Loss of scent while following plume results in search-like behavior with some evidence of reliance on geomagnetic cues in the nudibranch *Tritonia tetraquetra*

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Introduction

The Earth's magnetic field is often used by a variety of animals as a navigational tool. Animals may use their compass navigation to fix their position and determine their direction of movement. Oftentimes, a variety of complementary tools like, celestial cues may be used to assist compass navigation (Hill et al. 2012). These navigational abilities can promote reproductive success, food acquisition, and effective migration.

While compass navigation and orientation behavior has been well studied in birds (Wiltschko & Wiltschko 1972), sea turtles (Lohmann 1991), and other organisms, the underlying neural basis of these behaviors is less understood. In investigating the neurophysiology of vertebrate navigation, the animal is restrained and thus limited in exhibiting typical migratory behavior. Additionally, the complexity of vertebrate brain structure makes it difficult to identify specific neurons and neural circuits involved in navigation.

The large nudibranch mollusk, *Tritonia tetraquetra* (formerly *T. diomedea*) is known to orient to the Earth's magnetic field (Lohmann and Willows 1987). It has been hypothesized that *T. tetraquetra* use their magnetic sense in response to situations when primary navigational cues become undependable (Wyeth 2010). *T. tetraquetra* uses odor-gated rheotaxis (OGR) to detect predators, mates, and prey (Wyeth & Willows 2006). But, sometimes before the slug reaches the source of the odor, the odor plume may dissipate due to varying water flow direction. The slug may then benefit from switching to a secondary navigational tool, such as, magnetoreception (Wyeth 2010) when the odor cue is lost.

T. tetraquetra is a good model for studying the behavior and neural basis of navigation and magnetic sensing. Their navigational distances are short compared to other animals, allowing behavioral experiments to be done in the lab. Additionally, they have a centralized nervous system with large orange and white neurons that make them easy to visualize and identify (Willows 1971). Many of their neurons have been mapped and characterized. Past studies of the neural basis of *T. tetraquetra* magnetic sensing has begun to identify key neurons and potential uses of this navigational tool (Lohmann et al. 1991**)**.

Past studies of the neural basis of *T. tetraquetra* magnetoreception have used semi-intact and brain isolation methods (Lohmann et al. 1991; Popescu & Willows 1999; Pavlova et al. 2011). Semi-intact preparations are an ideal method that allows the slug to indulge in some normal behavioral activities. Using this method, pedal ganglion neurons (Pd5) have been shown to increase activity after a clockwise horizontal rotation of the magnetic field (Lohmann et al. 1991; Popescu and Willows 1999). The white peptidergic Pd5 cells comprise the largest neurons in the pedal ganglion (Lloyd et al. 1996). Pd5 cells extend axons ipsilaterally by Pedal Nerve 2 and 3 to the foot (Lloyd et al. 1996) and excite the cilia on the underside of the foot to drive locomotion. These ciliary motor neurons are known to play a role in crawling and may increase in activity in response to water currents (Murray et al. 1992) and magnetic field alterations (Lohmann et al. 1991; Popescu & Willows 1999). Cerebral nerve (Ce1), a known olfactory nerve (Wyeth & Willows 2006) has also been shown to be especially responsive to changes in magnetic field, and innervates sensory structures such as the rhinophores that may be involved in magnetoreception (Pavlova et al. 2011).

Previous studies of *T. tetraquetra* navigation and magnetic sensing, have only investigated unidirectional rotations (Lohmann et al. 1991; Popescu & Willows 1999; Pavlova et al. 2011). Furthermore, previous investigations did not compare the responses of homologous left and right nerves to determine if the difference might reflect information about the direction of the rotation. Here we ask whether there is a difference between the left and right neural recordings in response to counterclockwise and clockwise rotations of the ambient magnetic field. We also sought to determine, the use of magnetoreception in *T. tetraquetra*, and whether it may be used as a secondary navigational tool once flows vary and the odor plume is lost.

Materials & Methods

Animals

Slugs were collected in Langley, WA by SCUBA diving. Slugs were maintained at the University of Washington Friday Harbor Labs in fiberglass flow-through seawater tanks in areas where the total field intensity was ± 5% of the Earth's geomagnetic field intensity. They were kept in captivity for at least a week before they were used in behavioral and neurophysiology experiments. Captive slugs were fed sea pens (*Ptilosarcus gurneyi*), but were starved for 3 days to 3 weeks before behavioral chemotaxis trials Slugs were selected at random for behavioral or neural experiments.

Behavioral experiments:

For the behavioral experiments slugs were placed in a flow-through flume arena 100 cm wide by 200 cm long and 16 cm deep where water-flow was initiated at one side of the arena with a waterfall, and the resulting flow was uniform in speed across the width of the flume (Fig 1, Wyeth & Willows 2006). Grid lines were made on the base of the arena at 5 cm intervals for calibration of size and speed. A video camera was placed overhead to record time-lapse video 0.3 frames per second and 640x480 pixels with SecuritySpy (v. 2; Bensoftware) software. Two incandescent lights were placed overhead, one at each end of the arena to illuminate the arena, placed along the midline of the flume so as not to bias locomotion to the left or right of the flow stream. For at least thirty minutes to three hours before trials, the preferred prey of *T. tetraquetra*, the sea pens *Ptilosarcus gurneyi* were steeped in seawater to create an odored solution to use an attractive stimulus. Fluorescein was added to solution to mark the solution's odor plume movement in video recording. The odored seawater was run into the middle of the flow stream with latex tubing 1/4-inch inner diameter to match the speed of the water in the flume.

Ten slugs were placed approximately 1-m from the target with 16 trials each. Whether slugs were initially placed on the left or right side of the tanks, and whether a magnet was present, was randomized before each trial by flipping a coin. The produced magnetic distortion was assymetrical and located at the front of the arena (Figure 1). The slugs were started oriented sideways to the flow to obviate when the slug detected the odor source running in the center of the flow stream and began turning upstream. Once the slug caught the scent of the odor plume and moved towards the odor source approximately ½-m from the target, the odor solution was turned off to prevent odor-gated rheotaxis. Once odor plume passed slugs and the scent was lost, the water flow was turned off. A 1-meter square was dropped into the flume around the slug, to block flow and minimize rheotaxis. A drop of fluorescein-saturated seawater was injected 5 cm in front of the slug to determine residual flow direction due to turbulence after the uniform flume flow was blocked. ImageJ v.1.47 (National Institutes of Health) computer software was used to summarize the direction of slugs' directional movements.

Then, we measured change in directional heading after odor and flow was extinguished. We measured this from the behavioral tracking videos using Image J v.1.47 (National Institute of Health). In comparison, change in heading after the odor was turned off was compared to 40 seconds before odor was off, and 40 seconds after flow was turned off. In half of the trials, a random coin flip determined if a 2 cm wide, 3 mm thick neodymium magnet was placed on a platform suspended 5 mm over the surface of the water, which was in turn 16 cm over the bottom of the tank. So half of the trials challenged the slug to crawl in a distorted field (Fig 1), and half of the trials involved the normal geomagnetic field.

Neurophysiological recordings

Semi-intact animal preparations (Willows et al. 1973) were used for the neurophysiology recordings. The slugs were placed in still seawater with no flow. The water was kept cold by a bath of chilled freshwater located outside of the tank. This kept the inner slug tank at a temperature of 3-7°C. Slugs rested on a flat plexiglass platform capable of being adjusted vertically. Preparations were suspended near the surface of the tank with the foot extended in a normal crawling posture.

An incision was made on the anterior dorsal side of the slug providing access to cerebral, pedal, and pleural ganglia. The brain was guided onto a wax platform and immobilized with stainless-steel (non-magnetic) minuten pins while adjustable (non-magnetic tungsten) hooks attached to the side of the tank were used to hold the incision open. Once bilateral nerves and neurons were identified (Willows et al. 1973), recordings of the two were made simultaneously.

Coil systems

The tank was surrounded by two vertical Rubens coils, arranged perpendicularly to control the horizontal magnetic field as described by Lohmann et al. (1991). The coils were assembled by Dr. Shaun D. Cain in ~2000. Direct current was applied (~26V; 0.8 A) to one or the other coil system to produce the counterclockwise or clockwise magnetic rotations, respectively. Field strength was calibrated with a magnetometer and direction was analyzed with a stationary compass. The semi-intact preparation was placed within 20 cm of the centers of the two coils.

Extracellular and Intracellular Recordings

Extracellular recordings were made from chlorided silver wires inside seawater filled suction electrodes, and a reference bath electrode (Lohmann et al. 1991). Cut nerves were sucked into a glass microelectrode with the sharp tip broken off to the same diameter as the nerve, and the suction was provided by a hypodermic syringe. Nerve recordings were made using AM Systems Differential AC Amplifier model 1700. The low cut-off of neural signals was 100 Hz and the high cut-off was 5000 Hz. Intracellular recordings were prepared conventionally (borosilicate glass 1mm OD, 0.75mm ID, pulled by a Sutter model P-97 electrode puller) and held with micromanipulators used to insert microelectrodes filled with 3 M KAc (5-20 MOhms) into selected cells. Intracellular recordings were made using AM Systems Model 1600 Neuroprobe Amplifier. Digitization for intracellular and extracellular recordings was run by PowerLab 4SP

(10kHz extra-, and 2kHz intracellular), and were recorded in Windows LabChart Software 7.3.7 (AD Instruments) to determine the numbers of action potentials before, during, and after changes in magnetic field direction.

Intracellular and extracellular trials were made in 11 minute blocks: 5 minutes in the normal geomagnetic field followed by 1 minute of horizontal magnetic rotation, ending with 5 minutes or normal geomagnetic field. These 11 minute trials were completed 20 times, 10 trials with a 60° clockwise rotation and 10 trials with a 60° counterclockwise rotation. The change in total field intensity in the center of the coils was from 469 to 414 mG in clockwise rotations, and from 470 to 440 mG in counterclockwise rotations. Whether the trial was counterclockwise or clockwise was randomized (without replacement) before each trial by flipping a coin. Analysis of spikes was done with LabChart Software 7.3.7 (AD Instruments) using the Spike Histogram Extension with spike template matching and peri-stimulus time histograms were made triggered by the magnetic field rotation.

Results

Behavioral experiments

After odor and flow were turned off, slugs showed more turning behavior than before stimuli changed (Figure 2, P-value<0.0001). In 75.8% of trials, the change in directional heading 40 s after flow was turned off was greater than that in the 40 s before flow was turned off. When combined, 90.9% trials of change in directional heading after odor and flow extinguishment were greater than before odor was turned off. Additionally, it was found that slugs directional heading changed more in a distorted magnetic field than in a normal magnetic field (Figure 2, P-value<0.05). Overall, in both distorted and normal magnetic fields, they turn more after the removal of odor.

The behavioral tracks did not appear to follow different patterns in response to magnetic distortion or no magnetic distortion (Figure 2). Individual trials were compared in search of potential directional patterns (Figure 4-6). In two trials performed by different slugs, both moved to the right of the arena with distorted magnetic and normal field conditions (Figure 4). One slug moved in opposite directions for two normal field trials (Figure 5). One slug moved in the same direction for both distorted magnetic and normal field conditions (Figure 6).

Neural recordings

Both left and right pedal 5 and 6 intracellular recordings produced little response to clockwise and counterclockwise magnetic rotation. After clockwise rotation there was an increase in spiking 40 seconds after rotation in left pedal 5, but little change after counterclockwise rotation (Figure 7). In another set of trials, left pedal 6 produced a decrease after counterclockwise rotation, but little change after clockwise rotation (Figure 8). In right pedal 6 recordings, there was a decrease in spiking after clockwise rotation (Figure 9), but little response after counterclockwise rotation.

After clockwise rotation, left cerebral nerve 1 decreased spiking, but increased 100 seconds after counterclockwise rotation (Figure 10). In another animal, left cerebral nerve 1 increased in spiking 10 s after magnetic rotation (Figure 12). Right cerebral nerve 1 increased in spiking 20 seconds after clockwise rotation, but changed little after counterclockwise rotation (Figure 11), and in another recording a distinguishable peak was seen 112 s after clockwise rotation (Figure 13). In another recording of right cerebral nerve 1, a potential spike was seen 6-10 s after counterclockwise rotations (Figure 14).

Discussion

The function of the magnetic sense in *T. tetraquetra* is still unclear. It has been suggested that it may be used as a supplementary navigational tool in Wyeth's (2010) hypothesis. Under the experimental conditions of this study, our heading change results lend some support to some aspects of this hypothesis, but are not wholly consistent with it. Change in directional heading was significantly greater after odor was turned off and slightly more so when the magnetic field was distorted. This is the first evidence suggesting *T. tetraquetra* may use a magnetic sense as a supplementary navigational tool, but it also is not consistent with Wyeth's hypothesis that they crawl straight after losing on odor plume.

After losing the odor plume, slugs moved with no obvious pattern or direction. In some cases the trial in the normal field results did not differ from those in the distorted field, Our results suggests that while they may not be moving significantly in a particular direction in response to a distorted magnetic field, they may be changing directional heading more under these conditions.

One difference between natural conditions and our experimental conditions is that in Wyeth's hypothesis explains how the odor may be lost due to change in current direction (Wyeth 2010), but under our conditions the water flow was turned off, and did not change direction. In nature, the current flow rarely turns off, but rather changes direction. This could be another explanation why our results did not reflect Wyeth's hypothesis.

For our neural recordings the results indicate there may be an increase or decrease in spiking for some nerves and neurons. Right cerebral nerve 1 (RCeN1) increased spiking, whereas, left cerebral nerve 1 (LCeN1) is less definitive after clockwise rotation. LCeN1 increased spiking after counterclockwise rotation, while RCeN1 produced change in a different recording but not another. Both pedal 5 and 6 neurons produced little change after magnetic rotation. These nerves and neurons were chosen based on previous studies indicating these were most responsive (Lohmann et al. 1991; Popescu & Willows 1999; Pavlova et al. 2011). These results do not indicate strong evidence for being the primary nerves and neurons associated with magnetoreception in *T. tetraquetra,* however, changes in spiking after magnetic rotation indicate they may be involved in the pathway. Previous studies altered the magnetic field repeatedly to produce a neural response (Lohmann et al. 1991; Popescu & Willows 1999; Pavlova et al. 2011). Our experiment switched the magnetic coil once and left it sustained, which may be a more accurate simulation of what the slug may encounter in nature when it turns its body.

In addition, previous studies have found that *T. tetraquetra* living in shallow water are less sensitive to magnetic changes than deeper inhabitants (Cain, unpublished). The specimens we used were shallow living inhabitants, and may be less sensitive to the distortion produced in our behavioral experiments and rotation in our neural recordings.

Increasing interest in mapping neural pathways and organization has led to the development of alternative animal models to answer these questions. *T. tetraquetra* provides an excellent model for investigating neurobiology and physiology. The wealth of knowledge that has been discovered about the nervous system of *T. tetraquetra* provides information for basic neurobiology. Further investigation of the neural pathways associated with magnetoreception can provide insight into the ways the nervous system integrates multiple sensory cues (e.g. odor, current, and magnetic field) work together to produce movement.

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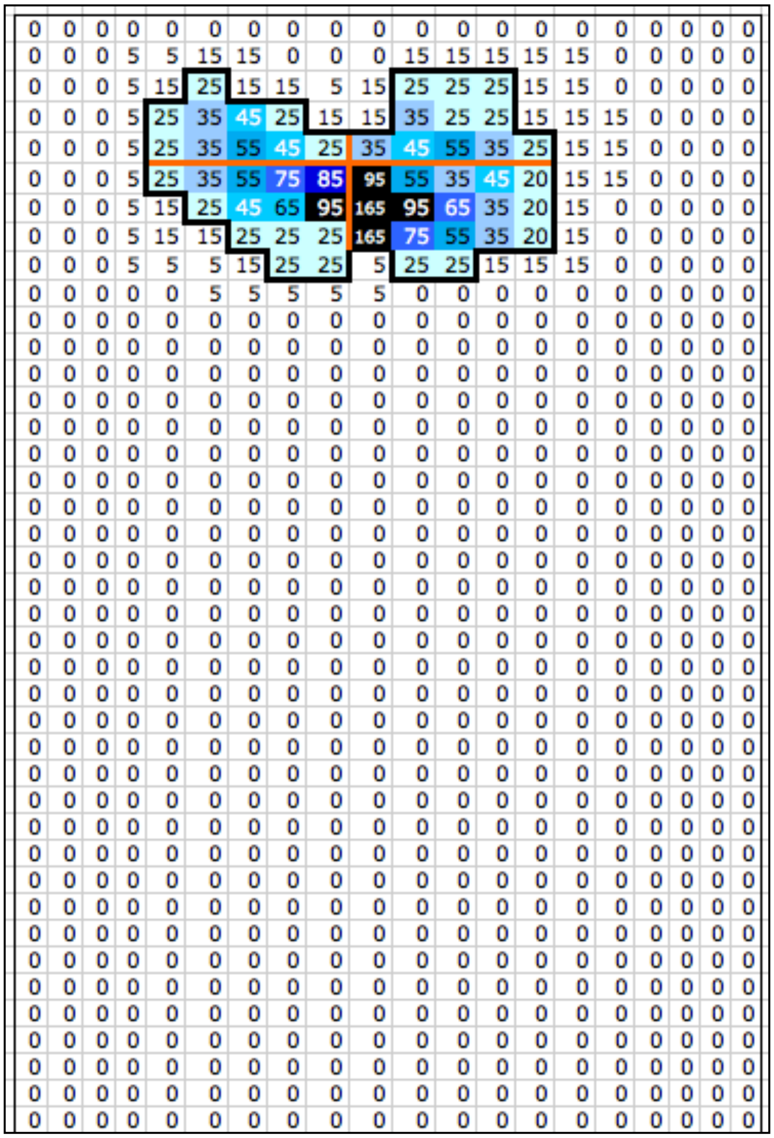

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Figure 1. Magnetic map. Degree deviation from normal magnetic field as the slug reaches the magnetic distortion in the behavioral experiments. The intersection of the orange cross represents the location of the magnet. Numbers within the thick black outline are deviations greater than 20 degrees. Each square is 5 cm by 5 cm, so the tank was 1 m wide and 2 m long.

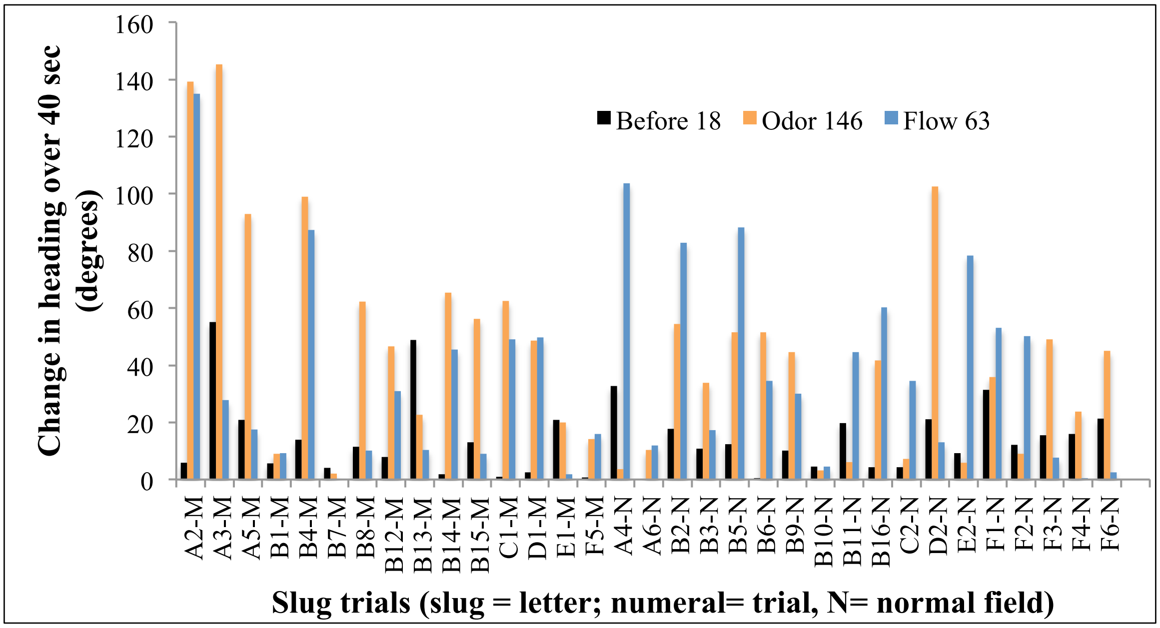

Figure 2. ***Tritonia tetraquetra*** **changes directional heading after odor is turned off.** Graph represents 40 s before odor is turned off (black), 40 s after odor is turned off (orange), and 40 s after flow is turned off (blue). Rotation of heading change is more in the 40 s after odor is turned off than the 40 s before (P-value<0.0001). Slugs turn more in distorted field than in normal magnetic field (P-value<0.05)

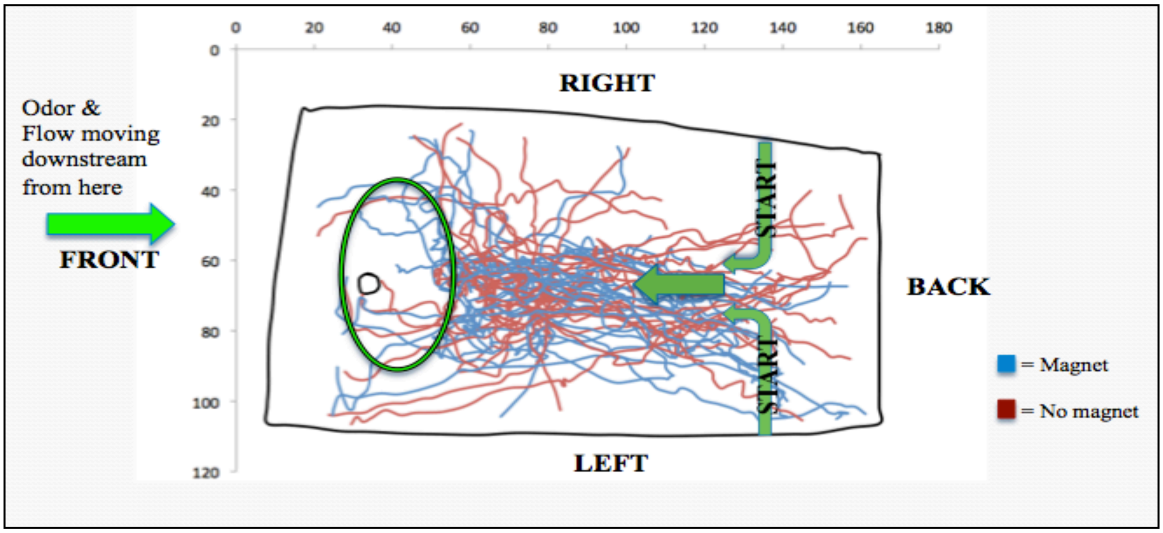

Figure 3. All behavioral trial trackings with and without magnetic distortion. Magnetically distorted trials are marked in blue and normal field trials (control) are in red. Slugs start at the back side facing the right or left. Once the slug catches the scent of the sea pen odor it is expected to turn upstream towards the source of the odor, by means of odor-gated rheotaxis. When slug reaches magnetic field odor and flow are turned off. The tank is actually 100 x 200 cm but the wide-angle lens placement produces a distortion in the video frame.

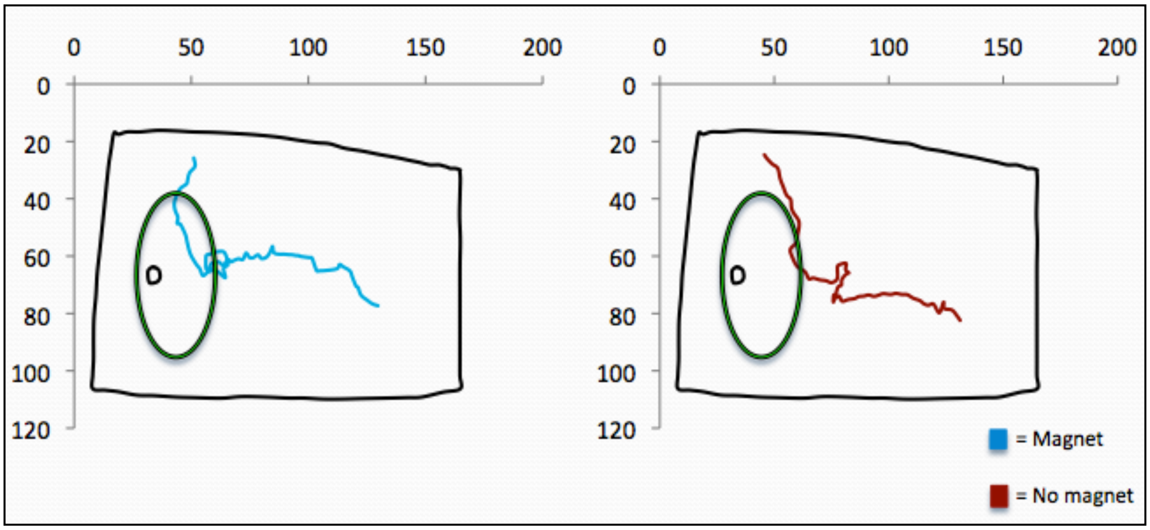

Figure 4. Two slugs moved in the same direction for magnetically distorted and normal field trials. Graph on the left represents the tracking from the magnetically distorted trial (blue), and the graph on the right is the normal field trial (red).

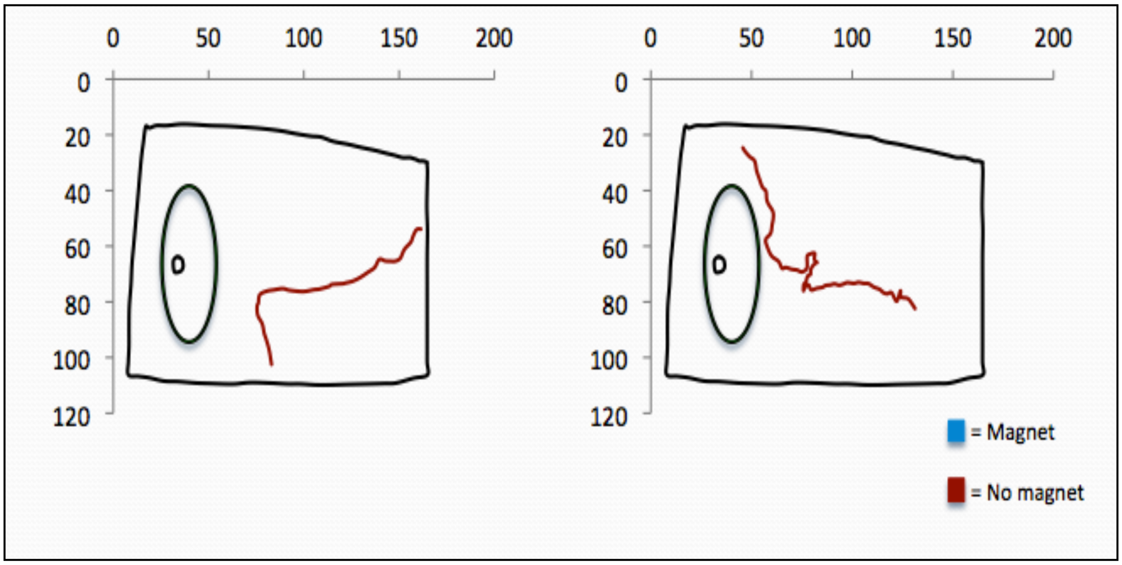

Figure 5. One slug moved in opposite directions for two normal field trials. Graph on the left represents the tracking from the magnetically distorted trial (blue), and the graph on the right is the normal field trial (red).

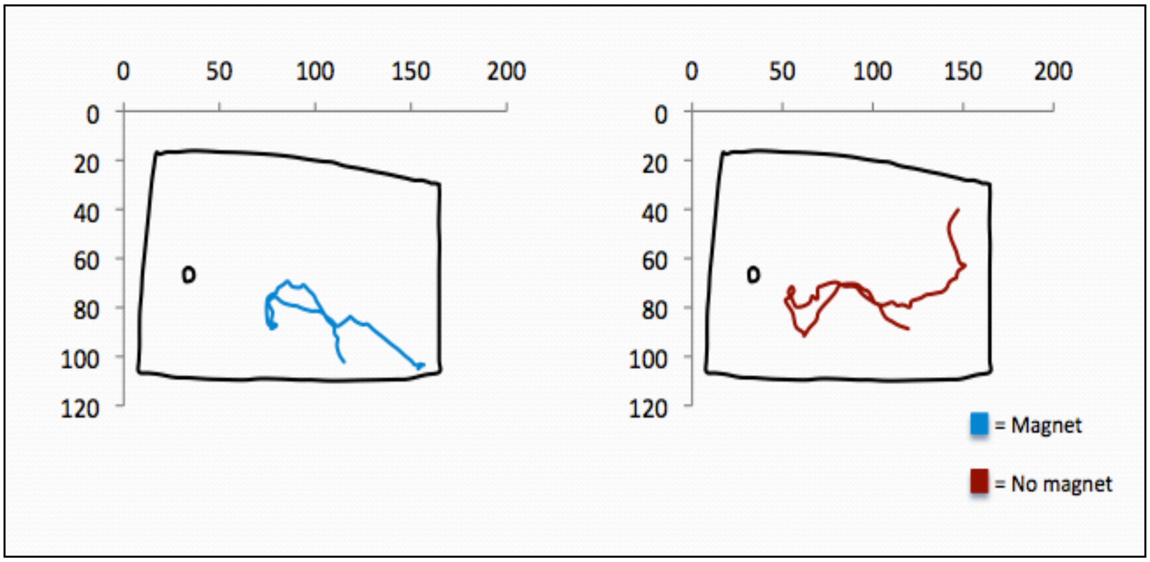

Figure 6. Two slugs that moved in the same direction for magnetically distorted and normal field trials. Graph on the left represents the tracking from the magnetically distorted trial (blue), and the graph on the right is the normal field trial (red).

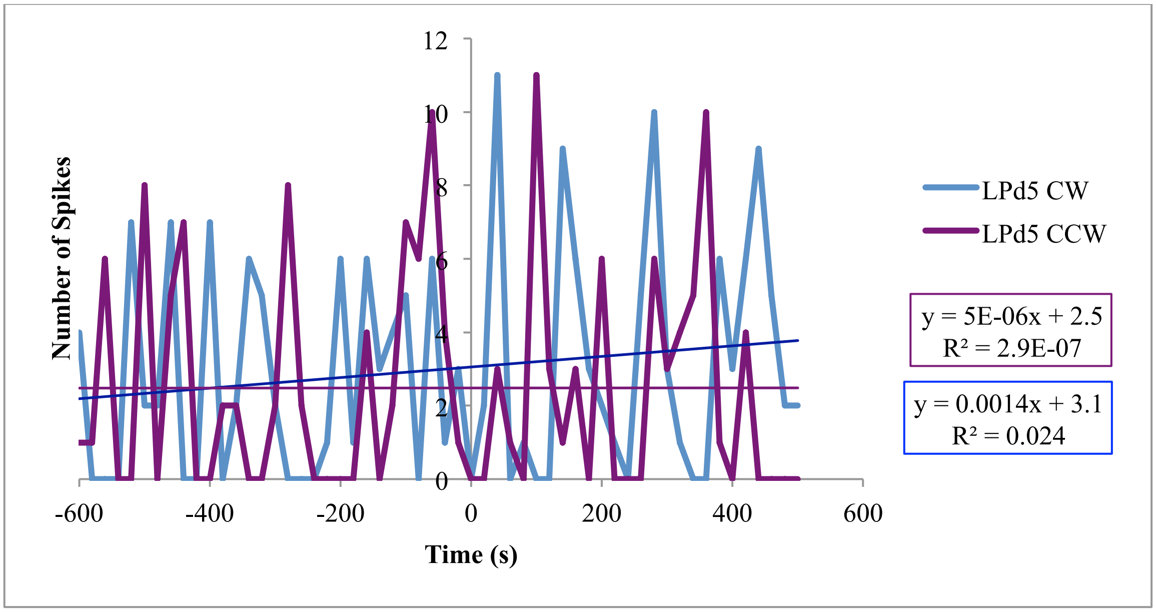

Figure 7. Left pedal 5 neuron response to clockwise and counterclockwise magnetic rotation. Number of spikes per 20 s interval. Possible small positive slope after clockwise rotation, with no change after counterclockwise rotation. 7 CW trials and 6 CCW trials.

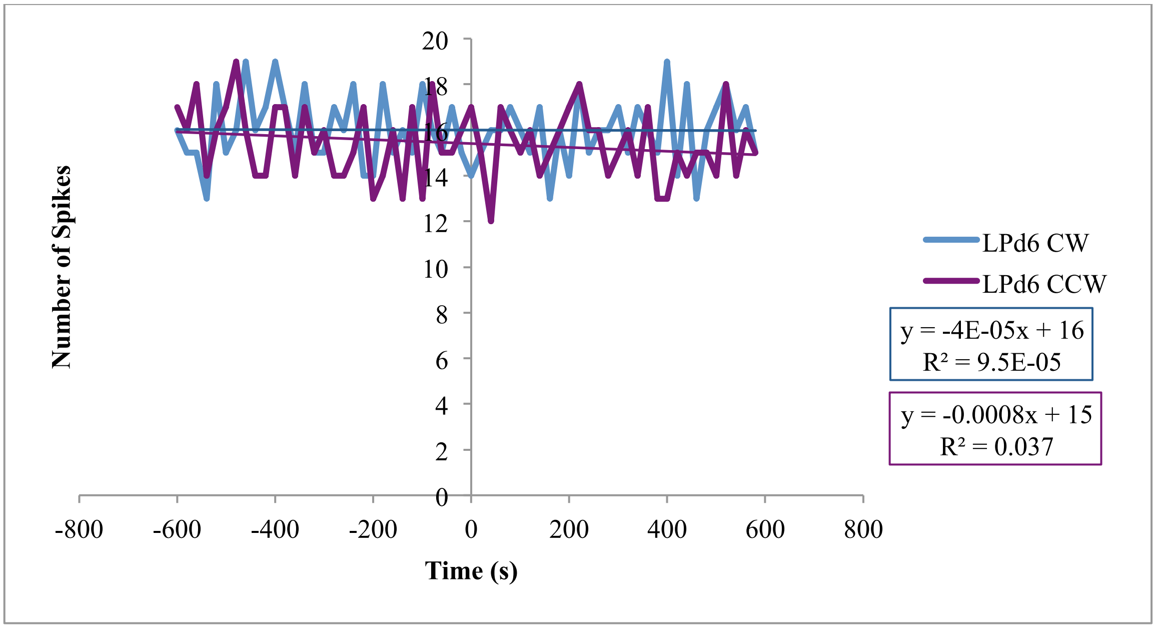

Figure 8. Left pedal 6 neuron response to clockwise and counterclockwise magnetic rotation. Number of spikes per 20 s interval. Possible small decrease after counterclockwise rotation, with no change after clockwise rotation. N= 2 trials each.

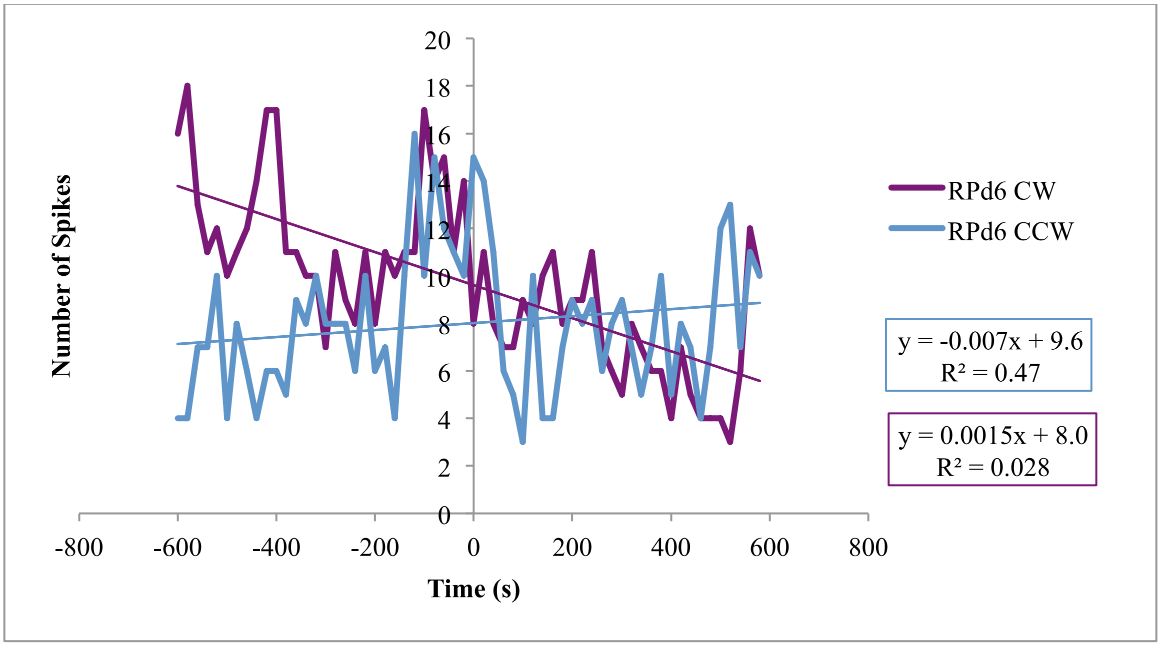

Figure 9. Right pedal 6 neuron response to clockwise and counterclockwise magnetic rotation. Number of spikes per 20 s interval. Possible decrease after clockwise rotation, and increase after counterclockwise rotation. N= 2 trials each.

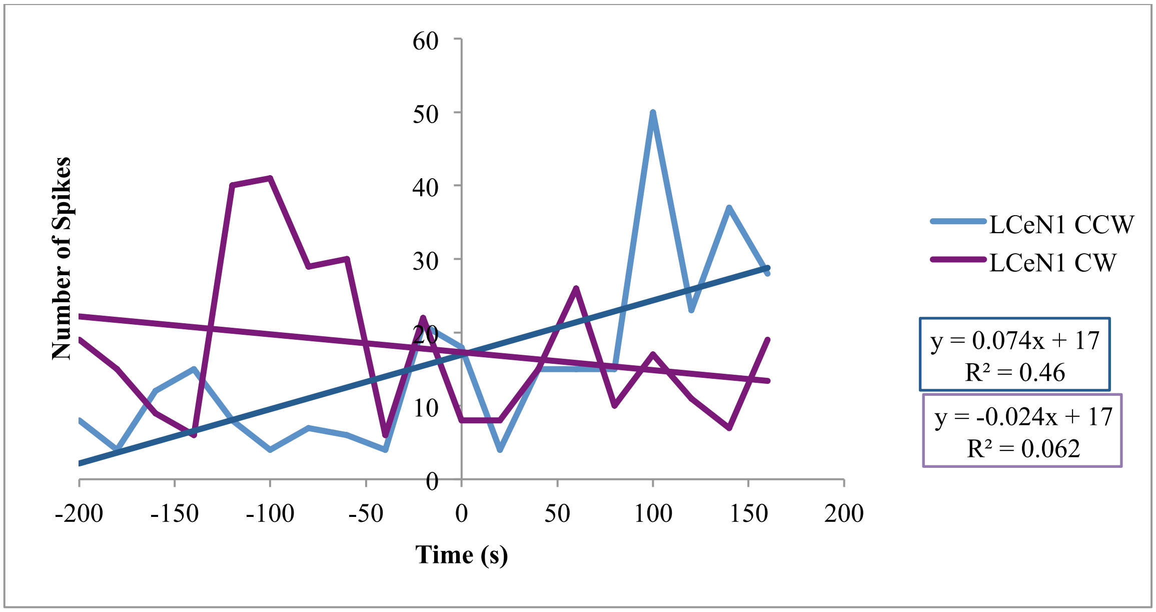

Figure 10. Left cerebral nerve 1 response to clockwise and counterclockwise magnetic rotation. Number of spikes per 20 s interval. Possible decrease after clockwise rotation, and increase after counterclockwise rotation. Summed activity of N= 10 trials each.

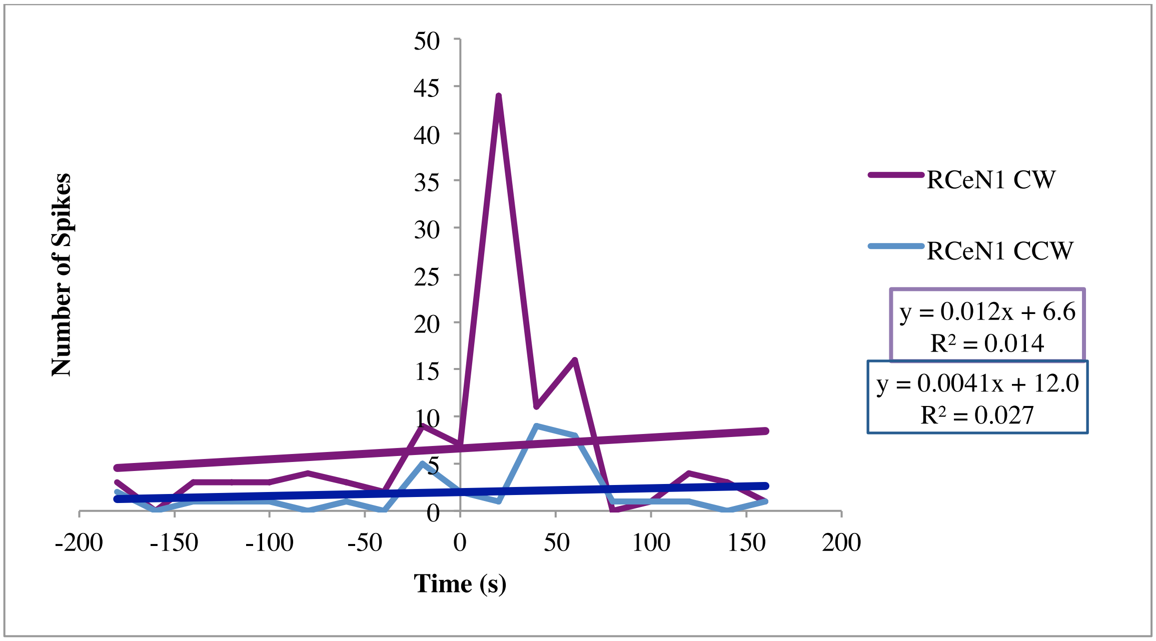

Figure 11. Right cerebral nerve 1 response to clockwise and counterclockwise magnetic rotation. A large increase was observed after clockwise rotation, but less increase after a counterclockwise rotation. **Number of spikes per 20 s interval. N= 10 trials each.**

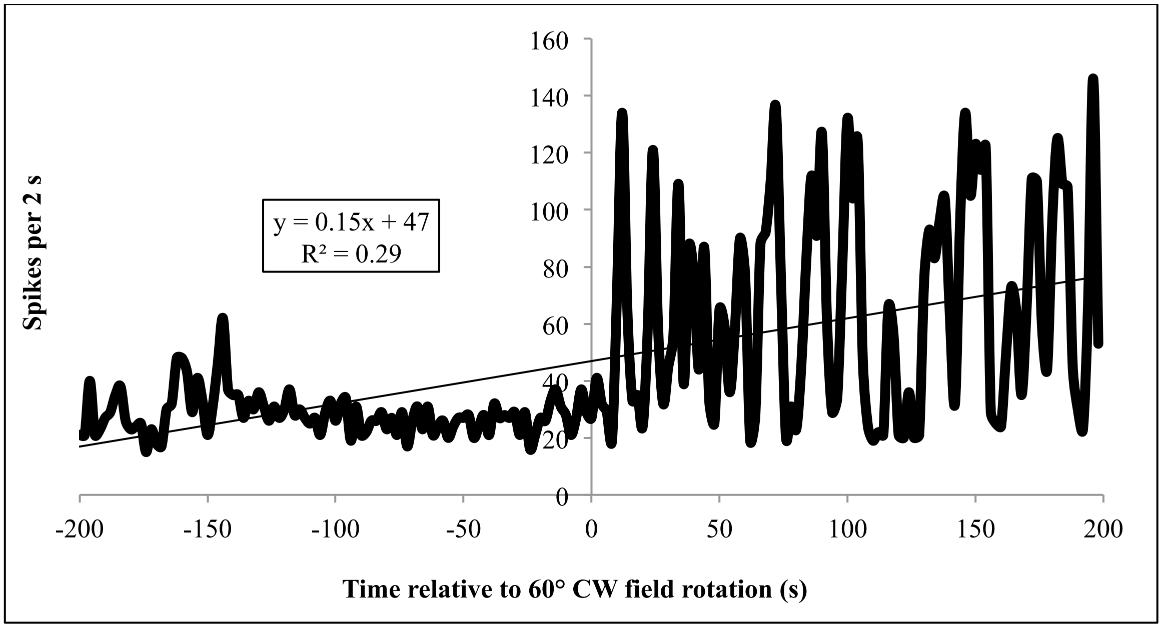

Figure 12. Left cerebral nerve 1 spiking increase after clockwise 60º magnetic field rotation. LCeN1 spiking increased 10 s after the 60º clockwise rotations that persisted for over 200 s (13 trials). Counter-clockwise showed no change in spike rate (data not shown; 11 trials).

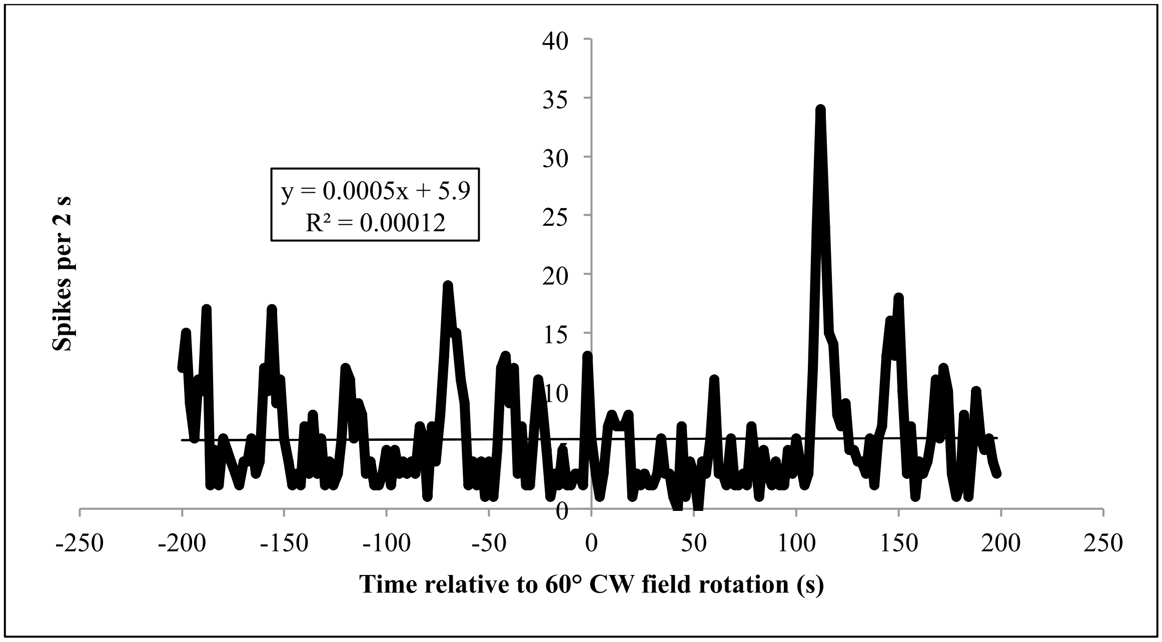

Figure 13. Right cerebral nerve 1 spike increased 120 s after clockwise 60º magnetic field rotation (13 trials).

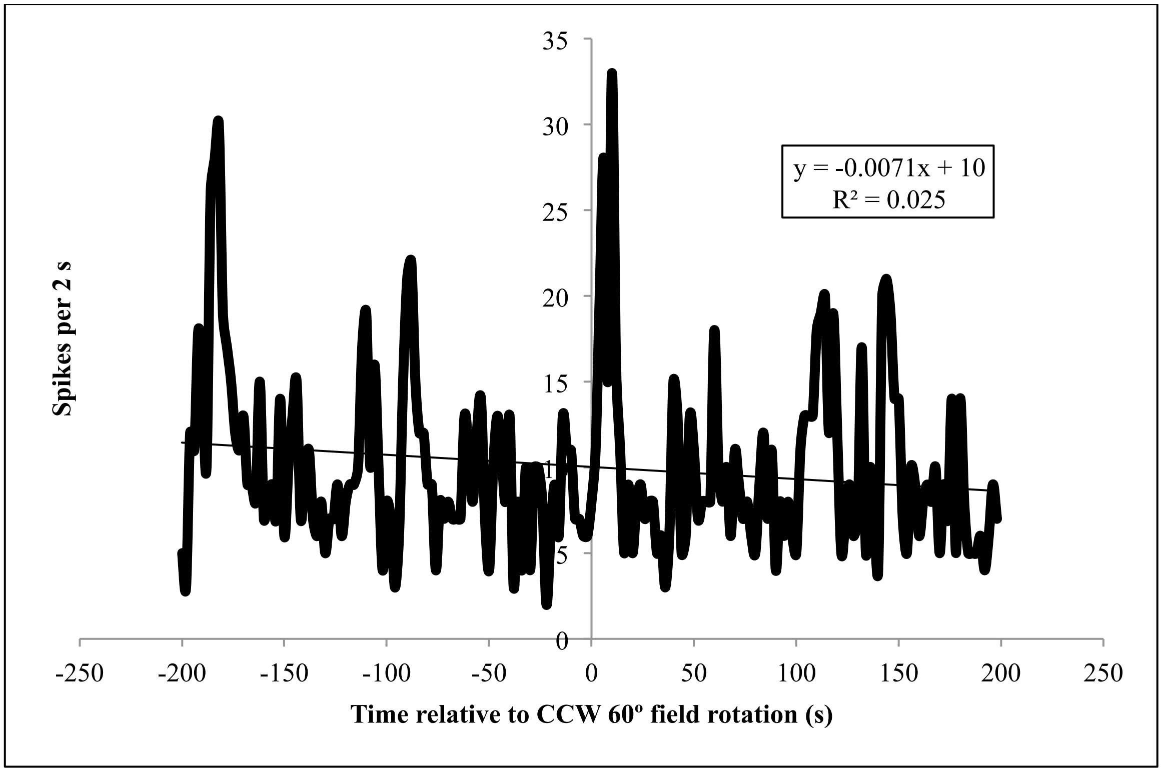

Figure 14. Right cerebral nerve 1 potential spike after counterclockwise 60º magnetic field rotation. Note an increased firing 6-10 s after the 60º counter clockwise rotations (11 trials).