnetic field detection in animals. *BioSystems* **13**, 181–201. (doi:10.1016/0303-2647(81)90060-5)

Kirschvink, J. L., Jones, D. S. & MacFadden, B. J. (eds) 1985 *Magnetite biomineralization and magnetoreception in organisms*. New York: Plenum Press.

Light, P., Salmon, M. & Lohmann, K. J. 1993 Geomagnetic orientation of loggerhead turtles: evidence for an inclination compass. *J. Exp. Biol.* **182**, 1–10.

Lohmann, K. J. & Lohmann, C. M. F. 1993 A light-independent magnetic compass in the leatherback sea turtles. *Biol. Bull.* **185**, 149–151.

Marhold, S., Wiltschko, W. & Burda, H. 1997*a* A magnetic polarity compass for direction finding in a subterranean mammal. *Naturwissenschaften* **84**, 421–423. (doi:10.1007/s001140050422)

Marhold, S., Burda, H., Kreilos, I. & Wiltschko, W. 1997*b* Magnetic orientation in common mole-rats from Zambia. In *Orientation and navigation—birds, humans and other animals*, paper 5. Oxford: Royal Institute of Navigation.

Mather, J. G. 1985 Magnetoreception and the search for magnetic material in rodents. In *Magnetite biomineralization and magnetoreception in organisms*, pp. 509–533. New York: Plenum Press.

Mather, J. G. & Baker, R. R. 1981 Magnetic sense of direction in woodmice for route-based navigation. *Nature* **291**, 152–155. (doi:10.1038/291152a0)

Němec, P., Burda, H. & Peichl, L. 2004 Subcortical visual system of the African mole-rat *Cryptomys anselli*: to see or not to see. *Eur. J. Neurosci.* **20**, 757–768. (doi:10.1111/j.1460-9568.2004.03510.x)

Phillips, J. B. 1986 Two magnetoreception pathways in a migratory salamander. *Science* **233**, 765–767.

Phillips, J. B. & Borland, S. C. 1992 Magnetic compass orientation is eliminated under near-infra-red light in the eastern red-spotted newt *Notophthalmus viridescens*. *Anim. Behav.* **44**, 796–797. (doi:10.1016/S0003-3472(05)80311-2)

Ritz, T., Adem, S. & Schulten, K. 2000 A model for photoreceptor-based magnetoreception in birds. *Biophys. J.* **78**, 707–718.

Ritz, T., Thalau, P., Phillips, J. B., Wiltschko, R. & Wiltschko, W. 2004 Resonance effects indicate a radical-pair mechanism for avian magnetic compass. *Nature* **429**, 177–180. (doi:10.1038/nature02534)

Schulten, K., Swenberg, C. & Weller, A. 1978 A biomagnetic sensory mechanism based on magnetic field modulated coherent electron spin motion. *Z. Phys. Chem.* **NF111**, 1–5.

Thalau, P., Ritz, T., Stapput, K., Wiltschko, R. & Wiltschko, W. 2005 Magnetic compass orientation of migratory birds in the presence of a 1.315 MHz oscillating field. *Naturwissenschaften* **92**, 86–90. (doi:10.1007/s00114-004-0595-8)

Wiltschko, R. & Wiltschko, W. 1995 *Magnetic orientation in animals*. Berlin: Springer.

Wiltschko, W. & Wiltschko, R. 2005 Magnetic orientation and magnetoreception in birds and other animals. *J. Comp. Physiol.* **191**, 675–693. (doi:10.1007/s00359-005-0627-7)

Wiltschko, R., Ritz, T., Stapput, K., Thalau, P. & Wiltschko, W. 2005 Two different types of light-dependent responses to magnetic fields in birds. *Curr. Biol.* **15**, 1518–1523. (doi:10.1016/j.cub.2005.07.037)

Yorke, E. 1979 A possible magnetic transducer in birds. *J. Theor. Biol.* **77**, 101–105. (doi:10.1016/0022-5193(79)90140-1)