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50 Hz Magnetic Field Effects on the Performance of a Spatial Learning Task by Mice

Zenon J. Sienkiewicz,* Richard G.E. Haylock, Rachel Bartrum, and Richard D. Saunders

National Radiological Protection Board, Chilton, Didcot, Oxfordshire, United Kingdom

Intense magnetic fields have been shown to affect memory-related behaviours of rodents. A series of experiments was performed to investigate further the effects of a 50 Hz magnetic field on the foraging behaviour of adult, male C57BL/6J mice performing a spatial learning task in an eight-arm radial maze. Exposure to vertical, sinusoidal magnetic fields between 7.5 μT and 7.5 mT for 45 min immediately before daily testing sessions caused transient decreases in performance that depended on the applied flux density. Exposure above a threshold of between 7.5 and 75 μT significantly increased the number of errors the animals made and reduced the rate of acquisition of the task without any effect on overall accuracy. However, the imposition of a 45-minute delay between exposure at 0.75 mT and behavioural testing resulted in the elimination of any deficit. Similarly, exposure to fields between 7.5 μT and 0.75 mT for 45 min each day for 4 days after training had no amnesic effects on the retention and subsequent performance of the task. Overall, these results provide additional evidence that 50 Hz magnetic fields may cause subtle changes in the processing of spatial information in mice. Although these effects appear dependent on field strength, even at high flux densities the field-induced deficits tend to be transient and reversible. Bioelectromagnetics 19:486–493, 1998.

Key words: ELF; magnetic fields; memory; power frequency; spatial learning; radial arm maze

INTRODUCTION

In a recent study, it was reported that immediate, prior exposure to a 50 Hz magnetic field at 0.75 mT for 45 min reduced the rate at which male mice learned to perform a spatial memory task in a radial arm maze [Sienkiewicz et al., 1998]. Exposure increased the number of errors the animals made in the maze especially in the first few days of testing, but overall accuracy was not impaired, because the exposed animals eventually learned the task as well as control animals. These findings confirmed and extended similar results originally reported using rats. Lai [1996] first showed that exposure of male rats to a 60 Hz field at 0.75 mT before daily training sessions in a 12-arm maze produced highly significant deficits in foraging, with the exposed animals consistently making more errors in the maze than those sham-exposed. It was speculated [Sienkiewicz et al., 1998] that differences in task difficulty may account for some of the difference in results between studies, although species and procedural differences must also make some contribution. Together these studies suggest that magnetic fields may disrupt spatial learning and working memory in rodents.

More recently, Lai et al. [1998] showed that place learning in a Morris water maze was also affected by prior exposure to 60 Hz magnetic fields. Animals exposed to a 1 mT field for 60 min learned to locate the submerged platform in the water maze during learning trials, possibly using nonspatial strategies, but they did not adopt an optimal search pattern to find the (missing) platform in the probe trial. A field-induced deficit in spatial reference memory was proposed to explain this result. In addition, Lai suggested that a decrease in central cholinergic activity in the frontal cortex and hippocampus, possibly as a consequence of field-induced activation of endogenous opioids, may account for these behavioural effects [Lai et al., 1993; Lai, 1996].

Taken together, these results add confidence to the belief that extremely low frequency magnetic fields

*Correspondence to: Dr. Z. J. Sienkiewicz, NRPB, Chilton, Didcot, Oxon, OX11 0RQ United Kingdom.

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may affect specific memory-related behaviours in animals [Salzinger, 1994]. They are also highly suggestive of a robust effect on spatial learning that generalises between species and does not require exact or unique experimental conditions and procedures to be observed. However, these behavioural studies suffer from a number of potential limitations that may restrict the more general application of their results. For example, the animals were exposed to a single value of flux density, so it is not known how the deficits in learning may change with variation in the magnetic field. Therefore, an experiment was conducted to investigate the relationship between change in behaviour and flux density (subsequently called the dose-response experiment). Another possible constraint is that all the animals in the previous studies were tested immediately after exposure to the field, so the length of time that these behaviours remain affected by the magnetic field is not known. Hence, a second experiment was conducted to investigate the effect of the introduction of a delay between exposure and behavioural testing (interval experiment). Finally, both radial arm maze studies investigated effects on the initial acquisition of the task and neither investigated whether the processing of previously learned information was affected by subsequent exposure to a magnetic field. Therefore, a final experiment investigated if repeated, short-term magnetic field exposure exerted any effect on the retention and performance of the task (retention experiment).

MATERIALS AND METHODS

Subjects

Male C57BL/6J mice at 12 weeks of age were purchased from MRC Laboratories, Harwell, Oxfordshire, United Kingdom. They were housed in individual polypropylene cages (29 cm × 15 cm × 12 cm) in a colony room adjacent to the behavioural laboratory and were given free access to standard laboratory diet (SDS RM-1) and water for 1 week before any procedure. Bedding was provided by commercial sawdust (Litalabo: SPPS, Argenteuil, France). The ambient conditions were maintained within the temperature range of 21 to 23 °C and 45 to 60% relative humidity. Lighting was provided from 0600 to 1800 hours. The background time-varying fields within the colony room were 0.1–0.4 μT, and the static field was 44 μT. All procedures were carried out in accordance with the Animals (Scientific Procedures) Act 1986.

Apparatus

Mice were exposed to a vertical, sinusoidal magnetic field at 50 Hz using a conventional yoked magnet. This device is composed of two sets of aluminium coils mounted in a laminated steel yoke and supported by a free standing iron frame. This magnet has been described in detail elsewhere [Kowalczuk et al., 1994]. The ambient temperature between the coils was maintained at 22 °C by an air conditioning unit and air extract fan within the laboratory. These devices also provided a background, masking noise of 55 dB(A) over the range of 20 Hz to 20 kHz. There was no perceptible vibration at any of the flux densities used in this study.

During exposure, the animals were housed in polycarbonate cages (33 cm × 15 cm × 13 cm). These cages contained no metallic parts. Water was available from a glass bottle fitted with a Melamine spout, and sawdust was provided as bedding. The cages were mechanically isolated from the magnet by resting on a free-standing, rigid Perspex table that straddled the lower coils of the magnet.

The radial arm maze was constructed from Perspex and consisted of a central, octagonal arena 24 cm in diameter and eight arms, each 32-cm long. The design was based on the original maze of Olton and Samuelson [1976] but was modified for mice after Pick and Yanai [1983]. Each arm had transparent side walls 3 cm high. The arena and arms were not enclosed except for the 10 cm of each arm proximal to the arena, which was covered by a transparent canopy to prevent the animals jumping directly between the arms. A small, circular food well (1 cm deep and 2 cm in diameter) was centred 3 cm from the distal end of each arm. Access to and from the arms was controlled by the use of opaque guillotine doors. These doors were remotely operated by the experimenter using a series of solenoid-activated pneumatic cylinders housed beneath the arena. The solenoids were powered by 24 V DC and produced a maximal field of 2 μT in the arena. The equipment within the laboratory was assumed to provide visual cues to guide behaviour [Olton and Samuelson, 1976]. Illumination was provided by overhead fluorescent lighting.

Behavioural Procedures

All mice were experimentally näive, and they were randomly assigned to one of the treatment groups. They were food deprived to 85% of their free-feeding weight over the 14 days before testing and were subsequently maintained at that level for the duration of the experiment. Water was always available in the home cages. Each experiment was performed using different batches of animals.

For preliminary training for all groups, each arm of the maze was baited with a food reward (45-mg food pellet: BioServ, Frenchtown, NJ), and the subject animal placed in the maze for one session lasting 5 min. Once the subject was in the maze, all doors were opened after about 5 s, and these doors remained opened until the end of the session. Each subject was under constant, remote surveillance using a system of video cameras and monitors, but its behaviour during this session was not recorded.

Before each testing trial, a subject was transported in its home cage to a nearby laboratory containing the exposure system, transferred into a separate exposure cage, and placed within the bore of the magnet. After 45 min of exposure or sham exposure, the cage was taken out of the magnet, and the subject was placed back in its own cage and returned to the behavioural laboratory. The distance between laboratories was about 100 m, and the maximal delay between the end of exposure and the start of the trial was about 1 min.

Animals in the dose-response experiment were weighed and then placed immediately within the maze to begin the trial. Animals in the interval experiment were first returned to the colony room for 45 min, after which they were weighed and placed within the maze to begin their trial. Animals in the retention study first received 10 daily trials on the task. They were not exposed to any source-generated magnetic field during this period. The animals were then exposed to the magnetic field (or sham-exposed) for 45 min each day for 4 days. After each exposure, these animals were taken back to the behavioural laboratory, weighed, and returned to the colony room. They were not tested in the maze on these days. Beginning on the day after the last exposure (or sham-exposure) the animals received an additional five daily trials in the maze. In all experiments, a maximum of three animals were exposed at one time within the magnet, with the start of exposure being staggered between successive animals by 15 min.

Subjects were exposed at 7.5 μT, 75 μT, 0.75 mT, or 7.5 mT. The magnetic flux density was continually measured using a Bell 9200 Gaussmeter equipped with either a MOW92-2506 Magnaprobe or a STB92-0404 transverse probe. The variation in flux density was less than ±5%. Control subjects were sham-exposed and underwent identical handling and behavioural procedures as their field-exposed counterparts but were only exposed to the ambient magnetic fields within the magnet. These fields were measured using an EMDEX II magnetic field dose meter and found to be less than 50 nT. The static magnetic field within the magnet was 40 μT. This was horizontal (±5°), aligned down the axis of the magnet and orthogonal to the applied field. The axis of the magnet itself was aligned in a NNE direction.

All subjects were required to learn the standard (win-shift) version of the task. They were confined in the central arena for about 5 s between arm choices to stop the use of kinaesthetic or other simple choice strategies. Visiting an arm was defined as the placement of all four feet within that arm. Because food rewards were not replaced during a trial, revisiting an arm during the same trial was scored as an error. The sequence of arms entered and the time to complete the trial were recorded. Times were measured to the nearest second using a hand-held stopwatch from the moment the guillotine doors were first opened until the last pellet was eaten or 15 min had elapsed. The subject was removed from the maze once it had visited all eight arms or after the maximal session length of 15 min. It was then returned to its home cage and fed its daily food ration. All surfaces of the maze were cleaned between trials using alcoholic wipes and compressed air.

Statistical Analysis

The results were analyzed by estimating the probability that an animal will not re-enter any given arm of the maze using maximal likelihood techniques, and then using these probabilities as the measure of performance of the task [Sienkiewicz et al., 1992]. To determine whether differences existed between treatments, various models were fitted to the performance scores of the treatment groups for each experiment. These models considered that there were either no differences in performance between the groups, or that there was a constant difference, an initial difference that tended to zero, or a difference in the rate of increase in performance. Other models considered a combination of these parameters. The models were compared by referring changes in the deviance divided by the associated changes in the degrees of freedom to the chi-squared distribution. These techniques are a generalization of analysis of variance (ANOVA) and may be considered equivalent to a two-way ANOVA, but using a binomial distribution for the underlying random variability.

RESULTS

All exposures and testing were performed between 0830 and 1730 hours. The order of testing of the treatment groups was determined by chance at the start of the experiment and was maintained in this order for all subsequent days. In the dose-response experiment, the subjects exposed at 75 μT were tested first in the morning followed by those exposed at 7.5 μT; and in the afternoon, the control subjects were tested first followed by those exposed at 7.5 mT. In the interval experiment, the exposed animals were tested in the morning, and the control animals were tested in the

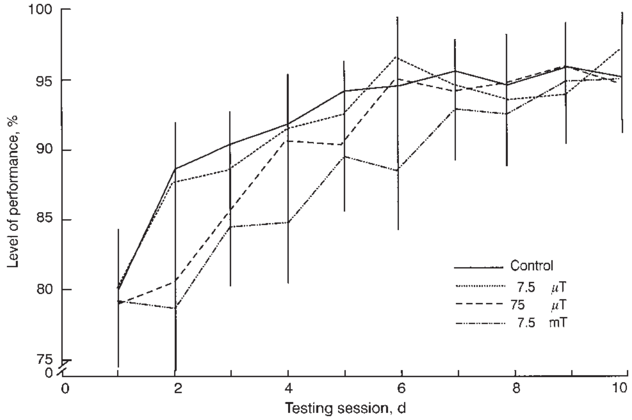

Fig. 1. Mean performance scores (±standard error) of mice during testing in a radial arm maze. Experimental animals (n = 6) were exposed to a 50 Hz magnetic field as indicated for 45 min immediately before testing; control animals (n = 6) were sham-exposed. Performance was measured as the probability of not re-entering any given arm of the maze and expressed as a percentage. The performances of the animals exposed at 7.5 mT were significantly different from those of the control group.

TABLE 1. Results of Statistical Analysis of the Dose-Response Experiment*

Treatment	Model	Deviance	Degrees of freedom	χ^2	*P*
7.5 μT	B	1411.63	1325		
	R	1410.95	1324	0.68	.4096
75 μT	B	1509.72	1386		
	R	1506.47	1385	3.25	.071
7.5 mT	B	1651.41	1472		
	R	1624.61	1471	26.80	< .05

*Eight different models were fitted to the results to compare the performances of the experimental and control groups [Aitkin et al., 1989]. The results of comparisons between the base model, which assumed no differences between treatment groups (model B), and the model, which assumed there was a difference only in the rate of improvement in performance (model R) are given. The latter provided the greatest improvement in fit compared with the base model for the animals exposed at 7.5 mT, and, hence, was the best fitting model to describe these data. Results of comparisons with the other models are not shown.

afternoon. This order became reversed for the retention experiment.

Figure 1 shows the change in performance with testing for the treatment groups within the dose-response experiment, performance being measured as the probability of not re-entering any arm of the maze. As shown in Figure 1, performance appeared to depend on the flux density. Exposure at 7.5 mT increased the number of errors made in the maze and significantly impaired performance, but the exposed animals finally reached the same level of accuracy as the controls. Statistical analysis showed that these data were best described by the model that assumed that the only difference between the treatment groups was in the rate of improvement of performance of the task. This model provided the greatest improvement in fit compared with the base model that assumed no differences between the groups (Table 1). There were no significant differences between treatment groups either on the initial or final levels of performance. Exposure at 75 μT also increased the number of errors made in the maze and slightly impaired performance, but the difference from the control group was not significant. These data were best described by the model that assumed no differences between treatment groups. Exposure at 7.5 μT had no significant effect on the number of errors made and had no effect on performance. These data were also best described by the model that assumed no difference between treatment groups.

Standard modelling techniques [Aitkin et al., 1989] were used to investigate the relationship between change in performance and flux density over the whole experiment. To improve the power to describe this relationship, the data for a group of 24 animals exposed at 0.75 mT and their 24 controls [Sienkiewicz et al., 1998] were included in this analysis. (These animals had been housed, maintained, and tested in this laboratory using identical methods and protocols to those of the present experiment, and the performance of these controls was not significantly different from that of the controls in the present experiment). The best fitting model to describe all these data was found to consist of two curves intersecting at day 1 (Fig. 2). One of

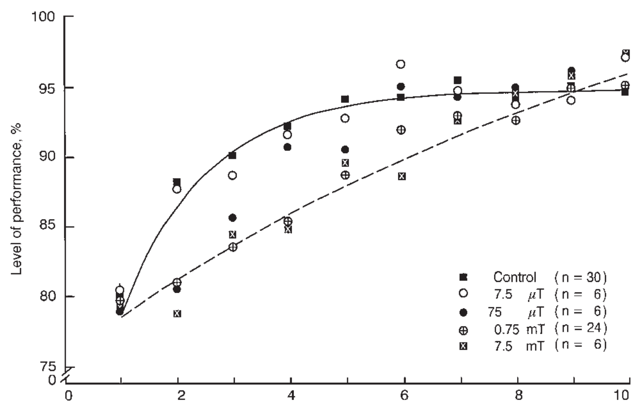

Fig. 2. The best fitting model to describe the performance of the animals in the dose response experiment compared with observed data. One curve (solid line) described the performance of the controls and the animals exposed at 7.5 μT, whereas the other curve (broken line) described the performance of the three other groups. The data for the animals exposed at 0.75 mT and additional controls are taken from Sienkiewicz et al. [1998].

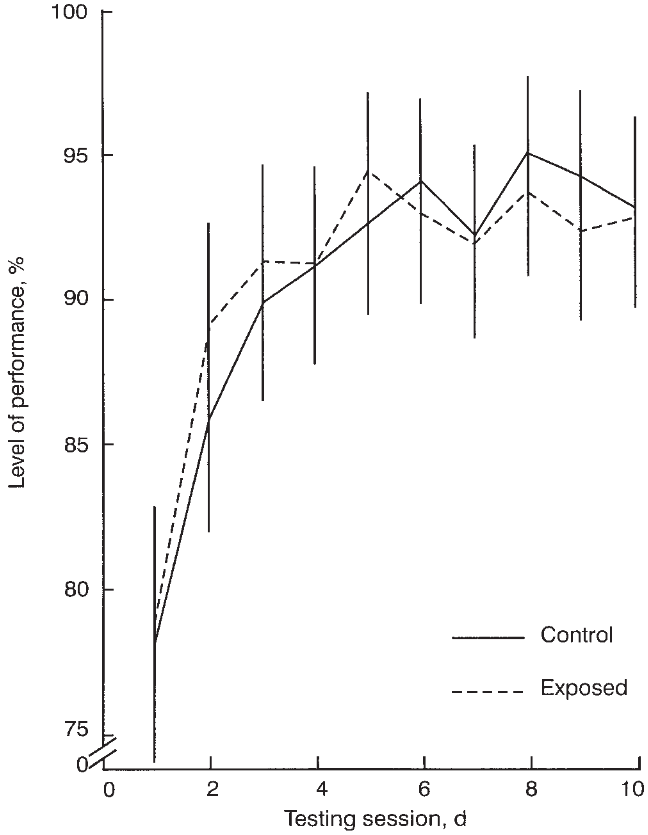

Fig. 3. Mean performance scores (± standard error) of mice during testing in the interval experiment. Experimental animals (n = 8) were tested in a radial arm maze 45 min after exposure to a 50 Hz magnetic field at 0.75 mT for 45 min; control animals (n = 8) were sham-exposed. Performance was measured as the probability of not re-entering any given arm of the maze and expressed as a percentage. Magnetic field exposure had no significant effect on performance.

these curves described performance of both the controls and the 7.5 μT group, whereas the other curve described the performance of the remaining three groups. The form of this model suggested that a threshold for a deficit in performance seemed to exist between 7.5 and 75 μT and that the magnitude of the deficit did not increase significantly with increasing flux density above this threshold. No further analysis of the relationship between impairment and flux density was undertaken.

Figure 3 shows the change in performance with testing for the interval experiment, performance again being measured as the probability of not re-entering any arm of the maze. Exposure at 0.75 mT did not affect performance 45 min after exposure, and any differences between treatment groups were not significant: these data were best described by the model that assumed no differences between groups (Table 2).

TABLE 2. Results of Statistical Analysis of the Interval Experiment*

Treatment	Model	Deviance	Degrees of freedom	χ^2	*P*
0.75 mT	B	1913.07	1762		
	I	1913.05	1761	0.02	.88
	F	1913.05	1761	0.02	.88
	R	1911.55	1761	1.52	.21

*Eight different models were fitted to the results to compare the performances of the experimental and control groups [Aitkin et al., 1989]. The best fit was provided by the base model, which assumed no differences between treatment groups (model B). All other models failed to provide significant improvements in fit. For comparison, the results for model I are given, which assumed an initial and sustained difference in performance between groups, model F, which assumed a final difference in performance, and model R, which assumed a difference in the rate of improvement in performance.

Figure 4 shows the changes in performance in the retention experiment, performance being measured as before. Animals were exposed at either 7.5 μT, 75 μT, or 0.75 mT. There were no significant differences between groups in the original learning phase of the task, nor were there any significant differences between treatment groups in the second, posttreatment phase of the task: in both phases of the experiment, these data were best described by the model that assumed no differences between groups (Fig. 5). As expected, all groups regardless of exposure condition tended to make a few more errors in the maze at the start of the second

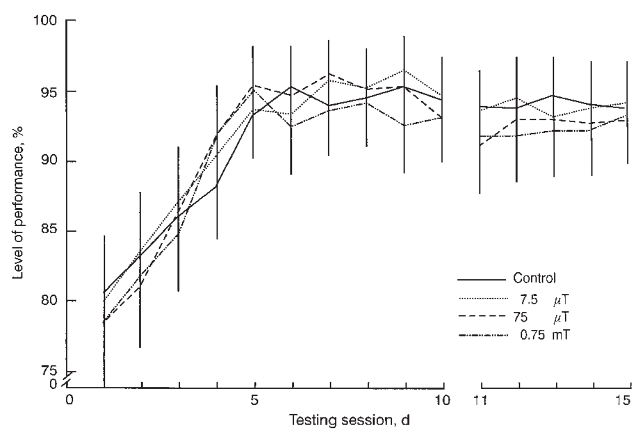

Fig. 4. Mean performance scores (± standard error) of mice during testing in the retention experiment. All groups of animals (n = 7 in all cases) were first tested on the task without overt exposure to any field. Experimental animals were then exposed to a 50 Hz magnetic field as indicated for 45 min each day for 4 days; control animals were sham-exposed. Performance was then reassessed in the maze for a further 5 days. Magnetic field exposure had no significant effect on performance.

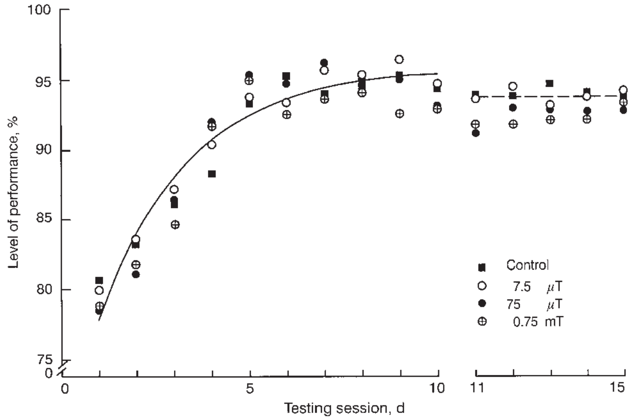

Fig. 5. The best fitting model to describe the performance of the animals in the retention experiment compared with observed data. A single curve (solid line) described the performances of all the four groups of animals during the 10 days of testing before treatment; likewise, another single curve (broken line) described all performances over the 5 days after treatment.

phase of the experiment; however, these differences were not significant (Kruskal-Wallis test: $H = 0.15$; $df = 3$; $P = .985$).

Every animal in each experiment managed to visit all eight arms within the 15-min period allowed each day. Across all experiments and treatment groups, the range of times to complete a trial was 197–836 s at the start of testing and 144–639 s at the end of testing. There were no significant differences between treatment groups in any of the three experiments in the times to complete the daily trials ($P > .05$, in all cases). This finding is in agreement with the results of previous studies [Lai, 1996; Sienkiewicz et al., 1998] which showed that exposure to a magnetic field did not significantly affect the time to complete foraging in a radial arm maze.

DISCUSSION

The present study investigated the effects of acute exposure to 50 Hz magnetic fields on foraging behaviour in a radial arm maze by adult male mice under a variety of conditions. It was shown again that animals exposed to magnetic fields immediately before testing made more errors in the maze that resulted in a significant decrease in the rate at which performance improved. However, as before, the animals learned to perform the task as well as controls, so there was no effect on overall accuracy. These deficits in performance depended on the intensity of the field with a threshold for significant effects being identified between 7.5 and 75 μT. Above this threshold the deficits in behaviour tended to increase, although the increase with flux density was not significant. In contrast, no deficits were seen if a simple delay was introduced between exposure and testing. Similarly, performance did not seem to be affected by exposure once the task had been learned. Overall, these results suggest again that acute exposure to magnetic fields may cause a deficit in spatial learning and working memory in mice, but long-term memory seems unaffected.

The finding that the deficits in performance did not significantly increase with increasing flux density above the apparent threshold for the effect is most interesting and merits further study. Nevertheless, it should be noted that the errors made in the maze by the exposed animals showed a tendency to increase with increasing flux density, but this increase was too modest to reach statistical significance. It is possible that a ‘‘floor effect’’ is being seen here in performance; a similar possibility has been considered by Lovely et al. [1991] with rats in an eight-arm maze. The C57BL performs the radial arm maze task compared very well with other strains of mouse [Ammassari-Teule et al., 1993], and in our experience, even a näive mouse will be successful in foraging in our maze after making roughly 30 or so errors. This number reduces rapidly within half a dozen sessions to become close to an asymptotic value. Therefore, further investigations are warranted before drawing explicit conclusions regarding the existence of a threshold. These studies should use flux densities at intermediate values to those used already, especially between 10 and 100 μT, and perhaps spatial learning tasks more challenging to the animals. These would not only help to clarify the relationship between flux density and behaviour, but also help to better define any putative threshold value.

Another interesting possibility raised by these studies is that even intense magnetic fields do not seem to cause long lasting or permanent changes in behaviour. First, it has been shown here that the number of errors the exposed animals make decreases steadily during the course of testing, and second, the results of the interval experiment clearly indicate that any initial effects induced by the magnetic field only persist for a very short time. A delay of only 45 min between exposure and testing was sufficient to completely abolish any deficits in behaviour. This finding suggests that normal homeostatic mechanisms can readily compensate for the field-induced changes that lead to the observed effects on behaviour. However, further studies are required using other flux densities to confirm the generality of this result.

The results of the final experiment clearly show that magnetic fields do not cause any significant changes in the retention of a well-established memory.

This finding is in agreement with the results of a previous preliminary study [Sienkiewicz et al., in press]. In the latter experiment, animals were also exposed to a magnetic field after receiving 10 daily trials in a radial arm maze; however, one group was exposed to a 0.75 mT field for a single session of 45 min, whereas another group was exposed for 45 min each day for 5 days. Performance was assessed using a single probe trial in the maze immediately after exposure. In both cases, exposure had no significant effect on performance during the probe trial. The present retention experiment investigated performance over the 5 days after exposure for 45 min each day for 4 days, and no significant field-dependent effects were seen, either at the start of or during the course of the retesting phase of the experiment. This result is also in general agreement with that of Lovely et al. [1992], who found that exposure to a combined AC and DC magnetic field had no effect on rats who had previously learned to forage within a radial arm maze. Thus, although the evidence available is very limited, it would seem to indicate that magnetic fields do not affect the retention of learned information even at levels that may affect initial learning.

Although these experiments were performed with mice, spatial memory function in rodents has been used as a model for understanding cognition and memory in humans. Therefore, it is not unreasonable to expect that humans exposed to intense magnetic fields under similar conditions may also show some transient cognitive or amnesic effect. It is not clear, however, that these conditions would be realised in either residential or occupational situations. The results of the dose-response experiment indicate that animals must be exposed above a threshold of between 7.5 and 75 μT to cause significant effects. This level is very much greater than the flux densities generally encountered in the public environment. In the United Kingdom, for example, most houses have ambient background fields of about 10 nT to 300 nT [NRPB, 1992], and the average (power frequency) fields even within homes close to high voltage overhead power lines are less than 1 μT [Merchant et al., 1994]. Nevertheless, the recommended restriction on human exposure to 50 Hz magnetic fields in the United Kingdom is 1.6 mT [NRPB, 1993], and fields of the necessary magnitude for effects in mice could be found directly under some overhead power lines [McKinlay et al., 1996] and be experienced in some industrial situations, such as within the power industry, when arc welding and using induction furnaces [NRPB, 1992]. However, exposures under the latter conditions are expected to be of intermittent and short duration, dependent largely on working practices [Chadwick, 1997]. Thus workers may not be continuously exposed to high fields for very long.

In the present experiments, all animals were exposed to magnetic fields for the same duration each day, so they contain no information on the possible effects of using different exposure periods. However, previously we found that short exposures of up to 15 min did not cause a significant effect on radial maze performance irrespective of flux density used [Sienkiewicz et al, 1996]. Together these results suggest that exposure must exceed a period of between 15 and 45 min to affect behaviour, although another study [Kavaliers et al., 1996] also suggests that shorter exposure periods may affect learning in some situations. Therefore, although it may be possible to experience fields of the magnitude used in these studies, it is not clear that the necessary conditions would be fulfilled to cause any significant effect in everyday circumstances. However, the possibility of an interaction between intensity and duration of exposure cannot yet be completely ruled out, and it is possible that significant effects might be found under some conditions with either short exposures to intense fields or long exposures to weak fields.

Overall these studies provide additional evidence that power frequency magnetic fields may affect the processing of spatial information in rodents and extend the conditions under which effects may be observed. The studies reported to date have identified that acute exposure at high field strengths can cause a transient and reversible effect on learned behaviour. Further investigations are planned to explore whether prolonged exposure at low flux densities can cause any significant effect on spatial learning and working memory.

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