Lesions of Area 5 of the Posterior Parietal Cortex in the Cat Produce Errors in the Accuracy of Paw Placement During Visually Guided Locomotion

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Lajoie K, Drew T. Lesions of area 5 of the posterior parietal cortex in the cat produce errors in the accuracy of paw placement during visually guided locomotion. J Neurophysiol 97: 2339–2354, 2007. First published January 10, 2007; doi:10.1152/jn.01196.2006. We developed a novel locomotor task in which cats step over obstacles that move at a different speed from that of the treadmill on which the cat is walking: we refer to this as a visual dissociation locomotion task. Slowing the speed of the obstacle with respect to that of the treadmill sometimes led to a major change in strategy so that cats made two steps with the hindlimbs before stepping over the obstacle (double step strategy) instead of the single step (standard strategy) observed when the obstacle was at the same speed as the treadmill. In addition, in the step preceding the step over the obstacle, the paws were placed significantly closer to the obstacle in the visual dissociation task than when the treadmill and the obstacle were at the same speed. After unilateral lesion of area 5 of the posterior parietal cortex (PPC), the cats frequently hit the obstacle as they stepped over it, especially in the visual dissociation task. This locomotor deficit was linked to significant differences in the location in which the forelimbs were placed in the step preceding that over the obstacle compared with the prelesion control. Cats also frequently hit the obstacle with their hindlimbs even when the forelimbs negotiated the obstacle successfully; this suggests an important role for the posterior parietal cortex in the coordination of the forelimbs and hindlimbs. Together, these results suggest an important contribution of the PPC to the planning of visually guided gait modifications.

INTRODUCTION

Visual information is critical for planning the modifications of gait that are necessary to walk over irregular terrain. Vision provides information on the size, shape, location, and distance (or time to contact) of an obstacle in one’s path, and this information is used to modify both the limb trajectory and where the foot is placed. For example, experiments in humans performing obstacle avoidance tasks or during long jumping have shown that preparatory adjustments to ensure appropriate foot positioning are made in the last few steps preceding the step over an obstacle and are highly dependent on visual cues about the target (Lee et al. 1977, 1982; Mohagheghi et al. 2004; Montagne et al. 2000; Moraes et al. 2004; Patla and Greig 2006; Patla and Vickers 1997).

In the cat, it has been shown that motor cortical neurons increase their discharge when cats modify their gait to step over obstacles attached to a treadmill belt (Drew 1988, 1993) but not in the cycles that precede the gait modification (Drew 1993; Drew et al. 1996). The motor cortex therefore seems to be primarily responsible for the execution of voluntary gait modifications and not for their planning. One candidate area that could contribute to the planning of these changes in gait is the posterior parietal cortex (PPC, areas 5 and 7), which is a site of integration of visual and somatosensory information (Beloozerova and Sirota 2003; Dubner 1966; Thompson et al. 1963) and which has strong projections to the motor cortex in the cat (Andujar and Drew 2005; Babb et al. 1984; Ghosh 1963) and which has strong projections to the motor cortex in the cat. More pertinently, Fabre and Buser (1981) showed that damage to the anterior suprasylvian cortex, including parts of area 5 and 7, led to deficits in reaching to a moving target but not to a stationary target. During locomotion, Beloozerova and Sirota (2003) have shown neurons in parietal area 5 that receive and integrate information about the heterogeneity of the surface on which the animal is walking and modify their discharge accordingly.

It is probable that the PPC makes a similar contribution in the cat. For example, Roelfsema et al. (1997) have shown that oscillatory activity in the visual, parietal, and motor cortices is synchronized during a visually guided reaching task, suggesting a contribution of the PPC to visually guided movements in the cat. More pertinently, Fabre and Buser (1981) showed that damage to the anterior suprasylvian cortex, including parts of area 5 and 7, led to deficits in reaching to a moving target but not to a stationary target. During locomotion, Beloozerova and Sirota (2003) have shown neurons in parietal area 5 that receive and integrate information about the heterogeneity of the surface on which the animal is walking and modify their discharge accordingly.

Together, these experiments suggest that the PPC in the cat contributes to motor control in general and locomotion in particular, especially when there is a need to adapt gait or modify movement to take into account a moving target. The nature of this contribution during locomotion, however, remains poorly understood. As part of a program to better elucidate the PPC contribution to visually guided locomotion, we developed a novel locomotor task in which the speed of obstacles attached to a moving belt can be varied independently of the speed of the treadmill on which the cat is walking (visual dissociation task). This task may be considered to be analogous to the situation in which a subject must step over a moving object, such as a rolling ball, or to the task used by Fabre and Buser (1981), in which cats reached to a moving object. In this visual dissociation condition, the cats must integrate information about the speed of the obstacle, which can be obtained only by using vision, with information about self-motion, obtained both from visual and proprioceptive information.

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cues. As a result, the visual dissociation task provides a greater challenge to the cat than the situation that we have used in the past in which the treadmill and the obstacles are at the same speed (Drew 1993). This latter task may be considered to be more analogous to the simpler situation in which a subject steps over a stationary obstacle or reaches to a static object.

As a first step to study the functions of the PPC in visually guided locomotion, we undertook a lesion study to examine the deficits produced when cats modify their gait to step over the obstacles. The study shows that the behavioral strategy adopted by the cats is modified in the visual dissociation task and that unilateral damage to area 5 of the PPC results in locomotor deficits that are likewise amplified in this condition.

Results from this work have been published in abstract form (Lajoie and Drew 2005).

**METHODS**

**Task and training**

Three adult male cats (4.3–7 kg) were trained over a period of 2–3 mo to step over obstacles attached to a moving treadmill belt. In the initial part of the training, the speed of the treadmill and that of the obstacles was identical and was fixed at 0.5 m/s. The second part of the training consisted in changing the speed of the obstacles over a continuum of speeds ranging from 0.3 to 0.6 m/s while the speed at which the cats walked remained constant (the visual dissociation condition). Cats adapted to this condition very quickly and successfully negotiated the obstacles with their forelimbs from the very first trial. However, they occasionally hit the obstacles with their hindlimbs in these first trails as they, presumably, failed to take into account the modified time taken for the obstacle to pass under the body (see RESULTS). It was also noticeable that the cats made larger and more variable changes in step cycle duration in the steps preceding the step over the obstacle in the first days of training in this condition (these data were not quantitatively analyzed). Training in the visual dissociation task continued over a period of ~1 mo until the animals were capable of stable locomotion for periods of 15–20 min. They were implanted for chronic recording.

**Implantation procedures**

All procedures followed the recommendations of the Canadian Council for the Protection of Animals and were approved by the Université de Montréal’s Animal Care and Use Committee. Surgery was carried out in aseptic conditions and under general anesthesia. Cats were pretreated with an initial intramuscular dose of ketamine (11 mg/kg), acepromazine maleate (atrvet, 0.005 mg/kg), and glycopyrrolate (0.01 mg/kg), and anesthesia was maintained after intubation with isoflurane (2–3% with oxygen). The cats were placed in a stereotaxic apparatus using atraumatic ear bars; petroleum jelly was placed on the cornea to prevent drying. Temperature was monitored continuously with a rectal probe and was maintained with a heating blanket. Fluids were administered through an intravenous line and antibiotics (penicillin, 40,000 IU/kg) and an analgesic (buprenorphine, 5 μg/kg) were given at the beginning and end of the surgical period.

Pairs of Teflon-insulated, braided, stainless steel wires were passed subcutaneously from a connector placed on the cranium and inserted into selected flexor and extensor muscles of the left (l) and right (r) fore- and hindlimbs to record EMG activity. In the forelimb, these muscles always included the anterior head of the sartorius (Sr), the semitendinosus (St), and the vastus lateralis (VL). The skin was sutured around the cranial implant, and cats were placed in an incubator to recover. An analgesic (buprenorphine, 5 μg/kg) was administered for the following 48–72 h, and antibiotics were given daily for the duration of the experiment.

**Protocol**

Experiments were carried out three to five times a week, and each session lasted ~2 h. Video recordings of all sessions were taken using a Panasonic WV-CL920 color CCTV camera (60 frames/s) and were synchronized with EMG data by means of a digital time code. Light reflecting markers were placed on the skin of the left forelimb over the following bony landmarks: the spine of the scapula, the head of the humerus, the olecranon process, the proximal end of the metacarpals, the proximal phalanges, and the tip of the distal phalanx. In the hindlimb, the markers included the ilium, the greater trochanter of the femur, the estimated center of the knee joint, the lateral malleolus, the tarsometatarsal joints, and the tip of the third digit.

Recordings were made while the cat walked on a custom-designed treadmill to which two obstacles were attached. One obstacle was cylindrical with a diameter of either 8 (cat PCM4) or 10 cm (cats PCM1 and PCM3). The other obstacle was smaller and either cylindrical (diameter 5 cm: cats PCM3 and PCM4) or rectangular (5 cm high by 8 cm wide: cat PCM1). Recordings were initially made when the speed of the treadmill and that of the obstacles was equal (0.5–0.5 m/s) for ~15 min or until cats had made 10–15 steps over each obstacle with each forelimb leading. We changed the speed of the obstacles and repeated the recordings. The two obstacles were set at equal distance on the treadmill belt (300 cm apart), and cats always took at least five steps between the time that the obstacle became visible to them and the time that they stepped over it. Signals for EMGs were amplified, filtered at 100 Hz to 3 KHz, and stored on a computer at a sampling frequency of 1 KHz.

**Lesion procedures**

After a period of control recordings of ~2–4 wk, the cats were anesthetized and prepared for surgery. Methylprednisolone sodium succinate (Solumedrol, 30 mg/kg) was administered to minimize cerebral edema. A craniotomy was made to allow access to the posterior parietal cortex, which was identified by the characteristic shape of the anserine sulcus. Blood vessels around the area to be lesioned were cauterized, and the lesion was subsequently made by aspiration. Unilateral lesions of the PPC were made in the left hemisphere for cat PCM3 and in the right hemisphere for cats PCM1 and PCM4. The cortex was covered with a hemostatic material (gel foam), and dental acrylic was used to close the craniotomy. Cats were placed in an incubator to recover and were retested for a period of ~2 mo after this lesion.

**Data analysis**

Data were selected for analysis from sessions with prolonged periods of stable locomotion as determined from examination of the videotapes of each experiment. For the kinematic analysis, data were digitized from the videotape using a MiroVideo DC30 series card. This card maintained the separation of each image into two fields so that the time between fields was 16.77 ms (1/60 s). We used a custom program to measure predetermined events from the images, classified according to the type of obstacle. These included J) the step cycle in which cats stepped over an obstacle; 2) the height at which each paw passed over the obstacle; 3) which forelimb was the first to step over the obstacle; 4) the strategy used to negotiate the obstacle; and 5) the placement of each paw with respect to the obstacle for the entire step over the obstacle, as well as one step before and one step after. This information was transferred to a commercial program (Systat V9.0) for statistical analysis. A two-way ANOVA was used to compare paw placement on the treadmill with respect to the obstacle in different conditions before and after the lesions. For the EMG data, an inter-
active program was used to identify the onset and offset of EMG activity and to identify the cycles preceding, during, and subsequent to the gait modification. This information was transferred to a custom program for statistical analysis.

Histology

On completion of each experiment, cats were anesthetized with pentobarbital sodium (40 mg/kg, ip) and perfused with formalin per cardia. The brain was removed and photographed. It was sectioned (40 μm) in the sagittal plane and stained with cresyl violet.

RESULTS

Prelesion locomotion

Kinematic and EMG data before the PPC lesion were recorded from each of the three cats for periods of 18 days. In the following subsections treating this prelesion period, data are presented only for the situation in which the right forelimb was the first (lead) limb to step over the obstacle. The strategies and results were identical in all important aspects when the left limb led.

Behavioral strategies

As shown previously by Widajewicz et al. (1994), when cats step over obstacles in their path, they use a strategy in which the first (leading) hindlimb to step over the obstacle is always ipsilateral to the leading forelimb; we refer to this as the standard strategy. This strategy is shown in Fig. 1A for the control condition when the speed of the obstacles was equal to that of the treadmill (0.5 m/s). In this example, the right forelimb (RFL) was the first (lead) limb to step over the obstacle (top), followed by the left forelimb (LFL, middle). The cat stepped over the obstacle with the right hindlimb (RHL, bottom) and finally with the left hindlimb (LHL). This sequence can be clearly seen in the simultaneously obtained EMG recordings in which increased activation of the rTrM precedes that in the lTrM and is followed in sequence by activity in the rSt and lSt (Fig. 1B).

When we decreased the speed of the obstacles with respect to the speed at which the cats were walking (the visual dissociation task), the obstacles took more time to pass under the cats’ body. Therefore cats had to adjust their gait to take this extra time into account. Theoretically, they could adapt to this increased time of passage by delaying the onset of hindlimb swing, increasing the duration of the hindlimb swing, or a combination of both. In practice, inspection of the video recordings and analysis of the EMG patterns suggested that all of the cats primarily adapted by increasing the duration of the hindlimb swing rather than the time of onset of hindlimb swing.

FIG. 1. A: when the speed of the obstacles was equal to that of the treadmill, the 1st hindlimb to step over the obstacle was always on the same side (homolateral) as the 1st (lead) forelimb; we refer to this as the standard strategy. In the example shown in A, the cat stepped over the obstacle 1st with the right forelimb (top) and then the left forelimb (middle). The left hindlimb was placed just in front of the obstacle (middle), and the right hindlimb stepped over the obstacle (bottom). B: EMG recordings obtained simultaneously with video recordings. Dotted lines indicate onset of 4 bursts of activity (1 in each limb) as the cat steps over the obstacle. Numbers refer to legs shown in traces in A. Diagonally oriented arrows emphasize sequence of activation of muscles in right and left limbs in the step over the obstacle for both forelimbs (FL) and hindlimbs (HL). l, left; r, right; St, semitendinosus; TrM, teres major.
swing. This is shown by several related findings. Figure 2A, for example, shows tracings taken from video recordings showing the relative position of the limbs and the obstacle for three different combinations of treadmill and obstacle speed. It shows that, in the normal situation (treadmill and obstacle both at 0.5 m/s), the obstacle had advanced halfway under the body at the moment of the right hindlimb swing onset. However, when the speed of the obstacles was slowed, the obstacle advanced progressively less far under the body at right hindlimb swing onset. This suggests that the onset of the hindlimb swing was determined by the time of passage of the forelimbs over the obstacle. That this is probably the case is shown by Fig. 2, B (left) and C, which show the relative onset of activity in the knee flexor, rSt, with respect to the end of the period of activity in the shoulder protractor, ICIB. The delay between these two events was almost constant across the range of obstacle speeds used (Fig. 2C). Only at the slowest speed used (0.35 m/s) was there a slight decrease in this relationship. As such, the cat must compensate for the increased time of passage of the obstacle by increasing the right hindlimb swing. This is shown by Fig. 2, B (middle) and D, which show a relative increase in the duration of the Srts as obstacle speed is decreased. Figure 2, B (right) and E, shows that there is likewise a linear increase in the phase of the end of the Srts activity (with respect to ICIB onset) as obstacle speed decreased.

When the obstacles were slowed to 0.35 m/s, the cats were frequently unable to use the standard strategy shown in Figs. 1 and 2. Instead, we observed a different strategy that we refer to as a double step strategy because the hindlimb on the same side

![Diagram of standard strategy: RFL leads](image)

**A** Standard strategy: RFL leads

- 0.5 m.s-1
- 0.4 m.s-1
- 0.35 m.s-1

**B** Step over obstacle

- rClB
- ICIB
- rSt
- Srts

End of activity in ICIB
- onset of activity in rSt (Ω)

**C** Box plots representing relative phase difference between offset of ICIB and onset of rSt (Ω), duration of Srts as a phase of the step cycle (Δ), and phase of end of period of activity of Srts with respect to onset of period of activity in rClB (E). All phase values are expressed with respect to the onset of rClB during the step over obstacle. Dotted lines in B illustrate measures shown in C-E. Asterisks in C-E indicate outliers. Ω, phase; Srts, sartorius.
as the lead forelimb takes an extra step before passing over the obstacle. As shown in Fig. 3A for the condition in which the RFL leads, the gait modification began normally with the RFL and LFL, respectively, stepping over the obstacle (1st and 2nd panels). Subsequently, however, the cats performed an extra step with the hindlimbs (Fig. 3A, 3rd panel) so that the RHL, instead of passing over the obstacle as in Fig. 1A, was placed in front of it. The cat stepped over with the LHL (Fig. 3A, bottom) and finally the RHL. This can also be seen in the pattern of EMG activity shown in Fig. 3B. The sequence of muscle activation for the forelimbs was identical to that seen in Fig. 1B. However, in the hindlimbs, it was reversed so that the increased activity in the LSt, corresponding to the step over the obstacle (now identified as 4), preceded that in the rSt (5).

Cats PCM1 and PCM4 used the double step strategy >50% of the time in the visual dissociation task in the prelesion condition; this was true for steps over both the large and small obstacle and when either the left or right limb led (Table 1). In cat PCM3, the double step strategy was used about one half the time when the right limb led but not at all when the left limb led. Cats never used the double step strategy when the speed of the obstacles was >0.35 m/s. When the speed of the obstacle was further decreased, to 0.3 m/s, cats PCM1 and PCM4 used only the double step strategy, whereas cat PCM3 always used this strategy when the right limb led but sometimes still used the standard strategy when the left limb led (data not shown).

**Paw placement**

Reducing the speed of the obstacle modified the position in which the paws were placed relative to the advancing obstacle. This was quantified by measuring the distance at which each paw was placed on the treadmill with respect to the obstacle. This is shown for a single experiment in Fig. 4 and for a series of experiments, in two cats, in Fig. 5. The black symbols in Fig. 4B and the black bars in Fig. 5, A and B, show the position of each paw when the speed of the obstacles was equal to that of the treadmill (0.5–0.5 m/s) and when the RFL was the leading limb. The starting position for the sequence is represented by RFL1, LFL1, RHL1, and LHL1, which are the positions of each limb in the step cycle that preceded the step over the obstacle (Fig. 4A). From this position, the sequence continues with the advance of first the left hindlimb (LHL2), then the left forelimb (LFL3), and the right hindlimb (RHL4). The cat stepped over the obstacle with the right forelimb (RFL5) followed by the LFL, RHL, and LHL as in Fig. 1. Note that the paw placement was very stable within the entire session, as shown by the relatively small SE in Fig. 4B.

Decreasing the speed of the obstacle to 0.35 m/s produced consistent and significant (ANOVA, \( P < 0.05 \)) changes in paw placement when the cat used the standard strategy (Figs. 4B, gray symbols, and 5, A and B, gray bars). In particular, each paw was placed closer to the obstacle in the step preceding the gait modification (RFL1–LHL1) when the speed of the obstacles was slower, as was that for the LHL2 (box 2) and LFL3. In the step over the obstacle, the hindlimbs were placed relatively closer to the obstacle on its far side when its speed was 0.35 m/s than in the control situation (e.g., RHL8 in box 3). This is presumably directly related to the increased time the obstacle takes to move a given distance at 0.35 m/s compared with 0.5 m/s.
The extent of the cortical damage in the two cats with the biggest lesions (PCM1, PCM3) is shown in Fig. 6. In each cat, the lesion encompassed both the rostral (primarily area 5a) and caudal (primarily area 5b) banks of the ansate sulcus, as well as the most rostral regions of the lateral sulcus (area 5b) but mostly spared area 7. In cat PCM3, the lesion began at ~2.8 mm from the midline and continued laterally for another 7 mm (Fig. 6A). The lesion therefore covered almost the entire ansate sulcus including those parts both medial and lateral to the lateral sulcus. In the more medial part of the ansate sulcus, the lesion affected primarily the caudal bank of the sulcus and the adjacent gyrus (Fig. 6B, sections 1 and 2) but extended to both the rostral and caudal banks of the sulcus in the more lateral sections where it was at its largest (Fig. 6B, sections 3 and 4).

In cat PCM1, the lesion was smaller, extending more than ~5.5 and was also located slightly more medially. It began ~1.1 mm from the midline and extended to ~7.5 mm from the midline (Fig. 6C). As a result, this lesion did not encompass the entire lateral branch of the ansate sulcus. As shown in the tracings of the histological sections in Fig. 6D, the lesion encompassed both the rostral and caudal bank of the ansate sulcus in more medial sections (sections 1 and 2) but affected mainly the caudal bank of the sulcus in more lateral sections (sections 3 and 4). The lesion in cat PCM4 (data not shown) was smaller than in the other two cats. It affected primarily the lateral branch of the ansate sulcus but extended in total from ~1.8 mm from the midline to ~9 mm lateral.

Postlesion deficits

Data were collected for a period of 15, 27, and 57 days after the lesion for cats PCM1, 3, and 4, respectively. Because the lesions were made on the right side in cats PCM1 and PCM4 but on the left side in cat PCM3, we refer to a given limb as being ipsilateral, or contralateral, to the lesion rather than left or right. We put the emphasis on the limb contralateral to the lesion, which can either be the first to encounter the obstacle (leads) or the second (after the ipsilateral limb), in which case we refer to it as the trail limb.

All cats were initially examined the day after the lesion. At this time, they were capable of normal locomotion and navigation in the laboratory, and no deficit was apparent in their normal behavior. However, when tested in the task, clear deficits were observable in all cats. We observed three categories of deficit: 1) the cats hit the front of the advancing obstacle with the forelimbs and/or the hindlimbs when bringing the limb over the obstacle (hits front); 2) they hit the obstacles on the other side after the gait modification (hits back); and 3) occasionally, the cats jumped over the obstacles either with all four limbs or with just the hindlimbs.

The overall deficits, encompassing all three categories, are shown in Fig. 7 for cats PCM3 and PCM1 for the situations when the limb contralateral to the lesion led (Fig. 7, A and E) or trailed (Fig. 7, B and F). In general, both cats showed severe deficits both when the treadmill and the obstacle were at the same speed (black bars) and in the visual dissociation task (gray bars). In all conditions, the deficits were more pronounced in the visual dissociation task. Over the 15- to 20-day period of testing shown in Fig. 7 for these two cats, there was a progressive reduction in the frequency of the deficits for most of the conditions, the exception being in cat PCM1 in the visual dissociation task when the contralateral limb led (Fig. 7E).

More detailed examination (Fig. 7, C and D) showed that most deficits in cat PCM3 were caused by the inability of the contralateral forelimb to clear the obstacle, both when it was the lead limb (Fig. 7C) and when it trailed (Fig. 7D). In cat PCM1, the deficits also resulted primarily from failure of the limb contralateral to the lesion site to clear the obstacle, although in this cat the most affected limb was the hindlimb (Fig. 7, G and H).

The same general observations apply for cat PCM4 (data not shown), although this cat hit the obstacle less frequently than the other two cats, and the effects were less prolonged. Indeed, when the speed of the obstacle and the treadmill was the same, cat PCM4 only hit the obstacle during the first 8 days after lesion. In the visual dissociation task, the cat still

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**TABLE 1. Frequency with which each cat used the double step strategy during the visual dissociation task**

<table>
<thead>
<tr>
<th>Cats</th>
<th>Condition</th>
<th>Large Obstacle</th>
<th>Small Obstacle</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Right leads</td>
<td>Left leads</td>
</tr>
<tr>
<td>PCM1</td>
<td>Prelesion</td>
<td>64% (2%)</td>
<td>42% (17%)</td>
</tr>
<tr>
<td></td>
<td>Postlesion</td>
<td>19% (16%)</td>
<td>0% (68%)</td>
</tr>
<tr>
<td>PCM3</td>
<td>Prelesion</td>
<td>43%</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Postlesion</td>
<td>59%</td>
<td>10%</td>
</tr>
<tr>
<td>PCM4</td>
<td>Prelesion</td>
<td>99%</td>
<td>75%</td>
</tr>
<tr>
<td></td>
<td>Postlesion</td>
<td>91%</td>
<td>89%</td>
</tr>
</tbody>
</table>

The table indicates the percentage of the steps over the obstacle in which the cat used the double step strategy (see Fig. 3). All data are taken during the visual dissociation task in which the speed of the treadmill was 0.5 m/s and the speed of the obstacle was 0.35 m/s. Cat PCM1 frequently jumped over the obstacle instead of stepping over it (box 3). A similar trend was observed in cats PCM1 (Fig. 5B) and PCM4 (data not shown).
hit the obstacle after 14 days, but only \( \sim 10\% \) of the time. This cat hit the obstacle with both the contralateral fore- and hindlimbs.

Cats PCM3 and PCM4 continued to adopt the double step strategy with about the same frequency postlesion as they did during the control, prelesion, period (Table 1). In cat PCM1, the frequency was much reduced. It should be noted that in the prelesion, control period, cats rarely, if ever, hit the obstacle, and only cat PCM1 occasionally resorted to jumping over the obstacle before the lesion (Table 1).

**Lead versus trail limb**

Cats hit the obstacle either on the front as it advanced toward them or on its back as the limb passed over the top and the cat prepared to replace it on the treadmill (Fig. 9A). For a subset of the data (select experimental sessions within the 1st 9 days postlesion, excluding trials in which the double step strategy was used), we determined whether the choice of lead limb had a determinant affect as to whether the cat hit the front or the back of the obstacle. That it did is shown in Fig. 8, A–C. When
the contralateral limb led, the cats almost always hit the obstacle with this limb (in only 1 trial did they hit the obstacle with the ipsilateral, trail limb). Moreover, in all three cats, the limb more frequently hit the back of the obstacle than the front. When the contralateral limb trailed, the cats still most frequently hit the obstacle with this limb (see Fig. 7), but in this case, they invariably hit the front of the obstacle (Fig. 8, A–C). On those occasions when the cats hit the obstacle with the leading, ipsilateral limb, they always hit the back of the obstacle. Cats PCM1 and PCM3 frequently jumped over the obstacle, regardless of which limb the cat was preparing to use to step over the obstacle.

Cat PCM1 also frequently hit the obstacle with the hindlimbs even when the forelimbs successfully negotiated the obstacle. In the subset of the data used for Fig. 8, this cat successfully negotiated the obstacle with its forelimbs in 107/146 trials; however, it hit the obstacle with one of the hindlimbs in 34/107 (32%) of these trials. In this situation, the cats mostly hit the obstacle with the contralateral hindlimb when it trailed (Fig. 8D). As for the forelimbs, the cats most frequently hit the front of the obstacle in this condition.

**Effect of paw placement**

To determine if there was a correspondence between the deficits observed and the location at which the paw was positioned, we made a quantitative analysis of the location of the paw for different conditions in all three cats. Figure 9 shows the results of this analysis for cat PCM3 in the condition when the contralateral forelimb led. As shown in Fig. 9B for the situation in which the treadmill and the obstacle speed were the same, and in Fig. 9C for the visual dissociation task, there was no significant difference between the position of the contralateral forelimb (coFL1) in the prelesion controls and in those steps in which the cat successfully stepped over the obstacle following the lesion (No Hits). In contrast, when the cat hit the front of the obstacle, the paw was placed closer to the obstacle, significantly so in the visual dissociation condition (Fig. 9C). When the paw hit the back of the obstacle, the paw was placed significantly further away than in the control situation (Fig. 9, B and C). These changes in the placement of the paw in this condition (coFL leads) were consistently observed in all three cats for both obstacles (large and small) and for both locomotor conditions (0.5/0.5 and 0.5/0.35 m/s).

Consistent changes in paw placement were also seen when the trailing contralateral limb hit the obstacle. When this trailing, limb hit the front of the obstacle (the most common deficit, see Fig. 8), the lead forelimb was placed closer to the front of the obstacle than in those steps in which the cat did not hit the obstacle (Fig. 10A). In this respect, the results are identical to those shown in Fig. 9 for the condition in which the contralateral limb led; i.e., the limb is always placed closer to the obstacle when it hits its front. In contrast, in cat PCM1, which frequently hit the front of the obstacle with the trail hindlimb, even though the forelimbs stepped over it without touching, we saw no consistent differences in the position of the hindlimb before the step (Fig. 10B).

**Height of the paw**

The height of the forepaw as it crossed over the obstacle is shown in Fig. 11 for cats PCM3 and PCM1. In the prelesion period (black bars), the height of each paw as it crossed the summit of the small obstacle was ~9 cm (Fig. 11, A and C). When the cats stepped over the larger obstacle (Fig. 11, B and D), the height of the paw scaled to the size of the obstacle and was ~13–14 cm. Postlesion, the height of the paw did not change in cat PCM3 and showed a small, but significant, increase in height in cat PCM1.

**Discussion**

We developed an innovative locomotor task that ensures that voluntary gait modifications are guided by visual information. In the visual dissociation condition, in which the speed of the obstacles is different from that of the treadmill on which the cat is walking, both the position in which the forepaw is placed and the speed of the obstacles are slowed to 0.35 m/s (single step strategy, \( n = 22 \) steps, gray bars; double step strategy, \( n = 34 \), white bars) calculated from 5 different sessions for cat PCM3 (small obstacle, RFL leads). B: same situation as in A for selected events from cat PCM1 (\( n = 42 \) steps for control, black bars; \( n = 19 \) for standard strategy at 0.35 m/s, gray bars; and \( n = 25 \) for double step strategy, white bars). Asterisks represent a significant difference (\( P < 0.05 \)) between 2 conditions.
front of the advancing obstacle and the coupling between the fore- and the hindlimbs is modified. Progressively decreasing the speed of the obstacle with respect to the speed of the treadmill ultimately requires the cat to modify the overall strategy used to negotiate the obstacle (double step strategy). Unilateral lesion of area 5 of the PPC produced motor deficits that were characterized by an inability to successfully step over obstacles attached to a moving belt. These deficits were exaggerated in the visual dissociation condition. Quantitative analysis of these deficits suggests that they are produced, in part, by an inability to appropriately position the paw on the treadmill belt in front of the advancing obstacle. These results support
the view that the PPC contributes to the sensorimotor transformations that are involved in the preparation of gait modifications when locomotion critically depends on visual information.

Behavioral strategy and importance of vision for the task

The basic locomotor task used in these experiments is identical to that used in previous studies from this laboratory designed to examine the contribution of different supraspinal structures to the control of voluntary gait modifications (Drew 1988, 1993; Prentice and Drew 2001). It is a task that requires the walking cat to judge the size and shape of the approaching obstacle, together with its relative velocity, and to appropriately modify its gait to step over that obstacle, smoothly, and without undue interruption of the ongoing gait. A priori, it is clear that the cat can only obtain the requisite information to perform this task from vision. The novel task that we present in this manuscript increases the demands on the cat to extract visual information about the attributes of the advancing obstacle, including its speed of approach, or time to contact, and to integrate this information with information concerning self-motion. The former information can be obtained only by using visual information; the latter can be obtained from both vision and proprioception. The challenge for the cat is to adapt its gait to take into account the difference in relative motion of the obstacle with respect to itself. We refer to the task as a visual dissociation task because the visual information provided by the obstacle is different from, or dissociated from, that which the animal would predict on the basis of the information concerning self-motion.

FIG. 7. Histograms showing percentage of steps in which the cat hit or jumped over the obstacle after lesion for cats PCM3 (A–D) and PCM1 (E–H). A, B, E, and F: data are shown for the situation in which the treadmill and obstacle speed were both at 0.5 m/s (black bars) and for the visual dissociation task when obstacle speed was slowed to 0.35 m/s (gray bars). For the visual dissociation condition, both standard and double step strategies are included without any distinction. C, D, G, and H: frequency with which the cat hit the obstacle with a given limb both when the contralateral forelimb led (C and G) and when it trailed (D and H). Data in C, D, G, and H are compiled from the entire postlesion test period and include data both when the treadmill and obstacle were at the same speed and in the visual dissociation task, including steps using both standard and double step strategies.
The results show that this visual dissociation required several modifications in strategy. For example, slowing the obstacle clearly modified the position in which the paws were placed in front of the obstacle in a significant and consistent manner (Fig. 4). Moreover, the fact that the last step was consistently placed in a small spatial window in front of the obstacle shows that the cats appropriately and consistently integrated the visual information from the advancing obstacle with information about their self-progress to ensure that the paw was precisely placed in a position that allowed the step over the obstacle to occur successfully. The importance of vision in modifying locomotor activity in this task is also evident from the changes in hindlimb activity that we observed in the visual dissociation condition. As the obstacle advances toward the cat, it provides direct visual input concerning the relative speed of advance, distance, and/or the time to contact. However, once the forelimbs step over the obstacles, this direct visual input is lost, and the hindlimbs have to be controlled on the basis of prior information. There is thus a need for short-term storage of this information between the passage of the fore- and the hindlimbs. That the cat is able to perform this processing is shown both by the changes in hindlimb swing duration as the obstacle speed is slowed (Fig. 2) and, particularly, by the change in strategy (Fig. 3) when the obstacle was slowed to 0.35 m/s (a ratio of ~0.7 with respect to the speed of the treadmill). Moreover, examination of Figs. 4 and 5 shows that a small, and consistent, change in forelimb paw position is the difference between the cat maintaining the standard strategy and changing its gait pattern to the double step strategy. Such a change in strategy may be made for several reasons. For example, it is possible that the cats initially plan to make a single step but make a last-second adjustment to the double step strategy because the paws are inappropriately placed. However, it is equally possible that the cats plan several steps ahead that they will adjust the position of the paws to allow an extra step to be taken with the hindlimbs (the double step strategy). This might facilitate the gait modification by removing the need to make a prolonged step with the hindlimbs. Although it is not possible to definitively choose between these two possibilities, the fact that there is very little variation in paw placement in either the single or double step strategies (Fig. 4) suggests that the double step strategy is planned in advance.

In addition, the visual dissociation condition requires the cat to modify the coupling between the forelimbs and the hindlimbs. As shown in Fig. 2, slowing the obstacle with respect to the speed of the treadmill forces the cat to progressively increase hindlimb swing duration. As such, the cats clearly need the capacity to store information on the required hindlimb gait modification from the time that the forelimbs step over the obstacles until the passage of the hindlimbs. A conceptually similar result concerning independence of control of the hindlimb was recently obtained by McVea and Pearson (2006), who showed that the gait modification in the hindlimbs can be delayed for several minutes if the passage of the cat over an obstacle is interrupted with the forelimbs on one side of the obstacle and the hindlimbs on the other. It is also important to note that, in the double step strategy, the cats completely modified the normal pattern of activity observed in the hindlimbs by reversing the normal sequence of the limbs. This suggests that the voluntary modifications of the forelimbs and the hindlimbs are, at least to some extent, controlled as separate processes.

**Fig. 8.** A–C: histograms showing percentage of steps in which each of the 3 cats hit either the front or the back of obstacle or jumped over it. Data are shown both for the limb contralateral (black bars) and ipsilateral (gray bars) to the lesion site both when the contralateral limb lead and when it trailed. D: steps in which the cat hit obstacle with 1 of the hindlimbs after successfully negotiating the obstacle with the forelimbs. Values for all 4 graphs are shown as a percentage of the total number of steps displayed in each histogram (value in top right of graph), so that the total for each graph is 100%. Legend in D applies to all 4 histograms. Data are taken from a subset of data shown in Fig. 7.

The results show that this visual dissociation required several modifications in strategy. For example, slowing the obstacle clearly modified the position in which the paws were placed in front of the obstacle in a significant and consistent manner (Fig. 4). Moreover, the fact that the last
Contribution of the PPC to the control of locomotion

In this study, we made relatively large lesions of the PPC to optimize our opportunities to determine the essential contribution, if any, of this structure to the control of visually guided locomotion. However, despite the extent of the damage, especially in PCMI and PCM3, none of the three cats showed any overt behavioral deficits in their regular overground locomotor behavior in the laboratory. This suggests that the deficits that we observed in our locomotor task reflect an important contribution of the PPC in situations in which there is a need to integrate visual information with information about self-motion and are not

FIG. 9. Position of lead limb with respect to position of the obstacle for different conditions (data from PCMI). A: tracings from video of 3 example steps in which the cat successfully stepped over the obstacle (top), hit the front of advancing obstacle (middle), or hit the far side (back) of the obstacle (bottom). Position of contralateral (right, lead) forelimb in the step before that over the obstacle is indicated (coFL1). B: quantitative analysis of the position of the paw for the 3 conditions shown in A when the treadmill and the obstacle were both at 0.5 m/s and for steps in which the cat jumped over obstacle (black bars, prelesion; gray bars, postlesion). C: data when obstacle was slowed to 0.35 m/s. Data in B and C are from the same dataset as Fig. 8. *Significant differences at $P < 0.05$. Note that control data are identical for each condition in B and C and are repeated to facilitate comparison.
the result of generalized problems of motor behavior. This is consistent with the results from the experiments of Fabre and Buser (1981), showing that lesions that included those regions examined in this study impaired reaching movements to moving visual targets but not those made to stationary ones. It is also compatible with the findings of Beloozerova and Sirota (2003), who found many cells in area 5 that were rhythmically active during locomotion and that increased their discharge frequency when the complexity of the locomotor task was increased. In this respect, it is also interesting to note that the extent of the deficits in our experiments was generally greater in the visual dissociation task (Fig. 7) than in the standard condition. This reinforces the suggestion that the PPC makes a particular contribution to the control of locomotion in situations in which information about a moving target has to be integrated with information about self-motion.

The lesions in all three cats covered a large region of the cortex around the ansate sulcus, particularly in the caudal bank. However, our histological inspection showed that the lesion in

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**FIG. 10.** A: placement of lead forelimb (ipsilateral to lesion) in steps in which the trail forelimb (contralateral to lesion) hit the front of obstacle. B: similar analysis for PCM1 for steps in which the forelimbs passed over obstacle but the trail hindlimb hit the front of obstacle. Data are shown for the situation when the obstacle and the treadmill are at the same speed (0.5/0.5), for the visual dissociation condition (0.5/0.35), and for large and small obstacles. Same dataset as Figs. 8 and 9.
PCM1 was larger in the more medial cortex and that in cat PCM3 was larger in the more lateral regions. The data in Fig. 7 show that cat PCM1 most frequently hit the obstacles with its contralateral hindlimb, whereas cat PCM3 most frequently hit the obstacle with the contralateral forelimb. This suggests some functional topographical organization of the PPC. This is compatible with anatomical and electrophysiological findings that the more lateral parts of the PPC project to the more lateral parts of the motor cortex in which the forelimb representation is located while more medial parts of the PPC project to the hindlimb representation of the motor cortex (Andujar and Drew 2005; Waters et al. 1982a,b). It is also compatible with the results from our unit recordings showing that cells related to forelimb activity during this locomotor task are located more laterally than those related to hindlimb activity (our unpublished observations). In cat PCM4, in which the lesion was smaller, but projected over a large area of the PPC, weak deficits in both the contralateral forelimb and hindlimb were observed.

Cats hit the obstacle most frequently with the limb contralateral to the site of the lesion both when it was the lead limb and when it trailed (Figs. 7 and 8). This suggests that the PPC contributes to the planning of the gait modification of a given limb in both the lead and the trail conditions. However, Fig. 7D shows that the cats also sometimes hit the obstacle with the ipsilateral limb, even when it was the lead forelimb. This result additionally suggests that the PPC in one hemisphere may influence activity in both the ipsilateral and contralateral limbs. This result is also compatible with our finding that neurons in the PPC discharge during gait modifications of both limbs (Andujar and Drew 2006; Lajoie and Drew 2006; unpublished observations).

The results shown in Figs. 9 and 10 suggest that one of the underlying causes of the cats’ inability to successfully negotiate the obstacles is inaccuracies in the placement of the paw. For the trials in which the cat cleared the obstacle, there were no significant differences in the position in which the paw was placed in the step before that over the obstacle postlesion as compared with prelesion control (Fig. 9). However, when the cats hit the front of the advancing obstacle, the lead forepaw was placed relatively closer to the obstacle than in the control situation, and it was placed relatively further away when it hit the other side of the obstacle (Figs. 9 and 10). This trend was consistent in all cats, although the differences were not always significant, primarily because of the small number of trials in some conditions. The paw was also placed significantly further from the obstacle in trials in which the cat resorted to jumping over the obstacle (see Fig. 9).

Our interpretation for those steps in which the cat hit the obstacle (i.e., excluding jumps) is that the limb trajectory used is planned on the basis of the expected, or planned, paw position. In other words, the cat plans a trajectory that would be adequate to step over the obstacle if the paw had been placed in the expected position. Of course, it is possible that the limb trajectory that is used is also inappropriately planned, and we cannot discount this. However, as our comparison of the height of the paw at the apogee of the step over the obstacle in those steps in which the limb clears the obstacle (Fig. 11) showed no statistical difference compared with the control, it is unlikely that the inability to step over the obstacle is simply because the limb was not raised sufficiently high.
All three cats, but especially cat PCM1, frequently hit the obstacles with the hindlimbs, even though the forelimbs successfully negotiated the obstacles. This finding suggests that the PPC makes an important contribution to the coordination of fore- and hindlimb activity in situations requiring visual guidance. However, we could not find any specific change in the position of the hindpaw in any of the cats in this condition suggesting that placement of the paw is not the predominant problem. An alternative possibility is that the cats are no longer able to calculate, or compensate for, the time of passage of the obstacle under the body in the absence of the PPC. Overall, these results suggest that fore–hindlimb coordination is controlled by different neural mechanisms depending on the circumstances. In undemanding circumstances, during walking over even terrain, fore–hindlimb coordination might rely primarily on spinal and brain stem mechanisms (Bem et al. 1995; Brustein and Rossignol 1998; English 1985). This is supported by the findings that decerebrate cats can generate relatively normal fore–hindlimb coordination patterns (Halbertsma et al. 1976; Miller et al. 1975). However, during visually guided locomotion, cortical structures, including the motor cortex (Drew et al. 1996, 2002; Widajewicz et al. 1994) and the parietal cortex (this study), are essential for producing the appropriate modifications of fore–hindlimb coordination.

One important issue is whether the deficits that we observed are caused by errors in perception of the obstacle or errors in planning the movement. Some answer to this issue is provided by the finding that, at least in cats PCM3 and PCM4, the frequency with which cats used the double step strategy was the same after the lesion as it was prelesion. Because the decision whether to use the standard strategy or the double step strategy seems to depend critically on the predicted position of the paws with respect to the advancing obstacle (Figs. 4 and 5), it seems probable that the cats were able to appropriately perceive the advancing obstacle after the lesion. As such, we suggest that the deficit is primarily because of a problem in motor planning. This is in agreement with the suggestion that the PPC plays a role in performing the sensorimotor transformations that are required for adapting actions to perceived objects (Goodale and Milner 1992; Rizzolatti and Matelli 2003) during reaching movements in humans and primates. Indeed, it is possible that the deficits observed in our experiments might be analogous to those observed in patients with optic ataxia who are able to describe objects that they see, including their orientation, but are unable to adjust their grip to seize those objects (Jakobson et al. 1991).

Conclusions

The development of this novel locomotor task, in which visual information from the advancing obstacle is dissociated from information provided by self-motion, provides an important tool for the study of the neural mechanisms that underlie visually guided locomotion. Our results show that, in this visual dissociation task, cats consistently modify their gait in the steps preceding the step over the obstacle and change the location in which the paws are placed in front of the advancing obstacle. Moreover, the visual dissociation task necessitates that the hindlimbs be controlled independently of the activity in the forelimbs. The results from our lesion study show that damage to the PPC leads to severe deficits in locomotion and that these deficits persist for periods of ≥2–3 wk. This speaks to the fact that the contribution from the PPC to visually guided locomotion is an important one that can only with difficulty be compensated by other cortical and subcortical structures. An important finding in these studies is that the lesions produced deficits in paw placement in front of the advancing obstacle and that these deficits were exaggerated in the visual dissociation task. This suggests an important role for the PPC in the preparation, and perhaps the initiation, of gait modifications under these circumstances. A challenge of future single unit recording studies will be to determine the neuronal mechanisms that are responsible for these functions.

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