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Rats avoid high magnetic fields: Dependence on an intact vestibular system

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Abstract

High strength static magnetic fields are thought to be benign and largely undetectable by mammals. As magnetic resonance imaging (MRI) machines increase in strength, however, potential aversive effects may become clinically relevant. Here we report that rats find entry into a 14.1 T magnet aversive, and that they can detect and avoid entry into the magnet at a point where the magnetic field is 2 T or lower. Rats were trained to climb a ladder through the bore of a 14.1 T superconducting magnet. After their first climb into 14.1 T, most rats refused to re-enter the magnet or climb past the 2 T field line. This result was confirmed in a resistive magnet in which the magnetic field was varied from 1 to 14 T. Detection and avoidance required the vestibular apparatus of the inner ear, because labyrinthectomized rats readily traversed the magnet. The inner ear is a novel site for magnetic field transduction in mammals, but perturbation of the vestibular apparatus would be consistent with human reports of vertigo and nausea around high strength MRI machines.

Keywords: Inner ear; Labyrinthectomy; Magnetic resonance imaging

1. Introduction

Increased resolution in magnetic resonance imaging (MRI) requires the use of high strength static magnetic fields (MFs): MRI machines with 8 tesla (T) magnets are now in use for human imaging [1], and up to 11.7 T has been employed for experimental animal imaging [2]. While it has been reported that many vertebrates can detect or orient to earth-strength MFs of ~50 μT, the sensory effects of high MF on mammals are largely unknown. As the MFs used in clinical and experimental MRI get stronger, the possibility of aversive sensory effects becomes more relevant. Indeed, engineers working with 4 T magnets reported a significant occurrence of nausea and vertigo in the vicinity of the magnets [3], and vertigo has been reported after head movements within 7 and 8 T magnets [1].

There has been little evidence that rodents are affected by 2 T or lower MFs [4–9]. We have previously found, however, that exposure to MFs of 7 T and above induced clear behavioral and neural effects. Immediately after restraint for 10 min or longer within high field magnets, rearing in an open field was suppressed and the rats walked in tight circles for up to 2 min; the direction of circling was dependent on the orientation of the rat within the magnet field [10]. When rats drank a novel sweet solution prior to MF exposure, they acquired a conditioned taste aversion such that they subsequently avoided drinking the solution [10,11]. At the neural level, MF exposure induced c-Fos, an immediate-early gene product frequently used as a marker of neuronal activity, in vestibular and visceral relays of the brainstem [12]. Taken together, these results suggested that MF exposure was an aversive stimulus, possibly akin to motion sickness due to vestibular perturbation.

Although rats show effects of high MF exposure in the minutes and days after restraint within magnets, it is not clear if rats can immediately perceive a high MF during exposure and alter their voluntary behavior based on MF detection. To determine if rats acutely perceive a MF as an aversive stimulus, we trained rats on a task that required voluntary entry and traversal of a 14.1 T MF.

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Our approach was similar to that of Weiss et al. (1992), who observed that rats avoided entering the arm of a T-maze which extended into the horizontal bore of a 4.5 T electromagnet.

Here we confirm and extend the observations of Weiss et al. by showing that rats trained to ascend a vertical “ladder” will avoid entering the bore of either a 14.1 T superconducting magnet or a large resistive electromagnet ramped up to 14 T. We also demonstrate using chemical labyrinthectomy that the inner ear is required for rats to learn an avoidance of the high MF. These results suggest that the mechanism of MF detection and avoidance requires an interaction of the MF and the peripheral vestibular apparatus.

2. Materials and methods

Two magnets located at the US National High Magnetic Field Laboratory (NHMFL) were used in this study: a superconducting 14.1 T NMR magnet and a resistive 20 T magnet.

2.1. Superconducting 14.1 T NMR magnet

A 600 MHz high resolution superconducting NMR magnet (Magnex Scientific, Ltd, Abingdon, England) was used in experiments 1 and 3. The magnet had an 89 mm bore and a fixed maximum field strength of 14.1 T at its center (B_0). The magnet contained shim magnets extending along the bore for approximately ±15 cm from the core, which were used to stabilize the MF and to give a central core field of uniform strength. The MF was orientated vertically with the positive pole at the top of the magnet. The magnets were operated without radiofrequency pulses, exposing rats to only static MFs.

To map the gradient of the magnet field along the vertical axis of the bore, a copper coil was pulled through the magnet at a constant speed [13]. As it ascended through the bore of the magnet, the current induced in the coil by the MF was recorded every 1 mm. The current measurements were integrated and calibrated with the peak field strength of the magnet to calculate the MF at all vertical positions (see Fig. 1B).

2.2. Resistive 20 T magnet

A large resistive magnet at the NHMFL was used in experiment 2 to test ladder-climbing at increasing field strengths (0–14 T) within a single magnet [15]. Direct current of up to 40 kA at 500 V (20 MW) is passed through copper coils, resulting in vertically-oriented, static MFs of up to 20 T. The field strength falls off rapidly with distance, so that when the field is 20 T in the center of the magnet, the field is near 0 T at 2 m distance from the center. The distribution of the MF produced by this resistive magnet is very similar to the field produced by the 14.1 T superconducting magnet [14].

2.3. Ladder

A ladder was constructed out of a 1.25 cm^2 plastic mesh rolled into a vertical cylinder 8 cm in diameter and 2.2 m in height. Two plastic boxes (30 cm wide × 15 cm deep × 20 cm tall) were connected to the bottom and top ends of the cylinder: a start box at the bottom and a goal box at the top. Sliding plastic doors at the juncture of the boxes with the ladder controlled access to the ladder.

2.4. Animals and training

Adult female Sprague–Dawley rats (175–200 g; Charles River, Wilmington, DE) were individually housed in polycarbonate, solid-bottom cages under a 12-h light, 12-h dark cycle in the temperature-controlled animal facility of the NHMFL. Rats had *ad libitum* access to water but were maintained on a food restriction schedule at 85% of their starting body weight.

Rats were trained early in the light period prior to their daily feeding time. The rats were trained to exit the start box at the bottom of the ladder, climb the ladder, and enter the goal box, which contained a palatable food reward (a mash of 70 g powdered rodent chow mixed with 14 g sucrose, 40 g chocolate syrup and 70 ml distilled water). Each day at the start of training, rats were placed for 1 min in the goal box at the top of the ladder and allowed to eat the food reward. They were then removed from the goal box and placed in the start box at the base of the ladder. Most rats climbed the ladder spontaneously; rats that did not start to climb the ladder within 1 min were given access to the food reward in the goal box again before returning to the start box. After rats reached the goal box, they were allowed to consume the food reward for 1 min before beginning the next trial.

Rats were given 5 climbing trials each day for 10–14 days, until all rats reached the goal box on all 5 trials within 1 min or less after exiting the start box. Rats that refused to climb to the goal box on all 5 trials by the fifth day of training were excluded. On the last few days of training, a 2-m long cardboard tube (the “sham-magnet”) was placed around the mid-section of the ladder to simulate the passage through the darkened bore of the superconducting NMR magnet. Rats readily climbed the ladder, and after several days would complete 5 consecutive trials with climb times of 10–60 s.

2.5. Experiment 1. Climbing a ladder through a 14.1 T magnet

Rats ($n = 8$) were trained to climb the ladder as above; 4 other rats failed to climb consistently on 5 consecutive trials per day and so were excluded from the study. The rats were tested on 3 consecutive days. On each day, rats ran 5 trials (each 3 min or less) and their climb time was recorded. Rats were run in 5 trials to be consistent with their training protocol, and to observe any differences in climb time across trials. If a rat did not leave the start box or if it started to climb the ladder but did not reach the goal box within 3 min, the trial was terminated and assigned a climb time of 180 s.

On the first day (pre-sham), the ladder was extended through the cardboard “sham-magnet” tube. On the second day, the ladder was inserted through the vertical bore of the 14.1 T superconducting magnet (see Fig. 1A). The rats began climbing from the start box at floor level, where the fringe field was 0.05 T. Rats were given 5 trials to reach the goal box above the magnet

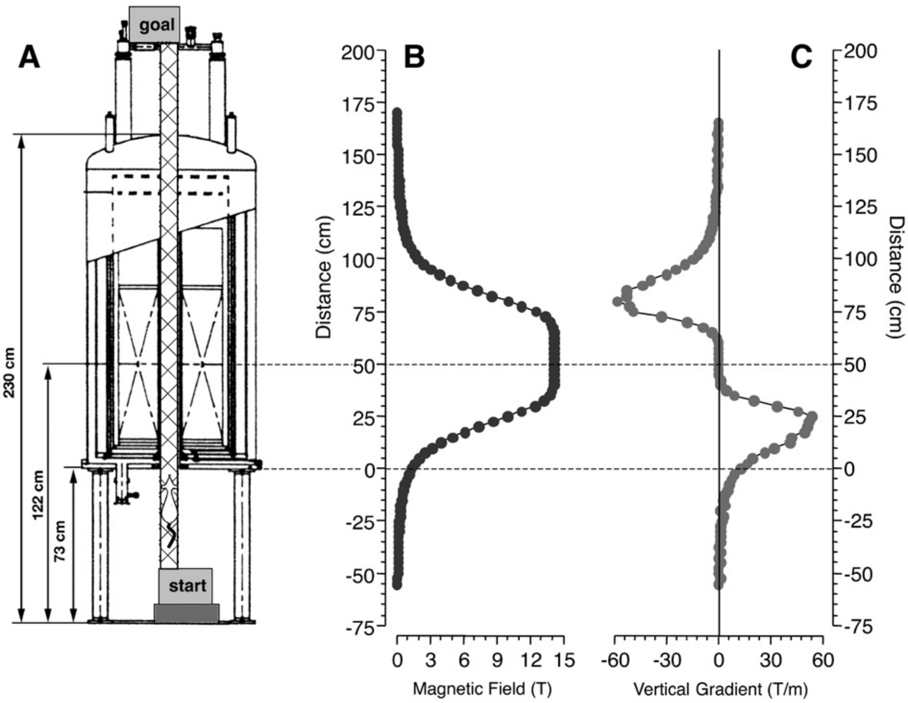

Fig. 1. A. Cross-sectional schematic of the 14.1 T superconducting magnet and the plastic mesh ladder inserted through the vertical bore. Rats were trained outside the magnet to climb the ladder from the start box to reach a food reward in the goal box. B. The magnetic field along the length of the ladder's path, relative to the opening of the bore at 0 mm. The magnetic field was close to 0 T at the ground level start box and at the goal box above the magnet. At the bore entrance, the field was just under 2 T, reaching a maximum of 14.1 T (B_0) between 350 and 650 mm above the ground. C. The field gradient along the vertical axis of the magnet (dB/dz) derived from the measured magnetic field.

(at 0.03 T), by climbing through the 14.1 T core field of the magnet. On the third day (post-sham), rats were given 5 more trials outside the MF with the ladder passing through the sham-magnet to assess any long-term effects of MF exposure.

On the magnet day, rats on each trial were videotaped with a digital video camera. The video from each trial was digitized on a Macintosh computer. By examining individual video frames in an editing program (iMovie), the maximum excursion towards the bore of the magnet made by each rat in each trial was measured; the maximum MF experienced by the rat on each trial could then be determined from the measured MF (Fig. 1B). (Rats that disappeared from view into the bore of the magnet were assumed to have exposed at least their heads to the maximum 14.1 T field, which lay only 35 cm within the magnet).

2.6. Experiment 2. Climbing a ladder through a resistive magnet

It is possible that rats avoided the bore of the 14.1 T NMR magnet in response to some property other than the presence of a MF (*e.g.* odor, illumination, vibration, etc.). To eliminate this possibility, a separate group of rats were tested in the large 0–20 T resistive magnet [15]. The resistive magnet has two advantages over the superconducting NMR magnet used in experiment 1. First, resistive magnets can be turned on and off; thus, the sham condition is identical to the MF-condition in all ways except for the presence of a MF. Importantly, rats that refuse to climb the ladder through a high MF can be retested at 0 T to determine if they are using non-magnetic cues (*e.g.* odor or light level) to avoid the magnet's bore. Second, the field strength of a resistive magnet can be set arbitrarily by varying the applied current. Thus, rats can be retested with arbitrary field strengths at the center of the magnet.

Rats were trained to run up the ladder to the goal box as before. Of the 12 rats trained to climb reliably (*i.e.* reaching the goal box in 5 consecutive trials per day), only the 6 rats with the fastest climb times were tested in the magnet, because of the limited time available on the resistive magnet. On the test day, the rats were transported from the animal facility of the NHMFL to the resistive magnet wing of the NHMFL, where the ladder was inserted through the 2-m long vertical bore of the 20 T resistive magnet. The resistive magnet was sequentially energized to 0, 1, 2, 4, 8, 12, and 14 T. All the rats were tested at one field strength before the MF was increased to the next field strength. As in experiment 1, rats were placed in the start box and their climb time to the goal box was recorded. Rats were given one trial at each field strength. If a rat failed to reach the goal box within 3 min, it was assigned a climb time of 180 s, and the trial was terminated. Rats that failed to climb through the 14 T field were retested within the resistive magnet at 0 T (the sham condition).

2.7. Experiment 3. Labyrinthectomized rats climbing through the 14.1 T magnet

Rats ($n=12$) were trained to climb the ladder as above. To test the role of the peripheral vestibular apparatus, rats (LBX, $n=6$) underwent chemical labyrinthectomy under halothane anesthesia by injecting sodium arsanilate through the tympanic

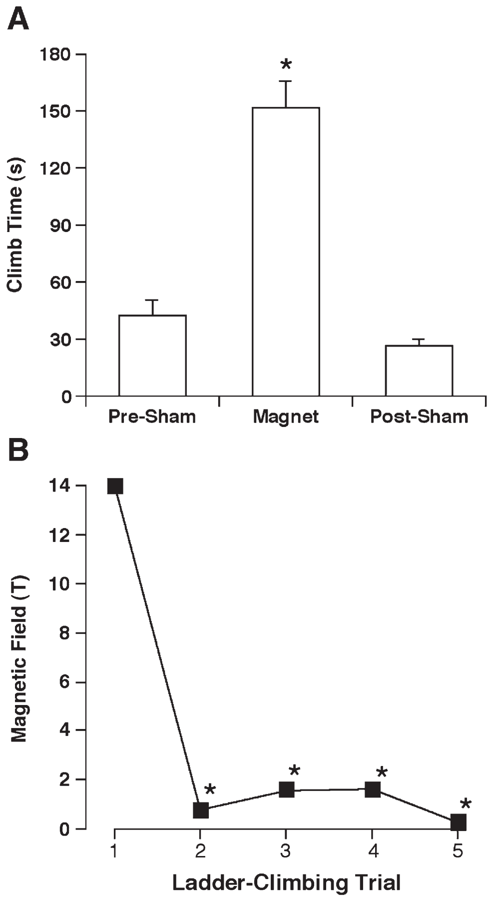

Fig. 2. A. Latency for rats ($n=8$) to climb the ladder through a cardboard "sham-magnet" (pre-sham and post-sham), or through the bore of the 14.1 T superconducting NMR magnet (magnet) to reach the goal box (average of 5 trials per rat). Most rats would not traverse the ladder through the magnetic field and were assigned a climb time of 180 s. *$p<0.05$ *vs* pre-sham test. B. Median of the maximum magnetic field reached by the rats when climbing through the magnet on 5 consecutive trials. After experiencing 14.1 T on the first trial, most rats would not climb past 2 T on subsequent trials. *$p<0.05$ *vs* first trial.

membrane into the inner ear (15 mg/50 µl of 0.15 M NaCl/ear). This procedure effectively destroys all sensory hair cells in the inner ear, rendering the rats unable to detect rotational or linear

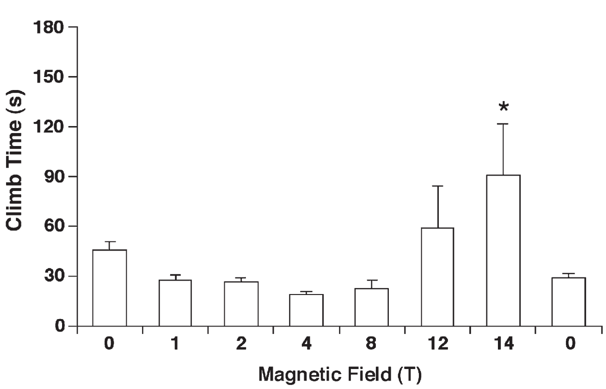

Fig. 3. Latency for rats ($n=6$) to reach the goal box by climbing through the bore of a resistive magnet energized to different magnetic field strengths. Rats were tested successively with one trial at each magnetic field strength. Half the rats refused to climb the ladder at 14 T, but climbed readily when retested at 0 T. *$p<0.05$ *vs* 0 T.

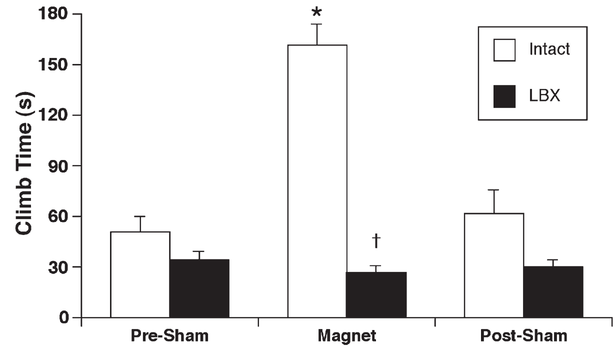

Fig. 4. Latency for intact (white bars, $n=6$) and labyrinthectomized rats (black bars, $n=6$) to climb the ladder. The ladder was placed outside the magnet (pre-sham and post-sham) or through the bore of the 14.1 T magnet (magnet). On most trials through the magnetic field the intact rats did not traverse the ladder; labyrinthectomized rats rapidly climbed the ladder both when it was outside the magnet and when it was extended through the magnet. *$p<0.05$ *vs* pre-sham, †$p<0.05$ *vs* intact-magnet.

acceleration [16,17]. Sham-lesioned rats ($n=6$) received intratympanic injections of 0.15 M NaCl (50 µl/ear). Three days after the injections, vestibular function was assessed using two tests to verify labyrinthectomy: 1) Rats were held upside down and then dropped from ~60 cm onto a foam rubber cushion. Unlike intact rats that right themselves and land on their feet, labyrinthectomized rats fail to right themselves in midair, and land on their backs. 2) Rats were placed upside down on a countertop, and an acrylic sheet was held against their feet. Sham rats quickly righted themselves and walked upon the countertop; labyrinthectomized rats remained upside down and "walked" with their feet against the underside of the acrylic sheet.

After labyrinthectomy or sham-labyrinthectomy, rats underwent 4 more days of training to climb the ladder. One rat in each group failed to maintain reliable climbing and was excluded, leaving five LBX rats and five sham-lesioned rats. Rats were tested on 3 consecutive days with 5 trials per day, as in experiment 1. On days 1 and 3, all rats were tested with the ladder outside the 14.1 T magnet (sham days); on day 2, all rats were tested with the ladder passing through the bore of the 14.1 T magnet. The time required to climb from the start box to the goal box was recorded; rats that did not leave the start box or reach the goal box were assigned a climb time of 3 min.

2.8. Statistical analysis

Significant differences were detected by ANOVA with repeated sampling of the same subjects across tests. *Post-hoc* comparisons were made using Tukey's HSD test (Kaleidagraph, Synergy Software). A non-parametric Kruskal–Wallis ANOVA was used to detect significant effects across median data in experiment 1.

3. Results

3.1. Climbing the ladder through a 14.1 T magnet

On the first day with the ladder running through the sham-magnet, all rats ran quickly and completed all 5 trials up the ladder and through the cardboard sham-magnet. When the ladder was extended through the 14.1 T MF, all rats entered the bore of the magnet during their first trial but took significantly longer to climb to the goal box: 3 rats climbed through the magnet and reached the goal box, while 5 rats entered the magnet but eventually returned to the start box (and so were assigned a climb time of 180 s). On subsequent trials, most rats would climb only part way up the ladder, stop short of the entrance to the bore, and then descend back to the start box. When tested the next day with the ladder extending through the sham-magnet, however, all rats climbed quickly and completed all 5 trials. (An example QuickTime video is available online at http://www.magnet.neuro.fsu.edu/laddervideo.mov.)

One-way ANOVAs across the 5 trials on each day of testing (pre-sham, magnet, and post-sham day) showed no significant effect of trial number on climbing time [pre-sham: $F(4,39)=0.19$, $p=0.94$; magnet: $F(4,38)=0.41$, $p=0.80$; post-sham: $F(4,39)$ 0.72, $p=0.59$], so the mean climbing time of each rat for each day was used in subsequent analysis. One-way ANOVA across the 3 conditions showed a significant effect of the magnet on climbing time [$F(2,23)=57.86$, $p<0.0001$]. Because most rats did not reach the goal box when climbing through the magnet, the average climb time was higher for trials in which the ladder traversed the 14.1 T MF compared to trials through the sham-magnet (Fig. 2A). Thus it appears that the bore of the 14.1 T magnet was aversive to the rats, such that they avoided re-entry after their first exposure.

After their first experience of the 14.1 T MF, rats appeared to detect the presence of the MF at intensities less than 14.1 T, because on subsequent trials the rats often stopped climbing even before entering the bore of the magnet. Video analysis was used to determine the maximum climbing height and thus MF exposure achieved by each rat on the 5 trials (including aborted climbs) through the magnet. The median values are plotted in Fig. 2B to represent the threshold of magnetic field effects (*i.e.* the point at which half the rats reversed direction). A significant effect across trials was found by both one-way parametric ANOVA [$F(4,39)=9.16$, $p<0.0001$] and by non-parametric Kruskal–Wallis ANOVA [$H(4)=162.49$, $p<0.001$], with all difference lying between trial 1 and trials 2–4. While all rats reached 14.1 T on the first trial, the median MF reached on subsequent trials was less than 2 T. Trials 2–4 were not significantly different from each other [$H(1.57)$, n.s.]. Thus it appears that the rats could detect some aspect of the MF at the 2 T field line, and possibly stopped climbing at 2 T because it predicted the presence of the 14.1 T MF further up the ladder.

3.2. Traversing a resistive magnet

In order to determine if avoidance of the 14.1 T MF was specific to the superconducting magnet, a separate group of rats were tested in an ascending series of MFs on a 0–20 T resistive magnet. Rats successfully reached the goal box at all field strengths until tested at 14.1 T; at 14.1 T, half the rats did not traverse the bore of the magnet but returned to the start box. One-way ANOVA across the different field strengths showed a significant effect [$F(6,41)=3.23$, $p<0.05$]. When the same rats that failed to reach the goal box were retested with a single trial at 0 T in the same magnet, they successfully climbed through the magnet and reached the goal box with an average climb time of 29±3 s (see Fig. 3; $p<0.05$ by paired *t*-test). These results suggest that rats avoided entering a high MF *per se*, and were not avoiding some other aspect of the apparatus generating the field.

3.3. Labyrinthectomy

As before, sham rats and LBX rats readily climbed the ladder through the sham-magnet on every trial. When the ladder traversed the superconducting magnet, however, only the LBX rats rapidly climbed through the 14.1 T MF to reach the goal box on every trial (see Fig. 4). A two-way ANOVA on average climb times with surgical group as one factor and repeated sampling of the same subjects across tests as the second factor showed a significant interaction of surgical group and testing condition [$F(1,2)=33.7$, $p<0.0001$]. Thus it appears that the peripheral vestibular apparatus was required for the rats to perceive and avoid a high MF.

4. Discussion

These results have 3 implications: 1) because rats will not voluntarily enter a 14.1 T MF after an initial exposure, 14.1 T is an aversive stimulus to rats; 2) because rats with experience of the 14.1 T MF subsequently stop near the 2 T field line, rats are able to detect some aspect of the MF or MF gradient at this point, and use it as a cue to avoid the aversive 14.1 T MF; 3) because labyrintechomized rats readily traverse the 14.1 T MF, the vestibular apparatus is required either for perceiving the aversive quality of the high MF, or detecting the lower fringe field or field gradient preceding the high MF, or both.

After one entry into or through the bore of the superconducting magnet, rats would not re-enter the magnet, and in fact would only ascend the ladder partway towards the magnet's bore. We ascribe the partial approach and reversal away from the bore to detection by the rat of the peripheral magnetic field or gradient that predicted the presence of the stronger field at the center of the magnet. It is possible, however, that the rats formed a more conventional place aversion and they avoided the magnet's bore based on auditory, visual, or olfactory stimuli associated with the superconducting magnet. Against this, rats that avoided the bore of the resistive magnet at 14 T subsequently entered the bore readily when the resistive magnet was unpowered at 0 T; the non-magnetic features of the resistive magnet are identical at both 0 T and 14 T. Thus, although rats may take advantage of environmental cues if present, a distinctive environment is not necessary for rats to discriminate the presence of the magnetic field.

These results confirm the prior observations of Weiss et al. (1992), in which rats avoided entry into an arm of a T-maze when it extended into a 4 T MF. Rats in the earlier T-maze study were more sensitive to the MF than the rats in this study, as the present rats did not avoid MFs below 12–14 T. This difference might be due to the training regime (here, rats were food-restricted and so highly motivated to climb the ladder), the physical configuration of the magnets (*e.g.*, the maximum gradient in the T-maze leading into the 4 T magnet was 13 T/m, while the gradient at the mouth of our 14.1 T magnet was 9 T/m), or even strain of rats (Long–Evans *vs* Sprague–Dawley). As in the current study, however, rats in Weiss et al. reversed direction upon reaching lower intensity MF that were not aversive *per se*, in order to avoid entry into higher MFs (4 T) further along the arm of the maze. The 1.75 T MF at the "reversal point" reported by Weiss et al. is in close agreement with the median maximum excursion to 2 T of the rats in this study.

Because rats stopped or reversed their climbing around the 2 T field line, they appear able to detect some aspect of the MF near that point. Candidate parameters include a magnetic or magnetohydrodynamic force [18] exerted by the 2 T field ($B_z\, dB/dz$), or an effect of the large vertical gradient (dB/dz) at that point. The vertical gradient at the 2 T field line, just inside the magnet, is 16.5 T/m. (The maximum gradient in the 14.1 T magnet is 54 T/m at 27 cm into the magnet). In particular, rapid movement through the static MF gradient is equivalent to exposure to a time-varying MF (dB/dt) of considerable strength. Time-varying MFs, or movement through high strength static MFs, are known to induce sensory effects in humans (*e.g.* magnetophosphenes and metallic taste), possibly by direct stimulation of receptive tissue or nerves in the eyes or mouth [19]. Thus, in future studies it will be important to explore the role of the rat's velocity through the MF.

After destruction of the peripheral vestibular apparatus of the inner ear, rats rapidly and repeatedly traversed the 14.1 T magnet. The peripheral vestibular apparatus is a novel site for MF transduction. In other vertebrates, the olfactory mucosa and trigeminal nerve of fish [20] or the retina [21] and trigeminal nerve [22] of migratory birds have been identified as sites of earth-strength magnetoreception that may contribute to prey detection or migration. The ability to detect high MFs would have no adaptive value to an animal in the wild, of course, and therefore the mechanism of vestibular action at 14.1 T is likely to be an artifactual manipulation of sensory elements within the inner ear.

The mammalian vestibular apparatus has two components, the semicircular canals and the otolith organs, each of which is a candidate to mediate MF effects. The semicircular canals are filled with conductive endolymph; the otolith organs (saccule and utricle) contain otoconia crystals composed largely of calcium carbonate [23]. Both the endolymph and the otoconia serve as inertial ballast that bends the sensory hair cells during rotational and linear acceleration, respectively. If the high MF or motion through the MF generates a force acting on either substance above the sensory threshold for rotational or linear acceleration, the central vestibular system would receive abberant input [9,18]. The perception of inner ear signals that conflict with input from the eyes and proprioceptive joint sensors is likely to be aversive in rats as in humans, in whom it causes motion sickness. Lower MFs must also generate a sensory effect that is detectable but non-aversive, because while naive rats will enter fields below 14.1 T, the same rats will not pass 2 T after exposure to 14.1 T. The vestibular apparatus could conceivably mediate both effects.

The demonstration of the inner ear as a locus for some sensory effects of MFs provides a neurological substrate for anecdotal reports of acute balance disorders such as nausea and vertigo [1,18]. Our results also suggest that as MRI field strengths are increased for higher resolution imaging (*e.g.* 8 or 11.4 T), the likelihood of aversive side-effects induced by MF activation of the vestibular system may also increase. Beyond undesired side-effects, however, exposure to high strength MFs may also serve as a novel way to manipulate the vestibular system non-invasively and without bodily motion.

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