A Contribution of Area 5 of the Posterior Parietal Cortex to the Planning of Visually Guided Locomotion: Limb-Specific and Limb-Independent Effects

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Andujar J-E, Lajoie K, Drew T. A contribution of area 5 of the posterior parietal cortex to the planning of visually guided locomotion: limb-specific and limb-independent effects. J Neurophysiol 103: 986–1006, 2010. First published December 16, 2009; doi:10.1152/jn.00912.2009. We tested the hypothesis that area 5 of the posterior parietal cortex (PPC) contributes to the planning of visually guided gait modifications. We recorded 121 neurons from the PPC of two cats during a task in which cats needed to process visual input to step over obstacles attached to a moving treadmill belt. During unobstructed locomotion, 64/121 (53%) of cells showed rhythmic activity. During steps over the obstacles, 102/121 (84%) of cells showed a significant change of their activity. Of these, 46/102 were unmodulated during the control task. We divided the 102 task-related cells into two groups on the basis of their discharge when the limb contralateral to the recording site was the first to pass over the obstacle. One group (41/102) was characterized by a brief, phasic discharge as the lead forelimb passed over the obstacle (Step-related cells). These cells were recorded primarily from area 5a. The other group (61/102) showed a progressive increase in activity prior to the onset of the swing phase in the modified limb and frequently diverged from control at least one step cycle before the gait modification (Step-advanced cells). Most of these cells were recorded in area 5b. In both groups, some cells maintained a fixed relationship to the activity of the contralateral forelimb regardless of which limb was the first to pass over the obstacle (limb-specific cells), whereas others changed their phase of activity so that they were always related to activity of the first limb to pass over the obstacle, either contralateral or ipsilateral (limb-independent cells). Limb-independent cells were more common among the Step-advanced cell population. We suggest that both populations of cells contribute to the gait modification and that the discharge characteristics of the Step-advanced cells are compatible with a contribution to the planning of the gait modification.

INTRODUCTION

Visual information is critical for locomotion over irregular terrain. Vision is used to assess not only the physical characteristics of obstacles—such as their shape and size—but also, for moving objects, their temporal characteristics (Drew et al. 2008; Fowler and Sherk 2003; Gibson 1958; Lee 1980; Sherk and Fowler 2000; Sun et al. 1992; Warren Jr et al. 2001). This information is then used to modify paw placement in front of the obstacle and to ensure the appropriate limb trajectory to step over it (Drew et al. 1996, 2008; Lajoie and Drew 2007; Marigold 2008; Mohagheghi et al. 2004; Moraes et al. 2004).

It is clear that multiple cortical and subcortical structures are involved in processing visual information for the control of locomotion (Armstrong and Marple-Horvat 1996; Beloozerova and Sirota 1993, 2003; Drew et al. 2008; Marple-Horvat et al. 1998) as they are for discrete voluntary movement of the arm or hand (Goodale and Milner 1992; Johnson et al. 1996; Rizzolatti and Luppino 2001; Rizzolatti and Matelli 2003; Scannell 1995). Among these structures, different regions of the posterior parietal cortex (PPC; areas 5a, 5b, and 7) have received particular attention in the primate because of their role in multimodal integration and the fact that cells in these regions discharge during tasks requiring visuomotor transformation (Andersen and Buneo 2002; Andersen et al. 1997; Burnod et al. 1999; Jeannerod et al. 1995; Johnson et al. 1996; Mountcastle 1995; Mountcastle et al. 1975; Wise et al. 1997). In addition, in instructed delay tasks, in which information about the upcoming movement is provided before the signal to move, many cells in regions of the PPC related to reaching or grasping show strong anticipatory activation (Jeannerod et al. 1995; Kalaska 1996; Kalaska and Crandall 1995; Sakata et al. 1997; Snyder et al. 1997, 2000). This suggests that the PPC not only may participate in the control of visually guided voluntary movements, but also may play an important role in their planning.

There are fewer studies on the PPC in the cat but there are reasons to believe that this structure also contributes to visuomotor transformations during both reaching and locomotion in that species (Drew et al. 2008). For example, in one study, lesion of the anterior suprasylvian gyrus (including areas 5b and 7) produced deficits in reaching for a moving object, whereas reaching for a fixed target remained unaffected (Fabre and Buser 1981). In addition, recent experiments have shown that lesions of areas 5a and 5b resulted in prolonged deficits in negotiating obstacles on a moving treadmill, particularly when the speed of the obstacles was different from that of the treadmill (Lajoie and Drew 2007). Further, single-neuron recording studies have shown that cell activity in area 5 is rhythmically modulated during locomotion and that it increases in tasks involving precise foot placement or when stepping over barriers (Beloozerova and Sirota 2003). Given that the PPC is strongly interconnected with more rostral cortical areas, including the motor cortex (Andujar and Drew 2007; Babb et al. 1984; Ghosh 1997; Waters et al. 1982a,b; Yumiya and Ghez 1984), and that it connects with the lateral cerebellum through the pontine gray nuclei (Kakei et al. 1995; Stein and Glickstein 1992) it has the potential to influence visually guided locomotion via multiple pathways.

Although the available evidence strongly suggests that the PPC in the cat contributes to the control of visually guided locomotion, the extent and nature of this contribution are still unclear. The only previous study on the characteristics of neurons in the PPC during visually guided locomotion is that of

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Beloozerova and Sirota (2003), in which cats stepped over a series of barriers or walked along the rungs of a horizontal ladder. These studies showed that neuronal activity was substantially increased in both tasks, although the repetitive nature of the behavioral tasks did not allow the authors to dissociate activity that may be involved in planning a step from that involved in the execution of that step. To address the issue of whether the PPC contributes to the planning of visually guided locomotion, we recorded activity from neurons from area 5 in a task that we have used previously to look at the contribution of the motor cortex to the control of visually guided locomotion (Drew 1988, 1993). In this task, cats walk on a treadmill and adjust their gait to step over an obstacle that advances toward them. The obstacle is visible for several steps prior to the requirement to modify gait and cells that are involved in planning such gait modifications should discharge substantially in advance of the step over the obstacle. Such is not the case for the majority of cells recorded in the motor cortex, which discharge only during the execution of the step over the obstacle (Drew 1993; Drew et al. 1996, 2008), suggesting that this structure does not make a major contribution to the planning of the gait modification. The results presented in this study show that, in contrast, a majority of cells in area 5 of the PPC show changes up to two full step cycles in advance of the step over the obstacle, supporting a contribution of this structure to the planning of visually guided gait modifications.

These results were previously presented in preliminary form (Andujar and Drew 2006).

**Methods**

**Training and surgery**

Data were collected from two male adult cats (weight 4–5 kg) trained to walk without interruption for a period of ≥20 min on a treadmill moving at speeds of 0.35 to 0.5 m s⁻¹ and to step over obstacles attached to a second moving belt. These obstacles spanned the complete width of the treadmill. The obstacles moved either at the same speed as the treadmill belt on which the cat was walking (matched task) or at a slower speed (visual dissociation task; Lajoie and Drew 2007). In this latter condition, the speed of the obstacle is decoupled from the speed of the treadmill. In the experiments described herein, the speed of the treadmill belt on which the cat walked was set at 0.5 m s⁻¹ and the belt to which the obstacle was attached was set at 0.35 m s⁻¹. The effect of this manipulation was to dissociate visual information obtained from the moving obstacle from that obtained from self-motion. In particular, in the visual dissociation task, the cat must calculate the onset of the gait modification on the basis of the relative speed of both the obstacle and the treadmill on which it walks, ensuring that visual information on the advance of the obstacle is critical for the planning of the gait modification. In practical terms, the task was more challenging to the cat and paw placement in front of the obstacle was modified with respect to the matched task (Lajoie and Drew 2007).

Following training, the cats were prepared for surgery under general anesthesia and under sterile conditions. In brief, the cats were premedicated with a mixture of acepromazine maleate (50 µg/kg), glycopyrrolate (10 µg/kg), and ketamine (11 mg/kg) and were then intubated and anesthetized with isoflurane (2–3% with oxygen). Fluids, as well as antibiotics (40,000 IU/kg, penicillin G sodium) and corticosteroids (methylprednisolone, Solu-medrol, 15 to 30 mg/kg) to prevent cortical swelling, were administered through a catheter. Heart rate and body temperature were monitored continuously. The animals were placed in a stereotaxic frame usingatraumatic ear bars coated with xylocaine; petroleum jelly was applied to the eyes to prevent desiccation of the cornea. A craniotomy was performed over the right PPC at the coordinates of the ansate sulcus, as determined prior to the surgery with a magnetic resonance imaging scan. A recording chamber (8 × 6 mm) was placed over the cranial aperture and fixed in place with dental acrylic (Drew 1993). Two arrays of microwires were stereotaxically implanted into the pontine gray nuclei (AP 0.0, L1.2 and AP 0.0, L3.5) by using a harpoon assembly (Drew 1993; Palmer 1978). A third microwire array was implanted into the pyramidal tract at coordinates P7 and L1.2. These electrodes were used to identify corticofugal neurons in layer V of the cortex. In one cat, wires were placed in the bony orbit to monitor eye movements. Analgesics (buprenorphine, 5 µg/kg) were administered for 3–4 days postoperatively. Antibiotics were given daily (cefadroxil, 100–200 mg).

In a second surgery, and using the same surgical procedures, pairs of Teflon-coated, braided stainless steel wires were implanted into selected muscles of the forelimbs, hindlimbs, and neck (Drew 1993; Drew et al. 1986). Cats were allowed to recover for 1–2 wk before beginning experiments.

All surgical procedures followed the recommendations of the Canadian Council for the Protection of Animals and protocols were approved by the local animal ethics committee.

**Protocol**

During each experimental session, a custom-made microdrive was attached to the recording chamber and a conventional glass-insulated, tungsten microelectrode (impedance of 0.5–1.5 MΩ) was advanced into the cortex. We report data only on neurons that were recorded from layer V of the cortex, which was identified by the presence of neurons discharging antidromically to stimulation of the electrodes implanted in the pontine gray nuclei or the pyramidal tract. Neurons that discharged at constant latency to the stimulation and that fulfilled the criteria of the collision test (Lipski 1981) were classified as corticofugal neurons. All isolated neurons (identified and unidentified) within layer V were recorded during locomotion. Recordings were restricted to layer V to obtain a relatively homogeneous database, at least with respect to the major projections of the cells.

For most neurons we initially recorded activity during 20–30 step cycles of unobstructed treadmill locomotion (control task). The neurons were then recorded for a period of 10–20 min during two kinds of voluntary gait modification as the cat stepped over the obstacles attached to the treadmill belt. In the matched task, the obstacles and the treadmill advanced at the same speed. Two obstacles (each with a round cross section) were attached equidistantly (3 m apart) to the treadmill belt and the cats normally executed 5–6 step cycles between each step over the obstacle. One obstacle had a diameter of 5 cm and the other 10 cm. This task simulated a stationary object approached by the walking cat. In the visual dissociation task, the obstacle moved more slowly than the treadmill (0.35 vs. 0.5 m/s), simulating a walking cat taking over a more slowly moving object. Neuronal activity was normally recorded for 5–10 min in the matched task and then for a similar time in the visual dissociation task. In both tasks, the obstacle was visible to the cat for at least five full steps before the gait modification. Electromyographic (EMG) activity was amplified, filtered, and then sampled off-line at a frequency of 1 kHz. Unit activity was sampled at 100 kHz.

When possible, each cell was tested to determine a receptive field. The entire body, as far as possible, was first explored to see whether a neuron discharged to light touch of the fur or skin. Such cells were classified as cutaneous. In the absence of a cutaneous field, we passively manipulated the limb to determine whether the cells could be discharged by proprioceptive inputs. In addition, we also tested each cell for visual responses by moving a rod in front of the cat. In addition to moving the rod vertically and laterally across the eyes, we also paid particular attention to whether the cell fired to a looming stimulus by moving the rod toward the cat. At the end of most
recording sessions (2–4 h), microstimulation was applied through the electrode (cathodal current, 11 pulses at 330 Hz, duration 0.2 ms, 5–50 μA) at the location of the last recorded neuron in layer V. Small electrolytic lesions (25–35 μA) were made in selected penetrations to aid in histological reconstruction.

DVD recordings were made of all experiments and synchronized to the EMG and unit data by recording a digital time code on both the DVD and the digitized data file. This allowed us to inspect the recordings off-line to ensure that only periods of stable walking were included for analysis.

**Histology**

At the end of the series of experiments, the cats were deeply anesthetized with an intraperitoneal injection of pentobarbital sodium (Somnotol, 40 mg/kg) and perfused per cardia with a formaldehyde solution. The brain was removed and photographed. The rostral part of the cerebral cortex, containing the PPC, was sectioned in the parasagittal plane (40 μm) and stained with cresyl violet. To accurately quantify the location of the recorded neurons, we calculated the location at which each penetration crossed layer V of the PPC. The anteroposterior location of the recorded cells was calculated as the linear distance of the cell from the fundus of the ansate sulcus as measured along the length of the straightened layer V. The mediolateral location of the cell was based on the histological section in which the recording site was located and the distance of that section from the midline. These two coordinates were used to plot the location of each cell on a flattened map of the cortex centered on the fundus of the ansate sulcus (for details see Andujar and Drew 2007; Rho et al. 1997). Cytoarchitectonic boundaries were determined on the basis of the criteria detailed in previous studies (Andujar and Drew 2007; Avendano et al. 1988; Ghosh 1997; Haslerr and Muhs-Clement 1964).

**Data analysis**

Neurons were selected for analysis if off-line inspection showed that their action potentials were well isolated throughout the recording period. A custom program was used to isolate and discriminate neurons based on time and amplitude. The recorded data were then processed similarly to those described in previous studies from this laboratory (Drew 1993; Lavoie and Drew 2002). The data were first displayed on a monitor and a custom program was used to mark the onset and offset of the locomotor activity of selected muscles to identify selected series of step cycles during the voluntary gait modifications. For each sequence of locomotion we identified whether the limb contralateral to the recording site was the first (lead condition) or the second (trail condition) to step over the obstacle. In addition, we separately identified steps over the smaller and larger of the two obstacles. We also separately identified each of the five steps preceding the step over the obstacle as well as the step following the gait modification. Last, data from the matched and dissociated tasks were also differentiated.

For each group of step cycles (e.g., all steps over the obstacle with the lead limb) we averaged the EMG and cell activity. EMG activity in each step cycle was normalized prior to averaging by resampling the activity into 512 equal bins. Because step cycle duration approximated 1 s in most trials, bin width averaged slightly <2 ms. Cell discharge activity was converted into instantaneous frequency (1,000/ interspike interval) and also normalized into 512 bins prior to averaging by using the method described by Udo et al. (1982). Averages were always synchronized to the onset of activity of either the cleidobrachialis (CIB) or brachialis (Br) muscles, each of which discharges at the onset of the swing phase of locomotion (Drew 1993). The discharge frequency of the cell during steps over an obstacle was compared with that during control locomotion. For the majority of cells, this latter variable was calculated from the averaged discharge activity when no obstacle was attached to the treadmill belt. However, for some cells, discharge activity was not recorded in the absence of the obstacles and, for these cells, control discharge activity was determined from the averaged activity four step cycles before the step over the obstacle. Comparison of these latter averages in cells in which unobstructed locomotion was also recorded showed no significant differences between the two. Cell discharge activity in a given condition was considered to be significantly different from control when it deviated from the interval of confidence (P < 0.01) of the SE of the control activity for >10% of the 512 bins comprising each cycle (≥51 consecutive bins; ~100 ms). In the displays herein that show averaged data during gait modifications, we generally display the averaged activity during the step over the obstacle together with the activity in the two to three steps preceding and the one to two steps following the gait modification. Each step cycle is normalized independently. Note that for the control traces, the cell activity during each step cycle is considered to be identical and is thus repeated in each displayed step cycle.

Raster plots, synchronized on the onset of activity of a given muscle, were constructed to visualize the temporal relationships between periods of cell discharge and the correlated muscle activity. Rasters were always rank-ordered according to the duration of the step cycle.

To determine whether a cell was phasically modulated during the control task, we used the Rayleigh test for directionality (P < 0.01) (Batschelet 1981; Drew and Doucet 1991). The period or phase of activity of a cell during control locomotion was calculated by using the method described in Lavoie and Drew (2002). In brief, the onset and offset of the period of burst activity were identified as the points at which the histogram of cell discharge frequency crossed the mean level of the discharge calculated from all trials (see RESULTS and Fig. 2, A and B). During the step over the obstacle, the phase of activity was defined as the period during which the discharge activity significantly differed from the interval of confidence of the SE activity during the control task. The phase and value of the peak discharge frequency were calculated from averaged traces low-pass filtered at 100 Hz (digital dual-pass Butterworth filter, fourth-order).

Cells were classified into groups using definitions similar to those in our previous studies examining the discharge characteristics of neurons in the motor cortex (Drew 1993) or the red nucleus (Lavoie and Drew 2002). Cells were first divided into two primary groups based on when the discharge activity significantly differed from control during the step over the obstacle. Cells in which discharge activity deviated significantly from control <200 ms before the onset of activity in the CIB or Br (swing onset) were classified as Step-related cells. Cells in which discharge activity differed significantly from control earlier than this were classified as Step-advanced cells. The Step-related cells were further subdivided into those in which the maximal significant deviation from control was restricted to the initial part of the swing phase, prior to the onset of EMG activity in the extensor digitorum communis (EDC; Phase I cells) and those with maximal changes at the end of swing, following the onset of activity in the EDC (Phase II cells). Cells in which discharge activity was significantly modified throughout the swing period were classified as Phase I + II. Some cells showed peak discharge activity after the swing phase in the modified cycle; these were referred to as Late cells. The Step-advanced cells were also subdivided into those in which discharge activity stopped at swing onset (Step-advanced only), those in which the discharge continued into the swing phase (Step-advanced swing), and those in which discharge continued after the swing phase (Step-advanced Late).

**Definitions**

Because of the complexity of the situation in which either the limb contralateral or ipsilateral to the recording site may be the first to pass over the obstacle, and cells may be related to either limb, we offer the
following definitions of terms used in this study. We refer to the situation in which the limb contralateral to the recording site is the first to pass over the obstacle as the lead condition; the contralateral limb is therefore the lead limb. In contrast, when the contralateral limb is the second to pass over the obstacle, we refer to this as the trail condition; in this situation the ipsilateral limb is the lead limb. When a cell is related to the same limb (always the contralateral limb in this study) in both the lead and trail conditions, we refer to this as a limb-specific cell. When a cell is related to the contralateral limb in the lead condition but the ipsilateral limb in the trail condition, we refer to this as a limb-independent cell. Note that in the latter case the cell is always related to the first limb to step over the obstacle.

RESULTS

Database

Recordings during locomotion were made from a total of 78 electrode penetrations in the PPC of two cats. Data reported herein are based on the analysis of 121 neurons, recorded from 46 of those tracks. These units were selected based on the following criteria: 1) all cells were localized in cortical layer V, as determined by antidromic stimulation or by histological analysis; 2) our initial on-line analysis suggested that the neurons showed phasic activity related to the forelimbs either during unobstructed locomotion or/during steps over the obstacles; 3) a minimum of 10 steps were recorded while the cat stepped over the obstacles; and 4) our subsequent off-line analysis showed no relationship with the hindlimb in the matched task. Cells not included in the analysis included cells related to the hindlimbs, those that discharged primarily to head movements, and those that showed no relationship to locomotion.

Histological reconstruction of these penetrations (Fig. 1) showed that the vast majority (103/121) of the analyzed neurons were located either within the rostral (26/121) or caudal (49/121) banks of the ansate sulcus or on the cortical gyrus adjoining the caudal bank of the ansate sulcus (28/121). A small number of cells (18/121) were located within the lateral sulcus where it joined the ansate sulcus. From a cytoarchitectonic perspective, 47/121 cells were recorded in area 5a and the adjacent area 2 and 74/121 in area 5b; no cells were recorded in area 7. Cells recorded together in a penetration generally showed similar properties, although this was not always the case.

![Histological examples and reconstructions made from the 2 cats used in this study.](http://jn.physiology.org/)

**FIG. 1.** Histological examples and reconstructions made from the 2 cats used in this study. Aa–Ac: 5 representative parasagittal histological sections taken from cats PCM2 (Aa, Ab) and PCM5 (Ac–Ae) illustrating the location of the penetrations in which some of the cells illustrated herein were recorded (in each tracing, “Tr” refers to the track or penetration). Each illustration (Aa–Ae) shows the gray matter (delimited between the 2 solid lines) and layer V of the cortex (dotted line). Rostral is to the left in each tracing and dorsal is to the top. Box Aa provides a surface view of the front half of the right hemisphere illustrating the location of the ansate sulcus and of cytoarchitectonic areas 1–7 of the cat. The horizontal lines (a–e) show the approximate location of the illustrated sections. The inset in Aa shows an expanded view of the ansate sulcus. B and C: the ansate sulcus and its adjacent gyri are illustrated in a flattened representation at the level of cortical layer V and aligned to the fundus of the ansate sulcus (ANS). Other solid gray lines indicate the fundus of the cruciate (CRU) and lateral (LAT) sulci and the lip of the adjacent gyri, identified here as the anterior ansate gyrus (AAG), posterior ansate gyrus (PAG), and the posterior sigmoid gyrus (PSG). The boundaries between cytoarchitectonic areas 1, 2, 5a, 5b, and 7 are delimited with dashed lines. Symbols on the plot indicate the location of all penetrations made in these 2 cats in which cells were recorded. Large open circles indicate penetrations in which cells discharging during the modified swing phase (Step-related cells) were recorded, whereas large filled circles indicate penetrations in which cells discharging in advance of the step over the obstacle (Step-advanced cells) were recorded. Circles with open and filled half sections indicate tracks in which both types of cells were recorded. The horizontal lines labeled a–e indicate the approximate location of the sections shown in Aa–Ae.
Parietal activity during normal locomotion: control task

Most cells (80/121, 66%) isolated during the experiments were first recorded during unobstructed locomotion for a minimum of 10 step cycles. In the other 41/121 (34%) cells, in which we did not record the activity of the cells in the absence of the obstacle, we used the discharge activity of the cell 4 cycles before it stepped over the obstacle (see METHODS); this corresponded to a minimum of two steps after the preceding obstacle.

On the basis of the Rayleigh test for directionality we determined that 64/121 (53%) neurons showed a nonuniform pattern of discharge activity during the periods of control locomotion. We used this as a working definition that the cell was phasically modulated during locomotion (Drew and Doucet 1991). Two examples of cells modulated during control locomotion are illustrated in Fig. 2, A and B. Both of these cells had receptive fields on the contralateral (co) forelimb that included the ventral surface of the paw and the forearm and both discharged maximally during the period of activity of the coClB, corresponding approximately to the swing phase of locomotion. The cell illustrated in Fig. 2B showed an additional, substantially smaller, burst of activity during the period of activity of the ipsilateral (i)Br, i.e., during ipsilateral swing. The horizontal lines in the central step cycle of Fig. 2, A and B indicate the period of activity of these cells, as defined in METHODS; the vertical dotted line indicates the phase of peak activity. The cell illustrated in Fig. 2A was recorded in the fundus of the ansate sulcus (Fig. 1, Aa and B), whereas the cell illustrated in Fig. 2B was recorded in a similar mediolateral location but just rostral to the fundus (not illustrated).

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**FIG. 2.** Neuronal activity during control locomotion. *A* and *B*: postevent histograms (PEHs) and raster displays of 2 examples of phasically modulated neurons together with recordings from selected muscles contralateral (co) and ipsilateral (i) to the recording site. Data are synchronized to the onset of the contralateral brachialis (coBr: straight vertical lines) and each cycle is repeated 3 times to emphasize the rhythmic nature of the discharge activity. The staggered vertical ticks indicate the phase of offset of the activity in the coBr. Horizontal lines on the unit trace in the middle step cycle indicate the period of cell activity and the vertical line indicates the phase of peak discharge (see METHODS). N indicates the number of step cycles in the average. The average duration of the step cycle is indicated below each average. The figurines represent the cutaneous receptive fields of the cells on the contralateral forelimb. *C*: the phase of peak discharge (filled circles) and the period of mean discharge (horizontal lines), as illustrated in *A* and *B*, for all 64 cells that showed a significant, phasic discharge during unobstructed locomotion according to the Rayleigh test for directionality. The data are synchronized either to the onset of the contralateral cleidobrachialis (coClB) or to the coBr (phase 0.0) and are normalized to the duration of the unobstructed step cycle (phase 1.0). The traces are rank-ordered on the basis of the phase of the peak discharge. Thicker lines indicate cells subsequently identified as Step-related during the gait modifications, whereas the thinner lines indicate cells discharging prior to the step over the obstacle (Step-advanced). The dotted lines indicate cells that did not increase their discharge activity during the steps over the obstacle. The large, gray rectangles indicate the average period of activity of the coClB and the iClB. The 2 cells shown in *A* and *B* are indicated with arrows. *D*: histogram showing the distribution of the phase of the peak discharge for the 64 cells illustrated in *C*. Filled histograms indicate the peak of the major burst of activity and hatched bars the phase of the smaller peak of activity (see, e.g., *B*). EDC, extensor digitorum communis; TriL, triceps brachii, lateral head.
The period of activity and the phase of peak activity of the entire population of 64 modulated cells are illustrated in Fig. 2C, which shows that the majority of cells discharged maximally during, or just after, the swing phase of locomotion. Overall, 53/64 (83%) cells discharged maximally in the first half of the step cycle (phase of 0.5) and the peak discharge activity of 33/64 (52%) of the cells occurred during the period of average coClB activity (see also Fig. 2D). These modulated cells were recorded throughout the area of the PPC that we explored with no signs of localization to any one particular area or region.

Some cells (11/64, 17%) showed a smaller, second period of activity, mostly during the period of activity of the iClB or iBr (second gray rectangle in Fig. 2C and hatched bars in Fig. 2D). The discharge frequency of this second burst was always less than the corresponding burst during the swing phase of the contralateral forelimb. In addition to this second number of cells discharging during the swing phases of both the left and right limbs, inspection of the raster displays of each cell, triggered on either coClB or iClB, showed that for 5/64 cells the discharge activity was best temporally related to the period of activity of the iClB. Taken together, these data show that 16/64 (25%) of cells showed a burst of activity related to the swing phase of the ipsilateral forelimb during the control task.

**Parietal activity during voluntary gait modifications**

Before performing the full analysis, we compared the discharge activity during steps over the larger of the two obstacles with that over the smaller one. For this analysis, we used only cells for which at least five steps over each obstacle were available. Because only a very few cells (9/121) showed any significant difference between the two conditions, we have combined the discharge activity for the two obstacles together in the analysis that follows.

When the limb contralateral to the recording site was the first to step over the obstacle (lead condition), 102/121 (84%) of the neurons significantly modified their discharge activity compared with the activity during unobstructed locomotion (Table 1). This population included 56/64 cells that were phasically modulated during control locomotion. It thus follows that only a few cells (8/121) were modulated in the control task but showed no change in activity during the voluntary gait modifications. In contrast, 46/102 cells showed a significant increase in discharge activity during the voluntary gait modifications but were either silent or discharged tonically during control locomotion.

We divided these 102 cells into the two major groups defined in Methods. In one group (41/121, 34%) the significant change in cell discharge began <200 ms prior to the onset of the activity of the ClB muscle and was maximal during the step over the obstacle; we refer to these as Step-related cells. In the other group, 61/121 (50%), cell discharge activity began >200 ms before ClB onset; we refer to these as Step-advanced cells. We present data first on the Step-related neurons because their discharge activity in the lead condition most closely resembles the patterns previously described in the motor cortex (Drew 1993).

**STEP-RELATED CELLS. Matched task: lead condition.** The change in peak discharge frequency of all 41/121 cells in this group occurred during the modified step. The majority of these cells increased their discharge activity with respect to the control activity (36/41); the other 5 showed decreased discharge activity. These 41 cells were separated into the four subgroups identified in Methods (see Table 1). Figure 3A illustrates an example of one of the 16/41 Phase I cells. This particular cell was recorded adjacent to the cell in Fig. 2A and had a similar tactile receptive field. It showed a weak peak of discharge activity (24 Hz) during the swing phase of locomotion during the control step cycles and a substantial increase in the level of this discharge activity, to 135 Hz (as measured from the filtered trace, thick black line), during the gait modification. Cell discharge activity was maximal during, and was restricted to, the period of activity of the coBr, as can be appreciated from the raster display (Fig. 3A, middle) and the averaged traces (Fig. 3A, right). The cell illustrated in Fig. 3B, which had a receptive field that encompassed the entire medial surface of the contralateral forelimb, also showed a substantial increase in its discharge activity during the step over the obstacle (from 48 to 189 Hz, as measured from the filtered traces). However, in this case the cell discharged late in the swing period and the significant change in discharge corresponded to, and was restricted to, the principal period of activity in the EDC; the cell was therefore identified as a Phase II cell. This relationship with the coEDC is emphasized by the vertical gray rectangle in the averaged display of Fig. 3B (right). A similar pattern was observed in 14/41 cells (Table 1). An increase in discharge activity throughout the period of activity of the ClB (Phase I + II cells) was less frequent and was observed in 6/41 cells. A further 5 cells began to increase their discharge frequency at the end of the swing phase and continued to discharge into the stance phase of locomotion.

The period of significantly modified activity for the population of these cells and the phase of their peak discharge are illustrated in Fig. 4, A and B. The peak discharge activity of all of these 41 cells occurred during the period of the coClB activity, i.e., during the swing period of the gait modification of the left forelimb. In 13/41 (32%) of the cells there was also a second burst of activity that occurred at phases of 0.5 to 0.9, corresponding to the period of activity of the iClB (Fig. 4, A and B). In 8/13 cells this activity was significantly increased with respect to control activity.

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**TABLE 1. General cell classification during lead condition**

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<th>Cell Group</th>
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<td>Step-related cells (41/121; 34%)</td>
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<td>Phase I</td>
<td>16/41 (39%)</td>
</tr>
<tr>
<td>Phase II</td>
<td>14/41 (34%)</td>
</tr>
<tr>
<td>Phase I + II</td>
<td>6/41 (15%)</td>
</tr>
<tr>
<td>Late cells</td>
<td>5/41 (12%)</td>
</tr>
<tr>
<td>Step-advanced cells (61/121; 50%)</td>
<td></td>
</tr>
<tr>
<td>Step-advanced Only</td>
<td>12/61 (20%)</td>
</tr>
<tr>
<td>Step-advanced Swing</td>
<td>45/61 (74%)</td>
</tr>
<tr>
<td>Step-advanced Late</td>
<td>4/61 (6%)</td>
</tr>
<tr>
<td>Nonsignificant cells (19/121; 16%)</td>
<td></td>
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</tbody>
</table>

This table indicates the number and percentage of cells identified in each major cell group. Definitions of Phase I and Phase II are provided in Methods. For the Step-advanced cells we define those in which discharge activity stopped at swing onset (Step-advanced Only), those in which it continued into the swing phase (Step-advanced Swing), and those in which it continued after the swing phase (Step-advanced Late).
In most cells the discharge frequency during the steps over the obstacle was substantially increased during the gait modifications (Fig. 4C), for both the primary (●) and, when present, the secondary (○) burst of activation. Average peak discharge frequency of the primary burst, for those 36/41 cells showing a significant increase in activity, was 59.0 ± 40.1 Hz during the gait modification compared with 36.2 ± 21.7 Hz for those 26 that were rhythmically modulated during control locomotion (Table 2). For the 9 cells with a secondary burst of activity, peak discharge was 54.0 ± 31.3 Hz during the step over the obstacle and 17.4 ± 5.9 Hz for these same cells during control locomotion.

**Matched task: trail condition.** The cat has the option of stepping over the obstacle first with either the contralateral or the ipsilateral limb; thus it is pertinent to ask whether the order of the limbs when the cat steps over the obstacle influences the discharge activity.

We found that 33/41 of the cells that were significantly modulated in the lead condition also showed a significant modulation of their discharge frequency in the trail condition. An additional 3 cells increased their discharge activity only in the trail condition, giving a total of 36 cells that modified their activity during the step over the obstacle in this condition. Eight cells were modified during the lead condition but not in the trail condition. Of the 33 cells showing modified activity in both conditions, 26/33 showed an increase in both conditions and 5/33 showed a decrease in both conditions; the other 2/33 showed increased discharge during the lead condition but decreased discharge during the trail condition.

In the majority (20/33) of the cells that were significantly modulated in both the lead and trail conditions, the change in discharge frequency was temporally related to the passage of the contralateral limb over the obstacle in both conditions. We refer to this as a **limb-specific** pattern of activity. This is illustrated for one cell in Fig. 5A (same example as in Fig. 3B). Discharge frequency in this cell was increased at the end of the period of activity of the coBr when the contralateral limb led (Fig. 5A, left). When the contralateral limb trailed (i.e., it followed the ipsilateral limb over the obstacle), the cell discharge maintained a constant relationship to the lead limb (i.e., the coBr; Fig. 5A, middle). There was no change in discharge activity (compared with control) as the ipsilateral limb stepped over the obstacle (Fig. 5A, right).

In contrast, in the other 13/33 cells, the discharge activity did not maintain a fixed relationship to the contralateral limb but instead showed a fixed relationship to the lead limb (i.e., the first limb to pass over the obstacle), regardless of whether this was the contralateral or the ipsilateral limb. We refer to this as a **limb-independent** pattern of activity. One example is illustrated in Fig. 5B. This cell discharged at the end of the period of the coBr when the contralateral limb led (Fig. 5B, left), in a manner similar to that of the cell illustrated in Fig. 5A. However, when the contralateral limb trailed, the cell discharge was displaced with respect to the coBr (Fig. 5B, middle) and instead now discharged at the end of the period of the iBr as the ipsilateral limb led over the obstacle (Fig. 5B, right). Note that only 1/13 of these limb-independent cells had a secondary burst of activity in the lead condition. Therefore the limb-independent
discharge represents a change in the temporal relationship of the primary, or only, period of activity in these cells.

The period of activity of all 36 cells showing modified activity when the contralateral limb trailed (solid lines), together with the 8 cells that increased activity during the lead but not the trail condition (dotted lines), is illustrated in Fig. 6A. The 16 cells whose activity was best related to the lead, ipsilateral, limb are indicated by the red lines. These 16 cells include the 13 limb-independent cells together with the 3 cells that were significantly active only in the trail condition. The maximal period of activity of most of these 16 cells was during the period of activity of the iClB and therefore substantially earlier than the period of activity of the ClB contralateral to the recording site (onset at phase = 0.0). This is to be compared with the situation when the contralateral limb led in which the significant change in activity of very few cells began prior to the onset of the coClB (Fig. 4A). In contrast, in the cells that maintained a relationship to the contralateral limb (black lines), the period of discharge activity during the trail condition (Fig. 6A) was very similar to that observed during the lead condition (Fig. 4A).

A direct comparison of the phase of the onset of the change in activity of the 33 cells modified during both the lead and the trail conditions, as measured with respect to the onset of activity in the coClB, is shown in Fig. 6B. The phase of the onset of activity of the population of cells that maintained a relationship to the contralateral limb (limb-specific cells, black symbols) was either scarcely changed in the trail condition (cells in top right quadrant of Fig. 6B) or was slightly phase advanced (bottom right quadrant close to the intersection of the

<table>
<thead>
<tr>
<th>Cell Group and Task</th>
<th>Lead Condition</th>
<th>Trail Condition</th>
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<tbody>
<tr>
<td>Step-related cells</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Matched task</td>
<td>59.0 ± 40.1 (n = 36)</td>
<td>49.6 ± 30.8 (n = 26)</td>
</tr>
<tr>
<td>Visual dissociation task</td>
<td>69.6 ± 42.4 (n = 35)</td>
<td>52.2 ± 37.6 (n = 28)</td>
</tr>
<tr>
<td>Control</td>
<td>36.2 ± 21.7</td>
<td></td>
</tr>
<tr>
<td>(n = 26)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Step-advanced cells</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Matched task</td>
<td>60.4 ± 44.3 (n = 51)</td>
<td>54.1 ± 37.6 (n = 51)</td>
</tr>
<tr>
<td>Visual dissociation task</td>
<td>59.9 ± 42.3 (n = 51)</td>
<td>51.7 ± 31.3 (n = 51)</td>
</tr>
<tr>
<td>Control</td>
<td>27.6 ± 16.2</td>
<td></td>
</tr>
<tr>
<td>(n = 24)</td>
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</table>

This table provides the averaged peak frequency (Hz) of the different classes of cells in each task and each condition tested. Only cells showing significantly increased periods of activity were included in the averages. There was no significant difference (P < 0.05) between the peak discharge during the lead condition versus that during the trail condition for any of the tasks.

FIG. 4. Neural activity of the population of Step-related cells during steps over the obstacle when the contralateral forelimb leads. A: phase of activity of the 41 cells showing significantly modified activity during the steps over the obstacle in the lead condition. General organization is as in Fig. 2C, with the following exceptions: 1) the horizontal black lines indicate the phase of activity of cells showing increased activity during the gait modification and 2) the horizontal gray lines indicate periods of decreased activity. The horizontal dotted lines (for the 2nd period of activity) indicate the presence of a phasic discharge, but no significant increase with respect to control. Open circles indicate the phase of peak activity of these cells during control locomotion (e.g., as in Fig. 2). Note that the duration of the ClB bursts (large gray rectangles) is asymmetric because the cat is stepping over the obstacle with the contralateral forelimb first. B: distribution of the phase of peak activity for the primary and, when present, the secondary period of cell activity: organized as for Fig. 2D. C: peak discharge frequency during the step over the obstacle as a function of the discharge activity during control locomotion for the main period of activity. The diagonal line indicates equal discharge activity in each condition. Circles indicate those cells showing significantly increased activity; squares represent cells showing decreased activity. Filled symbols identify those cells that were rhythmically active during control locomotion.
The characteristics of this population of cells are therefore similar to those described for motor cortical cells in a previous report (Drew 1993). However, the cells that were best related to the contralateral limb in the lead condition, but the ipsilateral limb in the trail condition (limb-independent cells, red symbols), show a substantial change in their location within the phase plot. The phase of onset is close to 0.0 in the lead condition but about $\pi/3$ in the trail condition, i.e., almost exactly antiphase. Such a population was not observed in the motor cortex.

The peak discharge frequency of the cells in both conditions was generally similar (Fig. 6C, Table 2), although most cells discharged slightly more intensely in the lead condition.

**Visual dissociation task.** All cells were also recorded in the visual dissociation task in which the speed of the obstacles was decreased with respect to that of the treadmill belt on which the cat was walking (see METHODS). This task produced several changes in the strategy that the cat used to step over the obstacle (Lajoie and Drew 2007). First, it changed the location in which the paw was placed in front of the advancing obstacle in the step before the step over the obstacle. Second, because of the relatively decreased speed of the obstacle, it increased the duration of the swing phase (see, e.g., coClB in Fig. 7).

Third, it frequently resulted in a major change in the overall strategy of the cat so that the order in which the hindlimbs stepped over the obstacle was modified (the double-step strategy; Lajoie and Drew 2007). We thus asked whether these changes in the planning and execution of the gait modifications were related to changes in the discharge activity of the cell.

As a first step in this analysis we compared cell discharge activity in steps in which the cats adopted the standard strategy with that obtained in the double-step strategy. Significant changes in activity were observed in only one cell that was tested in both conditions. We therefore combined data from the single- and double-step strategies in the subsequent analysis.

Most Step-related cells showed similar characteristics in the visual dissociation task to those observed in the matched task. However, changes in discharge pattern were observed in some cells. The most common difference was an increase in the frequency and the duration of the cell discharge during the step over the obstacle. This is illustrated in Fig. 7A for one example cell in which the change in duration was observed during both
the lead and the trail conditions. Such a change was observed in 8/41 neurons that showed significantly modified activity in the lead condition and in 7/36 of those showing modified activity in the trail condition. This increase in duration probably reflected the increased time required for the forelimb to step over the obstacle in the visual dissociation task, as indicated by the increased duration of the ClB activity. In a few cells (7/41 in the lead condition and 1/36 in the trail condition),

**FIG. 6.** Changes in phase and discharge frequency of Step-related cells when the contralateral limb leads or trails over the obstacle. A: plot of the phase of activity of 44 cells in the trail condition. The plot includes the 41 cells that were modified in the lead condition (Fig. 4A) as well as 3 additional cells that were activated only in the trail condition (see text). The general organization of the data is like that in Fig. 2C with the following exceptions: black (increased activity) and gray (decreased activity) lines indicate cells whose discharge is best temporally related to the contralateral limb in both the lead and trail conditions (limb-specific cells); red (increased activity) and rose (decreased activity) lines indicate cells related to the contralateral limb in the lead condition and the ipsilateral limb in the lead condition (limb-independent cells); dotted lines indicate cells that showed modified activity in the lead condition but not in the trail condition. The vertical gray rectangles indicate the period of activity of the iClB and coClB; data are aligned to the onset of the coClB. The outlined boxes A and B identify the 2 cells illustrated in Fig. 5. B: the phase of onset of the activity during the trail condition is plotted as a function of the phase of onset during the lead condition for all 33 cells showing increased activity in both conditions; the phase is calculated with respect to the onset of the coClB. C: peak frequency during the trail vs. the lead condition. Color codes in B and C as in A, but no distinction made between cells showing an increase and those showing a decrease.

**FIG. 7.** Changes in phase and discharge frequency of Step-related cells during the visual dissociation condition. A: averaged cell and EMG activity of a Step-related cell. The black lines show cell and EMG activity in the matched task, the red lines in the visual dissociation task. Dotted lines on the unit traces indicate the interval of confidence (P < 0.01) of the SE for the matched condition. The gray rectangles indicate the step over the obstacle by the contralateral limb. B and C: the phase of onset of the activity during the lead (B) and trail (C) conditions. For each plot, the phase of onset of cell discharge activity during the visual dissociation task is plotted as a function of the phase of onset during the matched task. In all cases the phase is calculated with respect to the onset of the coClB. D: peak frequency during the visual dissociation condition as a function of that during the matched condition in the lead condition.
the duration of the discharge was quite substantially prolonged and frequently continued until the passage of the subsequent hindlimb (not illustrated).

For a given cell, the timing of significant changes in obstacle-related activity was generally the same in both tasks (matched and visual dissociation). Moreover, this was the case for activity relating to both leading and trailing limbs (Fig. 7, B and C). Peak discharge frequencies in the two conditions were also similar (Fig. 7D, Table 2).

**STEP-ADVANCED CELLS.** *Matched task: lead condition.* Our other major group of 61 cells initiated their discharge >200 ms before the onset of the gait modification. Such cells may be involved in planning aspects of the gait modification prior to the step over the obstacle.

Examples of these Step-advanced cells are illustrated in Fig. 8. The cell illustrated in Fig. 8A showed a weak pattern of modulation during the two to three cycles before the step over the obstacle (Fig. 8A, right) and then showed a significant increase in discharge activity in the cycle preceding the step over the obstacle. The increase in discharge activity continued until the onset of the swing phase of the modified step. During the modified step, the discharge frequency of the neuron was significantly decreased below control levels. The example illustrated in Fig. 8B similarly started to increase its activity in the step cycle preceding the step over the obstacle but, in this...
case, showed a further increase in discharge activity during the swing phase of the modified step. Again, there was significantly decreased activity during the step over the obstacle. Finally, the cell in Fig. 8C showed a reciprocal pattern of activity, decreasing its discharge activity in the two steps prior to that over the obstacle and increasing its activity during the step over the obstacle.

Altogether, 12/61 (20%) Step-advanced cells showed a pattern of activity similar to that of Fig. 8A, in that the modification of the activity of the neuron ceased at approximately the onset of the modified step (Step-advanced only; Table 1). However, the majority of the Step-advanced cells (45/61, 74%) showed a discharge activity similar to that of Fig. 8, B or C in that the modification of the discharge activity continued into the swing phase (Step-advanced swing). In many cases, as in Fig. 8B, cells increased activity prior to the modified step frequently showed a further increase of activity during the swing phase of the modified step. A small number of cells (4/61) showed changes in activity that continued past the swing phase. Increased activity preceding the onset of the modified step was observed in 51/61 cells and decreased activity in the other 10/61 cells. Of the 61 neurons, 35 (57%) showed rhythmic activity prior to the obstacle (see Fig. 2C), whereas 26 cells (43%) were unmodulated or silent and discharged only as the obstacle approached the cat.

The period of significantly increased activity of all of the 61 Step-advanced cells is illustrated in Fig. 9A. This figure shows that many cells started to increase their discharge at least one step cycle before the gait modification. Indeed, the increase in discharge in 37/61 Step-advanced cells began greater than phase −0.5 before CIB onset and in 12/61 cells the change in onset occurred >1 step cycle before the step over the obstacle (Fig. 9, A and B). In some of these latter cells the change was a progressive one throughout the period in advance of the step over the obstacle (as in Fig. 8C), whereas in others it was represented as phasic, step-by-step, changes in discharge activity, as in the cell illustrated in Fig. 8A. Peak discharge activity in the majority of the Step-advanced cells (45/61) occurred just before (phases −0.2 to 0.0, 25/61) or just after (phases 0.0 to 0.2, 20/61) the onset of activity in the coCIB (not illustrated). Peak discharge frequency during the gait modification was substantially higher than that during control locomotion for the majority of the cells showing significantly increased activity (Fig. 9C, Table 2), including those that were modulated during control locomotion (●) and those that discharged tonically or were silent (○).

**Matched task: trial condition.** All of the 61 Step-advanced cells also showed significantly modified activity in the trial condition showing that they were not only related to planning activity when the limb contralateral to the recording site was the lead limb. In all except 2 cells, this change of activity was of the same sign (increase or decrease) in the two conditions. Moreover, as for the Step-related cells, many of the Step-advanced cells also showed limb-independent activity in that their discharge was best related to the first limb to pass over the obstacle in the lead and trail conditions rather than being time-locked to the contralateral limb irrespective of the condition. However, the proportion of Step-advanced cells (44/61, 72%) showing such limb-independent activity was much greater than that observed for the Step-related cells (13/33, 39%). One example of such a limb-independent cell is shown in Fig. 10A (same example as for Fig. 8B). In this cell, during the lead condition (Fig. 10A, left), the cell clearly discharged in advance of and during the onset of the swing phase of the contralateral (lead) limb. Discharge terminated abruptly at the end of the period of activity of the coBr. During the trial condition (Fig. 10A, middle and right), the cell was no longer well related to the contralateral limb and the activity of the coBr (Fig. 10A, middle) but, instead, now showed an excellent temporal relationship to the activity of the iBr (Fig. 10A, right).

In most cases the timing of the onset of firing relative to the contraction of the flexor muscle in the leading limb was the same.

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**FIG. 9.** Phase of activity and discharge frequency of the Step-advanced cells in the lead condition during the matched task. A: period of significantly increased activity of the 61 Step-advanced neurons. Basic organization of the display as in Fig. 2. The 3 cells illustrated in Fig. 8 are indicated (A–C). Horizontal black lines indicate increases in activity; horizontal gray lines indicate decreases in activity. Some cells showed more than one period of increased activity. Note the difference in the scale of the abscissa compared with that in Figs. 4 and 6. B: histogram showing the distribution of the phase of the onset of activity. Filled gray bars represent the principal change in activity before the step over the obstacle; hatched bars represent additional changes in activity occurring 1 to 2 steps prior to the step over the obstacle. C: comparison of peak discharge activity during the step over the obstacle as a function of the activity during control. Note that for the 28 cells that were rhythmically active, the control activity was based on the peak discharge of the cell (●); for the tonic cells we used the mean discharge frequency (○).
irrespective of whether this was the ipsilateral or contralateral limb. For example, the cell illustrated in Fig. 10A showed a significant deviation from the control activity at a phase (Φ) of −0.55 with respect to the onset of the coClB during the lead condition (Fig. 10A, left). This phase of activity was maintained with respect to the onset of the icIB in the trail condition (Fig. 10A, right). Consistent with this relationship the phase of cell onset with respect to the onset of the coClB during the trail condition was delayed by about 0.5 at −1.03 (Fig. 10A, middle). This relationship was similar for the majority of the population of limb-independent cells as illustrated in Fig. 10B, which plots the phase of cell onset as a function of the phase of CI onset in the lead limb in both conditions. Cells maintaining the same relationship to the onset of the lead limb CI in both conditions (filled circles), as in Fig. 10A, lie along the line of equivalency (solid diagonal line). Some cells are phase advanced by 0.5 (dotted line), indicating that they instead maintain the same relationship to the coCI in both conditions. The same data are expressed in a complementary manner in Fig. 10C, which plots the phase of onset as a function of the coCI in both conditions. In this case the cells discharging with the same relationship to the CI in the lead limb are phase delayed with respect to the line of equivalency and instead lie along the dotted line. Peak frequencies in the lead and trail conditions were almost identical (Fig. 10D, Table 2).

Visual dissociation task. In contrast to what was found for the Step-related cells, there were consistent changes in the phase of onset of many of the Step-advanced cells in the visual dissociation task. For example, in the cell illustrated in Fig. 11A there was a phase advance in the onset of the cell discharge during the lead condition (Fig. 11A, left), together with an increase in the duration, which was similar to that observed in the Step-related cells. A similar change in the cell discharge was observed in the trail condition in this cell (Fig. 11A, right). However, in the trail condition there was also a significant increase in the cell discharge in the two step cycles preceding the step over the obstacle. A more substantial change in the phase of cell onset during the lead condition is illustrated in the cell in Fig. 11B, whereas the cell in Fig. 11C shows a significant change in the amplitude and duration of the cell discharge, with no change in the phase of onset of the activity. Altogether, significant changes in the phase of onset were observed in 18/56 (32%) of the Step-advanced cells during the lead condition and in 22/56 (39%) of the cells tested in the trail condition. Nine (9/56, 16%) cells showed changes in both conditions. The phase of activity in the matched and dissociated tasks is illustrated in Fig. 11D for the lead condition and in Fig. 11E for the trail condition. The filled circles represent those cells in which the onset of the burst of activity during the visual dissociation task differed significantly from the onset of activity in the matched task. In the lead condition (Fig. 11D), most of these filled circles lay below the line of equivalence, indicating a phase advance of activity, although phase delays were occasionally observed. Phase changes in the trail condition were more variable. The peak frequency during the visual dissociation task was similar to that in the matched task. This is
During the lead condition, as in Fig. 11C, and 9/58 (16%) during the trail condition; the changes in amplitude were seen with and without significant changes in the phase of onset of the activity.
**Antidromic identification**

Approximately one half (48/93, 52%) of the neurons that we tested were activated antidromically by stimulation of either the microwire arrays in the pyramidal tract or the cerebral peduncle. Slightly more Step-related cells (23/37, 62%) than Step-advanced cells (25/56, 45%) were antidromically activated, although the difference is slight and might well be the result of sampling bias. However, substantially more Step-related cells (14/37, 38%) were identified from the electrodes in the pyramidal tract than were the Step-advanced cells (5/56, 9%). Although not detailed in this report, several cells were antidromically activated at different latencies from different wires in the arrays in the pontine gray nuclei. This would suggest we were activating collateral or terminal branches of the descending axons (see, e.g., Kably and Drew 1998).

**Localization**

The two categories of cells that we identified were differentially localized in the PPC, albeit with a degree of overlap. Of the Step-related cells, 27/41 (66%) were localized either within area 5a or within the adjacent area 2. In contrast, among the Step-advanced cells, the vast majority (51/61, 84%) were localized more caudally within area 5b. Step-related and Step-advanced cells were sometimes recorded in the same penetrations (Fig. 1). There was no clear distinction between the localization of limb-specific and limb-independent cells.

**Receptive fields**

As suggested by the figurines in Figs. 2, 3, 5, and 8, which illustrate the receptive fields of selected cells, our population of analyzed neurons included some with sensitive, cutaneous receptive fields restricted to the contralateral limb and others with no cutaneous receptive fields but that were only, or maximally, activated by movement of an object in the visual field. These different types of receptive fields were differentially represented in the two major populations of cells presented in this study. Of the 37/41 Step-related cells for which we tested to determine a receptive field, all except one (36/37) could be activated by light brushing of the skin and hairs on the contralateral forelimb. In addition, 6/37 cells were clearly activated by cutaneous input from the ipsilateral limb (this probably underestimated the bilateral input to this population of cells because we were not always able to test the receptive field on both forelimbs). On the other hand, only 2 cells discharged in response to moving an object toward (looming), away, or orthogonally across the visual field. We were able to test the receptive field of 48/61 of the Step-advanced cells. In contrast to the Step-related cells, 23/48 of the Step-advanced cells responded to movement of an object in the visual field, including looming stimuli. Thirteen (13/23) of these cells responding to visual input also had a receptive field on the contralateral forelimb. A further 5/48 cells had only cutaneous receptive fields. Eight (8/18) of the total number of cells responding to cutaneous input from the contralateral limb were also confirmed to have input from the ipsilateral limb. A few of the Step-advanced cells (6/48) had receptive fields that included the vibrissae. Although not tested in a controlled manner, many of these cells, both Step-related and Step-advanced, also discharged when the cats reached to a rod placed within their reach.

**Microstimulation**

Microstimulation (11 pulses each of 0.2 ms and at a frequency of 330 Hz) was applied at strengths of ≤50 μA in 17/27 sites from which Step-related cells were recorded. In all 17 sites the stimulation was ineffective in producing any noticeable movements or activation of any of the recorded EMGs. Stimulation was equally applied in 23/28 sites in which Step-advanced cells were recorded. This stimulation was ineffective in 18/23 sites. In the other 5/23 sites the stimulation evoked movement of the vibrissae; in 4/5 sites the threshold for this movement was >30 μA, whereas in the other site the threshold was 8 μA.

**Relationship to saccades**

Saccadic movements of the eyes were measured by wires placed in the bony orbits of one of the cats used in this study. Movements of the eyes did not occur in any constant relationship to the advance of the obstacle and in no case did we observe any consistent relationship between eye movements and cell discharge activity.

**DISCUSSION**

The data presented in this report demonstrate that neurons in area 5 of the PPC show major changes of their discharge activity in situations in which vision is required to modify gait. We identified two major groups of neurons. One group discharged during the step over the obstacle (Step-related cells). We suggest that this population contributes to the execution, or on-line modification, of the step over the obstacle. The other group discharged in advance of the step over the obstacle (Step-advanced cells). We suggest that this population is involved in different aspects of the planning processes that must precede the gait modifications. In both groups of neurons we found examples of cells that maintained a relationship with the limb contralateral to the recording site, regardless of which limb was the first to pass over the obstacle (limb-specific cells), and others that were related to either the contralateral or the ipsilateral limb depending on which limb was the first to step over the obstacle (limb-independent cells).

**Contribution of the PPC to the control of locomotion**

**LEAD CONDITION: STEP-RELATED NEURONS.** We believe that each of the two populations of neurons that we defined contributes to the control of visually guided locomotion. In the lead condition, the Step-related neurons showed properties that are generally similar to those that we have previously documented for neurons in the motor cortex in the same task (Drew 1988, 1993; Drew et al. 1996, 2008; see below). These neurons showed a discrete change in their discharge activity only as the leg passed over the obstacle. In general terms, as for most of the motor cortical cells that we previously described (Drew 1993), the majority of these Step-related cells can be divided into two subpopulations. One subpopulation (Phase I cells, e.g., Fig. 3A) was active just before and during the initial part of the swing phase of the step over the obstacle, whereas the...
second subpopulation (Phase II cells, e.g., Fig. 3B) was active in phase with the period of activity of the EDC, late in the swing phase, just prior to foot contact. Smaller subpopulations of cells were active throughout the swing phase of the modified step (Phase I + II) and later in the step cycle during the stance phase of the contralateral limb. As we have previously discussed (Drew 1993; Drew et al. 1996; Krouchev et al. 2006) with respect to the motor cortex, we suggest that the Phase I cells contribute to the modification of muscle activity in groups of synergistic muscles related to lifting the paw from the ground and bringing it above the obstacle. The Phase II cells would modify the activity of muscles related to preparing the paw for contact with the ground and the Phase I + II cells would regulate the activity of muscles involved in transporting the limb forward. However, although the motor cortex may influence motor activity directly, via the corticospinal tract, the PPC can exert an indirect effect only by modifying activity in other structures, including the motor cortex (see following text, Contribution of other structures). In this respect, it is possible that the Step-related cells modulate motor activity during the step over the obstacle on the basis of feedback and corollary discharge activity.

Although many of the Step-related cells that we recorded had peripheral receptive fields it is unlikely that the discharge activity that we observed simply reflected activation of that receptive field during locomotion (see also Beloozerova and Sirota 2003). Indeed, in many cases, cells were identified as having a receptive field that included the ventral surface of the paw but were inactive during the stance phase of locomotion and, instead, discharged during the swing phase of locomotion when the paw was not in contact with the ground (see, e.g., Figs. 2 and 3). This is reminiscent of what we previously observed in the motor cortex (Drew 1993; Drew et al. 1996) and suggests that the discharge properties of these Step-related cells are the result of a central drive related to the motor activity of the animal.

**LEAD CONDITION: STEP-ADVANCED NEURONS.** The majority of those cells showing modified activity in the task discharged in advance of the step over the obstacle (Step-advanced cells) and in some cases showed significant changes in discharge frequency two to three steps prior to the step over the obstacle. We suggest that these cells are involved in the preparation or the planning for the gait modification. Such a role is supported by our recent study (Lajoie and Drew 2007) in which we showed that cats with a unilateral lesion of the PPC showed persistent deficits in their ability to step over obstacles, particularly in the visual dissociation task. We showed that these deficits were linked to an inability to place the foot appropriately in front of the approaching obstacle. We suggest that the early discharge observed in this population of cells provides information that allows the cat to plan where to place its paws and when to initiate the step over the obstacle. Because the deficits in paw placement following PPC lesions were exaggerated in the visual dissociation task, we expected that cell discharge would be equally modified in this task. In agreement with this expectation, >30% of the Step-advanced cells showed a significant phase advance of their discharge activity in this task with respect to the onset of the gait modification and 20% showed a change in magnitude, further supporting a role for these cells in planning the gait modification. However, even in those cells showing changes, the basic pattern of the discharge activity was similar, suggesting that similar neuronal processes are involved in planning the gait modification in both the matched and the visual dissociation tasks.

Last, we found few cells that showed differences in discharge activity during steps over obstacles of different sizes. This result is somewhat surprising, given that determining limb trajectory on the basis of obstacle dimensions should be an important part of planning in this task. Whether this function is performed by different cortical structures or whether the signals were simply too noisy to demonstrate statistical differences in these conditions is not clear at this stage.

Among the Step-advanced cells, a majority continued to discharge during the gait modification, whereas a smaller number stopped discharging at the moment that the gait modification was initiated. It is possible that those cells that discharged during the gait modification—and especially those that showed increased activity superimposed on a rhythmic background—may regulate the precise step-by-step modifications both preceding and during the step over the obstacle, including paw placement. The cells that stop discharging just prior to the gait modification may have a more specific role in initiating the step over the obstacle. It is tempting to speculate that such cells may increase their discharge activity to a threshold level, at which time the modified step is initiated in the same way as has been found in cells in area 5 during self-initiated arm movements (Maimon and Assad 2006a,b) and in the lateral intraparietal area (LIP) during the decision-making process prior to saccade initiation (e.g., Roitman and Shadlen 2002). Moreover, similar ramp discharges have been described in both area 7 and the motor cortex in interception tasks (Merchant and Georgopoulos 2006). Indeed, it is possible that the same Step-advanced cells that discharge prior to the gait modification may also discharge in advance of self-initiated reaching movements. However, this was not tested in these experiments.

The extent to which the discharge before the step over the obstacle reflects obstacle attributes and the extent to which it reflects a motor plan cannot be easily distinguished on the bases of the current experiments. However, it is important to emphasize that the early responses observed in this population of PPC cells are very unlikely to be purely driven by the visual input from the approaching obstacle. Although many of these Step-advanced cells responded to movement of a rod into the visual field, the cells normally discharged only when the object was brought relatively close to the cat. This may correspond to the known property of many cells in the primate PPC to discharge only when a pertinent object is brought into the immediate extrapersonal space of the animal (Mountcastle et al. 1975). In a similar manner, the cells did not discharge when the obstacle became visible five or six steps prior to the step over the obstacle but discharged only in the two to three step cycles prior to the gait modification. The fact that the cell discharge was consistently linked to the onset of the gait modification would argue that it is contingent on the necessity to modify gait as opposed to the simple presence of an obstacle in the visual field. This suggestion is supported by preliminary findings showing that visual occlusion has relatively minor effects on cell discharge (Drew and Marigold 2008). It is also worth emphasizing that the relatively late discharge of the cells with respect to the period of time that the obstacle is visible to...
the cat is consistent with behavioral experiments in humans that have shown that most modifications of gait are made in the period immediately prior to the critical step or target rather than being spread out throughout the approach. For example, although long-jumpers have visual information concerning the take-off location for many steps prior to planting the foot, most modifications of gait to ensure appropriate placement of the foot are made in the two to three steps before take-off (Lee et al. 1982; Montagne et al. 2000).

One interesting possibility is that the cells may provide information on time to contact derived from an optic flow signal; this is normally referred to as Tau (Lee 1976, 1980). The idea that information from the radial expansion of the optic flow field could be used to guide locomotion was originally proposed by Gibson (1958). Subsequently, optic flow information has been shown to be used for navigation in many species, ranging from insects (Rind and Simmons 1999; Srinivasan 1992) to humans (Bruggeman et al. 2007; Lee et al. 1982; Warren Jr et al. 1986, 2001) and other mammals (Fowler and Sherk 2003; Sherk and Fowler 2000, 2001; Sun et al. 1992). For example, in the context of the present experiments, it is pertinent that Sherk and Fowler (2001) showed that the ability of cats to accurately position their paws in a cluttered environment was dependent on a motion-sensitive visual signal. Time-to-contact information, including Tau, has also been suggested to provide the information required to interrupt moving targets (see, e.g., Merchant and Georgopoulos 2006; Merchant et al. 2009). Moreover, cell discharge related to optic flow has been recorded in area 7a of the PPC and the motor cortex of primates (Merchant et al. 2001, 2003; Siegel and Read 1997; Steinmetz et al. 1987) and recent experiments in humans suggest that a time-to-contact signal may be encoded in the parietal cortex (May Tan et al. 2009). It should be noted, however, that it is unlikely that navigation and obstacle avoidance rely entirely on optic flow and Tau and several caveats to the general hypothesis have been proposed (e.g., Rushton et al. 1998; Tresilian 1999). Determining whether the discharge in the Step-advanced cells encodes a time-to-contact signal will require further experimental manipulation and analysis.

TRAIL CONDITION. Most cells activated during the lead condition were also activated during the trail condition. In the lead condition, the phasic modifications of cell discharge frequency were always best related to activity in the contralateral limb. However, in a proportion of both the Step-related (Fig. 5) and the Step-advanced cells (Fig. 10), the modified discharge activity in the trail condition was better related to activity in the ipsilateral limb than that to the contralateral limb. As stated earlier, the cell discharge in this population of cells was thus limb-independent, in that it was best related to the lead limb, regardless of which limb this was.

Such limb-independent cells are, in general terms, compatible with the population of bilateral cells recorded in a variety of tasks and in a variety of structures, in cats and primates (Cardoso de Oliveira et al. 2001; Chang et al. 2008; Cisek et al. 2003; Donchin et al. 2002; Greger et al. 2004; Hoshi and Tanji 2004; Kazennikov et al. 1999; Kermadi et al. 1998; Perfliev 2005; Steinberg et al. 2002; Tanji et al. 1988). Of particular pertinence to our results, the study of Chang et al. (2008) showed that the activity of 49% of the neurons in the parietal reach region (PRR) in the intraparietal sulcus of the PPC were limb independent in a manner similar to that described here; that is, that they discharged during the instructed delay period (memory task) prior to movements made by the limb either contralateral or ipsilateral to the recording site. A further 34% of neurons discharged only prior to movements of the contralateral limb (limb-specific). This is similar to the proportion of limb-independent neurons (i.e., discharging to both contralateral and ipsilateral limbs) described in the present study (57/94, 61% of all task-related neurons and 44/61, 72% of the Step-advanced cells).

Although our results concerning bilateral activity are outwardly compatible with those obtained in the primate reaching tasks, it is worth emphasizing that the situation during locomotion is not exactly the same as that in most of the experiments designed to examine the relationship of different cortical structures to bilateral movements. In most of the primate reaching tasks referenced in the preceding paragraph, the monkeys were trained to make movements either of the contralateral limb, or of the ipsilateral limb, or of both limbs simultaneously. However, during the gait modification, both limbs are always activated but their activity is sequential. In this respect, it is perhaps quite remarkable that the cells are related to the ipsilateral limb in the trail condition, even though there is still a requirement for control of the contralateral limb. Only a few studies (Kazennikov et al. 1999; Kermadi et al. 1998) have recorded neuronal activity specifically during a sequential, bimanual movement and in these studies, the same relative order of the limbs was used in all experiments, making it impossible to know whether neuronal discharge would change if the order of the arm movements was reversed.

The fact that the discharge activity of a large proportion of the cells was related to either the contralateral limb or the ipsilateral limb, depending on which was the lead limb, raises the question of the relative function of the limb-specific and limb-independent neurons. In the case of the limb-specific neurons, one can readily suggest that their major function is to contribute to the planning of the step over the obstacle by the contralateral limb in both the lead and trail conditions. In this case, the cell discharge specifies the changes in activity related to a single limb, irrespective of whether it is on-line correction of that limb or planning of the initiation of the gait modification. For the limb-independent neurons, the situation is less clear. In the case of these neurons, the discharge is specifying the action that is required and not the limb in which that action is required. In the case of the Step-advanced population, for example, we suggest that the discharge provides information as to when the gait initiation should occur and not in which limb that action should occur. This implies that there are other structures and pathways that are involved in selecting the appropriate action, and limb, based on information relating the position of the obstacle, and its speed of advance, to the location of the cat.

Comparison with the motor cortex

As detailed in the previous sections, many of the discharge characteristics of the cells recorded in area 5 of the PPC resemble those detailed previously in our recordings from the forelimb representation of the motor cortex (Drew 1988, 1993; Drew et al. 1996). This is particularly evident for the Step-related cells recorded in this study, which resemble the vast majority of the cells recorded in the motor cortex during
voluntary gait modifications. These Step-related cells, in both the motor cortex and the PPC, discharged in discrete bursts of activity during the step over the obstacle, with no change in activity in the steps preceding the step over the obstacle. Moreover, both populations include cells discharging at different times during the step cycle but with the majority of the activity (in the lead condition) occurring during the swing phase. However, there are several major differences in the characteristics of neurons in the two cortical areas.

At a relatively general level, there is a difference in the proportion of rhythmically modulated cells in the two cortical areas in the control steps compared with the steps over the obstacle. In the motor cortex, most cells were rhythmically active during control locomotion (80% in the studies of Armstrong and Drew 1984 and Drew 1993). In contrast, in the PPC, only 53% of the population was rhythmically modulated. During the gait modifications, however, 85% of the cells in the motor cortex showed a modulation of their discharge frequency (Drew 1993), which is similar to the proportion of cells (84%) in the PPC in the present study. This suggests that, whereas the motor cortex exerts a step-by-step control over locomotion in all conditions, many cells in the PPC are engaged only when there is a need to modify the discharge activity on the basis of visual information.

A more important difference lies in the existence of a large population of Step-advanced cells in the PPC; such cells accounted for 60% of all PPC cells showing modified activity. Although such cells were observed in the motor cortex (Drew 1993), they were a minority, forming only 16% of the total population of modified cells in the motor cortex. As we argued earlier, we suggest that these Step-advanced cells in the PPC are involved in the planning of the gait modification. Even allowing for the fact that a proportion of cells in the motor cortex might also have some role in planning, the much larger percentage in the PPC speaks to a major difference in the function of the motor cortex and the PPC in the control of locomotion. In general, this suggests that the motor cortex is primarily involved in the execution of the step over the obstacle, whereas the PPC has a supplementary role in the planning of these visually guided gait modifications in the two to three cycles preceding the modified step.

A difference also exists in the relationship between the frequency of the cell discharge and the size of the obstacle over which the cat steps. In the motor cortex, cell activity is increased for larger obstacles or barriers, often quite substantially (Beloozerova and Sirota 1993; Drew 1988, 1991). This is similar to the well-known relationship between motor cortical activity and the force required to produce a movement during primate experiments (Cheney and Fetz 1980; Evarts 1968, 1969; Kalaska et al. 1989; Sergio et al. 2005). However, only a very small proportion (7%) of the PPC cells recorded in this study showed any relationship with obstacle dimension despite a twofold increase in height and a fourfold increase in cross-sectional area.

Last, the most important difference between the characteristics of the cells in the motor cortex and the PPC during these voluntary gait modifications is the presence of the group of limb-independent cells in which cell discharge is related to the lead limb, regardless of whether that limb is contralateral or ipsilateral to the recording site. Such cells were never observed in the motor cortex in our task. This is compatible with a view that the PPC lies at a hierarchically higher level than that of the motor cortex in the planning and execution of these visually guided locomotor modifications.

**Contribution of other structures**

All of the cells recorded in this study were most probably located within cortical layer V of the PPC and 52% of them were positively identified as corticofugal neurons that projected at least as far as the cerebral peduncle. However, relatively few (20%) were identified as projecting as far as the pyramidal tract and, of those that did, most were Step-related neurons. As such, few neurons are likely to exert a direct influence on motor activity at the level of the spinal cord. Further, although some layer V neurons do send collaterals to more frontal cortical regions, including the motor cortex, this projection is relatively weak compared with the projection from layer III cells (Andujar and Drew 2007; Ghosh et al. 1987; Kakei et al. 1996; Yumiya and Ghez 1984). Therefore most of the cells recorded in this study can define or modify motor activity only indirectly via connections with subcortical structures, such as the basal ganglia and lateral cerebellum. In this respect, it is interesting that experiments in cats walking on a horizontal ladder have shown a population of cells in the later cerebellum that are active during visually guided step modifications (Marple-Horvat and Criado 1999; Marple-Horvat et al. 1998). Such cells may act in concert with cells in the PPC to plan and regulate visually guided locomotion.

**Comparison with other experiments on PPC in cats**

There have been few experiments that have examined the function of the PPC in the control of movement in the cat and only one that has specifically examined locomotion. As mentioned in the INTRODUCTION, Fabre and Buser (1981) implicated areas 5 and 7 of the PPC in the control of reaching movements, particularly to a moving target. Our finding that cells in the PPC are primarily active only when modifications of gait are required to step over moving obstacles would be compatible with their view of its particular importance in situations that require complex visuomotor coordination. As mentioned earlier, this is also suggested by our lesion experiments (Lajoie and Drew 2007), in which deficits were more evident in the visual disassociation task.

During locomotion, Beloozerova and Sirota (2003) recorded the activity in the PPC during a task in which cats were required to step from rung to rung of a horizontal ladder or to step over barriers on the ground. In the general findings our results are compatible with theirs. For example, a substantial proportion of PPC cells in both studies (34% in their study and 47% in ours) was unmodulated or silent during control locomotion. The small difference in relative proportions might reflect differences in methodology in defining modulated cells. In both studies the results showed an increase in PPC cell activity in the tasks involving visually guided locomotion, although the relative increase in discharge activity seems to have been greater in our study; again, this might reflect differences in methodology. Importantly, however, Beloozerova and Sirota (2003) reported that a majority of their cells (84%) showed two clear bursts of activity in each step cycle, with one burst in swing and one in stance. In contrast, a much smaller
proportion of cells showed a double burst in our task during the gait modifications (13/102, 13%, of all cells in the matched task, lead condition) and the second burst was always substantially smaller than the initial burst. Moreover, all of the cells showing a second burst of activity were found among the Step-related cells (13/41, 31%).

The reason for this substantial difference is not immediately clear. It is possible, for example, that it simply reflects a sampling bias although, as far as can be determined, the general extent of the PPC examined in both studies is similar. A further possibility is that the double burst cells reflect neurons that are related to forelimbs and hindlimbs. As we have reported in a brief report (Drew et al. 2008) such cells are found in area 5 of the PPC but are unlikely to have made up 80% of their population of cells. We suggest that an alternative explanation is task dependence. In our task, cats step over the obstacle with either the contralateral or the ipsilateral limb leading. Although we found a large population of limb-independent cells (>60% of the total population of cells and 72% of the Step-advanced cells), related to either limb, these cells fire only once in each step cycle, in phase with the lead limb. Why then do cells in the task of Beloozerova and Sirota (2003) in which cats step from rung to rung of a horizontal ladder or step over a series of barriers discharge twice in each step cycle? Our suggestion is that the PPC may plan each step (by each limb) independently in these tasks. In other words, during the ladder and barrier tasks, each limb may be considered by the PPC as being the lead limb as it performs a step. If this suggestion is correct then it would have conceptual consequences for the idea that locomotion is always controlled on the basis of a step cycle (e.g., onset of swing or stance in one limb to the next occurrence of swing or stance in that limb). Instead, in circumstances requiring equal visual guidance of each limb, there may be a need to control each step (e.g., the activity of each limb) in an independent manner, at least at hierarchically higher levels of control.

Localization of the cells and comparison with work in the primate

It is interesting to consider how these results compare with those obtained in the primate and the extent to which it is possible to relate the regions from which we recorded in these studies to those areas of the PPC from which reach-related activity has been recorded in the primate.

It is now generally accepted that area 5 in the primate may be subdivided into multiple functional regions (Colby and Duhamel 1991). From the perspective of the control of reaching, two major subdivisions are recognized (Colby and Duhamel 1991; Johnson et al. 1996; Kalaska 1996; Wise et al. 1997). The first of these lies in the dorsal regions of the superior intraparietal cortex and the adjoining rostral convexity in the primate. Many cells in this region are activated by peripheral receptors that would allow them to modulate activity in response to perturbation or error. In contrast, the Step-advanced cells are characterized by a strong and persistent activity prior to the modified step that would allow them to contribute to the visuomotor transformations, or planning, that allows the cat to place the paw appropriately in front of the obstacle and initiate the step over the obstacle. Again, although many of these cells receive visual input, the fact that the initiation of the neuronal discharge is better related to the initiation of the gait modification than to the appearance of the obstacle argues that the signal is more implicated in motor planning than in sensory processing, although this

Results from this study show that neurons in the PPC of the cat contribute to different features of the motor program needed to step over an obstacle during forward progression. The Step-related neurons discharge only during the step over the obstacle and may contribute to the execution of this step and to its on-line regulation. Although experiments in primates have emphasized the sensory nature of cells in the more rostral regions of the PPC, which we suggest to be analogous to area 5a in the rostral ansate sulcus (see preceding paragraphs), the dissociation between sensory receptive field and discharge activity observed in this study and that of Beloozerova and Sirota (2003) needs to be emphasized. This dissociation would argue that these Step-related cells receive a central, or corollary, signal in addition to any activation from peripheral receptors that would allow them to modulate activity in response to perturbation or error. In contrast, the Step-advanced cells are characterized by a strong and persistent activity prior to the modified step that would allow them to contribute to the visuomotor transformations, or planning, that allows the cat to place the paw appropriately in front of the obstacle and initiate the step over the obstacle. Again, although many of these cells receive visual input, the fact that the initiation of the neuronal discharge is better related to the initiation of the gait modification than to the appearance of the obstacle argues that the signal is more implicated in motor planning than in sensory processing, although this

Conclusions

It is clear from the preceding discussion that our two classes of cells show properties analogous to those of the cells in the two subdivisions defined in the preceding paragraph, albeit in the context of locomotion and not reaching. The Step-related cells clearly discharge in a manner similar to that in the more rostral regions of the primate PPC and the Step-advanced cells clearly show similarities to those of the cells in MIP and PRR. Moreover, as in the primate, the Step-related cells were located in more rostral regions of the PPC and the Step-advanced cells in the more caudal regions. Moreover, each of these two regions in the cat projects to different regions of the motor cortex, with the rostral cells projecting to more caudal regions of the motor cortex and the caudal parts to more rostral, and motor-related, parts of the motor cortex (Andujar and Drew 2007).

Taken together, the anatomical (Andujar and Drew 2007) and physiological (this study) results strongly suggest a certain conservation of the basic anatomy and properties of neurons in the PPC of cats and primates. However, the extent to which they should be considered true functional homologues will require further characterization in different contexts, with particular attention to the coordinate framework in which neuronal activity is encoded.
point remains to be more fully examined. Finally, the ability to study the discharge pattern of parietal neurons during a locomotor task requiring complex visuomotor transformations provides an important platform for understanding the contribution of this area not only to locomotor tasks but also to any task requiring interception of subject and object.

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