The Company of
Biologists

RESEARCH ARTICLE

Effect of magnetic pulses on Caribbean spiny lobsters: implications for magnetoreception

David A. Ernst* and Kenneth J. Lohmann

ABSTRACT

The Caribbean spiny lobster, *Panulirus argus*, is a migratory crustacean that uses Earth's magnetic field as a navigational cue, but how these lobsters detect magnetic fields is not known. Magnetic material thought to be magnetite has previously been detected in spiny lobsters, but its role in magnetoreception, if any, remains unclear. As a first step toward investigating whether lobsters might have magnetite-based magnetoreceptors, we subjected lobsters to strong, pulsed magnetic fields capable of reversing the magnetic dipole moment of biogenic magnetite crystals. Lobsters were subjected to a single pulse directed from posterior to anterior and either: (1) parallel to the horizontal component of the geomagnetic field (i.e. toward magnetic north); or (2) antiparallel to the horizontal field (i.e. toward magnetic south). An additional control group was handled but not subjected to a magnetic pulse. After treatment, each lobster was tethered in a water-filled arena located within 200 m of the capture location and allowed to walk in any direction. Control lobsters walked in seemingly random directions and were not significantly oriented as a group. In contrast, the two groups exposed to pulsed fields were significantly oriented in approximately opposite directions. Lobsters subjected to a magnetic pulse applied parallel to the geomagnetic horizontal component walked westward; those subjected to a pulse directed antiparallel to the geomagnetic horizontal component oriented approximately northeast. The finding that a magnetic pulse alters subsequent orientation behavior is consistent with the hypothesis that magnetoreception in spiny lobsters is based at least partly on magnetite-based magnetoreceptors.

KEY WORDS: Magnetite, Orientation, Navigation, Magnetoreceptor, Pulse magnetization, *Panulirus argus*

INTRODUCTION

Earth's magnetic field plays an important role in guiding the movements of diverse animals over a wide range of distances (Wiltschko and Wiltschko, 2005; Johnsen and Lohmann, 2005). The geomagnetic field is among the most pervasive and reliable of orientation cues, accessible day and night at nearly every location on the planet. Animals can derive two distinct types of information from the geomagnetic field. Many species use the field as a source of directional or 'compass' information, which enables them to maintain consistent headings (e.g. toward north or south) (Lohmann, 2010). In addition, Earth's magnetic field varies predictably across the surface of the globe, providing a source of

Department of Biology, University of North Carolina, Chapel Hill, NC 27599, USA.

*Author for correspondence (dernst@live.unc.edu)

D.A.E., 0000-0001-5134-1401

positional or 'map' information that some animals use to change direction at appropriate locations along a migratory route or to navigate toward particular geographic areas (Lohmann et al., 2001, 2004, 2007, 2012; Phillips et al., 2002; Putman et al., 2014).

Although many species evidently use the geomagnetic field as a compass, map or both, the transduction mechanisms that underlie magnetic field detection have not been clearly established in any animal. Several different hypotheses have been proposed to explain how animals might detect magnetic fields (Johnsen and Lohmann, 2008). Most recent research has focused on two possible biophysical mechanisms: (1) chemically mediated magnetoreception (Ritz et al., 2000; Maeda et al., 2008; Liedvogel and Mouritsen, 2010); and (2) magnetite-based magnetoreception (Kirschvink et al., 2001; Walker, 2008; Winklhofer and Kirschvink, 2010).

The magnetite hypothesis proposes that particles of the mineral magnetite (Fe_3O_4) provide the physical basis for the magnetic sense. Theoretical considerations suggest that single-domain magnetite crystals (crystals of a size that can sustain a permanent magnetic moment) are particularly well suited to function as magnetoreceptors (Kirschvink et al., 2001). Such particles might activate secondary receptors (e.g. stretch receptors or hair cells) as the particles twist into alignment with the geomagnetic field (Kirschvink and Gould, 1981; Johnsen and Lohmann, 2005; Winklhofer and Kirschvink, 2010). Magnetic particles have been detected in the tissues of a number of animals, many of which use the geomagnetic field as an orientation cue (e.g. Lohmann, 1984; Mann et al., 1988; Walker et al., 1997; Shaw et al., 2015).

One technique that has been used to investigate magnetite-based magnetoreception involves subjecting organisms to brief, strong magnetic pulses (Kirschvink et al., 2001; Shaw et al., 2015), a treatment that should have no lasting effect on chemically mediated magnetoreception (Wiltschko et al., 2002). In principle, a strong magnetic pulse applied in the right direction can realign the magnetic dipole moment of a single-domain magnetite crystal (Kirschvink, 1983; Kirschvink et al., 1985). As a consequence, the pulse treatment might cause incorrect magnetic information to be transduced to the nervous system, resulting in changes in orientation behavior. Magnetic pulses have been shown to alter the orientation of several vertebrate animals, including sea turtles (Irwin and Lohmann, 2005), migratory birds (Beason et al., 1995; Wiltschko et al., 1998, 2002; Holland, 2010; Holland and Helm, 2013) and mammals (Marhold et al., 1997a; Holland et al., 2008). In some cases, the treatment has disrupted existing directional preferences, resulting in random orientation; in others, it has elicited shifts in pre-existing directional preferences.

To our knowledge, all of the animals used in magnetic pulse experiments so far have been vertebrates; whether invertebrate animals are also affected by magnetic pulses has not been investigated. In the context of magnetoreception, a particularly interesting invertebrate is the Caribbean spiny lobster, *Panulirus argus* (Latreille 1804), the only invertebrate species known to have

both a magnetic compass (Lohmann et al., 1995) and a magnetic map (Boles and Lohmann, 2003; Lohmann and Ernst, 2014). Spiny lobsters undergo an annual mass migration and are capable of homing after nocturnal foraging or experimental displacements (Creaser and Travis, 1950; Herrnkind and McLean, 1971; Herrnkind and Redig, 1975; Herrnkind et al., 1975). In addition, concentrations of permanently magnetic material thought to be magnetite have been detected in the Caribbean spiny lobster (Lohmann, 1984).

As a first step toward determining whether magnetic particles are associated with magnetoreception in the spiny lobster, we studied the orientation behavior of lobsters subjected to strong magnetic pulses. Results indicated that a magnetic pulse altered subsequent orientation, a finding consistent with the hypothesis that magnetoreception in lobsters is based at least partly on magnetite-based magnetoreceptors.

MATERIALS AND METHODS
Animals
All experiments were conducted in Layton, Florida, USA, at the Keys Marine Laboratory (24.83°N, 80.81°W) in July 2013. Juvenile lobsters ranging from 55 to 86 mm in carapace length were captured in Florida Bay in the immediate vicinity of the laboratory by swimmers using hand-held nets. Each animal was visually inspected for signs of ill health. Healthy lobsters were placed into plastic buckets (18.9 liters) filled with seawater and transported to the laboratory for experiments. Those few animals that showed symptoms of PaV1 (*Panulirus argus* Virus 1, a virus that infects spiny lobsters) or other disease were not used. The collection of lobsters was authorized by the Florida Fish and Wildlife Conservation Commission (permit SAL-11-1333C-SR).

Magnetic pulse protocol
Lobsters were collected daily between 18:00 and 20:00 h and randomly assigned to one of three groups. Within 1 h of capture, lobsters in two of the groups were exposed to strong magnetic pulses (see below), while those in the third group (controls) were handled in the same way as the others, but not exposed to a magnetic pulse.

Magnetic pulses were generated by a magnetizer (model 7515-G) constructed by Magnetic Instrumentation (Indianapolis, IN, USA). The magnetizer consisted of a bank of capacitors (425 V max) that discharged to a solenoid (32 cm diameter×20 cm length). Magnetic pulses produced by the magnetizer had an intensity of 85 mT and a duration of 5 ms. Both values are within the range used in similar studies with other animals (Irwin and Lohmann, 2005; Holland et al., 2008; Holland, 2010; Holland et al., 2013; Holland and Helm, 2013).

Prior to placing the lobsters in the solenoid of the magnetizer, eye caps molded from polyvinylsiloxane impression material (Kerr Manufacturing Co., Orange, CA, USA) were placed over the lobsters' eyestalks to obscure their vision. Each lobster was then fastened to a small wooden board (approximately 5×75×2.5 cm, width×length×depth) with plastic cable ties. The board and lobster were then placed on non-magnetic supports and positioned so that the lobster was centered within the solenoid of the magnetizer and aligned along the magnetic north–south axis.

Because the effect of a magnetic pulse on magnetite crystals depends in part on how crystals are aligned relative to the pulse direction (Wiltschko et al., 2002; see Discussion), lobsters were treated under two sets of conditions. One group of lobsters was subjected to a magnetic pulse directed from posterior to anterior, with the pulse delivered parallel to the geomagnetic horizontal

component (i.e. toward magnetic north; Fig. 1A). A second group was also subjected to a magnetic pulse directed from posterior to anterior, but with the pulse delivered antiparallel to the geomagnetic horizontal component (i.e. toward magnetic south; Fig. 1B). An additional group of control lobsters was eye-capped, fastened to the wooden board and placed inside the solenoid, but not subjected to a magnetic pulse.

After lobsters were removed from the solenoid and detached from the wooden board, the eye caps were removed and lobsters were then housed outdoors in two rectangular fiberglass holding tanks (67×122×39 cm) placed side by side and filled with flow-through seawater from Florida Bay. Each tank was shaded from the sun and contained a cement block that the lobsters could use for cover. The two tanks appeared to be identical. Nevertheless, to ensure that the tank in which lobsters were housed did not influence the outcome, treatment groups were assigned to different holding tanks on different days of the experiment. The water temperature in both holding tanks was equivalent to that of Florida Bay.

All lobsters remained in the tanks overnight (for at least 10 h). The next morning, each lobster was tested a single time in the orientation arena (see below) and then released.

Orientation trials
Lobsters were housed and tested in the local magnetic field. The field was measured with a triaxial magnetometer (model 520A, Applied Physics Systems, Sunnyvale, CA, USA) and determined to have an intensity of 43.8 µT and an inclination of 53.7 deg.

All orientation trials were conducted between 07:00 and 14:00 h at a location approximately 200 m southeast of the capture site.
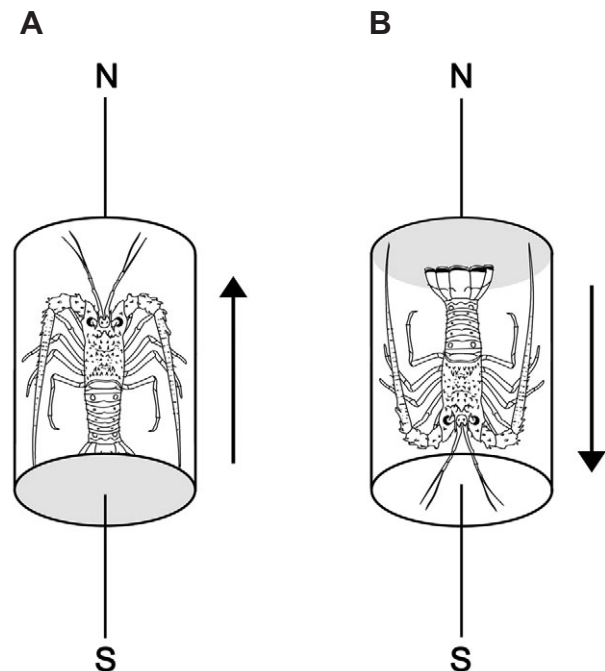

Fig. 1. Magnetic pulse treatment. All lobsters were placed tail-first into the solenoid of the magnetizer. (A) Parallel magnetic pulse condition: lobsters were treated with a magnetic pulse directed parallel to the horizontal component of the geomagnetic field (i.e. toward magnetic north) while facing north. (B) Antiparallel magnetic pulse condition: lobsters were treated with a magnetic pulse directed antiparallel to the horizontal component of the geomagnetic field (i.e. toward magnetic south) while facing south. The cylinder represents the solenoid while the arrow outside the solenoid indicates the direction of the magnetic pulse (N, north; S, south).

Before testing, each lobster was eye-capped to eliminate the use of visual cues. A plastic cable tie was secured around the posterior cephalothorax between the fourth and fifth pairs of pereopods. A small plastic ring (1 cm diameter) threaded onto the cable tie was positioned along the lobster's dorsal midline as an attachment point for a tether.

Lobsters were tethered with monofilament line within a circular, water-filled fiberglass arena (164 cm diameter; 29 cm water depth). One end of the tether was attached to a non-magnetic brass fishing swivel, which in turn was connected to the plastic ring on the midline of the lobster. The other end was attached to an electronic tracking system positioned on a support beam that extended across the center of the arena (Fig. 2). The tracking system consisted of a rotatable tracker arm, capable of pointing toward any direction in the horizontal plane, affixed to a digital encoder that transmitted the angle of orientation to a computer for data collection. The tether restrained lobsters to a circle with a radius of 25.5 cm.

Once tethered, lobsters were released randomly in one of the four cardinal directions and allowed to walk on a level, circular piece of acrylic positioned on the bottom of the tank. When the tether became taut, animals continued to walk at the same steady rate with their legs slipping continuously on the acrylic surface (Lohmann et al., 1995). The trial was then initiated, and each lobster's heading was recorded every 30 s for a period of 30 min.

After testing and prior to release, a circular notch was taken out of each lobster's right uropod. This ensured that each lobster could be identified upon recapture and that no lobster was inadvertently tested a second time.

All orientation experiments were carried out during a 7-day period (2–8 July) in 2013. The experiment was conducted in two phases. During the first 5 days, control lobsters and lobsters subjected to the antiparallel pulse were tested alternately in the arena; in other words, the first lobster tested was a control, the second was from the antiparallel pulse group, the third was a control, and so on. During the last 2 days of the experiment, we tested an additional group of lobsters that had been subjected to a parallel pulse.

Statistical analysis

Using standard procedures for circular statistics (Batschelet, 1981), a mean angle for each lobster was calculated based on all measurements obtained during the 30-min trial. Rayleigh tests were used to determine whether each group of lobsters was significantly oriented. The distributions of the three groups wer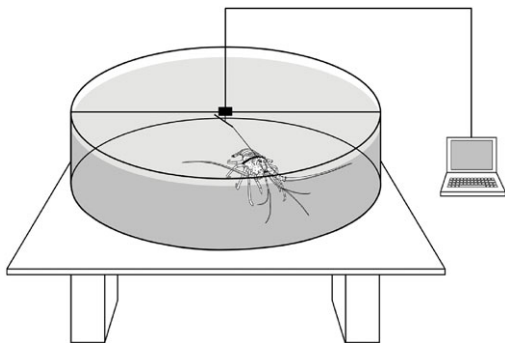e compared using the Mardia–Watson–Wheeler test; pairwise comparisons were made with the Watson test (Batschelet, 1981; Zar, 1999). In addition, to determine whether individual lobsters in some treatment groups held more consistent headings than lobsters in other groups, individual r-values (indicators of directional consistency) were compared across groups using a Kruskal–Wallis H-test (Siegel and Castellan, 1988).

RESULTS

Lobsters exposed to a magnetic pulse directed parallel to the horizontal component of the geomagnetic field (Fig. 1A) were significantly oriented with a mean angle of 259 deg (Rayleigh test, n=15, r=0.45, Z=2.98, P=0.048; Fig. 3A). Lobsters exposed to a magnetic pulse directed antiparallel to the geomagnetic field (Fig. 1B) were significantly oriented with a mean angle of 47 deg (Rayleigh test, n=14, r=0.53, Z=3.98, P=0.016; Fig. 3B), a direction approximately opposite that of the first group. By contrast, control lobsters (lobsters not exposed to a magnetic pulse) had orientation that was statistically indistinguishable from random (Rayleigh test, n=13, r=0.26, Z=0.886, P=0.42; Fig. 3C).

Significant differences existed among the three distributions (Mardia–Watson–Wheeler test, W=15.036, P=0.005). Pairwise comparisons indicated that the distributions of the parallel and antiparallel pulsed groups were significantly different (Watson test, U^2=0.323, P<0.005). In addition, the antiparallel group and control group were significantly different (Watson test, U^2=0.211, P<0.05). The distributions of the parallel group and control group were not significantly different (Watson test, U^2=0.091, P>0.2).

A comparison of the r-values of individual lobsters (calculated using all bearings recorded during the 30-min trial period) did not reveal any significant difference among the three groups (Kruskal–Wallis H-test, H=1.928, P=0.381), indicating similar levels of directional consistency regardless of treatment.

DISCUSSION

The results indicate that a magnetic pulse affected the subsequent orientation behavior of spiny lobsters. Control lobsters placed into the solenoid of the magnetizer, but not subjected to a magnetic pulse, were not significantly oriented as a group (Fig. 3C). By contrast, the two groups of lobsters that were exposed to a magnetic pulse each showed a significant directional preference, with the preferred direction apparently influenced by the alignment of the animal and magnetic pulse relative to Earth's magnetic field (Fig. 3A,B). The finding that a magnetic pulse affected orientation is consistent with the hypothesis that lobsters have magnetite-based magnetoreceptors (Kirschvink et al., 2001; Johnsen and Lohmann, 2005). Indeed, of the various mechanisms that have been proposed to underlie magnetoreception, only magnetite should hypothetically be affected by a strong magnetic pulse (Shaw et al., 2015).

All of the lobsters in this study were tested at a location within approximately 200 m of where they were captured. The lack of a directional preference in control lobsters is consistent with previous results, in which lobsters tethered in an underwater arena close to the capture site failed to orient consistently as a group, possibly because the animals were already in the immediate vicinity of their home dens (Lohmann et al., 1995).

Magnetic pulses similar to those used in the present study have been reported to alter the orientation behavior of several vertebrate animals, including sea turtles (Irwin and Lohmann, 2005), birds (Beason et al., 1995; Wiltschko et al., 1998, 2002; Holland, 2010; Holland and Helm, 2013) and mammals (Marhold et al., 1997a; Holland et al., 2008). The present study provides evidence that a
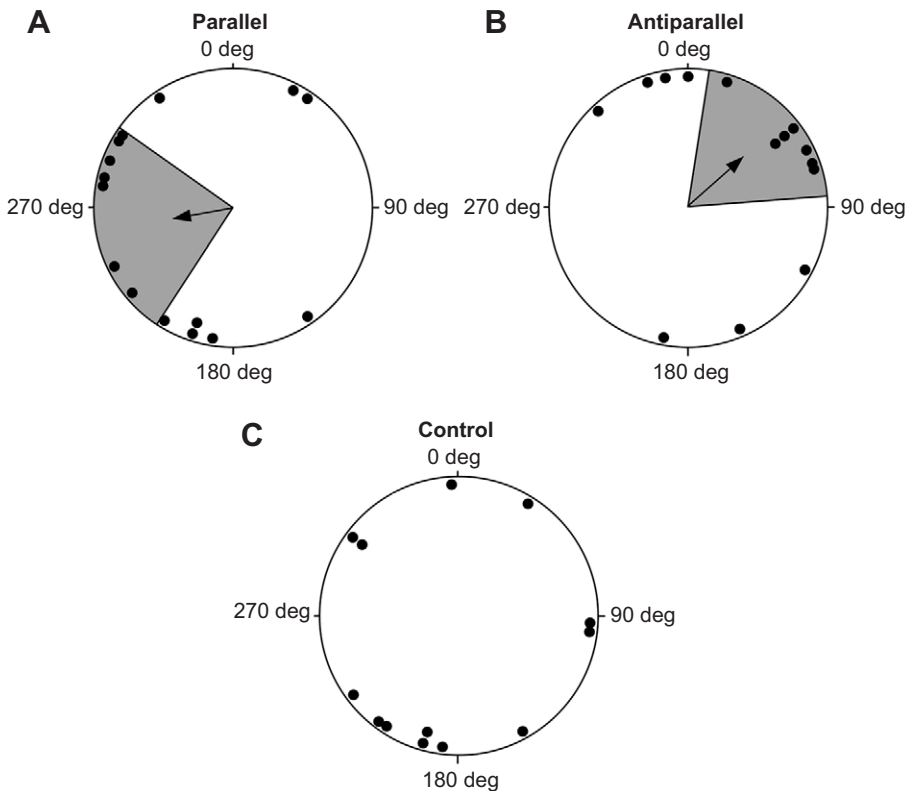

Fig. 2. Orientation arena. Lobsters were tethered within a circular arena to an electronic tracking system consisting of a tracker arm, digital encoder (black box above the lobster) and computer that monitored the angle of orientation. See Materials and methods for details.

Fig. 3. Lobster orientation trial results.
(A) Lobsters treated with a pulse directed parallel to the geomagnetic field were significantly oriented with a mean angle of 259 deg. (B) Lobsters treated with a pulse directed antiparallel to the geomagnetic field were significantly oriented in approximately the opposite direction, with a mean angle of 47 deg. (C) Control lobsters were not oriented as a group. Each black circle represents the mean heading of an individual lobster. Arrows indicate the mean direction of the group. Shaded areas represent the 95% confidence interval for the mean.

magnetic pulse can also alter the orientation behavior of an invertebrate animal.

Effect on magnetic map or magnetic compass?

Spiny lobsters are able to derive both directional ('compass') information and positional ('map') information from Earth's magnetic field (Lohmann et al., 1995; Boles and Lohmann, 2003). In principle, the magnetic pulse might have altered or impaired mechanisms underlying one or both of these abilities.

In migratory birds, a magnetic pulse has been hypothesized to affect a magnetite-based map sense. Birds that have completed at least one migration are thought to acquire a map through experience, whereas first-time migrants are thought to follow a consistent compass heading that does not require a map (Wiltschko and Wiltschko, 1995a,b, 2003). Consistent with this hypothesis, a magnetic pulse affected the orientation of Australian silvereyes (*Zosterops lateralis lateralis*) that had migrated at least once before, but had no effect on naïve birds migrating for the first time (Wiltschko et al., 1994, 1998; Munro et al., 1997).

In lobsters, one possibility is that the magnetic pulse altered magnetite-based receptors associated with a magnetic map sense (Lohmann et al., 2007), causing lobsters to perceive positional information incorrectly. If so, then an interesting speculation is that lobsters in the parallel pulse condition might have perceived erroneously that they had been displaced east of the capture site, whereas lobsters in the antiparallel pulse condition might have perceived themselves to be southwest of the capture site, resulting in attempts to home in opposite directions. Additional studies will be needed to confirm or refute this hypothesis.

Additionally or alternatively, it is possible that the magnetic pulse affected the magnetic compass. Interestingly, the lobster compass has different functional properties from those of several other animals including birds (Wiltschko and Wiltschko, 1972), sea

turtles (Light et al., 1993; Goff et al., 1998) and monarch butterflies (Guerra et al., 2014). Unlike lobsters, these animals all have inclination or axial compasses that are apparently blind to field polarity (Wiltschko and Wiltschko, 1972) and have properties compatible with chemical magnetoreception (Wiltschko and Wiltschko, 2010). By contrast, lobsters have a polarity compass with properties incompatible with chemical magnetoreception but consistent with magnetite (Lohmann et al., 1995; Johnsen and Lohmann, 2005; Lohmann and Ernst, 2014). It is noteworthy that mole rats and bats also have a polarity compass (Marhold et al., 1997b; Wang et al., 2007) and show altered orientation after a magnetic pulse (Marhold et al., 1997a; Holland et al., 2008), consistent with a magnetite-based compass in these animals.

Although it is also hypothetically possible that a magnetic pulse might affect orientation behavior via a general effect on lobster physiology, health or motivation, we consider this unlikely for several reasons. First, the finding that lobsters oriented in approximately opposite directions, depending on the direction of the magnetic pulse, is difficult to reconcile with a non-specific effect. Second, a significant recovery period (at least 10 h) elapsed between exposure to the magnetic pulse and orientation tests. Finally, no general effects of a magnetic pulse on physiology or behavior have been reported in similar experiments with other animals (Wiltschko et al., 1994, 1998, 2002; Beason et al., 1995, 1997; Wiltschko and Wiltschko, 1995b; Munro et al., 1997; Irwin and Lohmann, 2005; Holland et al., 2008).

Magnetoreceptor structure

Although evidence for magnetite-based magnetoreception has been accumulating, the exact structure of the putative receptors remains speculative. Hypothetically, a single-domain magnetite crystal able to rotate freely will continuously align itself with the direction of the ambient field (Johnsen and Lohmann, 2005). Little is known, however, about whether magnetite crystals are free to rotate or are

instead restricted to a narrow range of movement. In some models of magnetoreceptors, magnetite crystals can align in any direction (Kirschvink and Gould, 1981). In others, they are anchored in place and can move only over a limited range (Walker, 2008; Winklhofer and Kirschvink, 2010; Lohmann, 2016). The extent to which a magnetite particle can move has implications for how magnetite interacts with secondary receptors or ion channels and how the torque of a magnetite particle is ultimately converted into electrical signals during the transduction process for the magnetic sense.

In principle, a single-domain magnetite crystal subjected to a strong magnetic pulse directed parallel to the crystal's magnetic moment should remain functionally unchanged. By contrast, if a magnetic pulse is delivered antiparallel to the crystal's magnetic moment, the polarity of the magnetic moment will be reversed (Kirschvink, 1983; Kirschvink et al., 1985). Thus, the effect of a magnetic pulse depends on the alignment of the pulse relative to the dipole moment of a magnetite crystal.

In the present experiment, it is unclear whether magnetite crystals were able to rotate into alignment with the geomagnetic field prior to the pulse. This issue is of particular interest in the context of the parallel pulse group, which had a significant directional preference (Fig. 3A) whereas controls did not (Fig. 3C). One possibility is that some magnetite particles were unable to align with the geomagnetic field and were thus remagnetized in the opposite direction, resulting in altered orientation behavior as reported in some similar experiments with birds (Beason et al., 1995; Wiltschko et al., 2002). However, because the orientation of the parallel and control groups were not significantly different for the lobsters, caution is required in interpreting this part of the experiment and no firm conclusions can be drawn.

Regardless, the finding that magnetic pulses alter orientation responses in lobsters is consistent with magnetoreceptors based on single-domain magnetite crystals. Future work will be needed to definitively characterize the mechanisms that underlie magnetoreception in lobsters and other animals.

References
Batschelet, E. (1981). *Circular Statistics in Biology*. New York: Academic Press.
Beason, R. C., Dussourd, N. and Deutschlander, M. E. (1995). Behavioral evidence for the use of magnetic material in magnetoreception by a migratory bird. *J. Exp. Biol.* **198**, 141-146.
Beason, R. C., Wiltschko, R. and Wiltschko, W. (1997). Pigeon homing: effects of magnetic pulses on initial orientation. *Auk* **114**, 405-415.
Boles, L. C. and Lohmann, K. J. (2003). True navigation and magnetic maps in spiny lobsters. *Nature* **421**, 60-63.
Creaser, E. P. and Travis, D. (1950). Evidence of a homing instinct in the Bermuda spiny lobster. *Science* **112**, 169-170.

Goff, M., Salmon, M. and Lohmann, K. J. (1998). Hatchling sea turtles use surface waves to establish a magnetic compass direction. *Anim. Behav.* **55**, 69-77.
Guerra, P. A., Gegear, R. J. and Reppert, S. M. (2014). A magnetic compass aids monarch butterfly migration. *Nat. Commun.* **5**, 4164.
Herrnkind, W. F. and McLean, R. (1971). Field studies of homing, mass emigration, and orientation in the spiny lobster, *Panulirus argus*. *Ann. N. Y. Acad. Sci.* **188**, 359-376.
Herrnkind, W. F. and Redig, M. X. (1975). Preliminary study of establishment of den residency by spiny lobster, *Panulirus argus*, at Grand Bahama Island. *Hydro-Lab J.* **3**, 96-101.
Herrnkind, W. F., Van Derwalker, J. A. and Barr, L. (1975). Population dynamics, ecology and behavior of spiny lobsters, *Panulirus argus*, of St. John, USVI IV. Habitation, patterns of movement and general behavior. *Sci. Bull. Nat. Hist. Mus. Los Angeles County* **20**, 31-45.
Holland, R. A. (2010). Differential effects of magnetic pulses on the orientation of naturally migrating birds. *J. R. Soc. Interface* **7**, 1617-1625.
Holland, R. A. and Helm, B. (2013). A strong magnetic pulse affects the precision of departure direction of naturally migrating adult but not juvenile birds. *J. R. Soc. Interface* **10**, 20121047.
Holland, R. A., Kirschvink, J. L., Doak, T. G. and Wikelski, M. (2008). Bats use magnetite to detect the earth's magnetic field. *PLoS ONE* **3**, e1676.
Holland, R., Filannino, C. and Gagliardo, A. (2013). A magnetic pulse does not affect homing pigeon navigation: a GPS tracking experiment. *J. Exp. Biol.* **216**, 2192-2200.
Irwin, W. P. and Lohmann, K. J. (2005). Disruption of magnetic orientation in hatchling loggerhead sea turtles by pulsed magnetic fields. *J. Comp. Physiol. A* **191**, 475-480.
Johnsen, S. and Lohmann, K. J. (2005). The physics and neurobiology of magnetoreception. *Nat. Rev. Neurosci.* **6**, 703-712.
Johnsen, S. and Lohmann, K. J. (2008). Magnetoreception in animals. *Physics Today* **61**, 29-35.
Kirschvink, J. L. (1983). Biogenic ferrimagnetism: a new biomagnetism. In *Biomagnetism: An Interdisciplinary Approach* (ed. S. J. Williamson, G. L. Romani, L. Kaufman and I. Modena), pp. 501-531. New York: Plenum.
Kirschvink, J. L. and Gould, J. L. (1981). Biogenic magnetite as a basis for magnetic field detection in animals. *Biosystems* **13**, 181-201.
Kirschvink, J. L., Walker, M. M., Chang, S.-B., Dizon, A. E. and Peterson, K. A. (1985). Chains of single-domain magnetite particles in Chinook salmon, *Oncorhynchus tshawytscha*. *J. Comp. Phys. A* **157**, 375-381.
Kirschvink, J. L., Walker, M. M. and Diebel, C. E. (2001). Magnetite-based magnetoreception. *Curr. Opin. Neurobiol.* **11**, 462-467.
Liedvogel, M. and Mouritsen, H. (2010). Cryptochromes – a potential magnetoreceptor: what do we know and what do we want to know? *J. R. Soc. Interface* **7**, S147-S162.
Light, P., Salmon, M. and Lohmann, K. J. (1993). Geomagnetic orientation of loggerhead sea turtles: evidence for an inclination compass. *J. Exp. Biol.* **182**, 1-10.
Lohmann, K. J. (1984). Magnetic remanence in the western Atlantic spiny lobster, *Panulirus argus*. *J. Exp. Biol.* **113**, 29-41.
Lohmann, K. J. (2010). Q&A: animal behaviour: magnetic-field perception. *Nature* **464**, 1140-1142.
Lohmann, K. J. (2016). Protein complexes: a candidate magnetoreceptor. *Nat. Mater.* **15**, 136-138.
Lohmann, K. J. and Ernst, D. A. (2014). The geomagnetic sense of crustaceans and its use in orientation and navigation. In *Crustacean Nervous Systems and Control of Behavior* (ed. C. D. Derby and M. Thiel), pp. 321-336. New York: Oxford University Press.
Lohmann, K. J., Pentcheff, N. D., Nevitt, G. A., Stetten, G. D., Zimmer-Faust, R. K., Jarrard, H. E. and Boles, L. C. (1995). Magnetic orientation of spiny lobsters in the ocean: experiments with undersea coil systems. *J. Exp. Biol.* **198**, 2041-2048.
Lohmann, K. J., Cain, S. D., Dodge, S. A. and Lohmann, C. M. F. (2001). Regional magnetic fields as navigational markers for sea turtles. *Science* **294**, 364-366.
Lohmann, K. J., Lohmann, C. M. F., Ehrhart, L. M., Bagley, D. A. and Swing, T. (2004). Animal behaviour: geomagnetic map used in sea-turtle navigation. *Nature* **428**, 909-910.
Lohmann, K. J., Lohmann, C. M. F. and Putman, N. F. (2007). Magnetic maps in animals: nature's GPS. *J. Exp. Biol.* **210**, 3697-3705.
Lohmann, K. J., Putman, N. F. and Lohmann, C. M. F. (2012). The magnetic map of hatchling loggerhead sea turtles. *Curr. Opin. Neurobiol.* **22**, 336-342.
Maeda, K., Henbest, K. B., Cintolesi, F., Kuprov, I., Rodgers, C. T., Liddell, P. A., Gust, D., Timmel, C. R. and Hore, P. J. (2008). Chemical compass model of avian magnetoreception. *Nature* **453**, 387-390.
Mann, S., Sparks, N. H., Walker, M. M. and Kirschvink, J. L. (1988). Ultrastructure, morphology and organization of biogenic magnetite from sockeye salmon, *Oncorhynchus nerka*: implications for magnetoreception. *J. Exp. Biol.* **140**, 35-49.
Marhold, S., Burda, H., Kreilos, I. and Wiltschko, W. (1997a). Magnetic orientation in the common mole-rat from Zambia. In *Orientation and Navigation —Birds, Humans and other Animals*, p. 5. Oxford: Royal Institute of Navigation.

Marhold, S., Wiltschko, W. and Burda, H. (1997b). A magnetic polarity compass for direction finding in a subterranean mammal. *Naturwissenschaften* **84**, 421-423.

Munro, U., Munro, J. A., Phillips, J. B. and Wiltschko, W. (1997). Effect of wavelength of light and pulse magnetisation on different magnetoreception systems in a migratory bird. *Aust. J. Zool.* **45**, 189-198.

Phillips, J. B., Freake, M. J., Fischer, J. H. and Borland, C. S. (2002). Behavioral titration of a magnetic map coordinate. *J. Comp. Physiol. A* **188**, 157-160.

Putman, N. F., Scanlan, M. M., Billman, E. J., O'Neil, J. P., Couture, R. B., Quinn, T. P., Lohmann, K. J. and Noakes, D. L. G. (2014). An inherited magnetic map guides ocean navigation in juvenile Pacific salmon. *Curr. Biol.* **24**, 446-450.

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

Shaw, J., Boyd, A., House, M., Woodward, R., Mathes, F., Cowin, G., Saunders, M. and Baer, B. (2015). Magnetic particle-mediated magnetoreception. *J. R. Soc. Interface* **12**, 20150499.

Siegel, S. and Castellan, N. J. (1988). *Nonparametric Statistics for the Behavioral Sciences*, 2nd edn. New York: McGraw–Hill.

Walker, M. M. (2008). A model for encoding of magnetic field intensity by magnetite-based magnetoreceptor cells. *J. Theor. Biol.* **250**, 85-91.

Walker, M. M., Diebel, C. E., Haugh, C. V., Pankhurst, P. M., Montgomery, J. C. and Green, C. R. (1997). Structure and function of the vertebrate magnetic sense. *Nature* **390**, 371-376.

Wang, Y., Pan, Y., Parsons, S., Walker, M. and Zhang, S. (2007). Bats respond to polarity of a magnetic field. *Proc. R. Soc. B.* **274**, 2901-2905.

Wiltschko, W. and Wiltschko, R. (1972). Magnetic compass of European robins. *Science* **176**, 62-64.

Wiltschko, R. and Wiltschko, W. (1995a). *Magnetic Orientation in Animals*. Berlin: Springer.

Wiltschko, W. and Wiltschko, R. (1995b). Migratory orientation of European robins is affected by the wavelength of light as well as by a magnetic pulse. *J. Comp. Physiol. A* **177**, 363-369.

Wiltschko, R. and Wiltschko, W. (2003). Avian navigation: from historical to modern concepts. *Anim. Behav.* **65**, 257-272.

Wiltschko, W. and Wiltschko, R. (2005). Magnetic orientation and magnetoreception in birds and other animals. *J. Comp. Physiol. A* **191**, 675-693.

Wiltschko, R. and Wiltschko, W. (2010). Avian magnetic compass: its functional properties and physical basis. *Curr. Zool.* **56**, 265-276.

Wiltschko, W., Munro, U., Beason, R. C., Ford, H. and Wiltschko, R. (1994). A magnetic pulse leads to a temporary deflection in the orientation of migratory birds. *Experientia* **50**, 697-700.

Wiltschko, W., Munro, U., Ford, H. and Wiltschko, R. (1998). Effect of a magnetic pulse on the orientation of silvereyes, *Zosterops l. lateralis*, during spring migration. *J. Exp. Biol.* **201**, 3257-3261.

Wiltschko, W., Munro, U., Wiltschko, R. and Kirschvink, J. L. (2002). Magnetite-based magnetoreception in birds: the effect of a biasing field and a pulse on migratory behavior. *J. Exp. Biol.* **205**, 3031-3037.

Winklhofer, M. and Kirschvink, J. L. (2010). A quantitative assessment of torque-transducer models for magnetoreception. *J. R. Soc. Interface* **7**, S273-S289.

Zar, J. H. (1999). *Biostatistical Analysis*. Upper Saddle River, NJ: Prentice Hall.