Corticoreticular Pathways in the Cat. II. Discharge Activity of Neurons in Area 4 During Voluntary Gait Modifications

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Kably, Bouchra and Trevor Drew. Corticoreticular pathways in the cat. II. Discharge activity of neurons in area 4 during voluntary gait modifications. J. Neurophysiol. 80: 406–424, 1998. We propose that the descending command from area 4 that is responsible, in part, for the change in limb trajectory required to step over an obstacle in one’s path also plays a role in triggering the anticipatory postural modifications that accompany this movement. To test this hypothesis, we recorded the discharge characteristics of identified classes of corticofugal neurons in area 4 of the cat. Neurons were identified either as: pyramidal tract neurons (PTNs) if their axon projected to the caudal pyramidal tract (PT) but not to the pontomedullary reticular formation (PMRF); as corticoreticular neurons (CRNs) if their axon projected to the PMRF but not to the PT; and as PTN/CRNs if their axon projected to both structures. Altogether, the discharge properties of 212 corticofugal neurons (109 PTNs, 66 PTN/CRNs, and 37 CRNs) within area 4 were recorded during voluntary gait modifications. Neurons in all three classes showed increases in their discharge frequency during locomotion and included groups that increased their discharge either during the swing phase of the modified step, during the subsequent stance phase, or in the stance phase of the cycle preceding the step over the obstacle. A slightly higher percentage of CRNs (39%) discharged in the stance phase prior to the gait modification than did the PTNs or PTN/CRNs (20% and 17% respectively). In 37 electrode penetrations, we were able to record clusters of 3 or more neurons within 500 μm of each other. In most cases, PTN/CRNs recorded in close proximity to PTNs had similar receptive fields and discharged in a similar, but not identical, manner during the gait modifications. Compared with adjacent PTNs, CRNs normally showed a more variable pattern of activity and frequently discharged earlier in the step cycle than did the PTNs or PTN/CRNs. We interpret the results as providing support for the original hypothesis. We suggest that the collateral branches to the PMRF from corticofugal neurons with axons that continue at least as far as the caudal PT provide a signal that could be used to trigger dynamic postural responses that are appropriately organized and scaled for the movements that are being undertaken. We suggest that the more variable and earlier discharge activity observed in CRNs might be used to modify the postural support on which the movements and the dynamic postural adjustments are superimposed.

INTRODUCTION

As we discussed in the preceding article (Kably and Drew 1998), the corticoreticulospinal pathway may play an important role in ensuring that postural responses are scaled appropriately to the voluntary movements that they accompany. However, most of the evidence for this claim is indirect and is based largely on the results of cortical stimulation (e.g., Gahery and Nieoullon 1978) or cortical lesions in animals (Ioffe et al. 1988) and humans (Massion 1992; Viallet et al. 1992).

Certainly, the abundant connections between the pericruciate cortex and the pontomedullary reticular formation (PMRF), shown in a number of anatomic (Berrevoets and Kuypers 1975; Kiezer and Kuypers 1984; Kuypers 1958; Matsuyama and Drew 1997; Newman et al. 1989; Rho et al. 1997) and electrophysiological (Canedo and Lamas 1993; He and Wu 1985; Jinnai 1984; Lamas et al. 1994; Magni and Willis 1964a; Pilyavsky 1975) studies, and detailed in the companion paper, provide a substrate by which the motor cortex could trigger postural responses from the PMRF. Moreover, it is of particular interest that a substantial proportion of the neurons in area 4 that project to the PMRF have a receptive field restricted to the forelimb (Kably and Drew 1998). Such cells might be expected to be activated during locomotion and to increase their discharge frequency during voluntary gait modifications.

The role of the PMRF in the control of posture is based in part on a consideration of the known anatomy and physiology of this structure, which indicates that reticulospinal neurons branch widely within the spinal cord (Matsuyama et al. 1988, 1997; Peterson et al. 1975), conduct at fast speeds (Drew et al. 1996a; Eccles et al. 1975; Magni and Willis 1964b; Peterson et al. 1979; Wolstencroft 1964) and may influence the level of excitability of both flexors and extensors in each of the four limbs (Drew and Rossignol 1990a,b; Mori 1987; Mori et al. 1992; Peterson 1979) and, in part, on the effects produced by lesions of this structure or of its descending component (e.g., Brustein et al. 1993; Kuypers 1963, 1964; Lawrence and Kuypers 1968). In addition, the more direct evidence from the experiments of Luccarini et al. (1990) and Sakamoto et al. (1991), introduced in the companion paper, as well as recent results from our laboratory (Prentice and Drew 1995) suggest that the PMRF plays a role in the production of the dynamic postural responses that accompany voluntary activities, including locomotion (see Lavoie et al. 1995).

The present study was primarily designed to determine whether cortical neurons in area 4 that project to the caudal pyramidal tract (PT) and that send collaterals to the PMRF (PTN/CRNs) discharge phasically during gait modifications and thus could provide a signal that could be used to trigger the postural responses that accompany the gait modification. The discharge patterns observed in these cells are compared with those observed in neurons that project directly to the
METHODS

Task and training

All cats used in these experiments were trained to step smoothly over a cylindrical obstacle (10-cm cross-section) that was attached to a moving treadmill belt. As detailed previously (Drew 1993), at the treadmill velocity normally used in this study (0.35 m/s), the cats could see the obstacle for 2–3 s before stepping over it. These experiments were carried out on the same four cats as in the companion paper (Kably and Drew 1998), in which all surgical and experimental manipulations are described. Given the crossed nature of the projection from the motor cortex to the spinal cord, all analyses were performed with respect to the limb contralateral to the motor cortical recording site.

Data analysis

Sections of data in which stable, single, action potentials were recorded from cortical neurons during periods of locomotion of ≈10 steps over the obstacle were selected for analysis. Action potentials were discriminated on the basis of their shape and amplitude and were sampled, together with the electromyographic (EMG) activity from the recorded muscles, at a frequency of 1 kHz on a microcomputer. As described in Drew (1993), custom-written software was used to mark the beginning and end of each burst of EMG activity and to identify step cycles according to whether they were before, during, or subsequent to the step over the obstacle. That step cycle that occurred two steps before the step over the obstacle was designated as the control cycle. The first leg to be brought over the obstacle was identified as the lead leg and the second as the trail leg. All analyses, unless otherwise specified, were performed when the lead limb was that contralateral to the cortical recording site, this is referred to as the lead condition.

The data were initially examined using two custom procedures. In one, the data in each class of identified cycle were averaged, and the activity in the step over the obstacle compared with that observed in the control cycles. In all cases, the discharge activity of neurons with a receptive field on the forelimb was synchronized with respect to the onset of activity in the contralateral sartorius (coSrt) EMG. The onset and duration of the activity in this muscle corresponds, approximately, to the onset and duration of the swing phase of the forelimb (see Drew 1993). For neurons with a receptive field on the hindlimb, the discharge activity was synchronized with respect to the onset of activity in the contralateral flexor hallucis longus (coClB) EMG. The onset and duration of the activity in this muscle corresponds approximately to the onset and duration of the swing phase in the hindlimb (see Widajewicz et al. 1994).

The instantaneous frequency of the cell and the EMG activity in that cycle were normalized to 256 bins (see Drew 1993; Drew and Doucet 1991; Udo et al. 1982) before being averaged. Unit and EMG activity in the preceding and subsequent steps were treated in the same manner to provide displays of the type illustrated in Figs. 2, 3, 6, 8, 9, and 11–13. The interval of confidence (P < 0.01) for the averaged control traces also was calculated and significant changes in unit activity during the gait modifications were defined as those in which the two traces differed for >25 consecutive bins (Drew 1993).

In the other analysis, unit activity was displayed in the form of raster displays that were aligned, in turn, to the onset of each of recorded EMGs. Displays of this form (see Figs. 2 and 3) allowed a ready appreciation of the temporal correlation of the discharge activity of the cell and the pattern of EMG activity (see Drew 1993; Drew et al. 1986).

To identify the phase of the step cycle in which cells were active during the gait modifications, they were classified as in our previous publications (Drew 1993; Widajewicz et al. 1994).

Briefly, for neurons in the forelimb representation of area 4, the averaged postevent histograms were used to define four groups of neurons: those neurons in which peak discharge occurred early in the swing phase, after the onset of activity in the coClB but before the onset of activity in the coSrt ( stance cells ); and those cells the peak discharge of which occurred later in swing, after the onset of activity in the coClB (phase 2 cells); those cells the peak discharge of which occurred after the cessation of activity in the coClB (corresponding approximately to the onset of stance) and before the onset of the next period of activity in the coSrt ( phase 1 cells ); and those cells in which the increase in discharge frequency began >200 ms before the onset of swing ( early ). Those few cells (5/212) in which the peak discharge of the cell was during either phase 1 or phase 2 but in which the increase in discharge began >200 ms before the onset of activity in coClB were also classed as early. For neurons in the hindlimb representation, the same classification was used with respect to the onset of activity in the coSrt.

In addition, most cells were examined using a vectorial analysis. For this analysis, circular statistics were used to define the mean phase of the cell discharge. As described in detail elsewhere (Drew 1993; Drew and Doucet 1991), the discharge frequency of cells that showed a significant (see earlier text) and unimodal increase in activity and the discharge of which was directionally significant (Rayleigh test for directionality) was converted into a vector (see also Georgopoulos et al. 1983, 1984). This vector indicated the mean direction of the cell discharge and is referred to in the text as the mean phase (ϕ) with a value of 0.0 indicating the onset of activity in coClB or coSrt and a value of 1.0 indicating the end of the step cycle. The length of the vector (r) is dependent on the dispersion of the distribution and gives an indication of whether the neuron discharged tonically (uniform distribution and, therefore, values close to 0.0) or phasically (highly directional discharge and values close to 1.0). This value of r multiplied by the maximum averaged discharge frequency of the cell (determined from averages compiled as above) gives a value (F) that is indicative of the overall discharge activity of the cell. This analysis allows a ready comparison of the discharge patterns and frequency of a population of neurons during locomotion.

It should be emphasized that in this study neurons were recorded throughout area 4 and that we have pooled the data from all neurons when discussing the general properties of the population (e.g., Figs. 1 and 4). However, where it was important to have a more homogeneous population, we have used only the data from the neurons recorded in the forelimb representation of area 4 (e.g., Figs. 5, 9, 12, and 13). In determining the phase of activity of the population and in the plots of Fig. 10, the data from neurons in both the forelimb and hindlimb representations are used and, in these cases, the latency, or phase, of the forelimb neurons is measured with respect to the coClB, and of the hindlimb neurons to the coSrt.

RESULTS

Database

The data presented in this article are based on the recordings made from 212 identified neurons (109 PTNs,
TABLE 1.  Classification of neurons recorded during the voluntary gait modifications

<table>
<thead>
<tr>
<th>Class of Neuron</th>
<th>n</th>
<th>Forelimb</th>
<th>Hindlimb</th>
<th>Mixed</th>
<th>Head</th>
</tr>
</thead>
<tbody>
<tr>
<td>PTNS</td>
<td>109</td>
<td>36+</td>
<td>17+</td>
<td>5+</td>
<td>3+</td>
</tr>
<tr>
<td>PTN/CRN</td>
<td>66</td>
<td>28+</td>
<td>5+</td>
<td>2+</td>
<td>1+</td>
</tr>
<tr>
<td>CRN</td>
<td>37</td>
<td>15+</td>
<td>0</td>
<td>0</td>
<td>3+</td>
</tr>
<tr>
<td><strong>Totals</strong></td>
<td><strong>212</strong></td>
<td><strong>79+</strong></td>
<td><strong>22+</strong></td>
<td><strong>7+</strong></td>
<td><strong>7+</strong></td>
</tr>
</tbody>
</table>

The table indicates the number of neurons that were recorded in each class [pyramidal tract neurons, (PTNs) PTN/CRNs, and CRNs]. The data are divided according to the receptive field of each neuron and to whether the cell showed a significant increase in its discharge during the gait modification (+), whether it showed a significant decrease (-), or whether there was no change. Number of neurons are in parentheses.

66 PTN/CRNs, and 37 CRNs) recorded from area 4 (see Table 1). These neurons form a subset of those presented in Kably and Drew (1998). Most of the neurons (140/212) either had a receptive field that included the forelimb and/or were recorded in loci in which microstimulation evoked twitch responses in the forelimb musculature. A smaller number of cells (43/212) had a receptive field restricted to the hindlimb, and a few neurons had a receptive field on both the fore- and hindlimb (mixed: 10/212). A further 19/212 neurons had a receptive field

**FIG. 1.**  A: locations of the penetrations in which identified projection neurons were recorded during locomotion. ●, cells with receptive fields restricted to the forelimbs; open circles, those restricted to the hindlimbs; open triangles, those with a receptive field on both the fore- and the hindlimbs; filled triangles, those with a receptive field on the face and/or neck. Solid lines, fundus of the cruciate sulcus (CRU) and the rostral and caudal lips of the cruciate sulcus (see Kably and Drew 1998 for further explanation). B: conduction velocity of the axons of each class of projection neuron. Note that only 33/37 of the CRNs could be activated antidromically from electrodes in the pyramidal tract (PT).
FIG. 2. Example of the projections and discharge characteristics of a PTN/CRN recorded from cat MC19. A: antidromic identification of the neuron from selected electrodes in the PT and the pontomedullary reticular formation (PMRF; latencies indicated at the top left of each trace); the vertical dotted line on the traces indicates the onset of the stimulus. Location of each electrode is shown on standardized sagittal sections of the brain stem taken from Berman (1968), and the size of the circles indicates the estimated current spread according to the study of Hentall et al. (1984; see Kably and Drew 1998). Inset: cutaneous receptive field of this neuron. B: raster displays and postevent histograms (PEHs) aligned on the onset of the contralateral cleidobrachialis (coCIB), showing the discharge characteristics of this PTN during control locomotion and during steps over the obstacle when the forelimb contralateral to the recording site led. Staggered vertical line indicates the cessation of electromyographic (EMG) activity in this muscle. C: normalized and averaged discharge of this cell and 3 forelimb muscles in the limb contralateral to the recording site. Thinner traces illustrate the activity in the control cycles, and the thicker lines the activity during steps over the obstacle. TrM, teres major; TrIL, triceps brachii, lateral head. EMGs illustrated in this and in all subsequent figures were contralateral to the recording site in area 4.
that was restricted to the face and/or neck (head). Although almost one-third (33/109) of the PTNs that we recorded had a receptive field restricted to the hindlimb, only 9/66 (14%) of the PTN/CRNs and only 1/37 of the CRNs were recorded in the hindlimb representation. In contrast, the majority of the head-related neurons (14/19, 74%) projected directly or via a collateral to the PMRF.

**Location and conduction velocity**

The cortical location in which each type of identified projection neuron was recorded is illustrated in Fig. 1A, which shows that all three types of neurons were widespread throughout the rostral aspect of area 4. However, whereas PTNs were recorded in both the rostral and caudal bank of the cruciate sulcus, including both the forelimb and hindlimb representation, the CRNs (with 1 exception) were recorded only from the forelimb and head representation in the rostral bank of the cruciate sulcus. As shown by the histograms of Fig. 1B, the conduction velocities of these populations resembled those illustrated in Fig. 7 of the preceding paper for the total population. The majority of PTNs (62/109, 57%) and of CRNs (21/33, 64%) had slowly conducting axons (<20 m/s) (Kably and Drew 1998; Takahashi 1965), whereas the majority of the PTN/CRNs (51/66, 77%) were classified as fast PTNs.
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This neuron was activated antidromically from the PT at the level of the decussation at a latency of 1.47 ms, as well as from a number of electrodes located in the brain stem, ipsilateral (bundle C), and contralateral (bundles E and F), to the recording site in the motor cortex. In this example, the collateral branches projecting in the vicinity of the C, E and F bundles conducted at 3.6, 1.6, and 4.2 m/s, respectively, whereas the root axon in the PT conducted at 29.9 m/s.

During locomotion, in the absence of any obstacles (control), this neuron discharged phasically during, and subsequent to, the latter part of the period of activity of CoClB, i.e., during the latter part of swing and the initial part of stance (Fig. 2, B and C). The average peak discharge frequency during this period was 10 Hz. In the lead condition, there was a large increase in the discharge frequency of the cell, to an average peak frequency of 80 Hz, when the cat stepped over the obstacle. In addition, there was a change in the period that the cell was maximally active such that cell discharge was now confined within the time that the CIB was active, i.e., the neuron discharged only during the latter part of swing.

Figure 3 shows three examples of other cells recorded in the same trajectory as that illustrated in Fig. 2, emphasizing that all three classes of neurons showed modulation of their discharge frequency in the lead condition.

The overall changes in the magnitude and mean phase of the activity in the three classes of neuron are illustrated in Figs. 4 and 5 and summarized in Table 2. Figure 4 shows that, on a population basis, all three classes of projection neuron showed similar properties with respect to the sign and the relative magnitude of the changes in discharge during the gait modifications. Altogether, 61/109 (56%) of the PTNs showed a significant increase in their discharge frequency, compared with 36/66 (55%) of the PTN/CRNs and 18/37 (49%) of the CRNs. However, the increase in discharge frequency of the CRNs, in general, was relatively modest compared with the increase in frequency seen in the PTNs and PTN/CRNs. Only 1/18 (6%) of the CRNs showed an increase in discharge that was >200% of control compared with 21/109 (19%) of the PTNs and 14/66 (21%) of the PTN/CRNs.

These changes in magnitude also can be seen in Fig. 5, which illustrates in vector format the mean discharge (F) and the mean phase (Φ) of the activity of those cells recorded in the forelimb representation of the motor cortex, both during control locomotion and during steps over the obstacle. Examination of the vectorial plots in the Fig. 5, left, indicates that all three classes of neuron showed similar low levels of discharge frequency during the control condition. During the gait modification, all three populations showed an increased level of discharge activity, indicated by the increased length of the vectors in Fig. 5, middle, with the majority of this activity occurring during the swing phase of locomotion. Nevertheless, as shown by inspection of Fig. 5, right, all classes of neurons were represented by cells that discharged at different times in the step cycle (see Table 2). PTNs and PTN/CRNs generally exhibited similar patterns of activity, with 37/60 (62%) of PTNs and 25/36 (69%) of PTN/CRNs discharging maximally during the swing phase of locomotion.
the modified step. A slightly smaller percentage of CRNs discharged during swing, 9/18 (50%), and a slightly higher percentage, 7/18 (39%), discharged in the step preceding the gait modification than did PTNs, 12/60 (20%), or PTN/CRNs, 6/36 (17%).

Analysis of the discharge of each of the three classes of neurons during the control cycle showed no population differences. The mean phase of activity of 32% of the PTNs and 35% of both the PTN/CRNs and CRNs occurred between phases 0.0 and 0.4, corresponding approximately to swing, whereas 27, 24, and 22% of the PTNs, PTN/CRNs, and CRNs, respectively, discharged between phases 0.4 and 0.8, corresponding approximately to stance.

COLUMNAR ORGANIZATION. A particular interest in this study was to determine whether neurons having different projection patterns but recorded in close proximity (within 500 μm, in the same track) discharged similarly. The three cells illustrated in Fig. 3 were recorded in the same cell layer and within 200 μm of the PTN/CRN illustrated in Fig. 2; the receptive fields of 3 of 4 of these cells were restricted to the caudal margin of the upper arm and to the axilla (the other cell was lost before the receptive field could be determined). All four of these projections neurons discharged similarly, albeit not identically. During control locomotion, all four cells were silent during the initial part of the swing phase and discharged maximally at the end of swing and the beginning of stance. More importantly, during the step over the obstacle, all of the cells increased their discharge frequency at the end of the swing phase.

Altogether, we could record three or more neurons within 500 μm of each other in 37 penetrations. In 24 of these penetrations, the neurons were within 300 μm of each other. The sample included both the forelimb (29/37) and hindlimb (7/37) representations of the cortex; in 1/37 clusters, the neurons had receptive fields on both the fore- and hindlimbs. Two examples of penetrations included in this part of the database are illustrated in Fig. 6. In the example illustrated in Fig. 6A, which includes three PTNs and one PTN/CRN, three of the neurons had a similar receptive field, and all showed an increase in their discharge frequency during the swing phase of locomotion during the gait modification, three in phase 1 and the other in phase 2. The five neurons in Fig. 6B, one PTN, two PTN/CRNs, and two CRNs, also showed similarities in their discharge patterns but these were more diverse than those in Fig. 6A. For example, cells A and B1 (both CRNs) increased their discharge frequency in the period before the limb initiated its swing phase, whereas neurons B2, C, and D all increased their discharge frequency in the early part of the swing phase. Note that in this example, units B1 and B2 discharged differently during the gait modification even though they were recorded simultaneously. All three classes of neurons were intermingled in each penetration with no evidence that any one class of neuron was located relatively more or less deep than any other.

The variation in the discharge pattern of the population of neurons that were recorded in close proximity is illustrated in Fig. 7, which, for each class of corticofugal neuron, plots the mean phase of activity in a given neuron relative to the mean phase of activity in the earliest discharging PTN that was encountered in a penetration. For example, in Fig. 6A, the mean phase of the earliest discharging (reference) PTN (cell B) was 0.24, that of cell A was 0.36, and that of cell F was 0.19 (circular statistics were not used on cell C as its discharge pattern was bimodal). Consequently, the relative phase of cell A with respect to cell B was 0.12, and of cell F with respect to cell B was −0.05. Figure 7A shows that the mean phase of 17/26 (65%) PTNs that were recorded in a cluster (i.e., within 500 μm of other) was within 0.2 of the reference neuron (see Fig. 6A). A slightly more dispersed pattern was observed for the PTN/CRNs (Fig. 7B), but even so, 19/31 (61%) of these neurons discharged within 0.2 of the reference PTN. In the case of the CRNs, however (Fig. 7C), only 6/16 (38%) discharged within the same window, and the relative phases were, in general, more dispersed than for the other two classes of neurons. In addition, as for the examples in Fig. 6B, a majority of these CRNs fired relatively earlier in the step cycle than the reference PTN.

It is possible that this diversity in discharge patterns may be because some of the cells in the cluster were recorded from different columns. We therefore examined more closely 17 pairs of cells that were recorded simultaneously. One such pair is illustrated in Fig. 6B (units B1 and B2) and a further four pairs are shown in Fig. 8, A–D. Although some...
pairs of neurons discharged in a very similar manner, e.g., Fig. 8, A and B, others, such as those in Fig. 8, C and D, and in Fig. 6B, showed more variability. For 12 pairs of neurons in which the average peak discharge could be calculated from the circular statistics for both cells, a similar proportion (8/12, 67%) discharged within 0.2 of each other as for the PTNs and PTN/CRNs illustrated in Fig. 7. Although the sample of simultaneously recorded neurons is small, the results suggest that the variability in the discharge patterns of the simultaneously recorded neurons is as high as that found within the clusters of neurons.

We also examined the discharge patterns of PTN/CRNs and CRNs that were recorded in the same clusters as the subpopulations of PTNs that increased their discharge frequency during early or late swing of the forelimb (phase 1 and phase 2 PTNs, respectively). Figure 9 confirms the results shown in Figs. 6–8 by illustrating that the average discharge patterns of the PTN/CRNs in the two graphs were generally similar to the average discharge pattern of the reference PTNs. However, as seen in Fig. 9A, although the discharge patterns of the PTN/CRNs recorded in the same clusters as the phase 1 PTNs were similar, they were not identical. Rather, the peak discharge of the PTN/CRNs occurred later, in the latter half of the swing phase. On the other hand, despite the differences in the discharge patterns of the phase 1 and phase 2 PTNs, inspection of the discharge patterns of the two populations of PTN/CRNs (phase 1 and phase 2) indicates that they were almost identical. This suggests that although the two populations of PTNs may subserve different functions during the gait modification (see Drew 1993), the PTN/CRNs recorded in these same regions may subserve a common function. Only a few CRNs were

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**FIG. 6.** A and B: examples of neurons recorded in close proximity along 2 different electrode penetrations. PEHs for each of the neurons in each penetration are displayed at the same scale. Values in parentheses indicate the distance of the recorded neuron (in mm) from the 1st PTN recorded in the trajectory. Receptive field of each of the neurons (when available), as well as the location of the penetration, are shown above each series of PEHs. Filled areas represent a cutaneous receptive field, whereas arrows represent that the neurons also were activated by passive movement around the indicated joint. Small arrows in neuron c in B indicate that the discharge activity in this neuron was increased by pressure on the paw. Effects of microstimulation at these loci are illustrated by the figurines inside the cortical contours.
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**FIG. 7.** A–C: histograms illustrating the relative differences in mean phase between cells recorded within 500 μm of each other. For each cluster of neurons, the average phase of each cell was calculated with respect to the mean phase of the earliest discharging PTN recorded in a cluster. Plots thus indicate the relative phases of the other neurons with respect to this reference PTN (see text for details). Recorded in these penetrations. However, in agreement with the data plotted in Fig. 7C, those CRNs recorded in penetrations in which PTNs discharging in phase 1 were found discharged before the gait modification and before the onset of the activity in the PTNs. Little change in activity was observed in the four CRNs recorded in the penetrations in which the phase 2 PTNs were recorded.

### Discharge characteristics during locomotion in the trail condition

Comparison of the discharge of the three classes of neurons when the fore- or hindlimb contralateral to the recording site trailed, showed little difference in the characteristics of the PTNs and PTN/CRNs, although the CRNs again were more variable. For example, with respect to the number of cells that discharged in both conditions, Table 3 indicates that 28/37 (76%) of the PTNs and 19/25 (76%) of the PTN/CRNs that discharged in swing (phase 1 + phase 2) in the lead condition also increased their discharge in the trail condition (although not necessarily in the same phase, see further). In contrast, only 2 of 9 (22%) of the CRNs that increased their discharge in swing in the lead condition also increased their discharge in the trail condition. In most cases, for both the PTNs and the PTN/CRNs, the increase in discharge was greater in the lead condition than in the trail condition; 22/37 (60%) of the PTNs and 13/25 (52%) of the PTN/CRNs exhibited a greater increase in their discharge frequency of the swing phase during the lead condition than in the trail condition.

Examination of the relationship between the latency of the discharge (with respect to the onset of activity in coClB for cells in the forelimb representation and with respect to coSrt for cells in the hindlimb representation) when the limb led and when it trailed illustrates the tendency for most cells to discharge earlier in the trail condition than in the lead condition (Fig. 10). This also can be seen from inspection of the examples illustrated in Fig. 11. For example, Fig. 11A shows a PTN that discharged in phase 1 in the lead condition; its discharge frequency increased after coClB onset in the lead condition but preceded it in the trail condition. Figure 11B illustrates a CRN that discharged well before the onset of activity in the coClB in both the lead and trail conditions (early); note, however, that the increase in discharge was earlier in the trail condition than in the lead condition. In some cases, these differences were quite exaggerated. For example, a few neurons that discharged in stance in the lead condition, discharged well before the onset of activity in the coClB in the trail condition (see Fig. 11C). Others that were classified as discharging in phase 1 in the lead condition discharged well before the onset of activity in the coClB in the trail condition (Fig. 11D).

Figure 12 illustrates the discharge of the same clusters of neurons as were illustrated in the lead condition in Fig. 9. Comparison of these two figures shows that, as for the total population, most of these subgroups of neurons also discharged earlier in the trail condition than when the limb led. Again, there was close correspondence between the average discharge pattern of the PTNs and PTN/CRNs that discharged during phase 1 in the lead condition, although with less evidence of the relative phase shift that was observed in the lead condition (Fig. 9A). As for the lead condition, the few CRNs recorded in these trajectories were phase advanced and fired relatively earlier than in the lead condition. Comparison of the time of this discharge with respect to the changes observed in the EMG activity raises the possibility that this discharge might be better related to the time of passage of the ipsilateral (lead) limb over the obstacle than of the contralateral limb. Those PTNs that discharged during phase 2 in the lead condition showed no change in discharge in the trail condition, presumably because the relative amplitude and phase of the dorsiflexor muscles with respect to the onset of the coClB is also unchanged. However, the PTN/CRNs recorded simultaneously with these PTNs showed, as a population, a slight increase in their discharge frequency before the step over the obstacle. There was, thus, a dissociation of the discharge properties of these two classes of neurons in the lead and trail condition. The CRNs showed a decrease in their discharge frequency that started well before the gait modification of the trail limb, at a time similar to that seen for the CRNs in Fig. 12A.
Receptive fields and microstimulation

The characteristics of the population of neurons in area 4 with respect to the receptive fields and the effects of microstimulation are given in the preceding paper (Kably and Drew 1998). As indicated therein, cells of all three classes included neurons with a receptive field that included the more distal limb and were recorded from loci where microstimulation produced movements around either the shoulder, elbow, or wrist at threshold. Examination of the subpopulation used for the present analysis showed no major differences with respect to the overall population. For example, CRNs included only slightly fewer cells with a receptive field that included the paw and wrist (60%) than did PTN/CRNs (81%) and PTNs (76%). Similarly, all three classes included similar numbers of cells in which the receptive field included the shoulder (52–53%). However, if only those cells that showed an increase in discharge frequency in the lead condition were considered, then although a high percentage of PTNs and PTN/CRNs (73 and 76%, respectively) had a receptive field that included the paw and wrist, only 38% of CRNs had a similar field. Indeed, most CRNs (46%) that showed increases in discharge frequency had a receptive field on the scapula and shoulder. Microstimulation in loci from which PTNs and PTN/CRNs were recorded evoked movements primarily around the elbow or the shoulder but also around the wrist, whereas microstimulation in loci in which CRNs were recorded were without effect or evoked almost exclusively, either retraction of the shoulder or elbow flexion.

DISCUSSION

The major result of these studies is the observation that the descending commands that are sent to the spinal cord from the motor cortex are also sent to the brain stem. We believe that this signal is responsible, at least in part, for ensuring that the postural responses that accompany the voluntary gait modifications are appropriately distributed and scaled to the magnitude and duration of the limb movements.

Database

The locations of the recording sites used for this paper were similar to those that made up the larger database in the companion paper (Kably and Drew 1998) and examined in our previous reports (Drew 1993; Widajewicz et al. 1994). This sampled region included most of that part of area 4 (mostly referred to as rostromedial) from which the major portion of the corticoreticular pathways in the cat originate (Keizer and Kuypers 1984; Kuypers 1958; Rho et al. 1997). However, relatively few recordings were made from the most lateral regions of area 4 that contain the most distal representation of the paw (Armstrong and Drew 1984b; 1985).

FIG. 8. A–D: 4 examples of pairs of neurons that were recorded simultaneously during the task, together with the averaged activity of the CIB and the TriL (E). Data are arranged as previously. Phase values (Φ) above each average indicate the mean phase of the discharge as calculated from the circular statistics.
Fig. 9. Summary of the activity of the PTN/CRNs and CRNs recorded within 500 μm of reference PTNs classified as discharging in phase 1 or phase 2 of the step cycle in the lead condition. Averaged traces are arranged as in Fig. 2. Number of neurons that were averaged in each class is indicated to the right of each average (N). Note that 2 PTN/CRNs and 1 CRN are included in both set of averages because PTNs discharging in both phase 1 and phase 2 were recorded in 3 of these penetrations (see e.g., Fig. 6A).

Nieoullon and Rispal-Padel 1976). Comparison of the conduction velocities of the axons of the projection neurons that we recorded (Fig. 1) with those of the database as a whole (Fig. 7 of the companion paper) again suggests that the population recorded here was representative of the larger population.

The population of neurons recorded from the four cats active during swing, the change in discharge frequency, the latency of the discharge when the limb led and when it trailed, and the number of cells with a receptive field that included the paw and wrist were almost identical in the two studies. The population of neurons recorded from the hindlimb representation of area 4, and those with a receptive field on both the fore- and the hindlimb, likewise resembled that described earlier by Widajewicz et al. (1994). We therefore believe that the sample of cells included in this publication reflects well the properties described in more detail in our previous reports.

Table 3. Neurons that showed increases in discharge frequency in both the lead and trail condition

<table>
<thead>
<tr>
<th>Class</th>
<th>Phase 1</th>
<th>Phase 2</th>
<th>Stance</th>
<th>Early</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>PTN</td>
<td>19/22 (86)</td>
<td>9/15 (60)</td>
<td>10/11 (91)</td>
<td>10/12 (83)</td>
<td>48/60 (80)</td>
</tr>
<tr>
<td>PTN/CRN</td>
<td>15/17 (88)</td>
<td>4/8 (50)</td>
<td>4/5 (80)</td>
<td>3/6 (50)</td>
<td>26/36 (72)</td>
</tr>
<tr>
<td>CRN</td>
<td>1/3 (33)</td>
<td>1/6 (17)</td>
<td>1/2 (50)</td>
<td>6/7 (86)</td>
<td>9/18 (50)</td>
</tr>
<tr>
<td>Total</td>
<td>35/42 (83)</td>
<td>14/29 (48)</td>
<td>15/18 (83)</td>
<td>19/25 (76)</td>
<td>83/114 (74)</td>
</tr>
</tbody>
</table>

Each cell in the table indicates the number of neurons that discharged in the trail and in the lead condition; the values are also given as a percentage (in parentheses).

Characteristics of PTNs, PTN/CRNs, and CRNs

On a population basis. All three classes of neurons, including CRNs, were phasically modulated during locomotion.
FIG. 10. A–C: relationship between the latency of the onset of the increase in discharge frequency when the contralateral limb leads and when it trails over the obstacle for PTNs (A), PTN/CRNs (B), and CRNs (C). All neurons that showed an increase in both conditions are plotted, irrespective of receptive field. Latencies were measured with respect to the onset of coClB for neurons in the forelimb representation of area 4 (see Drew 1993) and with respect to the onset of coSrt for neurons in the hindlimb representation (see Widajewicz et al. 1994). Symbols identify to which group the PTNs were allocated on the basis of the phase of their peak discharge in the lead condition (key in A). All neurons with similar latencies in the 2 condition would fall on the diagonal dotted line; neurons discharging earlier in the trail condition than in lead fall to the right of this line.

In the present experiments, it was not possible to ensure that all penetrations were orthogonal to the cortical surface, although those closest to the cruciate sulcus approximated this orientation. On the other hand, it should be emphasized that all of our recordings were made from neurons that were confined to layer V of the cortex, and even in penetrations that were not orthogonal to the surface, the recorded neurons were very close to each other. In most cases, neurons that were recorded from a single cortical layer had receptive fields that were similar (see e.g., Figs. 2, 3, and 6). This is in agreement with previous reports that suggest that neurons within a column in the motor cortex receive afferent input from the same spatial location, although not necessarily of the same modality (Asanuma 1975; Asanuma et al. 1968; Welt et al. 1967). In other cases, including some in which the electrode penetration was oblique, the receptive fields showed some changes in location from the most superficial to the deepest neuron that was recorded. Although this may reflect that our penetrations were passing from one cortical column to another, it should be noted that other studies have also found that clusters of cells recorded in close proximity may receive afferent inputs from different regions of the body (Armstrong and Drew 1984a; Lemon 1981).

Few studies have made a detailed examination of the discharge properties of neurons recorded in close proximity during movements, and fewer still have compared the discharge characteristics of neurons recorded in the same column but with different projections patterns. One of the most detailed studies of this issue was made by Lemon (1981), who, as in this study, recorded a large number of neurons in clusters of 500 μm (although not all neurons were in layer V as in the present study). Lemon reported that most neurons recorded in clusters in which the afferent feedback was identical also behaved similarly during a reaching task. This is in agreement with our overall examination of the discharge properties of the clusters of neurons that demonstrated that each of the three classes of projection neuron encoded a similar, although not identical signal.

On the other hand, the neurons that were recorded in the
Fig. 11. A–D: examples of neuronal discharge during the lead and trail conditions. Data are displayed in the same manner as in the preceding figures. FL, forelimb; HL, hindlimb. Data are aligned to the onset of activity in the coCIB in A–C and to the onset of activity in contralateral sartorius (coSt) in D.
FIG. 12. Summary of the activity of the same neurons as illustrated in Fig. 9 during the trail condition. Data are synchronized to the onset of activity in the coCIB during the trail condition.
clusters, and even some of those recorded simultaneously, did not always discharge identically. For example, the simultaneously recorded PTN/CRN and CRN illustrated in Fig. 6B showed very clear differences in activity, and, although the sample was small, it was noticeable that CRNs recorded in close proximity to PTNs and PTN/CRNs often discharged earlier in the step cycle. This tendency for PTN/CRNs to discharge in a similar manner to PTNs and for CRNs to discharge dissimilarly is also illustrated by the data shown in Figs. 7–9. Given that most of our recordings were restricted to layer V, we believe that these results provide evidence that at least some of the differences in discharge characteristics that we saw in the different classes of neurons reflect differences in function.

The discharge characteristics of cortical neurons projecting to subcortical structures were also studied by Fromm and his colleagues, who studied the properties of corticorubral (Fromm 1983) and corticostratial (Bauswein et al. 1989) neurons in primates trained to move a lever. The present results have both points of similarity and others of difference with those studies. For example, Fromm found that the discharge patterns observed in those neurons with exclusive projections to the red nucleus resembled more the patterns of activity observed in rubrospinal neurons than those observed in adjacent PTNs, even when they were recorded simultaneously. Those neurons that projected to the red nucleus via collaterals had properties that were related more closely to the activity patterns of the adjacent PTNs (see also Humphrey and Reed 1983). In their study of corticostriatal neurons, which projected mostly exclusively, Bauswein et al. (1989) reported that their discharge characteristics were similar to the target population onto which the neurons projected. The results from the present study are consistent with these observations in that we found that neurons that projected to the PMRF via collateral branches were generally similar to those of adjacent PTNs (Figs. 7–9), whereas those that projected directly were more distinct (although it is not possible at the present time to state that they discharge in a similar manner to their target neurons in the PMRF).

This similarity suggests that it may be a general principal of the organization of the corticofugal pathway that cortical neurons that send a collateral to a target structure discharge similarly, although not identically, to those that project directly to the spinal cord, whereas cells that project directly to a target, without projecting to the spinal cord, discharge in a manner that is distinct from the command for voluntary movement and that may encode attributes of the movement that are specific to that target structure.

Functional implications

These results provide some direct evidence for the hypothesis that the motor cortex, via its collateral branches to the PMRF, may form part of the neuronal mechanism that en-
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