



## Static otolithic drive alters presynaptic inhibition in soleus motor pool



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### ABSTRACT

The vestibular system has both direct and indirect connections to the soleus motor pool via the vestibulospinal and reticulospinal tracts. The exact nature of how this vestibular information is integrated within the spinal cord is largely unknown. The purpose of this study was to identify whether changes in static otolithic drive altered the amount of presynaptic inhibition in the soleus H-reflex pathway. Changes in static otolithic drive were investigated in sixteen healthy participants using a tilt table. Two presynaptic pathways (common peroneal and femoral) to the soleus H-reflex were tested in three weight conditions (supine, non-weight bearing, and weight bearing). The dependent variable was the peak-to-peak amplitude of the soleus H-reflex. Inhibition to the soleus motor pool through the common peroneal nerve pathway differed significantly during weight conditions and tilt. During tilt and non-weight bearing there was greater inhibition of the soleus H-reflex compared to supine, however, this effect was reversed during tilt and weight bearing. Facilitation from the femoral nerve pathway was reduced by tilt compared to supine, but this reduction was unaffected by weight condition. This supports a role of the vestibular system as providing complex, task-dependent presynaptic input to motoneurons in the lower limbs.

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### 1. Introduction

The vestibular system relates the position of the head in space relative to gravity and plays an integral role in maintaining balance and supporting posture (Nashner, 1971). Whereas the semicircular ducts have been implicated in alerting a person to potential falls (Nashner, 1971), the otolithic organs may have an important role for conveying ongoing information about the body with respect to gravity and may be more relevant to postural regulation (Watt, 1981a, 1981b; Greenwood and Hopkins, 1976; Lacour et al., 1978).

Otolithic information is transmitted to all levels of the body primarily via the vestibulospinal and reticulospinal tracts (Nyberg-Hansen, 1965; Nyberg-Hansen and Mascitti, 1964). The information conveyed by these two tracts is organized reciprocally and is functionally coupled, so that different muscles will receive different, complementary, information from each tract about the position of the head relative to gravity (Orlovsky, 1972; Grillner et al., 1968). Recent research further demonstrates that this coupled, reciprocal patterning of information in the lower limbs is

both muscle and task dependent (Dakin et al., 2013; Bent et al., 2004, 2002).

There has been much investigation examining the various factors responsible for appropriate regulation of posture and dynamic maintenance of balance. The picture painted by these studies demonstrates that postural regulation is a task dependent on many factors, from somatosensory inputs (Bove et al., 2006; Inglis et al., 1994; Horak, 2006; Inglis and Macpherson, 1995) and cortical inputs (Barra et al., 2006; Bernard-Demanze et al., 2009; Shinya et al., 2016; Taube et al., 2008), to vestibular inputs (Peterka et al., 2011; Horak, 2009) and each of these factors is relatively weighted in its effect on the postural system (Dichgans and Diener, 1989; Fetter et al., 1990; Horak et al., 1990; Carriot et al., 2015). Vestibular inputs are integrated with and weighted against all of these other inputs for the dynamic modulation of postural responses. Interestingly, however, while these other factors affect long-latency postural responses, vestibular inputs also affect short-latency postural responses like the H-reflex (Kennedy and Inglis, 2001). Vestibular input to short-latency postural responses and the H-reflex have been demonstrated in both dynamic (Greenwood and Hopkins, 1976; Taube et al., 2008; Knikou and Rymer, 2003) environments where a drop or a tilt is initiated and also static environments (Knikou and Rymer, 2003; Aiello et al., 1983) where a tilt is sustained. However, the mechanism of vestibular integration within the spinal networks remains unknown. Several authors have posited that this integration hap-

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pens presynaptically (Kennedy and Inglis, 2001; Knikou and Rymer, 2003; Iles and Pisini, 1992). Gaining insight into these mechanisms could potentially lead to a deeper understanding of how specific vestibular disorders affect postural networks within the spinal cord. The soleus motor pool has long been studied for its relevance to postural regulation. Two well-defined presynaptic pathways to the soleus motor pool include common peroneal nerve conditioning and femoral nerve conditioning. For a full understanding of these pathways, please refer to Hultborn and colleagues (Hultborn et al., 1987a, 1987b; Morin et al., 1984).

Based on the anatomy alone, the vestibular system could potentially affect the soleus motor pool presynaptically through the motor neurons directly, Ia afferent fibers, first-order primary afferent depolarization (PAD) interneurons, and/or second-order PAD interneurons (Nyberg-Hansen, 1965; Nyberg-Hansen and Mascitti, 1964). Recognizing the relationship between vestibular and somatosensory inputs, and coupled with the fact that weight-bearing has been shown to down-regulate the soleus H-reflex in humans (Koceja et al., 1993) we also sought to examine how the vestibular system interacts with weight-bearing mechanisms to more fully understand the complexities of vestibular input to spinal networks. The purpose of this study was to examine the role of the vestibular pathways in mediating soleus motoneuron excitability in both a weight-bearing and a non-weight-bearing condition.

## 2. Materials and methods

Twenty healthy subjects (14 female) between the ages of 18–35 years participated in this study. Subjects were excluded for self-report of known neurological disorder, balance disorder, and/or participation in high levels of physical activity. Prior to participation, all subjects read and signed an Informed Consent Form in accordance with the Declaration of Helsinki and approved by the Human Subjects Committee of Indiana University.

Surface EMG was collected after preparing the skin with alcohol, using Ag electrodes (Delsys, Bagnoli 16) configured in a parallel array with 1-cm spacing and their output was pre-amplified with a gain of 1000. The electrodes were placed on the subject's right leg, parallel to muscle fibers, over the soleus, medial and lateral gastrocnemius, tibialis anterior, and rectus femoris muscles. Signals were monitored, using an online oscilloscope (Tektronix, Model TDS 3012), throughout the experiment to ensure appropriateness of EMG recording.

### 2.1. H-reflex procedures

Percutaneous electrical stimulation was used (GRASS S88D stimulator) to stimulate the appropriate mixed nerve and elicit the H-reflex or the conditioning stimulation. All H-reflex and conditioning stimuli were delivered using a 1 ms square-wave pulse (GRASS, S88stimulator), and monitored online using an oscilloscope (Tektronix, Model TDS 3012), according to standard lab procedures (Hugon, 1973). Briefly, the ideal testing site for the soleus H-reflex was determined by holding the electrode over the popliteal fossa while very slowly increasing the intensity delivered to the subject until the H-reflex appeared on the oscilloscope, in the absence of an M-wave. Once the intensity was high enough to evoke a small H-reflex, the experimenter slightly shifted the position of the electrode within the popliteal fossa to find a location where the largest measurable H-reflex existed at the same intensity of stimulation. Once this optimal location within the popliteal fossa was found, it was marked and the electrode was secured in that position. After the electrode was fully secure, it was double-checked to be sure that an H-reflex equivalent to the earlier size

was still present, yet there was no M-wave present. The same overall procedure was repeated for the common peroneal nerve stimulation, with the electrode placed at the head of the fibula, and the femoral nerve, with the electrode placed in the inguinal crease. Optimal placement of the electrodes was periodically checked throughout the experiment to ensure that there was no movement of the electrodes over the course of the experiment. A soft ankle splint was placed on the subjects' feet, fixing the angle of the ankle to 90° so that changes in muscle length due to ankle angle did not confound the results. Furthermore, subjects wore a blindfold in all of the conditions, to prevent any visual cues that may have influenced the soleus H-reflex. Finally, the subject was asked to keep their head in a neutral and comfortable position, resting against the tilt table, for the duration of the testing. This head position was visually monitored by the experimenter throughout the testing.

All data were recorded on a laboratory computer (Optiplex GX280, Dell Computer Corporation) using custom data acquisition software (AcqKnowledge, version 3.7.3, BioPAC systems Inc.), sampled at 2000 Hz, and stored for offline analysis.

Once all electrodes, ankle splint, harness, and blindfold were secured, the subject was asked to lay supine, eyes closed, on the tilt table and M-max of the soleus muscle was determined by slowly increasing the stimulation intensity until the M-wave saturated. Once the M-max value was determined, all further data were obtained by setting the stimulation intensity at an amplitude sufficient to elicit the soleus H-reflex at 15% of M-max. Because the soleus H-reflex was the dependent variable, only M-max of the soleus muscle was obtained. While, theoretically, M-max should be the same across all conditions (McNulty et al., 2012), in our experience M-max has been seen to shift slightly in the same subject over time or in different conditions. This instability has also been documented by others (McNulty et al., 2012). Therefore, M-max was determined for each subject independently in the three weight conditions (supine, non-weight bearing, and weight bearing) and the H-reflex amplitude for each of the three weight conditions was set at 15% of the M-max for that individual condition.

### 2.2. Tilt table procedures

The clinically-approved tilt table (Tri W-G, model TW6131.HD) moved at a constant slow speed of 4.3°/s (equivalent to 0.01 Hz). During the non-weight bearing condition, a harness assured that as the table angle changed the subject was not supporting any of his/her body weight. During the weight-bearing condition, we estimated that at a tilt of 60° the subject was bearing 86.6% of his/her body weight.

### 2.3. Experimental procedures

There were three different stimulus conditions (soleus H-reflex alone 'test', common peroneal nerve conditioning, and femoral nerve conditioning) and three different weight conditions (supine 'control', tilted to 60° and non-weight bearing, and tilted to 60° and weight bearing). For all three of the weight conditions, subjects experienced all three of the stimulus conditions, 10 trials for each conditioning stimulus. The test H-reflexes were interleaved with the conditioning stimuli so that prior to one conditioning stimulus there were a minimum of three test H-reflexes at the appropriate stimulation intensity. This is a necessary control due to the nonlinearity of the H-reflex recruitment curve (Crone et al., 1990). The presentation order of stimulus condition and weight condition was counterbalanced across all subjects. All stimuli were presented randomly with an interstimulus interval no shorter than 9 s. Between each of the weight conditions subjects were returned to a supine position and given short breaks. Upon return to the exper-

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