Independent and Convergent Signals From the Pontomedullary Reticular Formation Contribute to the Control of Posture and Movement During Reaching in the Cat

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Submitted 10 December 2003; accepted in final form 26 May 2004

Schepens, Bénédicte and Trevor Drew. Independent and convergent signals from the pontomedullary reticular formation contribute to the control of posture and movement during reaching in the cat. J Neurophysiol 92: 2217–2238, 2004. First published June 2, 2004; 10.1152/jn.01189.2003. We have addressed the nature of the postural control signals contained within the discharge activity of neurons in the pontomedullary reticular formation, including reticulospinal neurons, during a reaching task in the cat. We recorded the activity of 142 neurons during ipsilateral reaching movements that required anticipatory postural adjustments (APAs) in the supporting limbs to maintain equilibrium. Discharge activity in 82/142 (58%) neurons was significantly increased before the onset of the reach. Most of these neurons discharged either in a phasic (22/82), tonic (10/82), or phasic/tonic (41/82) pattern. In each of these 3 groups, the onset of the discharge activity in some neurons was temporally related either to the GO signal or to the onset of the movement. In many neurons, one component of the discharge sequence was better related to the GO signal and another to the onset of the movement. Based on our previous behavioral study during the same task, we suggest that reticulospinal neurons in which the discharge activity is better related to the GO signal contribute to the initiation of the APAs that precede the movement. Neurons in which the discharge activity is better related to the movement signal might contribute to the initiation of the movement and to the production of the postural responses that accompany that movement. Together our results suggest the existence of neurons that signal posture and movement independently and others that encode a convergent signal that contributes to the control of both posture and movement.

INTRODUCTION

Voluntary movements of a limb are preceded and accompanied by anticipatory postural adjustments (APAs) that prepare the body for the expected disturbance of the center of mass that will be produced by that movement (Bouisset and Zattara 1981; Horak and Macpherson 1996; Massion 1992). Such APAs are particularly evident for large movements of the arm or trunk or when that limb supports the body (Belenki et al. 1967; Béraud and Gahéry 1995; Bouisset and Zattara 1981; Brown and Frank 1987; Burleigh et al. 1994; Crenna and Frigo 1991; de Wolf et al. 1998; Horak et al. 1984; Lee et al. 1990; Mouchinno et al. 1992; Nasher and Forsberg 1986). The postural adjustments that precede the movement, often by more than 100 ms, have been referred to as preparatory APAs (pAPAs; Gahéry 1987). There are also postural responses that occur during the movement and that serve to stabilize the body or body segment during the execution of the movement itself. These postural responses are also anticipatory in nature because they occur before there is any possibility of feedback from the movement itself influencing the response (Massion 1992). They are referred to by Gahéry (1987) as accompanying APAs (aAPAs).

The control mechanisms responsible for the production of these different types of postural response and for their integration with the movement are only poorly understood and the extent to which posture and movement are expressed either as a unity or as independent signals is a controversial issue (Massion 1992). There is certainly evidence to support some level of independence in the signals responsible for the production of the pAPAs and the movement (Brown and Frank 1987; Cordo and Nasher 1982; de Wolf et al. 1998; Horak et al. 1984; Massion 1992), including our own recent study (Schepens and Drew 2003a). However, it is difficult to determine whether the dissociation of timing in the pAPAs and the movement that we observed reflects independence of planning or independence at a later stage in the execution of the movement. In the case of the postural responses that accompany the movement, the data, at least in the cat, suggest that they are tightly coordinated with the movement (Alstermark and Wessberg 1985; Schepens and Drew 2003a) and might be initiated by a single motor command (see Gahéry and Nieuwoud 1978; Kably and Drew 1998b).

The neural signals responsible for the production of the postural responses and for their integration with the cortical commands for movement are even less well understood. Nevertheless, there is abundant evidence from lesion studies to suggest that the brain stem reticular formation makes an important contribution to this function. For example, Kuypers (1963; Lawrence and Kuypers 1968) demonstrated that damage to the reticulo- and vestibulospinal tracts, in both cats and primates, leads to gross ataxia and a wide variety of balance problems while leaving fine control of the distal arm mostly intact. Similarly, during locomotion, damage to these same tracts also leads to problems in balance control as well as in weight support (Afelt 1974; Brustein and Rossignol 1998; Eidelberg 1981; Gorska et al. 1990). In addition, studies by Luccarini et al. (1990) have shown that injection of a cholinergic agonist into the pontine reticular formation reduces the postural responses elicited by cortical stimulation. This sup-
ports a role for the reticular formation in the integration of posture and movement, although it leaves open the nature of the contribution. Indeed, there have been very few studies that have examined the activity of neurons in the pontomedullary reticular formation (PMRF) during discrete voluntary movements (Gibson et al. 1998; although, for information in primates on the contribution of the mesencephalic reticular formation, see Stuphorn et al. 1999; Werner et al. 1997) and none that was directly related to the question of how the reticulospinal system contributes to the regulation of posture.

The present study was designed to address this issue by recording the activity of neurons in the PMRF, including reticulospinal neurons (RSNs), during a reaching task in the cat. Our recent kinetic and electromyographic (EMG) study of the strategy adopted by cats during a reaching task (Schebens and Drew 2003a) showed that the pAPAs followed the oo signal instructing the cat to make the movement at a relatively fixed latency and were temporally decoupled from the movement itself. Consequently, the latency of the onset of the movement itself showed no fixed relationship to the stimulus. This temporal decoupling provides an ideal theoretical framework in which to determine the extent to which neurons in the PMRF are related to different components of the overall reaching strategy. For example, changes in activity in neurons that contribute to the initiation of the pAPAs would be expected to be tightly linked to the stimulus for the movement (the oo signal) and would be temporally decoupled from the movement. Conversely, changes in activity in neurons related to the initiation of the movement, or to the postural responses that accompany the movement, would bear no temporal relationship to the stimulus and would covary with the onset of the movement. The results suggest that both types of neurons may be found within the same areas of the PMRF.

Preliminary results of these findings were previously published in abstract form (Schebens and Drew 2000, 2001, 2003b).

METHODS

Training and surgery

Experiments were performed on the same 2 animals as used in a previous publication (Schebens and Drew 2003a). All training procedures and most surgical interventions were documented in that publication. In brief, the animals were trained to reach to a tube placed medially and at shoulder height and to retrieve a morsel of food. Between trials the tube was closed by a opaque shutter that was opened, under computer control, to provide access to the food (Fig. 1). After a period of training, the cats were anesthetized with isoflurane (2–3% with oxygen) and prepared for surgery. A stainless steel, rectangular plate (internal dimensions 8 × 6 mm) was attached to the cranium to form a recording chamber that gave access to the PMRF. Three microwires (50 μm diameter) were implanted in the lumbar spinal cord (L2) to allow antidromic identification of RSNs (Drew et al. 1986; Prentice and Drew 2001). Pairs of stainless steel wires were inserted into the bellies of selected muscles in all 4 limbs to record EMG activity. Note that the recording chamber was implanted over the left PMRF: EMGs from the left limbs are thus ipsilateral to the recording site. All procedures were approved by the institutional Ethics Committee and followed national guidelines.

Protocol

Experiments were started 1 wk after the surgery. In each experimental session, a conventional, glass-insulated, tungsten microelec-

trode (impedance 0.5–1.5 MΩ), held in a custom-made microdrive, was advanced to a position just above the brain stem while the cat was held on the experimenter’s lap. The cat was then transferred to a treadmill where it rested quietly while the electrode was advanced slowly through the brain stem. As the electrode was advanced, stimuli were applied to the most effective spinal electrode to help in isolating RSNs with low or no spontaneous activity. When a neuron was isolated, stimulation was applied to each of the spinal electrodes in turn to determine whether the cell could be activated antidromically from the spinal cord. Cells that were activated at constant latency from the spinal stimulation and that exhibited collisions with spontaneous spikes at appropriate latencies (Lipski 1981; see Fig. 1) were classed as RSNs. All other cells were classified as Unidentified neurons. Both classes of neurons were recorded during the task, providing that the recording was stable.

All isolated neurons, with the exception of those that showed only saccade-related activity (found in and close to the abducens nucleus), were recorded during a period of locomotion. The cat was then transferred to the apparatus used for the reaching task and neuronal activity was recorded while the cat stood with each foot on a force platform (Fig. 1; see also Schebens and Drew 2003a). When the cat was standing quietly, data collection was initiated while the cat reached with the left or the right forelimb. Sets of data in which the cat reached with the left or right forelimb were normally interspersed in blocks of 5 or 10 trials. During experimental sessions in which neuronal recordings remained stable, further data trials were recorded either with the reaching target placed at different heights or distances. The electrode was then advanced and another cell isolated. Experimental sessions lasted 2–4 h and ended when the cats were no longer willing to work for a food reward. In this paper, we report only on the neuronal discharge characteristics of the cells during reaching to a standard target position with the left, ipsilateral limb. In cat RS22 the target was normally either 29 (30% of recordings) or 27 (69%) cm from the center of the front force-platforms and at a height of 22 cm (81% of recordings), whereas in cat RS23 it was 22 cm (96% of recordings) from the center of the front force-platforms and at a height of 16 cm (100% of recordings).

All neuronal and EMG data were recorded on-line during the experiments together with the forces (F) and moments exerted by the cat against the platform in all 3 planes (subscripts: V, vertical; AP, anteroposterior; and ML, mediolateral). Force and EMG data were sampled at 1 kHz. Neuronal data were sampled at 100 kHz. Video recordings were made of all experiments and a digital time code recorded simultaneously on the computer and on the video recordings allowed these recordings to be synchronized to the EMG and neuronal recordings.

Data analysis

Because of the inherent incertitude in ensuring adequate on-line cell discrimination during experiments in unrestrained animals, all neuronal recordings were discriminated off-line. The recordings of neuronal activity were displayed on a computer monitor and an interactive, time-amplitude, software-discrimination routine was used to identify individual neurons. Because only neurons that appeared well isolated during the experiments were recorded, no special spike-isolation routines were necessary. Normally, only one cell was isolated from each record; in exceptional cases 2 cells were sometimes clearly identifiable using time-amplitude discrimination. Given that the goal of the analyses in these experiments was to determine the relationships between cell activity and behavior, we rejected from the analysis only those trials in which the cat began the movement before the oo signal (end of tone and opening of shutter). Variability in the reaction time and in the force levels was advantageous for performing regression analyses between different aspects of the neuronal discharge activity and the behavioral measures (see following text). Force data were filtered and the bias removed as described in our previous
Only neurons for which a minimum of 5 reaches with the limb ipsilateral to the recording site were included in the database.

Initially, each trial was examined individually and the onset and offset of the period of activity in selected flexors and extensors was marked using a cursor and interactive software; we also marked the onset and offset of the periods of cell activity, when they were sufficiently discrete. The onset of activity in the ipsilateral cleidobrachialis (iClB) and in the ipsilateral brachialis (iBr) muscles was always measured because one or the other of these simultaneously activated muscles was used as the standard indicator of movement onset (Prentice and Drew 2001; Schepens and Drew 2003a). Raster displays and postevent histograms (PEHs) were always generated with respect to the opening of the shutter (GO signal) and to the onset of the iClB. Rasters and PEHs were sometimes generated for other events and muscles depending on the nature of the discharge activity. Scatterplots and linear regressions were automatically generated for the time of onset and offset for the cell discharge as a function of the time and offset of each recorded muscle.

We always calculated linear regressions for both the onset of cell discharge and lead time as a function of the onset of movement. In an analogous manner to our analysis of the relationship between the onset of EMG activity and the onset of the APA in our previous paper (Schepens and Drew 2003a), lead time was defined as the onset of movement minus the onset of the variable under study (e.g., onset of cell discharge or onset of initial force change) (see Fig. 2). This latter relationship was used to determine whether the onset of cell discharge, or of the respective variable, was better related to the GO signal or to the onset of the movement itself. A slope of 1.0 for lead time versus movement onset indicates that the variable is better related to the GO signal, whereas a slope of 0.0 indicates a better relationship to the movement (Chapman et al. 1986; Vicario et al. 1983) (Fig. 2). Only cells for which the regression was significant ($P < 0.05$) were classified as being unambiguously related to either the GO signal or the movement.

When compiling the average latency measures of cell activity (see Fig. 2), we used the same criteria for inclusion as in our previous publication (see Fig. 4 in Schepens and Drew 2003a). For cat RS22, force onset had to begin within 210 ms of the GO signal and for cat
The latency of cell discharge but the same label could be used to define an event that follows the Go signal at a constant latency will show no schematic representation of the relationship between cell latency and lead time.

An event that precedes movement (preparatory anticipatory postural adjustment (pAPA)) as defined in a previous paper (Schepens and Drew 2003a). B: schematic representation of the relationship between cell latency and lead time. An event that follows the Go signal at a constant latency will show no relationship to the time of iCIB onset when plotted directly (left) but will show a linear relationship when plotted as lead time (right). ΔiFL or first detectable change in force; equivalent to the onset of the anticipatory postural response that precedes movement (pAPA).

RS23 within 112 ms. To ensure that average values were not unduly biased by slow movements we also calculated the mode and inter-quartile ranges for the same data set for the onset of activity in the iCIB. On this basis, to be included in the averages, the onset of iClB had to be <563 ms in cat RS22 and <400 ms in cat RS23. No limits were used when compiling any of the linear regressions.

To examine the quantitative relationships between cell-discharge frequency and the magnitude of the EMG activity or the force, we divided the individual trials into temporal slices. The binwidth of these slices varied between 20 ms (if we examined the relationship only for the reaction time or the movement time) and 50 ms (if we examined the relationship for the whole trial). Within each bin, we integrated the EMG activity or the force data and we calculated the average instantaneous cell-discharge frequency within this bin. Linear regressions were then automatically made between the intensity of the cell discharge and the magnitude of all of the EMG and force traces that were recorded (~64 measures in all). These were then rank-ordered according to the coefficient of determination.

For the purposes of classifying cells, neuronal discharge activity was synchronized with respect to the onset of activity in the iCIB of the reaching limb and averaged. This averaged trace was then filtered using the same digital filter as that for the EMGs (see Fig. 4). The initial classification of neurons into those that showed or did not show a significant change in discharge activity during the task was based on whether cell discharge after the Go signal significantly deviated from the control level of discharge (increase or decrease of ±2SD). Cells that showed no significant deviation from control levels were classified as unresponsive; cells that showed significant changes in activity were classified either as cells showing an increase or a decrease in discharge according to the sign of the initial significant change.

Cells exhibiting a significant increase in discharge frequency were further objectively classified as discharging phasically, tonically, or with a phasic/tonic pattern (see Fig. 4). As a basis for this classification, we automatically measured cell discharge at 3 defined times during the trial: 1) The level of control activity was measured for a 1 s period beginning 2 s before iCIB onset (control period). 2) Dynamic activity during the reach was defined as the overall maximum cell discharge that occurred from the onset of the period of activity in iCIB to the time that the paw entered the tube (dynamic period); in situations in which information on the time of entry into the tube was not available we used a fixed movement time of 300 ms. 3) The level of cell discharge after the reaching movement, indicating the level of maintained, or tonic, discharge was measured for a period of 500 ms beginning 1 s after iCIB onset (static period). Phasic cells (Fig. 4A) generally exhibited a ratio of tonic level/control level of <150%. Because many of these cells had very low levels of activity during the control period, we also included in this category cells in which the discharge frequency during the static period did not exceed that during control by more than 10 spikes/s. Tonic cells (Fig. 4B) exhibited a ratio of tonic/control level of >150% and showed a maintained discharge after the time that the paw reached the tube in which the ratio of the maximum discharge during the movement/tonic period was ≤125%. Phasic/tonic cells (Fig. 4C) equally exhibited a ratio of tonic/control level of >150% and exhibited a ratio of movement/static period of >125%.

**Histology**

At the end of the recording sessions, electrolytic lesions (20–50 μA) were made at selected regions within the recording area. The cats were deeply anesthetized and perfused through the aorta. The brain stem was removed and processed before being stained with cresyl violet. The location of each penetration was traced onto standard sections of Berman’s atlas (1968) using the electrolytic lesions as a guide. This allowed us to determine the approximate stereotaxic location of each of the recorded neurons (see Fig. 3).

**RESULTS**

**General features of the task**

The reaching task that we used in this study required that the cat adjust its posture before initiating the movement. This can be seen from inspection of Fig. 1, which shows selected, averaged force and EMG data during a left (ipsilateral to the recording chamber) reach. As detailed in a previous publication (Schepens and Drew 2003a), the reach is preceded by a loading in the ipsilateral reaching limb (iFLV) and an unloading in the contralateral, supporting, limb (coFLV) that define the preparatory anticipatory postural responses (pAPAs) (Fig.
2). Their presumed function is to produce a transfer of the center of mass over the supporting limbs, ensuring stability and contributing to the initiation of the movement (Ioffé et al. 1982; Schepens and Drew 2003a). There is also a loading of the ipsilateral hindlimb (iHLv) and an unloading of the contralateral hindlimb (coHLv). All of these changes are actively produced as they are preceded and accompanied by EMG changes in the appropriate muscles. Figure 4D, for example, illustrates the change in activity in the iTriL that precedes the first detectable change in force in the reaching limb (iFLv). Similarly, the decrease in activity in the coTriL precedes the decrease in force observed in the respective force recording (coFLv).

In our task, we define the onset of movement as coinciding with the onset of activity in the iClB or iBr. As demonstrated in Schepens and Drew (2003a), onset of activity in these muscles is tightly correlated to the lift of the limb (force under the paw drops to zero) and precedes lift by an average of 83 ms in cat RS22 and by 64 ms in cat RS23. The onset of activity in the iClB is accompanied by an increase in activity in the extensor muscles of the supporting forelimbs (see coTriL). The change in activity in the iClB and the coTriL is coincident and strongly correlated (Alstermark and Wessberg 1985; Schepens and Drew 2003a). These postural changes in the supporting forelimb thus occur as feed forward signals that anticipate the destabilization produced during the movement. Following Gañéry (1987) and Massion (1992), we refer to these changes as anticipatory postural responses that accompany the movement (aAPAs). Note that some muscles (e.g., coTriL) may contribute to both the preparatory responses before the movement as well as to the postural responses that accompany the movement (Schepens and Drew 2003a).

Database and general characteristics

A total of 142 neurons (89 in cat RS22 and 53 in cat RS23), histologically determined to have been recorded within the PMRF, and which fulfilled all of the criteria detailed in METHODS, were recorded during ipsilateral reach. Of these 142 neurons, 60 (42%) were identified as RSNs.

The location of these neurons is illustrated in Fig. 3, A and B on a standard section taken from the atlas produced by Berman (1968). The majority of the neurons was recorded within the nucleus reticularis gigantocellularis (NRGc), primarily in the more rostral regions. A smaller proportion of cells was recorded from the caudal region of the nucleus reticularis pontis caudalis (NRPc) and from within the nucleus reticularis magnocellularis (NRMc). Both RSNs and Unidentified neurons were recorded throughout the explored area and all neurons were located within 1.6 mm of the midline. Within the population of RSNs, the majority of the neurons that we recorded had axons that conducted at velocities >90 m s⁻¹ (mean 98 m s⁻¹); similar values were obtained in each cat (Fig. 3C). As such, in terms of both location and conduction velocity of axon, the characteristics of this database are generally similar to those used in our previous studies of PMRF function during locomotion (Drew et al. 1986; Prentice and Drew 2001), albeit with a smaller proportion of cells from the NRPc. Differences in the populations of RSNs and Unidentified neurons, when present, are addressed later.
FIG. 4. Examples of the neuronal recordings and of the 3 major types of discharge patterns observed among those neurons that increased their discharge activity before the onset of activity in the iClB muscle. A: cell discharging in a phasic pattern. B: cell discharging in a tonic pattern. C: cell discharging in a phasic/tonic pattern. Each part of the figure illustrates (left to right) 2 examples of the untreated spike discharge, taken from trials relatively early and late in the recording session and aligned on the go signal; expanded traces of the neuron showing its form; and a histogram of averaged neuronal discharge (n = number of trials in the average) during left (ipsilateral) reaches, triggered on the activity of the iClB muscle. Note that because of the large amplitude of the action potentials in B and C, some records were cropped during acquisition. Each histogram shows unfiltered (thinner line) and filtered (thicker line) averages. Thin horizontal and dotted lines illustrate the control ±SD level of activity. Numerical values within the histogram indicate, from left to right, average discharge frequency during the control period; maximal discharge during the dynamic phase of the reach; and average discharge frequency in the 500-ms period beginning 1 s after the onset of the iClB. Discharge frequencies were calculated from the filtered traces. D: averaged vertical forces and electromyographic (EMG) activity taken from the example illustrated in B. Data on the left are triggered on the go signal (opening of the shutter); data on the right are triggered on the onset of activity in iClB.
signal and of these about one half (9/15) were completely silent throughout the task.

Peak discharge rates for neurons showing increased activity during the task were relatively high (Table 1). Neurons with a tonic or phasic/tonic pattern of activity discharged at notably higher rates of discharge during the dynamic period than did those with a purely phasic pattern of activity. Control rates in the 3 groups were relatively similar. As expected, on the basis of the definitions used for classifying these cells, the discharge rate in the static period was greatest in neurons discharging tonically and least in phasic neurons.

Cells showing increased activity before the onset of activity in the iClB

Overall, the discharge patterns of the neurons in the 3 major groups that we defined formed a continuum, from cells that discharged in a purely tonic pattern to those that discharged in a purely phasic pattern (Fig. 5). Thus although objective criteria were used to define 3 groups of cells that accord with the classifications most commonly used by neurophysiologists, the data do not support a clearly demarcated division between them. For this reason, we have chosen to treat the database as a whole, emphasizing the major differences between tonic, phasic, and phasic/tonic neurons where appropriate. Moreover, as explained in the introduction, one of the major goals of these experiments was to determine whether the temporal relationships of the reticular cells to the go signal and to the onset of movement were similar to those that were previously detailed in our behavioral study (Schepens and Drew 2003a) for the kinetic and EMG measures.

Cells temporally related to the go signal

Figure 6 illustrates one example of a neuron in which the initial change in discharge activity was temporally related to the go signal. Activity in this neuron increased shortly, and abruptly, after the go signal. It then diminished before again increasing and remaining elevated throughout the dynamic stage of the reach (Fig. 6, A and B). Examination of the discharge activity on a trial-by-trial basis showed that, in most trials, the onset of the period of increased discharge activity began at a relatively constant latency after the onset of the go signal (Fig. 6B) and preceded the initial change in force (ΔF_L). The later bursts of activity were more variable and occurred later in trials in which movement was delayed (Fig. 6, A and B, right). As a result, the initial increase in activity is most obvious in the PEH triggered on the Shutter (Fig. 6A, left) and the later burst is clearer in the PEH triggered on the movement (Fig. 6A, right).

![Table 1](image)

<table>
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<th>Group</th>
<th>Control Period</th>
<th>Dynamic Period</th>
<th>Static Period</th>
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<tr>
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<td>59.0 ± 37.4</td>
<td>16.7 ± 21.7</td>
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<td>Tonic</td>
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<td>81.9 ± 30.2</td>
<td>76.1 ± 28.2</td>
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<tr>
<td>Phasic/tonic</td>
<td>19.6 ± 12.9</td>
<td>94.7 ± 40.5</td>
<td>49.8 ± 22.0</td>
</tr>
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Averaged peak discharge rates (±SD) calculated from average postevent histograms similar to those illustrated in Fig. 4 for all cells in the 3 main groups showing increased activity.

![Chart 1](image)

**FIG. 5.** Ratio between the maximal discharge activity during the dynamic phase of the movement and the average discharge frequency during the static phase of the movement for all 73 neurons classified as belonging to the Phasic (●), Tonic (○), and Phasic/Tonic (▲) groups. Insert: histograms illustrate example neurons.
Some of these relationships are represented in a quantitative manner in the scatterplots illustrated in Fig. 6C. The graph illustrating the relationship between the latency of the initial change in force ($\Delta iFLV$) and the latency of the onset of activity in the iCIB shows that the slope ($m = 0.06$; open symbols) of the relationship is closer to zero than to 1, confirming the temporal dissociation of these 2 components of the reach. Even for reach movements that were initiated relatively slowly, the initial postural change was elicited at an almost constant latency. As we previously demonstrated, this relationship is maintained over a wide range of reaction times (see Fig. 12A; Schepens and Drew 2003a). In contrast, plotting the lead time of the force onset as a function of the onset of activity in iCIB reveals a much stronger relationship between these 2 values.

**FIG. 6.** Example of a neuron whose change in discharge was related to the go signal. A: perievent histograms (PEHs) and raster displays of the cell discharge triggered on the go signal (shutter onset: left) and the onset of the iCIB (right). Thicker vertical bars in the raster displays indicate the onset of the activity in the ipsilateral brachialis (iBr; left) or the offset of activity in this same muscle (right). B: 2 examples of neuronal discharge pattern, the vertical force in the ipsilateral forelimb (iFLV) and the activity in the iBr during single trials, emphasizing the stability of the latencies (inset values) in the cell and force traces and the variation in the latency of the iBr. Arrows on the iFLV trace indicate the onset of the force change. C: scatterplots illustrating the relationship between the latency of the initial change in activity of each of these 3 variables with respect to the onset of activity in the iCIB. Each graph plots both the latency of the onset of activity in the variable (○) and the lead time (●) (onset of activity in iCIB minus the onset of activity in the respective measure; see METHODS) as a function of the latency of iCIB onset. Abbreviations: m, slope of the linear regression; N, number of trials; $R^2$, coefficient of determination.
and the onset of the iClB (not illustrated). Distinct bursts of activity in this neuron is temporally linked to the change in activity in the iClB and shows no temporal relationship to the GO signal, as indicated by the plot of iBr lead time as a function of iClB onset. As we previously discussed in detail (Schepps and Drew 2003a), this simple analysis provides an excellent method of determining whether a component of the reaching strategy is better related to the GO signal, and by extension to the initial changes in force that define the pAPA, or to the onset of activity in iClB, and by extension the reaching movement and the postural responses that accompany that movement.

Figure 6C (right) plots the onset of the initial change in cell activity in the same manner as for \( \Delta iFL \) and iBr. For this analysis, we measured the onset of cell activity only in those trials in which there was a clear change in frequency that corresponded to the initial peak observed in the PEH. This scatterplot clearly shows that the temporal relationships of this reticular neuron are very similar to those observed for \( \Delta iFL \).

That is, the onset of activity in this neuron is temporally decoupled from the onset of movement and is much more strongly related to the GO signal, as illustrated by the plot of cell lead time as a function of iClB (\( m = 1.04, R^2 = 0.92 \); filled symbols). This neuron could thus contribute to the initiation of the preparatory APA that follows the GO signal with a similar time course (Fig. 6B, see also Fig. 12). This suggestion would be strengthened by directly showing a relationship between the onset of cell activity and either \( \Delta iFL \) or the onset of one of the shoulder or extensor muscles that show a similar temporal link to the GO signal. However, in this and in most of the other cells, all such regressions were nonsignificant (not illustrated). This is not surprising, given the small variation in latency between these 2 values. Similar nonsignificant relationships, for a similar reason, were observed between the onset of activity in the extensor muscles and \( \Delta iFL \) (see Fig. 12G; Schepps and Drew 2003a).

Similar relationships between the onset of the initial period of increased activity in cell discharge and the GO signal were observed in 6/11 of the phasically discharging neurons for which we were able to measure the latency of the change in discharge activity in individual trials. Similar relationships were also quantitatively verified in 14/29 of the neurons discharging with a phasic/tonic pattern of activity that showed an initial increase in discharge activity (see, e.g., Fig. 10).

This neuron also showed later periods of activity that are clearest in the individual traces of Fig. 6B. The earliest of these periods occurred just before the onset of activity in the iClB (Fig. 6A, right). However, a similar analysis of the temporal relationship of this period of activity was inconclusive because significant relationships were obtained to both the GO signal and the onset of the iClB (not illustrated). Distinct bursts of activity during the movement were also observed in 3/6 other phasic neurons that showed early activity related to the GO signal. In 2 of these, the activity began after the onset of activity in the iClB and in the other cell there was no significant temporal relationship with either the GO signal or the onset of activity in the iClB. In contrast, the end of the overall period of activity was well related to the end of the period of activity in the iBr in both the neuron illustrated in Fig. 6 and in the other 3 neurons. In 2 of these, activity terminated after the end of activity in iBr (as in the example in Fig. 6) and in the other 2 before the end of activity in iBr.

These data suggest that, whereas the initial period of activity in these phasic neurons might be better related to the initial postural response (pAPA; see Discussion), some of them probably also contribute to the dynamic period of the reach. Similarly, in the tonic and phasic/tonic cells that showed an initial period of discharge related to the GO signal, the more pronounced and maintained discharge activity that followed this almost certainly contributed to the movement and/or to the postural responses occurring during the movement (aAPAs).

In a number of the tonic and phasic/tonic neurons there was a clear decrease in the level of cell activity. One example of such a RSN is illustrated in Fig. 7. Quantitative analysis of this decrease of activity (Burst_1) showed that there was a strong relationship between lead time and the onset of activity in the iClB (Fig. 7B, left) confirming that it was better related to the GO signal than to the movement. Note that the intercept of the regression (66 ms) is similar to that observed for the increase in cell activity illustrated in Fig. 6 (80 ms). After the decrease in cell activity there was a large increase in cell discharge (Burst_2). Analysis of this increase showed that, although the coefficient of determination for the relationship between lead time and the onset of activity in the iClB was only slightly >0.5 (Fig. 7B, right), it was significant, suggesting that this period of activity was also better related to the GO signal.

Altogether, 11 reticular cells showed a decrease in activity that we were able to measure in individual trials. In all of these cells this decrease was temporally related to the GO signal. A secondary increase related to the GO signal could be measured in 8 neurons.

**Cells temporally related to the initiation of the movement**

A large proportion of the cells showed an initial change in cell discharge that was better related to the movement than to the GO signal. Figure 8 shows one such phasically discharging neuron. In this example, there was a discrete burst of activity that occurred progressively later in trials in which the onset of movement was delayed. This can be readily seen in both the PEH and raster displays of Fig. 8A as well as in the individual trials illustrated in Fig. 8B. The scatterplots of Fig. 8C indicate that there was a strong linear relationship between the onset of the cell discharge and the onset of the iClB (\( m = 0.77, R^2 = 0.81 \)) but only a weak relationship between the lead time and the onset of activity in the iClB (\( m = 0.23, R^2 = 0.27 \)). This is the opposite of the relationship demonstrated by the cell illustrated in Fig. 6. A similar relationship to the movement was observed in 2 other phasically discharging neurons. The cessation of the period of discharge of this neuron occurred coincidently with the end of the period of activity of the iBr (Fig. 8A, right). This relationship was significant, as it was in the other 2 phasic movement–related neurons (not illustrated).

Movement-related activity was more frequently observed in the tonic and phasic/tonic cells. In these categories, 16 neurons showed an initial period of activity that was significantly correlated to the GO signal. Figure 9 shows 2 such examples, one of a tonic neuron (Fig. 9A) and the other of a phasic/tonic cell (Fig. 9B). In both cases, the onset of the discharge showed significant relationships with the onset of activity in the iClB.
with an intercept close to the origin. By definition, these tonic and phasic/tonic neurons continued to discharge throughout the time that the reaching limb was in the air and the weight was distributed among the 3 supporting limbs. Note that this population of cells differs from that described in the previous section in that the cells contain no discharge activity temporally related to the GO signal.

In some cells, including neurons showing phasic, tonic, and phasic/tonic patterns of activity, there was some evidence that individual cells might receive 2 different input signals and thus contribute to the \textit{initiation} of both the initial postural adjustments (aAPAs) and of the movement and postural adjustments (aAPAs) that followed. Such neurons displayed 2 distinct, temporally decoupled periods of activity, as illustrated in the example of Fig. 10. One period of activity, identified as Burst_1, occurred at a relatively fixed time after the occurrence of the GO signal. The other, identified as Burst_2, occurred at a longer latency and showed a progressively delayed time of onset in trials in which the onset of movement was delayed (see, e.g., the \textit{middle traces} in Fig. 10A, [Trial 4]). In the averaged displays of Fig. 10B, these characteristics are mostly lost because of the effects of temporal smearing. In the display triggered on the GO signal, Burst_1 is clear as a sharp increase of activity because it begins at a relatively constant latency after the GO signal. The second increase in activity, Burst_2, however, is less clear because of the variation in latency of the
onset of the movement. In contrast, in the displays triggered on the onset of activity of the iClB, the initial change in activity is no longer evident, whereas the second period of increased activity becomes more pronounced because the activity is well related to the triggering event, the onset of the iClB. The quantitative relationship of these 2 components of the discharge activity is illustrated in Fig. 10C, which shows the positive relationship of Burst_1 to the go signal and of Burst_2 to the onset of the iClB.

Summary of temporal relationships

Analysis of the temporal relationships between neuronal activity and the 2 major components of the reaching strategy (the go signal and the onset of the iClB) was performed for a total of 71 periods of modified cell-discharge activity measured in 51 cells. A majority of these events (58/71, 82%) were significantly related to either the go signal or to the movement (Fig. 11A). The remaining 13 periods of activity either showed

FIG. 8. Example of a phasic neuron in which the change in discharge activity was best related to the onset of the movement. A: PEHs and rasters organized as in Fig. 6. B: 2 individual trials showing the variation in both the cell and the iBr activity with respect to the go signal. C: scatter-plot illustrating the relationship between the onset of cell-discharge activity and the onset of activity in the iClB.

FIG. 9. A and B: examples of cells with a tonic (A) and phasic/tonic (B) component to their discharge that were related to the onset of the movement.
no significant relationship to either event \((n = 7)\) or showed a significant relationship to each \((n = 6)\). In the latter case, this could be explained by a lack of variation in the reaction times in these experiments. The slopes of those neurons showing a significant relationship to one or the other event formed 2 distinct groups (Fig. 11B). This bimodal distribution is similar to that obtained, in the same experiments, from plotting the slopes calculated from regressions of the onset in the change of force and the time of lift as a function of the onset of activity in iClB (Fig. 11C).

An overall summary of the latency of the onset of the change in cell activity for those neurons showing a significant relationship either to the go signal or to the onset of activity in the iClB is provided in Fig. 12 and is tabulated in Table 2. In cells showing multiple responses (e.g., Fig. 10), values for each component are included. Based on the results illustrated in Figs. 6–10, we divided the discharge patterns of the neurons into a number of different classes according to the relationship of the discharge to the go signal or to the movement. The earliest changes in activity, occurring at about 70–80 ms after the go signal (Table 2), were exhibited as either a primary increase or decrease in activity that was strongly related to the go signal (Fig. 12, A and B). Primary decreases in cell discharge were obligatorily observed only in tonically discharging cells (see, e.g., Fig. 7), whereas primary increases were observed in both phasically and tonically discharging neurons (Figs. 6 and 10). As can be seen from the histograms to the left of Fig. 12, A and B (see also Fig. 6), these changes in cell-discharge activity (gray), on average, preceded the initial changes in force that were measured in the same trials.

In those neurons that showed evidence of a secondary period of excitation that was also related to the go signal (e.g., Fig. 7),
the change in activity occurred at an average latency of 140 ms (Table 2). As illustrated by the histograms of Fig. 12C, this change in cell discharge occurred, on average, subsequent to the initial change in force but well in advance of the onset of movement.

A large proportion of the neurons exhibited changes in activity that were better related to the movement than to the go signal (Table 2 and Fig. 12D). The overall average latency of the onset of activity in these movement-related cells was 239 ms (Table 2). Although the average latency in the phasic cells was less than that in the other 2 groups, there was complete overlap with the shorter latency responses of the neurons in the tonic group. In most cases, the onset of the change in activity in these movement-related cells followed the initial change in force and preceded the onset of the change in activity in the iClB (Fig. 12D).

As demonstrated by the scatterplots of Fig. 12, the relationship between the latency (or lead time) of each population of neurons and the onset of the iClB was similar to that illustrated for each of the individual cells of Figs. 6–10. This supports the view that those measured events that showed significant relationships either to the go signal or to the onset of the iClB form a part of 2 separate signals related to different events in the behavioral strategy.

Quantitative relationships with the level of EMG and force

A quantitative analysis of the intensity of cell discharge as a function of EMG and force magnitude was performed for all cells. For phasic neurons we used a binwidth of 20 ms and analyzed only the data from the go signal to the time that the paw entered the tube, whereas for the other cells we used a binwidth of 50 ms and examined the whole trial, from the initial tone to 3 s after the shutter opened.

For the phasic neurons, only relatively weak correlations \((R^2 < 0.25)\) were seen, despite the fact that the discharge frequency in each cell was regressed against the total of 64 EMG or force traces. For the neurons showing a tonic component there was some evidence of stronger correlations. Figure 13 illustrates some of the results from 4 cells: 2 tonic cells (Fig. 13A, 2 leftmost cells) and 2 phasic/tonic cells (Fig. 13A, 2 rightmost cells). In all 4 examples, there was a \textit{fair} linear correlation between cell discharge and the level of activity in the contralateral triceps (coTrIL), which is increased throughout the reaching (see Figs. 1 and 4). Examination of the value of \(R^2\) for this relationship, for the whole population of tonically discharging cells, showed that 26/51 (51%) cells showed a value of \(R^2 > 0.3\) and 12/51 (24%) had a value >0.4 (see Fig. 13B). However, as illustrated in Fig. 13, A and B, it should be emphasized that the correlation with the coTrIL was not noticeably better than that obtained with some of the other variables. For example, the correlation with the Fv in the left hindlimb (iHLv) was as good as that with the coTrIL in cell RS22T07G and the correlation with iClB was as good as that with the coTrIL in cell RS22T23B. Nevertheless, it is noteworthy that of the 64 variables with which cell intensity was correlated for each cell, the relationship with coTrIL was found in the top 5 correlations in 21/51 (41%) of the tonically discharging cells, and iClB was in the top 5 in 25/51 (49%) of the cells. In comparison, iHLv was in the top 5 correlations in only 6/41 (15%) of the cells, although either iHLv or iVL was in the top 5 in 14/51 (28%) cells.

Other cell types

Three other types of cell discharge were observed in more than 10 cells.

In one of these subpopulations the neurons (11/142) showed a decrease in activity that continued throughout the trial. Figure 14A illustrates an example of such a neuron. Inspection of this figure shows that this decrease in activity began relatively late and followed the onset of activity in the iClB. Indeed, in this example, the decrease in activity began at about the same time as the paw entered the tube to obtain the food reward (not illustrated). This pattern of activity was typical for those cells showing a sustained decrease in activity. From 29 individual trials, taken from 4 cells, in which it was possible to accurately measure latencies, the onset of activity in the iClB began 233 ± 84 ms after the go signal, whereas the initial decrease in cell activity began at 425 ± 224 ms after the go signal (the large SD was caused by one cell in which the decrease began noticeably earlier).

Figure 14B illustrates an example of the second of these subpopulations (18/142 neurons), which was characterized by neurons that showed an initial decrease in activity followed by an increase in activity that began \textit{after} the onset of activity in the iClB. The latency of the initial decrease in discharge rate in these neurons was relatively short (91 ± 35 ms, \(n = 35\) trials, 8 cells) and is thus comparable to that observed in the neurons described in the preceding sections (Table 2). On the other hand, the latency of the onset of the increase in activity that followed this inhibition was relatively late (449 ± 135 ms), and was similar to the latency of the decrease observed in neurons of the type illustrated in Fig. 14A.

The other pattern of discharge activity that we observed (16/142 cells) included all of those neurons that showed an initial increase in activity that followed the onset of activity in the iClB (Fig. 14C). The onset of activity in many of these neurons was frequently well related to events occurring at the end of the movement. In 6/8 cells for which latencies could be...
measured, the onset of cell discharge was significantly related to the end of the period of activity in the iBr or to the time that the paw entered the food tube ($P < 0.05, R^2: 0.51–0.95$). The average latency of the onset of activity in these cells was $426 \pm 148$ ms (71 trials, 8 cells).

Discharge activity during the pretrigger period

For most neurons, the initial change in activity occurred after the go signal. However, in a number of neurons there were ramp increases or decreases of activity that occurred before the go signal. Of the 73/142 phasic, tonic, and phasic/tonic neurons, 26/73 (36%) showed significant changes in activity during this pretrigger period. We refer to this activity in the current manuscript as pretrigger activity to avoid confusion with the terminology used to describe the different types of anticipatory postural activity that are subsequent to the go signal but before the movement.

An example of one such cell, showing one of the largest changes that we observed, is illustrated in Fig. 15. This neuron showed a phasic/tonic pattern of discharge after the go signal but also showed a significant increase in activity before the onset of the go signal that occurred at approximately the same time as the onset of the Cue tone (Fig. 15B). At the same time, there was a significant modification of the anteroposterior component of the center of vertical pressure (CVP) during this same period, indicating that the cat was leaning forward in anticipation of the opening of the shutter. There was also a slight increase in the FV exerted by the 2 forelimbs (e.g., iFLV in Fig. 15A) and there was an increase in activity in the ipsilateral acromiotrapezius (iAcT) muscle at about the same time. Although these changes were clear in the illustrated cell,
they were not so obvious in some of the other cells. Moreover, even in the illustrated example (Fig. 15), a clear change in pretrigger activity was evident only in the iAcT, although at high gain, increases could also be seen in the coAcT and in the iTrM. The changes in CVP thus likely reflect the aggregate sum of subtle changes in activity in a number of muscles, rather than large changes in a few muscles.

Examination of the quantitative relationship between the integrated level of the cell discharge during the Cue period and the integrated level of all of the recorded analogue channels revealed a relatively low level of correlation (not illustrated). The best correlation was with the iAcT ($R^2 = 0.30$) and similar correlations were observed with the anteroposterior component of the CVP ($R^2 = 0.25$) and with the anteroposterior component of the force recorded from the contralateral forelimb ($R^2 = 0.29$). Similar values for the coefficient of determination with iAcT were obtained in 3/8 cells recorded from cat RS23 along the region of the brain stem and that the NRPc and NRMc were only poorly represented in the overall database.

**RSNs versus unidentified neurons**

The populations of cells showing temporal relationships to the initial changes in posture and to the movement included both identified RSNs and Unidentified neurons. Overall, a comparison of the characteristics of the RSNs and the Unidentified neurons showed no differences, although it should be noted that phasically discharging neurons were predominantly Unidentified (18/22: 82%). Nevertheless, even among the phasic group the Unidentified neurons included cells related both to the GO signal and to the movement. Similarly, within the phasic/tonic group there was no one pattern of discharge that was found only in RSNs or Unidentified neurons. For example, the complicated discharge pattern observed in the Unidentified neuron illustrated in Fig. 10 was also observed in RSNs. The only other distinction that was observed was a tendency for cells showing decreased activity to include more Unidentified neurons than RSNs (23/29: 79%).

We also examined whether the cells organized into the different classes with respect to the relationship of the discharge to the GO signal or to the movement (see, e.g., Fig. 12) showed any differences with respect to the number of RSNs or Unidentified neurons. However, RSNs and Unidentified neurons were almost equally represented in each class.

**DISCUSSION**

This is the first study to examine the relationship between the neuronal discharge patterns in the PMRF and the behavioral components of a reach from a standing position. The results are consistent with the hypothesis that reticular neurons contribute both to the postural responses that precede the

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**TABLE 2. Latency of change in cell discharge**

<table>
<thead>
<tr>
<th>Initial Decrease (related to go signal)</th>
<th>Initial Increase (related to go signal)</th>
<th>Secondary Increase (related to go signal)</th>
<th>Movement-Related (related to iClB onset)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Phasic ($n = 0$)</td>
<td>Phasic ($n = 0$)</td>
<td>Phasic ($n = 0$)</td>
<td>Phasic ($n = 0$)</td>
</tr>
<tr>
<td>Tonic ($n = 4$)</td>
<td>Tonic ($n = 0$)</td>
<td>Tonic ($n = 14$)</td>
<td>Tonic ($n = 13$)</td>
</tr>
<tr>
<td>(36) $16.0 \pm 26.3$</td>
<td>(98) $89.1 \pm 51.6$</td>
<td>(98) $153.8 \pm 48.1$</td>
<td>(87) $260.4 \pm 105.5$</td>
</tr>
<tr>
<td>Phasic/tonic ($n = 7$)</td>
<td>Phasic ($n = 6$)</td>
<td>Phasic/tonic ($n = 6$)</td>
<td>Phasic/tonic ($n = 13$)</td>
</tr>
<tr>
<td>(42) $70.0 \pm 29.6$</td>
<td>(49) $135.8 \pm 48.1$</td>
<td>(49) $153.8 \pm 48.1$</td>
<td>(135) $238.7 \pm 101.6$</td>
</tr>
<tr>
<td>Total ($n = 11$)</td>
<td>Total ($n = 20$)</td>
<td>Total ($n = 8$)</td>
<td>Total ($n = 19$)</td>
</tr>
<tr>
<td>$78.0 \pm 28.0$</td>
<td>$147.8 \pm 46.7$</td>
<td>$139.7 \pm 42.8$</td>
<td>$135.8 \pm 101.6$</td>
</tr>
</tbody>
</table>

Latencies of onset of the changes in discharge activity (in ms) for cells with different discharge patterns (see text and Fig. 4). *n*, the number of neurons that were quantitatively identified as belonging to the indicated class. Values below each group indicate the number of individual trials for which latency values could be measured (in parentheses) and the mean and SD of the latency values. Only trials for which latencies fell within the limits identified in the METHODS were included in these averages.
movement (pAPAs) as well as to the movement itself and, by extension, the postural responses that accompany that movement (aAPAs). We suggest that there are independent channels within the PMRF that contribute to the initiation of the postural responses preceding movement and of the movement itself as well as convergent channels that play a privileged role in integrating posture and movement. These ideas are summarized in Fig. 16, which forms a basis for the discussion that follows.

General characteristics of the cell discharge

Reticular neurons showed a wide range of discharge characteristics including periods of increased and decreased discharge activity. In the former population, the level of cell-discharge activity was frequently >80 Hz (Table 1) during the dynamic phase of the reach. This is similar to the discharge levels reported for the mesencephalic reticular formation during reaching movements in the primate (Gibson et al. 1998; Werner et al. 1997) and is higher than the level of activity recorded from RSNs during treadmill locomotion (Drew et al. 1986) or during voluntary gait modifications (Prentice and Drew 2001). Moreover, this level of discharge is comparable to that observed in neurons in the primate (see, e.g., Fetz et al. 1989) and cat (Vicario et al. 1983) motor cortex during voluntary movements. Because microstimulation in the PMRF in the awake cat evokes potent responses in the limb musculature.

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**FIG. 13.** A: scatterplots of average cell discharge as a function of selected EMG and force traces for 2 neurons discharging with a tonic pattern (RS23T07A, same cell as in Fig. 7 and RS22T07G) and 2 neurons with a phasic/tonic pattern (RS22T23B, same cell as in Fig. 9B, and RS22T08C). Plots are compiled from 50-ms temporal slices of activity measured from individual trials (see METHODS). B: range of values for the coefficient of determination ($R^2$) obtained from all cells with a tonic component for 4 representative measures. AU, arbitrary units.
(Drew 1991; Drew and Rossignol 1990), these general characteristics suggest that reticular neurons contribute strongly to motor activity during reaching.

General considerations concerning the database and interpretation

Reticulospinal neurons and Unidentified neurons showed generally similar characteristics and were represented in all of the classes of neurons that are illustrated in this paper. In part, this reflects the difficulty in identifying RSNs in the awake preparation. Only RSNs projecting to the ipsilateral spinal cord were positively identified and, even then, the relatively low-intensity stimulation would not activate all lumbar-projecting axons. Unidentified neurons must also include those projecting only to the cervical spinal cord or to the contralateral lumbar cord. Nevertheless, the ability to positively identify at least one class of RSNs, and the fact that there was little difference between these and Unidentified neurons, suggests that the data provide a true indication of the nature of the reticular signals that contribute to the control of posture and movement.

Although our RSNs were identified from the lumbar spinal cord while the task involved voluntary movements of the forelimbs, we emphasize that these movements require postural adjustments in both fore- and hindlimbs and that these occur with similar time courses (Schepens and Drew 2003a). In addition, many cells with lumbar projecting axons also innervate the cervical spinal cord and thus may influence activity in both fore- and hindlimbs (Matsuyama et al. 1988, 1997; Peterson et al. 1975). Further, cells projecting only to cervical levels could influence hindlimb activity by long propriospinal neurons (Alstermark et al. 1987). As such, these neurons could contribute to activity in either or both limb(s). For this reason, we place the emphasis herein on the more general contribution of these cells to the APAs preceding the movement, observed in both fore- and hindlimbs, and to the initiation of the movement and the postural responses that accompany them.

Contribution to the production of the pAPAs

Our previous examination of the EMG activity and ground reaction forces (GRFs) that occur during a reach (Schepens and Drew 2003a) provide a firm foundation for the interpretation of the neuronal discharge patterns presented herein. In the previous paper we showed that movement is preceded by APAs that are defined by characteristic changes in both EMG and force...
Moreover, these pAPAs followed the Go signal at a relatively constant latency and were temporally decoupled from the reach (see also Fig. 6). Similar dissociation between pAPAs and voluntary movement have been described in humans (e.g., Brown and Frank 1987).

A similar relationship between neuronal activity and the Go signal was observed in many reticular neurons, including RSNs. These neurons followed the Go signal at a fixed latency and were temporally decoupled from the onset of the reach. Moreover, the latency of this discharge activity (Table 2) was, on average, shorter than the earliest change in force (Fig. 12) and the earliest changes in activity in limb muscles (60–90 ms: Schepens and Drew 2003a). They are thus unlikely to be the result of afferent feedback. The data presented are thus compatible with a role for these neurons in the production of the initial changes in EMG activity underlying the pAPAs preceding the movement. The initial increases in cell-discharge activity in our study could contribute to the increases in extensor activity that are observed in the ipsilateral forelimb and contralateral hindlimb at this time, whereas the initial decreases in cell activity could contribute to the concomitant decreases in activity observed in the contralateral forelimb and ipsilateral hindlimb (Figs. 1 and 4; Schepens and Drew 2003a). This interpretation is compatible with the fact that a number of electrophysiological (Floeter et al. 1993; Jankowska et al. 2003; Peterson et al. 1975) and anatomical (Matsuyama et al. 1988, 1997) studies, as well as the results from recording and stimulation studies carried out during locomotion (Drew 1991; Drew and Rossignol 1990; Drew et al. 1986), have shown that neurons in the PMRF may influence muscle activity both

**FIG. 15.** Example of a neuron showing increased activity during the pretrigger period. **A:** PEH and raster display, together with the average FV from the ipsilateral, reaching, forelimb. This figure also illustrates the transfer of the center of vertical pressure (CVP) in the anteroposterior (AP) plane as well as EMG activity recorded from the ipsilateral acromiotrapezius (iAcT) muscle. CVP was calculated from the changes in FV exerted by all 4 limbs (Schepens and Drew 2003a). AP changes in the CVP are illustrated as changes from a normal level of 60% body weight supported on the forelimbs (Macpherson 1988). **B:** 2 individual trials of the same neuron illustrating pretrigger increases in cell discharge, AP displacement of the CVP, and iAcT activity. Open triangles and first vertical dotted line indicate the onset of the cue. **C:** scatterplot illustrating the relationship between the onset of the change in activity in the cell as a function of the onset of the CVP. Data are measured from individual trials in 5 cells (including that illustrated in A) in which clear pretrigger activity was observed. **D:** a similar plot for cell activity as a function of the onset of the AP displacement of the CVP.
ipsilaterally and contralaterally. As such, both the primary augmented and decreased responses may contribute to the loading of the reaching limb that produces the transfer of the center of mass over the supporting limb. In this respect it is worth noting that a previous study by Werner et al. (1997), which examined the discharge properties of mesencephalic reticular neurons during a reach, reported no evidence of any cell activity related to the GO stimulus that triggered the movement. This may reflect that the primates were seated and thus there was little need for any postural activity to maintain equilibrium. Alternatively, it might reflect differences in the function of neurons in the mesencephalic and pontomedullary regions of the reticular formation.

The secondary period of increased cell discharge that we described was also significantly related to the GO signal but, by definition, followed an earlier change in activity. We suggest 2 possibilities for the contribution of this response. One is that these signals contribute to the activation of unrecorded shoulder or trunk muscles that become active between the onset of the APA and the reach. The other is that they are involved in preferentially modifying postural activity in groups of hindlimb muscles that become active later, especially during slow movements (Schepens and Drew 2003a). At the present time, it is not possible to further differentiate between these, or other, explanations for the occurrence of this secondary signal.

**Contribution to the production of movement and of the aAPAs**

A substantial proportion of reticular neurons showed increases in activity that were significantly related to the movement. The majority of these cells contained a tonic component in their discharge. This maintained discharge could contribute to the reach itself, to the postural responses that accompany it (aAPAs), or to both. Because the onset of the activity in iCIb and the changes in activity in the extensor muscles in the supporting forelimb (e.g., coTriL) are simultaneous (Alstermark and Wessberg 1985; Fig. 11H in Schepens and Drew 2003a), it is difficult to distinguish between these 2 possibilities on the basis of temporal data. Moreover, given that all the reaches illustrated in this manuscript were to a single location, it is equally difficult to differentiate these components on the basis of their relative magnitude. However, we did find that the best linear regressions were more frequently obtained for the coTriL (Fig. 13) than with any other muscle, supporting a role for these neurons in the production of the postural responses.
accompanied by the movement. Moreover, we also emphasize that the tonic discharge in the neurons was maintained despite the fact that the active movements of the reaching limb involved both a protraction to the tube as well as a retraction to replace it on the platform.

Because the discharge activity in these neurons began after the onset of the initial pAPA, it is more difficult to demonstrate that the discharge is a feed-forward motor signal than it is for those cells discharging before any movement. For example, movement-related neurons may discharge in response to the shift in the center of mass of the body. However, the strong temporal dissociation between onset of the APA and the onset of the reach (Fig. 6: Schepens and Drew 2003a) and the fact that all of these cells, by definition, discharged before the onset of the reach (and showed a significant temporal relationship with it) support our view that such neurons contribute to the production of these events.

Many of the movement-related cells with a tonic component also showed a clear phasic discharge during the reaching movement and some cells discharged phasically and had no tonic component. This activity probably contributes to the dynamic movement of the reaching limb toward the target. Those cells showing both a phasic and a tonic component could signal aspects of both the movement and the maintained period of postural support. This latter interpretation is compatible with the results from our studies during locomotion that show that microstimulation at a given point frequently activates flexor muscle activity in the limb ipsilateral to the recording site and extensor muscle activity in the contralateral forelimb, as well as in the hindlimb muscles (Drew 1991). Such a complex pattern of activity would explain why stronger relationships were not observed between cell-discharge activity and the level of activity of individual EMG or force measures in our linear regression analysis.

Independent and convergent channels for the control of posture

We were able to identify 2 temporally decoupled signals in the discharge patterns of the reticular neurons: one that follows the GO signal at a relatively fixed latency and the other that is related to the initiation of the movement. In the preceding paragraphs, we argue that the former may contribute to the pAPA and the latter to the movement and the postural responses accompanying the movement (aAPAs). In some cells, these signals were seen in isolation, arguing for independent control of the 2 parts of the behavioral strategy. This was particularly true for the movement-related cells. However, in many cells, the overall discharge activity of the cell was not related to only one of these components but showed a convergent signal in which both components could be identified. We suggest that such convergent signals are responsible for the activation of the different groups of muscles active at the different times in the reach as well as of those muscles that contribute to both (e.g., iTrIL).

Overall, the data suggest that the variety of cell responses that we observe may result from the combination of a smaller number of components that converge onto individual reticular neurons (see Fig. 16).

The first and most elemental of these components is the response defined as a primary increase that is temporally related to the APAs preceding the movement. This component is seen in isolation in a few cells (not illustrated) but is normally seen combined with other components related to movement. We consider that the primary decrease is the mirror image of the primary increase and that these 2 responses should be treated as a single component that contributes to the initiation and the regulation of the pAPA. The second component is a phasic signal related to the initiation of the movement. This component can also be seen in isolation (e.g., Fig. 8), but is more frequently seen in combination with other components, either together with the component that defines the pAPA (e.g., in phasic cells) or together with the component specifying the aAPA (see following text). The third major component is the tonic signal that is related to the initiation of the movement and to the postural responses that accompany it. This component can also be seen either in isolation (Fig. 9) or combined with other components (e.g., Fig. 10). The response identified as a secondary response related to the GO signal may provide a 4th component. Finally, there may also be yet another component that is activated at the end of the dynamic phase of the reaching movement, either as an increase in discharge (Fig. 14, B and C) or as a decrease (Fig. 14A). However, we believe that this signal should be considered together with the 2nd (phasic movement) component as contributing to the phasic activity of the limb. This latter interpretation serves to emphasize that the components that we define represent types of response rather than a specific pattern active only at one moment during the activity. As in the study of Werner et al. (1997), different populations of neurons are active at slightly different times throughout the reaching movement. Similarly, it is equally clear that the latency of the initial period of discharge activity, related to the GO signal, is also variable (Fig. 12, A and B). Such flexibility within a type of component is required to produce pAPAs (see, e.g., Benvenuti et al. 1997) and movements that can be adapted to the specific requirements of the behavioral need.

Pretrigger activity

A subpopulation of neurons exhibited modified discharge activity before the GO signal. In primate cortex, this type of precocious discharge activity during a delayed-instruction task has been shown to be involved in the processing of sensory information related to the instructed movement (Crammond and Kalaska 1994, 2000; Di Pellegrino and Wise 1993; Wise and Kurata 1989).

Given the clearly demonstrated participation of the PMRF in postural control, we start with the assumption that the pretrigger activity observed in our task is more likely to reflect precocious postural adjustment than high level planning or sensorimotor transformations. The data illustrated in Fig. 15 support this viewpoint by demonstrating the relationship between cell-discharge frequency and the forward transfer of the anteroposterior component of the CVP. Coefficients of determination for the linear regression analysis of cell discharge as a function of EMG or GRF were low, possibly reflecting a contribution to more global aspects of the response (see also preceding paragraphs). We also emphasize that phasic changes in EMG activity in the pretrigger period were observed only in selected muscles, even in situations in which there were quite obvious changes in CVP. This speaks to the issue that rela-
tively small changes in relatively large numbers of muscles may lead to changes in posture that are detectable only by global kinetic measures.

Conclusions

This paper details the nature of the control signals responsible for the initiation and regulation of posture during a reaching movement made from a standing position in the cat. We identify 3 types of major signals in the discharge patterns of reticular neurons in the PMRF: 1) phasic signals related to the pAPA; 2) phasic signals related to the dynamic phase of the reaching movement; and 3) tonic signals related to the aAPAs. These signals, which are expressed independently or, more frequently, in the form of convergent signals, result from inputs from other, hierarchically higher regions of the nervous system (Fig. 16). On the basis of the known functional anatomy of the corticoreticular system (Berrevoets and Kuypers 1975; Canedo and Lamas 1993; Kably and Drew 1998a; Matsuyama and Drew 1997; Rho et al. 1997) and of previous studies performed in this laboratory in walking cats (Kably and Drew 1998b), it is probable that both the phasic and tonic signals related to movement arise as feed-forward signals transmitted by corticoreticular axons. The corollary nature of this discharge would ensure that the timing and the magnitude of these postural adjustments are appropriately related to the exact nature of the movement being made. The origin of the signal responsible for providing the phasic signals related to the pAPA is less clear. Possible candidate structures include the premotor or supplementary areas of the cortex or a direct input from the basal ganglia, although we cannot rule out that this signal may also originate, at least partly, within area 4.

Acknowledgments

We thank J. Bérichon and G. Richard for constructing the apparatus; M. Bourreau and P. Drapeau for electronic and programming assistance, respectively; N. de Sylva for help during the experiments; and Drs. S. Rossignol and A. Smith for comments on this manuscript.

Grants

This work was supported by the Canadian Institutes of Health Research. B. Schepens was supported by a Jasper Fellowship and by a Human Frontier Science Program long term fellowship.

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