Electromyographic Responses From the Hindlimb Muscles of the Decerebrate Cat to Horizontal Support Surface Perturbations

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Honeycutt CF, Gottschall JS, Nichols TR. Electromyographic responses from the hindlimb muscles of the decerebrate cat to horizontal support surface perturbations. J Neurophysiol 101: 2751–2761, 2009. First published March 25, 2009; doi:10.1152/jn.91040.2008. The sensory and neural mechanisms underlying postural control have received much attention in recent decades but remain poorly understood. Our objectives were 1) to establish the decerebrate cat as an appropriate model for further research into the sensory mechanisms of postural control and 2) to observe what elements of the postural response can be generated by the brain stem and spinal cord. Ten animals were decerebrated using a modified premamillary technique, which consists of a premamillary decerebration that is modified with a vertical transection near the subthalamus to eliminate spontaneous locomotion. Horizontal support surface perturbations were applied to all four limbs and electromyographic recordings were collected from 14 muscles of the right hindlimb. Muscle activation was quantified with tuning curves, which compared increases and decreases in muscle activity to background and graphed the difference against perturbation direction. Parallels were drawn between these tuning curves, which were further quantified with a principal direction and breadth (range of directions of muscle activation), and data collected by other researchers from the intact animal. We found a strong similarity in the direction and breadth of the tuning curves generated in the decerebrate and intact cat. These results support our hypothesis that directionally specific tuning of muscles in response to support surface perturbations does not require the cortex, further indicating a strong role for the brain stem and spinal cord circuits in mediating directionally appropriate muscle activation patterns.

INTRODUCTION

The mechanisms underlying the ability of terrestrial animals to remain upright and maintain stability in the face of mechanical perturbations have received considerable attention in recent decades (Allum et al. 1998; Bloem et al. 2000; Chanaud and Macpherson 1991; Deliagina et al. 2006; Diener et al. 1988; Fung and Macpherson 1995; Henry et al. 1998; Jacobs and Horak 2007; Lockhart and Ting 2007; Macpherson 1988a,b; Maurer et al. 2006; Mergner et al. 2003; Nashner 1976; Stapley et al. 2002; Torres-Oviedo et al. 2006). In a classic series of studies, Macpherson (1988a,b) used radial, horizontal movements of a support surface to evoke coordinated postural responses from cats trained to stand quietly on a platform. Muscle activation patterns were quantified through creation of tuning curves that compared increases and decreases in muscle activity to background and graphed the difference against perturbation direction. Muscles were found to have a principal direction of activation, but were also found to have a substantial breadth or range of directions over which the muscle was active. In general, tuning curves were found to be broadly tuned, occupying ≥25% of the perturbation space and often overlapped the activation space of other muscles. Subsequent analysis of these tuning curves demonstrated that muscles are recruited in groups or synergies (Ting and Macpherson 2005). However, no clear consensus has been reached detailing the important sensory mechanisms and neural structures necessary for the production of appropriate postural corrections.

A significant debate exists as to whether the neural networks in the brain stem and spinal cord can mediate the observed directional tuning or whether circuits in cortical areas are required as well. It has been argued that isolated spinal circuits with intact musculoskeletal systems are responsible for quite sophisticated motor tasks (Edgerton et al. 2001; Stein and Daniels-McQueen 2004; Timoszyk et al. 2002) and sensorimotor transformations (Bosco and Poppele 2001; Poppele and Bosco 2003). In contrast, the poor postural responses of spinalized cats (Fung and Macpherson 1999; Macpherson and Fung 1999; Pratt et al. 1994) have been interpreted to indicate that spinal pathways are not adequate for appropriate muscle activation. It should be noted, however, that the spinal lesion interrupts neural communication between forelimbs and hindlimbs and may interfere with postural networks that depend on propriospinal pathways. Furthermore, chronic spinal injury in cats is accompanied by widespread clasp-knife inhibition (Bonasera et al. 1994; Nichols et al. 1999), increases in inhibitory neurotransmitters, and reorganization of spinal synapses (Edgerton et al. 2001), all of which likely influence spinal cord functionality. More recent studies suggest that spinal circuits can support postural control as long as supraspinal influences remain intact (Deliagina et al. 2006, 2008; Lyalka et al. 2005; Musienko et al. 2008). Although cortical circuits influence most motor behaviors, the extent to which these circuits are required for the expression of the postural response remains unknown (Jacobs and Horak 2007). Therefore the location of the required neural integration and the degree to which this integration is distributed among areas in the CNS remain elusive.

For the above-cited reasons, we asked whether the decerebrate cat preparation might be used for further investigation of both the sensory and neural mechanisms used during postural control. The decerebrate cat has been used extensively to study many mechanisms of motor control, includ-
ing motor unit recruitment (Cope and Clark 1991; Cope et al. 1997), spinal pathway organization (Houk 1979; Nichols 1989, 1999; Nichols et al. 1999; Sherrington 1898), pattern-generating circuits (McCrea et al. 1995; Mori 1987; Pearson 1995; Shik et al. 1968), and integration of feedback from the vestibular system and from neck proprioceptors (Gottschall and Nichols 2007; Wilson et al. 1984, 1986). Our objectives were 1) to establish the decerebrate cat as an appropriate model for further research into the sensory mechanisms of postural control and 2) to observe what elements of the postural response can be generated in the absence of the cerebral cortices. We hypothesize that directionally appropriate muscle activation does not require the cerebral cortices.

We have developed a reduced preparation that exhibits directionally appropriate muscle responses in the absence of the cerebral cortices. This preparation, consisting of a modification of the premammillary decerebration, retains responsiveness to postural perturbations but does not exhibit spontaneous stepping. A description of the activation patterns of selected hindlimb muscles in response to horizontal platform perturbations is included in this study. The data from this preparation are also compared with those obtained from intercollicular decerebrate cats and the implications of this comparison for the role of supraspinal circuits in the expression of the force constraint strategy are discussed. Preliminary results have been published in abstract form (Honeycutt and Nichols 2005).

METHODS

Ten cats, used in accordance with the issued standards of the National Institutes of Health and the Emory Institutional Animal Care and Use Committee, are described in the following report. Animals will be referred to by the date of the experiment (6/8, 9/7, 9/11, 9/13, 9/29, 10/8, 11/7, 12/18, 1/22, 2/23). Under isoflurane anesthesia, a tracheotomy was performed to monitor anesthesia levels and an IV was inserted in the external jugular vein for hydration and drug delivery. Bipolar electrodes, constructed from Teflon-coated braided wire, were inserted into the belly of the medial gastrocnemius (MG), lateral gastrocnemius (LG), vastus lateralis (VL), vastus medialis (VM), semitendinosus (ST), semimembranosus (SM), gracilis (Grac), iliofemoris (Ilio), internal oblique (IO), anterior sartorius (aSart), anterior biceps femoris (aBF), posterior biceps femoris (pBF), and gluteus medius (Glut) muscles in the right hindlimb.

We used two decerebration techniques: intercollicular and a modified premammillary. The more traditional intercollicular decerebration consisted of a vertical transection through the superior colliculus (Mori 1987; Sherrington 1898). All brain material rostral to the transection was removed. The intercollicular decerebration technique did not produce consistent postural responses (see RESULTS) so we used a modification of the premammillary decerebration, a preparation usually used to obtain spontaneous stepping (Grillner and Shik 1973; Whelan 1996). Following the premammillary transection and removal of all brain tissue rostral to the cut, a second, vertical transection was made at the level of the mammillary bodies to prevent spontaneous locomotion. The resulting preparation was considerably more responsive to mechanical perturbations than animals prepared with intercollicular transections.

**Experimental protocol**

After the initial surgery, the animal was positioned using a stereotaxic frame to support the head and a sling to support the body. Additionally, a clamp was fixed at the base of the tail to support the hindquarters of the animal. The clamp did not interfere with hip rotation and allowed for a more natural hip angle and movement than fixation of the hip or spinal clamps. The sling was detached after isoflurane was removed and weight bearing was established. Anatomical measurements, collected on intact animals during standing, were used to position the hip height, head height, and paw spacing (both transverse and sagittal planes). The feet were placed over four force transducers (ATI Industrial Automation) located on a support platform. The natural turnout of the foot was used for each animal. Electrical signals from the bipolar electrodes were passed through a preamplifier, with a gain of 200 (overall gain of 1,000), and band-pass filtered from 10 to 1,150 Hz. Electromyographic (EMG) data from the electrodes and three-dimensional force data from the transducers were collected using a LabVIEW program designed specifically for this project.

Animals were gradually removed from anesthesia over the course of 30–45 min to minimize sudden increases in blood pressure. Muscle activity in response to support surface perturbations was present within 5 min of anesthesia removal. However, data were not evaluated until the animal was completely removed from anesthesia for 30 min. Data during these initial trials were compared with data taken later during the day to ensure similarity. Once the animal was completely removed from anesthesia, the support surface was translated in 16 different, horizontal directions using two motors: rotational and linear. The rotational motor positioned the linear motor for the perturbation. This technique ensured a linear perturbation. Support surface translations were delivered in random order. In all but one case, the support surface was perturbed 4 cm over 400 ms, with an acceleration of 0.5 m/s². In one animal (6/8), the platform was moved 8 cm over 400 ms. The perturbation parameters were chosen based on previous studies in intact cats for comparison purposes (Macpherson 1988a,b, 1994). Unique to the decerebrate cat, the animal’s head and tail were in a fixed position. Thus the limbs were perturbed, held at the extended position for 1,000 ms, and then returned 4 cm over 400 ms to the initial position. In one animal (10/8), the hold position was only 500 ms.

**Data analysis and quantification**

EMG data were notch filtered for 60-Hz noise, demeaned, high passed at 30 Hz (to remove movement artifacts), and rectified. EMG data were additionally averaged across three trials for figures; however, statistical analysis was completed one trial of 16 directions individually (see preceding paragraph). EMG data were compiled only for trials where muscle responses were present in all 16 directions. Latencies were estimated by visual inspection. An increase in firing amplitude or firing rate greater than the maximum amplitude or firing rate during the background for a minimum of 5 ms was considered an active response. The muscle responses were evaluated during several 200-ms windows during the perturbation (dynamic phase) and the hold (steady-state phase). The background mean EMG activity, from a 200-ms window preperturbation, was subtracted from the mean EMG activity of each 200-ms window. The resulting responses were graphed against perturbation direction to create a tuning curve (see Figs. 1 and 2 in RESULTS for further description). EMG tuning curves are portrayed in two formats: radial and linear. Tuning curves were normalized to maximum activation before quantification. Inhibitory responses were normalized to maximum excitation to maintain individual muscle scale.

To quantify the tuning curves, the breadth and principal direction were calculated for each muscle response. The breadths of the excitatory and inhibitory responses are quantified by calculating the area under the respective normalized tuning curves. A large breadth represents a muscle that is active over many perturbation directions. The principal direction represents the maximum direc-
tion of activation. To determine the principal direction, muscle responses from each direction were converted to a vector and $x$ and $y$ components were averaged to find the primary vector or principal direction of the response. The principal direction represents the average direction of all directional muscle activity. Statistics were computed 1) to define the characteristics of our data set and 2) to compare two different time epochs of the modified premammillary decerebrate animals’ muscle responses. Statistical comparison of means of principal direction and breadth were completed with a two-tailed $t$-test of equal variance. F-tests were used to confirm equal variance and Lillifores tests were used to confirm normalized distributions in samples with more than four observations. In the rare case that the populations exhibited nonnormalized distributions, a Kolmogorov–Smirnov (KS) test, which does not assume normalized distribution, was used. In the rare case that the F-test indicated an unequal variance, a $t$-test of unequal variance was performed. To be included in statistical analysis, the muscle must have responded in a minimum of three trials for the full set of 16 directions in each animal. Degrees of freedom for statistical significance were adjusted appropriately based on the number of observations in each muscle (see tables for observation numbers); $t$-tests were performed at a 0.95 confidence interval or $P$ value of 0.05. Results were compared qualitatively between the intercollicular and modified premammillary preparations and between the modified premammillary decerebrate preparation and the intact animal.

RESULTS

Modified premammillary preparation

The muscles of the decerebrate cat responded to horizontal support surface perturbations with varying amounts of excitation or inhibition. Figure 1 shows the raw (three trials averaged) EMG traces for each of the 16 directions of perturbation for the gluteus medius muscle (10/8 experiment). EMG traces are depicted in order of perturbation direction starting with trace 1 at 0° (lateral direction) and proceeding counterclockwise. Perturbation direction angles are shown graphically in Fig. 2A. Excitation and inhibition in all muscles were estimated to occur at latencies of 20–30 ms (Fig. 1). As can be seen from traces 3–8 (Fig. 1), activity generally increased in firing frequency during the ramp. In the case of inhibitory responses (traces 11–16), firing frequently ceased during the ramp. Some traces showed little excitation or inhibition and appear to be transition phases between the two states. Quantification of these changes in muscle activity as tuning curves is further described in Fig. 2.

The muscles of the decerebrate cat produced broad tuning curves usually encompassing $\pm 25\%$ of the perturbation space. The raw traces depicted in Fig. 1 were quantified by comparing the initial mean response (0–200 ms) to mean background activity. The change in mean activity was then graphed against perturbation direction to give a visual representation of what directions cause muscle activation or inhibition.
inhibition. The time period (0–200 ms) was chosen for comparison to intact animal data (Macpherson 1988b). The excitatory and inhibitory tuning curves of the gluteus medius muscle (10/8 experiment) are depicted in two formats, radial (B) and linear (C), in Fig. 2. All tuning curves (also see Fig. 3) appear broad in nature, demonstrating a graded and smooth increase to maximum activation and then a smooth decrease to a maximum inhibition. Therefore muscles show a steady rise in activation until a maximum is reached, rather than being turned on and off in a switchlike behavior. While activated or inhibited over multiple directions, each muscle tuning curve had a principal direction where it is most active or most inhibited. We quantified both the principal direction of each tuning curve along with the breadth. The linear tuning curve in Fig. 2C shows the quantified principal direction of the excitatory tuning curve (arrow) along with the regions used for breadth quantification are shaded.

Tuning curves were obtained from a wide variety of muscles in the decerebrate cat. Figure 3 displays the typical radial tuning curves of all surveyed muscles. These tuning curves are arranged according to principal direction starting at 0° (lateral side of the animal) and continuing counterclockwise. Although the tuning curves span all 360° of perturbation space,
none of the muscles surveyed had a principal direction exclusively in the lateral direction (0°). Inhibitory tuning curves are often present and are generally directed oppositely to the excitatory tuning curves (Table 1). However, on an individual muscle basis, inhibitory principal directions can be as much as 25–30° away from directional opposition (180° difference from excitatory principal direction). More typically, however, these inhibitory responses are within 10–15° of 180°. For quantification, inhibitory tuning curves are normalized to maximum activation of each muscle. All muscles (with the exception of pBF) demonstrated inhibitory tuning; however, not all muscles demonstrated inhibitory tuning in all experiments since inhibitory tuning curves are limited by the presence of background activity.

Quantification of principal directions revealed that some muscles are highly consistent across experiments, whereas others demonstrate more variability. Table 1 displays the quantification of the excitatory and inhibitory tuning curve’s principal directions and breadths for all muscles surveyed. Muscles are in the order based on the excitatory tuning curve principal direction to correspond to Fig. 3. The excitatory principal directions ranged from 69 to 274°, which again demonstrates the lack of principal direction in the lateral (0°) direction. The inhibitory principal direction range was more broad, representing 3.5 to 330°; however, there is a lack in the medial direction from 107 to 258°. Some muscles, such as Grac, ST, LG, and Ilio, appeared to have very consistent excitatory principal directions (small SDs), whereas others, such as MG, VL, and VM, had significant principal direction variance across experiments. Inhibitory principal directions on average demonstrated larger variance across experiments than excitatory principal directions (Glut, VL, and VM being the exceptions). Furthermore, there were similar levels of variance for the excitatory and inhibitory directions in some muscles (MG, SM:caudal) but not in others (Grac, Ilio, LG).

Quantification of breadth demonstrated that a large excitatory breadth does not correlate to a large inhibitory breadth. The largest average excitatory breadths were present in the Grac, LG, pBF, and aBF muscles, whereas the smallest were in the VL, Ilio, and Glut muscles (Table 1). The largest average inhibitory tuning curve breadths, however, were different from their excitatory counterparts. The largest inhibitory breadths were present in VL and MG and the smallest were in IO, cSM, and ST. Again, inhibitory tuning curves are limited by the presence of background activity. Therefore it is expected that the largest inhibitory breadths would be found in the antigravity muscles that are typically spontaneously active in these preparations.

## Dynamic versus steady-state epochs

Excitation and inhibition seen during the perturbation (dynamic: 0–400 ms) continued through the platform hold (steady-state: 400–1,400 ms). Figure 4 presents the muscle responses during the ramp-and-hold of muscles near their principal direction of excitation and inhibition. The first gray box marks the forward perturbation and the second gray box the backward (or return) perturbation. The increase of EMG activity during the dynamic response persists through the steady-state period with little adaptation in firing rate or amplitude. Inhibition generally persists through steady state. However, some adaptation (or return of firing) was noted in a few cases (aBF, MG, IO in Fig. 4). The magnitudes of these responses varied between muscles and experiments; however, the generalized response was a burst of activity or inhibition during the initial perturbation that was usually held constant through the hold.

Despite subtle variability in response magnitudes, quantification of tuning curves throughout both the dynamic and steady-state phase showed that tuning remained constant through the time epoch. The data in Fig. 5 illustrate the tuning curves for two time bins during the dynamic (0–200, 200–400 ms) and steady-state (500–700, 700–900 ms) time periods. To compare amplitude shifts that might occur through the time epochs, tuning curves were normalized to the maximum activation of the first time epoch. All tuning curves generally demonstrated the same gradual rise in

### Table 1. Quantification of principal direction and breadth of tuning curves evaluated from 0 to 200 ms in the modified premammillary decerebrate animal

<table>
<thead>
<tr>
<th>Excitatory Response</th>
<th>Inhibitory Response</th>
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<tbody>
<tr>
<td><strong>Prin. Dir.</strong></td>
<td><strong>Breadth</strong></td>
</tr>
<tr>
<td>Gracilis</td>
<td>69 (3.4)</td>
</tr>
<tr>
<td>Semitendinosis</td>
<td>74 (8)</td>
</tr>
<tr>
<td>Posterior biceps femoris</td>
<td>91 (11)</td>
</tr>
<tr>
<td>Medial gastrocnemius</td>
<td>105 (40)</td>
</tr>
<tr>
<td>Semimembranosis (caudal)</td>
<td>106 (15)</td>
</tr>
<tr>
<td>Anterior biceps femoris</td>
<td>112 (19)</td>
</tr>
<tr>
<td>Semimembranosis (cranial)</td>
<td>114</td>
</tr>
<tr>
<td>Internal oblique</td>
<td>118</td>
</tr>
<tr>
<td>Gluteus medius</td>
<td>121 (14)</td>
</tr>
<tr>
<td>Lateral gastrocnemius</td>
<td>128 (8.9)</td>
</tr>
<tr>
<td>Vastus lateralis</td>
<td>195 (33)</td>
</tr>
<tr>
<td>Vastus medialis</td>
<td>216 (23)</td>
</tr>
<tr>
<td>Anterior sartorius</td>
<td>246</td>
</tr>
<tr>
<td>Iliopsoas</td>
<td>274 (4.6)</td>
</tr>
</tbody>
</table>

Depicts the quantification measures for all tuning curves across experiments for 0–200 ms. Prin. Dir., principal direction; N(e), number of excitatory curves; N(i), number of inhibitory curves. SDs are depicted in parentheses. Muscles are arranged based on principal direction starting at 0° (lateral side of the animal) and continuing counterclockwise. Both excitatory and inhibitory regions were quantified when present.

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activation until a maximum was reached (described in Fig. 3). Although there were subtle differences in the tuning with slight increases or decreases in inhibition or breadth alterations, the overall tuning remained the same. Principal directions and breadth during the last time period (700–900 ms) were further quantified and are reported in Table 2.

Quantification for the dynamic (0–200 ms; Table 1) and steady-state (700–900 ms; Table 2) responses showed no statistical difference in the principal direction and breadth across the time epochs. F-tests and t-tests were performed comparing principal direction and breadth (excitatory and inhibitory) for the dynamic (0–200 ms) and steady-state (700–900 ms) time epochs. All tests (t-test of equal and unequal variance and the KS) confirmed no statistical difference between the principal direction and breadths of all muscles between the 0- to 200-ms and the 700- to 900-ms epochs; t-tests were performed with a 95% confidence interval (P value of 0.05).

**Intercollicular preparation**

Tuning curves were rarely obtained (3 of 28 animals) from the muscles in the intercollicular decerebrate cat; however,
when present these curves were of similar direction and breadth to those of the modified premammillary preparation. Figure 6 shows example tuning curves and raw EMG from animals that demonstrated quantifiable EMG responses to horizontal perturbation. With the exception of the Grac muscle, all muscles that gave responses were extensor muscles. Raw EMG was similar in expression to that of the modified premammillary preparation; however, the magnitude of the response was decreased from the modified preparation. Tuning curves were similar in expression (both principal direction and breadth) to that of the modified premammillary preparation. Table 3 displays the quantification of all tuning curves that were produced. The principal directions of the muscle responses generated in the intercollicular animal were all within the mean and SDs of the principal directions reported in the modified premammillary animals. Breadths were difficult to accurately compute due to the decreased magnitude of the responses; however, in two cases (LG and Grac) the breadths were within those values reported in the modified premammillary animal, although the other values were more variable. In conclusion,
with the exception of small differences in breadth, tuning curves obtained from the intercollicular preparation were remarkably similar to those observed in the modified premamillary preparation.

**DISCUSSION**

**Summary**

We have obtained active responses from 14 muscles in the right hindlimb of unanesthetized decerebrate cats in response to horizontal platform perturbations. These animals had not undergone training on the task prior to the terminal experiment. These responses could be evoked in a small proportion of those animals prepared with intercollicular decerebration and in nearly all animals subjected to premamillary transaction, modified by an additional transection near the subthalamic nucleus to eliminate spontaneous locomotion. The electromyographic responses obtained from the right hindlimb of each animal during the radial ramp-and-hold perturbations resembled those obtained by other researchers in intact animals both in direction and breadth. The responses were characterized by excitatory and inhibitory tuning curves that varied little in breadth and direction between the dynamic and static phases of the perturbations. The presence of appropriately tuned responses implicates a strong role for the brain stem and spinal cord in generating the direction of muscle responses to postural perturbation. The development of this decerebrate cat preparation will allow us the ability to further investigate the role of various sensory system mechanisms underlying responses to postural disturbances.

**Comparison with studies of intact animals**

The excitatory and inhibitory tuning curves obtained in these studies were qualitatively comparable in principal direction and breadth with those obtained in intact animals (Macpherson 1988b; Torres-Oviedo et al. 2006). Despite methodological differences including electrode placement and limb choice, the excitatory tuning curves for Grac, aBF, LG, and VM (Fig. 3) generally correspond to the tuning curves of the same muscles obtained in intact animals (Macpherson 1988b). Furthermore, the principal direction for pBF is shifted laterally to the principal direction of aBF (Tables 1 and 2), as is the case for the intact animal (Chanaud and Macpherson 1991). The variability (SD) present in direction and breadth (Table 1) is also similar when evaluating the tuning curves reported in the literature (Chanaud and Macpherson 1991; Macpherson 1988b; Torres-Oviedo et al. 2006). In addition, both excitatory and inhibitory responses are present in the decerebrate cat, as reported in Macpherson’s original work in the intact animal (Macpherson 1988b).

Our primary objective was to determine whether the decerebrate animal could be used for further investigation of postural mechanisms. The decerebrate cat has been used extensively to study many mechanisms of motor control, including motor unit recruitment (Cope and Clark 1991; Cope et al. 1997), spinal pathway organization (Houk 1979; Nichols 1989, 1999; Nichols et al. 1999; Sherrington 1898), pattern-generating circuits (McCrea et al. 1995; Mori 1987; Pearson 1995; Shik et al. 1968), and integration of feedback from the vestibular system and from neck proprioceptors (Gottschall and Nichols 2007; Wilson et al. 1984, 1986). The observation that the muscles of the decerebrate cat can produce appropriately directed tuning suggests that this preparation is appropriate to further evaluate the sensory mechanisms and neural substrates driving these responses.

**Sensory mechanisms**

By choosing to fix the decerebrate animal’s head in a stereotaxic frame and performing ramp-and-hold perturbations, we were able to evaluate the muscle responses without the influence of vestibular and visual feedback. In the experiments of Macpherson (1988b, 1994), animals stabilized themselves over the moving platform to restore the original relationship of the center of mass to the placement of the four paws. Vestibular inputs are used under these conditions, as demonstrated by balance insufficiencies and improperly scaled muscle re-
sponses following vestibular loss (Macpherson and Inglis 1993; Thomson et al. 1991). Macpherson and Inglis, however, also reported that these animals were capable of producing appropriately directed muscular responses, which argues that the direction of these responses does not require vestibular input. Knowing that the decerebrate cat can also produce appropriately tuned muscular responses in the absence of visual and vestibular feedback supports this notion and further implies a critical role for cutaneous and muscle receptors in the production of appropriately directed muscle activation.

We favor the hypothesis that muscle receptors, specifically muscle spindles, provide the directional tuning for these muscle responses (Nichols et al. 1999). Supporting evidence comes from muscle spindle recordings in the anesthetized animal that display similarly directed tuned responses to their muscle of origin in response to limb perturbations of the same parameters (Honeycutt et al. 2007). In addition, reinnervated muscles, which have a surgically induced loss of muscle receptor feedback, do not exhibit a quantifiable excitatory response to postural perturbations in the anesthetized modified pre-mammillary decerebrate cat (Honeycutt et al. 2008). These reinnervated muscles remain functionally intact, capable of force production, and demonstrate appropriate motor unit recruitment (Abelew et al. 2000; Cope and Clark 1993; Haftel et al. 2005). Accordingly, muscle spindles are likely furnishing important directional information to the nervous system regarding postural perturbations. Nevertheless, there is considerable evidence that cutaneous feedback potently contributes to postural control (Kavounoudias et al. 1998, 2001; Maurer et al. 2001; Meyer et al. 2004; Roll et al. 2002; Stal et al. 2003; Stapley et al. 2002; Ting and Macpherson 2004). This new decerebrate preparation is being used in ongoing studies to evaluate the relative contributions of these two sources of sensory feedback. Our findings indicate that directional tuning is unaffected by loss of cutaneous feedback of the foot soles in the decerebrate cat (Honeycutt 2009).

Excitatory and inhibitory directional tuning may have differing control mechanisms. We noted that inhibitory tuning curves, although generally directed oppositely to excitatory tuning curves, could be as much as 30° off from complete numerical opposition (180°). In addition, data show that muscles with the highest excitatory principal direction variability did not correlate to muscles with the highest inhibitory tuning curve variability. Although this may be a result of the distorting effects of changes in background activity, it could also indicate that mechanisms driving excitatory responses are distinct from those driving inhibitory responses. We suggest that antagonistic muscles, which have well-studied reciprocal inhibition, may contribute significantly to the directionality of Table 3. Quantification of principal direction and breadth of tuning curves evaluated from 0 to 200 ms in the intercollicular decerebrate animal

<table>
<thead>
<tr>
<th>Muscle</th>
<th>Excitatory Response</th>
<th>Inhibitory Response</th>
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<tbody>
<tr>
<td>Lateral gastrocnemius</td>
<td>Prin. Dir. 126 (27)</td>
<td>261 Prin. Dir. 200</td>
</tr>
<tr>
<td></td>
<td>Breadth 5.6 (1.8)</td>
<td>0.7 Breadth 1</td>
</tr>
<tr>
<td></td>
<td>N(e) 3</td>
<td>N(i) 1</td>
</tr>
<tr>
<td>Gluteus medius</td>
<td>116 (38)</td>
<td>— —</td>
</tr>
<tr>
<td>Gracilis</td>
<td>62</td>
<td>— —</td>
</tr>
<tr>
<td>Vastus medialis</td>
<td>236</td>
<td>24</td>
</tr>
<tr>
<td>Medial gastrocnemius</td>
<td>136</td>
<td>— —</td>
</tr>
</tbody>
</table>

Depicts the quantification for all muscles that gave EMG responses to translation for the intercollicular preparations. The principal directions are comparable to those reported in the modified pre-mammillary animals, although the variability of the LG muscle is slightly increased. The breadths demonstrate more variation from the modified pre-mammillary preparation. The gluteus medius shows an increased breadth from the modified preparation, whereas the vastus medialis and medial gastrocnemius show decreased breadths.

FIG. 6. Raw EMG and tuning curves from the intercollicular decerebrate cat: example traces of raw (3 averaged traces) EMG (A, B) and radial tuning curves (C) from the intercollicular preparations. The top trace of each raw EMG trace (A) is from the maximal excitatory direction and the bottom traces (B) are from the most inhibitory direction. The perturbation is depicted in the last trace (C). The raw EMG and radial tuning are remarkably similar to those of the modified pre-mammillary preparation. Further quantification is reported in Table 3. Intercollacellular responses were rare, with only 3 of 23 animals giving quantifiable EMG activation in response to translation.
inhibitory responses since torque exerted by antagonistic muscles can depart from direct opposition to the agonist (Lawrence 3rd and Nichols 1999).

Central mechanisms

There is substantial evidence that the cortex (Adkin et al. 2006; Beloozerova et al. 2003, 2005; Jacobs and Horak 2007; Taube et al. 2006), brain stem (Delagana et al. 2006, 2008; Mori 1987; Mori et al. 1989; Musienko et al. 2008), and spinal cord (Bosco and Poppele 2001; Lyalka et al. 2005; Stein 2008) all contribute to postural control. Classical literature illustrates that the decerebrate cat generates several postural tasks including the righting reflex (Magnus 1926), suggesting a strong role for brain stem and spinal cord circuits. Yet, more recent evidence alludes to a role for the cortex in unpredictable postural disturbances (Adkin et al. 2006; Jacobs and Horak 2007). It is plausible that these structures exist within a hierarchical framework in which each unit is responsible for increasingly complex integration of sensory and environmental information. Based on this report and data from the spinalized animal, we therefore propose that the directionally selective muscle tuning comes from the lowest levels of this hierarchy.

Our data demonstrating that robust and directionally appropriate muscle activation is present without the cerebral cortices strongly argue that the spinal cord and brain stem are responsible for the direction information driving appropriate muscular responses to horizontal perturbations. Yet, knowledge that the abF, aSart, Glut, RF, and VM muscles of the spinalized cat generate appropriately directed muscular responses (Macpherson and Fung 1999) further implies that the brain stem is not required for directional tuning. Although directionally appropriate, responses were not of sufficient strength or duration to generate the necessary force to oppose the perturbation. This is likely the result of the clasp-knife inhibition condition, where even small muscular force production is quickly followed by rapid inhibition (Nichols and Cope 2001), and not the result of insufficiencies of the spinal cord circuitry. We know that spinal cord participates in a variety of postural functions including stiffness regulation of muscle, joints, and limb (Nichols 1989; Nichols and Houk 1976). Furthermore, the spinal cord is known to mediate diverse motor tasks including wiping actions (Poppele and Bosco 2003; Stein and Daniels-McQueen 2004) and locomotion (Edgerton et al. 2001). Based on these considerations, we hypothesize that the spinal cord contains the circuitry required for directionally appropriate muscle activation.

A role for the upper brain stem in mediating these responses comes from our data showing that the muscular responses of the modified premammillary decerebrate cat are considerably more robust and present in a larger set of muscles than either the intercollicular or spinalized animal. When muscular responses were present in either the modified premammillary or intercollicular animal, they always generated similarly tuned responses to one another and the intact animal. However, 88.9% of animals prepared with the modified premammillary decerebration were able to generate muscular responses compared with only 11.7% of intercollicular decerebrated animals, implying an important role for the upper brain stem in controlling the expression of the tuned responses generated by the lower circuitry. This notion is corroborated by reports demonstrating that simultaneous stimulation of upper and lower brain stem regions enhance the lower brain stem effects on postural tone (Mori 1987). It has been clearly demonstrated that lower brain stem regions, specifically the ventral and dorsal segmental fields (VTF and DTF), respectively, can excite or inhibit postural tone (Mori 1987). Mori et al. (1989) additionally used horseradish peroxidase to determine which regions, stimulated through their passing axons, enhanced the VTF and DTF effects. They determined that the most effective VTF stimulation sites also stimulated upper brain stem regions, such as the hypothalamus and subthalamic nucleus, whereas the most effective DTF stimulation sites corresponded with the diencephalon and the dorsal posterior and lateral hypothalamus. The upper brain stem’s role in postural control appears analogous to its role in locomotion where the subthalamic nucleus controls the expression of locomotion generated by the mesencephalic locomotor region of the lower brain stem (Mori et al. 1989). The close association of the postural tone regions (VTF and DTF) to the expression of locomotion further indicates that these two systems are likely similarly controlled. These observations strongly imply that the upper brain stem controls the expression of the lower brain stem regions associated with postural tone.

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