Contribution of cells in the posterior parietal cortex to the planning of visually-guided locomotion in the cat: effects of temporary visual interruption.

by

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Abstract

In the present study, we determined whether cells in the posterior parietal cortex (PPC) may contribute to the planning of voluntary gait modifications in the absence of visual input. In 2 cats we recorded the responses of 41 neurons in layer V of the PPC that discharged in advance of the gait modification to a 900 ms interruption of visual information (visual occlusion). The cats continued to walk without interruption during the occlusion which produced only minimal changes in step cycle duration and paw placement. Visual occlusion applied during the period of cell discharge was without significant effect on discharge frequency in 57% of cells. In the other cells, the visual occlusion produced either significant decreases (18%) or increases (21%) of discharge activity (in one cell there was both an increase and a decrease). The mean latency of the changes was 356 ms for decreases and 252 ms for increases. In most neurons, discharge frequency, when modified, returned to the same levels as during unoccluded locomotion when vision was restored. In some cells, there were significant changes in discharge activity after the restoration of vision; these were associated with corrections of gait. These results suggest that the PPC is more involved in the visuomotor transformations necessary to plan gait modifications than in continual sensory processing of visual information. We further propose that cells in the PPC contribute both to the planning of gait modifications on the basis of only intermittent visual sampling and to visually-guided online corrections of gait.

(249 words)
Introduction

When walking in a natural environment it is frequently necessary to adjust gait to step over or around stationary or moving obstacles. Visuomotor planning for such a task requires interpretation and control over both spatial and temporal aspects of an animal’s locomotor cycle. In particular, the animal needs to judge the distance or time to the approaching obstacle and to integrate this with an estimation of the state (e.g. spatial location and relative orientation) of its body and limbs. Furthermore, it needs to determine where to place its feet in front of the obstacle and decide when to initiate the gait modification to step over the object (Marigold et al. 2011). Clearly, visual information is essential for this task. At the same time, however, there is abundant information to show that continual visual information is not essential to modify gait. Indeed, subjects are able to follow complex trajectories (Patla et al. 1996; Pham and Hicheur 2009), to step over obstacles (Patla 1998; Rietdyk and Rhea 2006) or step onto precise targets (Hollands and Marple-Horvat 1996; Patla et al. 1996; Wilkinson and Sherk 2005) on the basis of an initial view of the environment or with only intermittent sampling of the route. A major question is how subjects are able to execute these complex movements in the absence of continual visual information.

Our recent work suggests that the posterior parietal cortex (PPC) may be involved in this process. The PPC is well known to contribute to the planning and execution of visually-guided reaching movements and has been suggested to be a site of sensory coordinate transformation and body/limb state estimation (Andersen and Buneo 2002; Buneo and Andersen 2006; Shadmehr and Krakauer 2008). For instance, multiple experiments in primates have shown that neurons in the superior bank of the intraparietal sulcus discharge before and during reaching movements and may encode the metrics of the movement and provide a signal to trigger the movement (Cui and Andersen 2007; Kalaska 1996; Maimon and Assad 2006a,b; Mountcastle et al. 1975; Snyder et al. 1997).

Recent experiments also suggest that the PPC may make a substantial contribution to the planning and execution of visually guided locomotion. Beloozerova and Sirota (2003), for example, reported neurons in the PPC that discharge rhythmically during visually-guided locomotion. Recently, we have detailed a population of PPC neurons in area 5b of the cat that discharge 1-2 step cycles in advance of the step over an approaching obstacle and which we
suggest may be involved in planning visually-guided gait modifications (Andujar et al. 2010; Drew et al. 2008). Furthermore, lesions to this region result in locomotor deficits that are characterized by contact with the obstacle during the gait modification (Lajoie and Drew 2007). Analysis showed that these deficits were the result of errors in paw placement in front of the obstacle. Perhaps most interestingly, however, we have proposed that cells in area 5 of the PPC may play a role in storing visual information in working memory that can be used to modify future locomotor adjustments (Lajoie et al. 2010).

A major unanswered question raised by our previous results is whether the properties of PPC neurons can also account for subjects’ ability to plan and execute accurate gait modifications in the absence of direct visual information. If cells in the PPC are implicated in this process, one would expect that removing visual input should have little or no effect on the discharge activity of these cells. This would be in agreement with a view that the discharge activity reflects more a motor plan than continual sensory processing. In contrast, if these cells are activated by direct, continual visual input and passively driven by object motion, temporary removal of visual information should abolish or dramatically reduce the discharge.

Here, we trained cats to step over obstacles that moved towards them during locomotion while recording neurons in the PPC. Vision of the obstacle and surroundings was briefly interrupted 1 – 3 step cycles prior to stepping over the obstacle. We found that in approximately one half of the neurons removal of visual information was without significant effect on cell discharge, supporting a role for these cells in motor planning rather than sensory processing.

Preliminary results have been published in Abstract form (Drew and Marigold 2008).
Methods

Training and Task

Two adult male cats (PCM7 and PCM9, weight 4.5 kg and 6.6 kg, respectively) were trained over a 3 – 4 month period to walk without interruption for ~ 20 minutes on a treadmill and to step over two identical, cylindrical, obstacles (diameter 8 cm) attached to a second, moving belt. The obstacles were spaced equidistantly on the treadmill belt with 3m between each obstacle so that the cats normally executed between 6–7 step cycles (or 12–14 steps) between each obstacle. The treadmill was constructed such that when the cat was in the center of the treadmill belt on which it walked, the obstacles were visible to the cat for 2m before it stepped over them. This corresponded to at least 5 full step cycles before the gait modification, approximately 5 -7s depending on the speed of the obstacle. The cats were initially trained with the obstacles set to the same speed as the treadmill belt (0.45 or 0.5 m.s⁻¹: matched task). Training in this condition continued until the cats were able to maintain a stable position on the treadmill belt and to step smoothly over the obstacles with minimal disruption of their progression. The cats were then trained when the obstacle was decoupled from the treadmill belt (visual dissociation task: Lajoie and Drew 2007). In this latter condition, the speed of the belt to which the obstacles were attached was slowed to 0.30 or 0.35 m.s⁻¹. This condition made the task more difficult for the cat and may be compared to a situation in which a moving subject has to intercept a moving object (for example, a soccer player hitting a moving ball). In our task, however, the cat has to step over the obstacle rather than hit it.

The cats were then habituated to temporary removal of visual information. In this situation the laboratory was illuminated only by three series of LEDs located above and to the side of the treadmill and all extraneous light sources from equipment were masked (Fig. 1). The LEDs were then extinguished for short periods extending eventually to 900 ms (the approximate duration of 1 step cycle, or two steps). We refer to this situation as visual occlusion. In the occluded condition, the luminance of the obstacle was 1.7*10⁻⁵ cd/m². Visual occlusion was applied in the visual dissociation task, initially in the absence of obstacles and then in their presence. Visual occlusion was applied 1, 2 or 3 step cycles before the step over the obstacle. This resulted in visual information again becoming available at slightly different times before, or during, the step over the obstacle (Fig. 1). Note that even with the earliest occlusion (blue
rectangle in Fig. 1), the obstacle was visible to the cat for several seconds before the occlusion began. Training continued until the cats continued walking with minimal changes to their gait pattern during the visual occlusion, even when this occurred just before, or during, the step over the obstacle.

Surgical Procedures

All handling and surgical procedures followed the recommendations of the Canadian Council for the Protection of Animals and protocols were approved by the animal ethics committee at the Université de Montréal. Surgeries were carried out in aseptic conditions and under general anesthesia. The cats were pre-medicated with an initial intramuscular dose of a mixture of Ketamine (11 mg/kg), glycopyrrolate (0.01 mg/kg), and acepromazine maleate (0.05 mg/kg). Subsequently, the animals were intubated and anesthesia was induced and maintained with isoflurane (2-3% with oxygen). During the surgery, the animals were placed in a stereotaxic frame with the use of atraumatic ear bars and petroleum jelly was placed on the cornea of both eyes to prevent drying. Fluids were administered via an intravenous line along with antibiotics (Penicillin 40,000 IU/kg), a corticosteroid (Solu-medrol 30 mg/kg) to prevent cortical swelling, and an analgesic (Buprenorphine 0.005 mg/kg). Heart rate and body temperature were monitored continuously; the latter was maintained with a heating blanket and lamp.

A craniotomy was performed over the right PPC at the coordinates of the ansate sulcus, as determined prior to surgery with a MRI scan. A stainless-steel rectangular base plate was fixed over the craniotomy with dental acrylic (Drew 1993) and formed the recording chamber. Microwire arrays were implanted into the cerebral peduncle and pyramidal tract using a harpoon assembly (Drew 1993; Palmer 1978) to allow the antidromic identification (Lipski 1981) of corticofugal neurons from layer V of the PPC. Pairs of Teflon-coated, braided, stainless-steel wires were passed subcutaneously from a connector placed on the cranium and were inserted into selected flexor and extensor muscles of the left and right fore- and hind-limbs to record electromyographic (EMG) data. The muscles of interest in the present experiment included the shoulder protractor and elbow flexor, the cleidobrachialis (ClB) and the elbow flexor, the brachialis (Br), each of which becomes active at the approximate onset of the swing phase of locomotion (Drew 1993). In addition, a small connector was placed on the midline of the
cranium to allow attachment of a short rod (~5cm) during the experiments. This was used to
monitor head position (see below).

After the surgery, analgesics (Buprenorphine, 0.005 mg/kg) were administered for 72
hours and the animals were allowed to recover for 1–2 weeks. Antibiotics were given during the
experimental period when necessary.

Protocol

During each experimental session, a custom-made microdrive was attached to the
recording chamber and a conventional glass-insulated, tungsten microelectrode (impedance 0.5–
1.5 MΩ) was manually advanced into the PPC. Each isolated neuron was initially tested to
determine if it could be antidromically activated (see Lipski 1981) from one of the stimulating
electrodes in the cerebral peduncle. Such cells were considered to be located within layer V of
the cortex. Neurons that were antidromically activated, together with those neurons recorded in
close proximity (200–300 μm), were recorded during locomotion when their discharge activity
was judged, on-line, to be altered prior to the gait modification necessary to step over the
obstacle. Data were recorded only from layer V neurons to ensure a relatively homogeneous
database consisting only of corticofugal neurons. The activity of these PPC neurons was first
recorded during the matched task for 5-10 mins and then in the visual dissociation task. After 2-3
mins of locomotion in the visual dissociation task, we started the visual occlusion paradigm.
Visual occlusions of 900 ms were triggered to begin 1–3 step cycles before the step over the
obstacle (Fig. 1).

During the task used in these experiments the cat may step over with one forelimb first or
the other. In this paper, as in others from this laboratory (Drew 1993, Andujar et al. 2010), when
the first (lead) limb is the limb contralateral to the cortical recording site, we refer to this as the
lead condition. When this limb is the second to pass over the obstacle, we refer to this as the trail
condition (the limb ipsilateral to the recording site is the lead limb in this instance).

Visual occlusions always began 200 ms after the onset of the contralateral Br (coBr)
activity in one cat and 300 ms after the onset of the contralateral ClB (coClB) activity in the
other cat. As a consequence, the occlusions were not symmetrical in the lead and trail conditions
and occlusion in the trail condition was effectively phase-shifted by 0.5 step cycle with respect to
the flexor muscle activity. In other words, while the occlusion occurred 200 ms after the
contralateral flexor muscle (e.g. coBr) activity in the lead condition it occurred prior to the onset of the activity in the (following) ipsilateral flexor muscle activity (e.g iBr) in the trail condition (See Fig. 1). Nonetheless, to simplify the text we refer to occlusions during both the lead and trail conditions as being applied 1, 2 or 3 step cycles before the step over the obstacle (see Fig. 1). These differences in the phase of occlusion are appropriately considered in our analysis and interpretation.

Visual occlusion was performed intermittently during 5 – 20 mins of locomotion in the visual dissociation task. Occlusion was performed only in the visual dissociation task because of the difficulty in holding cells for prolonged periods of time and because this was the most challenging task for the cat. Occluded and non-occluded gait modifications were interspersed during the 5 - 20 min recording period.

Each session was recorded using a Panasonic (model WV-CL920) color video camera (60 Hz) and written to DVD. In addition, a 6-camera movement analysis system (M2 cameras, Vicon Motion Systems, Oxford, UK, frequency of acquisition 100 Hz) using infrared strobes was used to monitor the locomotion in all tasks, including during the visual occlusion. The position of the cat with respect to the obstacle was obtained by measuring the coordinates of reflective markers placed on a rod attached to the connector on the cat’s cranium and other reflective markers attached to the moving obstacles. In one cat (PCM7), reflective position markers were secured to the skin bilaterally on the forelimbs at the end of third digit of the paw, the metacarpal phalangeal joint, and laterally on the ankle joint to track paw movement. These markers were used to measure the distance of the paw from the obstacle at paw contact. All kinematic recordings were synchronized with EMG and cell data by using a digital time code. Cell discharge activity was digitized on-line at 100 KHz and discriminated off-line. The EMG data were amplified and sampled at 1 KHz.

After recording each cell, we evaluated (when possible) the cutaneous receptive field of the cell and tested each cell for any response to a looming stimulus by advancing a hand-held wand towards the cat. In some experimental sessions, small lesions (25 μA cathodal DC current) were made at known locations within the recording chamber to facilitate histological reconstruction of the electrode penetrations.
The behavioral effects of the occlusion on locomotion were determined by measuring step cycle duration as well as the location in which the paw was placed prior to the step over the obstacle (Lajoie and Drew 2007). Step cycle duration was measured as the time of the onset of activity in one burst of activity in Br until the time of onset of the subsequent period of activity. The distance of the paw from the obstacle was calculated as the distance between a marker on the obstacle and the marker on the paw. Measures of the duration of the step cycle were made for the two step cycles preceding the step over the obstacle. Measures of the distance of the paw from the obstacle were made for the 3 steps (not step cycles) prior to the step over the obstacle (Fig. 2D). All measures were made in the unobstructed condition as well as when occlusion was applied 1, 2, or 3 step cycles before the step over the obstacle. Measures were made separately according to which leg was the first to step over the obstacle. Data were analyzed with a one-way ANOVA for step cycles 1-2 (Fig. 2A) and for steps 1-3 (Fig. 2D) and then by using Bonferroni post-hoc tests. Statistical significance was set at p < 0.05.

Custom written software was used to isolate and discriminate neurons based on time and amplitude. Subsequently, a custom program was used to select the onset and offset of the CIB and/or Br muscles, paw contacts from the position markers, and the visual occlusion period. For each sequence of locomotion, the step over the obstacle was identified along with whether the forelimb contralateral or ipsilateral to the recording site in the right PPC was used to step over first (i.e., lead limb). We also identified step cycles occurring in the period between the steps over the obstacles, which we treated as control or unobstructed cycles (see Andujar et al. 2010). Finally, sequences of locomotion data were identified to differentiate unoccluded and visual occlusion conditions during the visual dissociation task.

We initially analyzed the data to determine the pattern of cell activity before and during the step over the obstacle as in Andujar et al. (2010). In brief, we averaged the cell and EMG activity in steps in which the cat stepped over the obstacle first with the limb contralateral to the recording site (lead limb). EMG activity was normalized by resampling the activity in each step cycle into 512 bins before averaging. As the duration of the step cycles on average was between 900 and 1000 ms (Fig. 2B, C), each bin was slightly less than 2ms duration. For the cell traces,
we calculated the instantaneous frequency of the discharge by calculating the reciprocal of the interspike interval in ms (1000 ms/interspike interval in ms) in each step cycle before also normalizing the traces by resampling into 512 bins (Doucet and Drew 1991; Udo et al. 1982). Averages were always synchronized to the onset of activity in the coClB or coBr. We also calculated the averaged cell discharge activity in the unobstructed cycles. As in our previous publications (Drew 1993; Andujar et al. 2010) cell discharge during the steps over the obstacles was considered to be significantly different from the unobstructed condition when discharge deviated from the interval of confidence (p< 0.05) of the standard error of the mean of the unobstructed discharge for a period of 50 bins (=10% of a normalized step cycle). Raster displays were made by triggering cell activity on the onset of the coClB or coBr. Trials were rank-ordered according to the duration of the burst in the triggering muscle.

To determine whether occlusion significantly affected cell discharge activity during the task, averages were constructed synchronized to the onset of the coClB or coBr burst that was used to trigger the occlusion. This ensured that activity during the occlusion was appropriately synchronized to this event. For this analysis, the data were not normalized to the average cycle duration (see preceding paragraph) but instead were displayed for a fixed period before and after (generally 1500 ms before and 3200 ms after) the triggering event. (Because these displays are not normalized, the bursts of EMG activity in the superimposed profiles become progressively less synchronized further away from the triggering EMG.) When averaging the cell discharge frequency in these non-normalised displays, binwidth was set at 2 ms. One would expect that if cell discharge were influenced by visual input it should be significantly reduced or abolished for the 900 ms duration of the occlusion. In the present analysis we used a more conservative approach, classifying a cell as significantly responsive to the occlusion if average cell discharge during any 450 ms interval (during the occlusion) fell either above or below the interval of confidence.

When quantifying the magnitude of the effect of the occlusion we integrated the cell discharge activity for the entire period of the occlusion (900ms). This value was expressed as a percentage of the integrated discharge activity of the cell in the same period in the absence of occlusion. The latency of a response was taken as that time when the discharge activity in the
occluded condition deviated from the interval of confidence of the cell discharge in the unoccluded condition.

**Histology**

Before perfusing the cat with formaldehyde we made a series of marking lesions in the PPC in the regions from which we had recorded to aid in the histological reconstruction of the experiments. After perfusion, the relevant area of the cerebral cortex was blocked and then sectioned (40 µm) in the parasagittal plane. Penetrations were identified with the aid of the marking lesions.
Results

Behavioral Effects of Visual Occlusion during Obstacle Avoidance

Once fully trained, both cats used in these experiments continued to walk without hesitation during occlusions applied at different times prior to and during the step over the obstacle. They also continued to step over the obstacle with minimal qualitative change in gait although in some steps the cats hit the obstacle as they stepped over (this rarely, if ever, occurred with full vision). This speaks to both the ability of the cats to step over the obstacles on the basis of visual information obtained one or two step cycles before the gait modification and the fact that this stored information did not always contain sufficient detail to perform the task without error. Both of these features were evident in the behavioral analysis detailed in Fig. 2.

Figure 2 shows measures of the step cycle duration taken from the coBr of both cats during the lead condition (see Fig. 2A). There were no significant changes in step cycle duration two cycles before the step over the obstacle in either cat (Figs. 2B,C) regardless of condition. For the step cycle immediately before the step over the obstacle, there were significant increases in duration when occlusion was given at the same time (1 step before the step over the obstacle, green bars) and, in cat PCM7, when the occlusion was applied 2 step cycles before the step over the obstacle (pink bar). Similar results were obtained for the step cycle measured from the iBr in the trail condition (not illustrated) when considering occlusion applied 2 and 3 step cycles before the step over the obstacle (see Fig. 1). However, in the trial condition, some changes were also observed two step cycles before the step over the obstacle. In all cases, the significant changes in cycle duration were relatively small, ranging from 31-91ms in cat PCM7 and from 53-141 ms in cat PCM9 (3.4-14% of the average unoccluded step cycle).

We have previously shown (Lajoie and Drew 2007) that cats place their paw at a relatively restricted distance from the obstacle in the steps immediately before that over the obstacle. As a further measure of the effect of occlusion, we therefore calculated the distance that the paw was placed in each of the three steps before the step over the obstacle (Fig. 2D) in the unoccluded condition and when vision was occluded one or two step cycles before the gait modification. The result from this analysis for the lead condition in cat PCM7 is shown in Fig. 2E, which illustrates the mean and standard deviation (SD) of the distance of the paw from the obstacle in each of the 3 steps before the step over the obstacle. Despite the occlusion, the paw in
each of the three illustrated steps was placed at a similar, restricted, distance from the obstacle. 

Post hoc tests showed that the only significant difference (p < 0.001) was for step 3 (i.e., 3 steps before stepping over the obstacle) between the unoccluded condition (black circle) and that when the occlusion was applied two step cycles before the step over the obstacle (pink bar in Fig. 2D and pink circle in Fig. 2E).

As has been reported in human studies (Patla and Greig 2006; Patla 1997; Lee et al. 1982) the SD of the distance from the entire population in the unoccluded condition was least for the last step immediately before the step over the obstacle (Fig. 2F). This decrease in the SD was also observed for the occlusion two step cycles before the step over the obstacle but was not observed (arrow) when the occlusion was applied one step cycle before the gait modification (Fig. 2F). This suggests that the cat did not have sufficient visual information to appropriately judge where to optimally place the paw in the latter condition. Similar findings were made for the trail condition. Data were not available for the distance of the paw from the obstacle for cat PCM9.

The results of the behavioral analysis show that the effect of the occlusion on the locomotion was small and was primarily characterized by small changes in step cycle duration and, to a lesser extent, paw placement, especially when vision was not available in the step cycle before the step over the obstacle. These data show that cell activity was recorded during similar behavioral conditions in the occluded and unoccluded condition.

**Neuronal Database**

From our total database of > 200 neurons, we initially selected 69 neurons recorded from the PPC in two cats (37 in PCM7 and 32 in PCM9) in which the onset of the change in activity began at least 200ms before the onset of the activity in the coBr or coClB during the step over the obstacle. We refer to such cells as step-advanced cells as in our previous publication (Andujar et al. 2010). We restricted our analysis to these step-advanced cells because of our previous suggestion that such neurons are involved in the planning of the gait modification (see Discussion). Of these step-advanced cells, 41/69 (30/37 in PCM7 and 11/32 in PCM9) were tested under conditions of visual occlusion during the obstacle avoidance task and form the basis of the present report. Thirty-six (36/41) PPC neurons demonstrated an increase in discharge activity prior to the step over the obstacle and 5/41 a decrease in activity. Of the cells showing
increased activity, discharge ceased at the onset of the step over the obstacle in 19/36 but continued during the step over the obstacle in the other 17/36.

Histological localization showed that the majority of the cells were located in area 5 (mainly area 5b) as in our previous study (Andujar et al 2010) although some cells were located further caudally in area 7. Twenty-three (23/41) cells were antidromically activated from the stimulating electrodes in the cerebral peduncle and were therefore confirmed as being localized within layer V of the PPC. The other 18/41 neurons were recorded in very close proximity to these identified neurons. The responses of 21/41 cells tested with visual occlusion were examined for visual inputs outside the context of the task by moving a rod towards the cat (looming) or across the visual field; 15/21 responded to such stimuli. Cells responding to a looming stimulus included equal numbers (N=5) showing no change, increased or decreased activity to occlusion (see below).

**Effects of Visual Occlusion on PPC Neuron Discharge Activity**

We first considered together all periods of occlusion, regardless of when they occurred with respect to the period of modified cell discharge, and determined whether the cell discharge frequency was significantly modified during the time that occlusion was applied. This analysis showed that a substantial proportion of the cells (17/41, 41%) never showed any significant change in activity to occlusion, regardless of when the occlusion occurred with respect to the step over the obstacle, or whether occlusion was applied in the lead or trail condition (Table 1, **All Occlusions**). In 28 cells, one of the periods of occlusion completely overlapped the period of increased discharge prior to the step over the obstacle in the visual dissociation task. In this more restricted situation, 57% of the cells showed no significant change in discharge activity during the occlusion (Table 1, **Full Overlap**) at a time when the activity in the cell is most likely to contribute to the planning of the gait modification. Examples of cells showing no change during full overlap are shown in Figs. 3 and 4.

Figure 3 shows the discharge activity of three cells in the trail condition (ipsilateral limb first to step over the obstacle). The step over the obstacle in this and all other figures is indicated by the gray rectangle. All three of the cells showed a ramp increase in discharge frequency that began approximately one to two step cycles before the step over the obstacle by the ipsilateral forelimb. These general properties are consistent with those detailed in a previous publication.
Occlusion was applied 2 step cycles before the step over the obstacle (pink rectangles), during the period of maximal discharge in each of the three cells. In none of the examples illustrated in Figs. 3A-C did the occlusion have any significant effect on the cell discharge activity (data superimposed on the right).

Occlusion during the step over the obstacle also had no significant effect on cell discharge in many cells. Three examples are illustrated in Fig. 4; two of them show occlusion during the trail condition (Figs. 4A, B) and the third during the lead condition (Fig. 4C). Note that in the example in Fig. 4C there was an increase in discharge activity when vision was restored. The reasons for this increase are discussed in a later section.

In the other 24/41 (59%) cells, visual occlusion caused significant changes in discharge activity for at least one of the periods of occlusion. Changes could be either an increase or a decrease in cell discharge frequency. Overall, decreases in activity were observed in 9/41 (22%) cells and increased cell discharge was observed in 14/41 (34%) cells in at least one of the visual occlusion conditions (Table 1, All Occlusions). In one cell (1/41, 2%), discharge activity showed either an increase or a decrease depending on when the occlusion occurred. Increased activity when the occlusion occurred during the period of increased cell activity was less frequent (21%, Table 1, Full Overlap) than when considering all periods of occlusion (34%, Table 1, All Occlusions). Examples of decreased and increased cell activity in response to visual occlusion in the period preceding the step over the obstacle, in both the lead and trail conditions are illustrated in Fig. 5.

The example in Fig. 5A shows the responses of a cell to occlusion at two different times preceding the step over the obstacle in the lead condition (left column) and the trail condition (right column). In the unoccluded condition, the cell showed an increase in activity that began more than two step cycles before the step over the obstacle and ended at the onset of the gait modification (gray rectangle). This cell showed a limb-independent pattern of discharge (Andujar et al. 2010) in that discharge was related to the first limb to step over the obstacle in both the lead and trail conditions. In the lead condition, when occlusion occurred 2 step cycles before the step over the obstacle (Fig 5A, top left) there was a clear and significant decrease in the cell discharge (arrow). However, this decrease in activity did not reach significance until 640 ms after the onset of the occlusion. Occlusion in the cycle preceding the step over the obstacle
(Fig 5A, bottom left) also produced a decrease but this was not significant because of the short duration (<450 ms) of the modified discharge. In the trail condition, occlusion both two (Fig 5A, top right) and three (Fig 5A, bottom right) step cycles before the step over the obstacle also caused clear and significant decreases in cell discharge activity beginning at latencies of 276 and 304 ms from the onset of the occlusion, respectively.

The cell illustrated in Fig. 5B showed increased discharge activity to the occlusion in both the lead and trail conditions. This increased activity was superimposed on the normal burst of activity in the lead condition and preceded the normal period of activity in the trail condition. The latency of this increase following visual occlusion in the lead condition was 142 ms and discharge frequency was increased to 180% of control: in the trail condition the values were 310 ms and 301%.

Additional examples of changes in discharge activity produced by the occlusion are illustrated in Fig. 6. In the example illustrated in Fig. 6A, cell discharge during the step over the obstacle in the unoccluded situation was similar to the examples illustrated in Fig. 3. However, in this cell, the occlusion produced a complete arrest of the discharge, which showed an immediate return to the level of activity during unoccluded steps once the lights were switched back on. The cell in Fig. 6B illustrates a decrease in cell activity that occurred in advance of any overt changes in cell discharge related to the step over the obstacle, while the examples in Figs. 6C, D show that increases in cell activity were occasionally substantial in response to visual occlusion. The example in Fig. 6D also illustrates a rare example in which the occlusion caused changes in cell discharge frequency that were both of short latency and equal to the duration of the occlusion.

Magnitude of the responses

The overall changes in magnitude of the cell discharge produced by visual occlusion are illustrated in the histogram of Fig. 7A where we plot the relative magnitude of the discharge activity during occlusion as a percentage of the unoccluded discharge activity. Values greater than 100% represent increased activity during the occlusion compared to the control condition. Cells showing a significant decrease in activity were mostly active at 25-75% of their activity during control. Cells showing a significant increase in activity ranged quite widely from a low of 126% of control to over 400% of control although in the majority the change was less than 300%. As would be expected, cells showing no significant change in activity showed only
modest differences between the control and the occluded traces and were centered on 100%. Some cells with no significant change in activity deviated from 100% because of intense, but brief, changes in activity. The median values of each group were 105% for the unchanged populations and 45% and 243% for those showing a decrease and an increase, respectively, in discharge activity.

Latency of the responses
The latency of significant changes in activity was defined by the difference between the onset of visual occlusion and the onset of a deviation from the 95% confidence intervals (from the averaged, filtered traces). We found the median (± interquartile range) latency for a significant change in discharge to be 252 (±284) ms for increased firing and 356 (±194) ms for decreased firing. Latencies < 50 ms were rare, occurring for only 10% of the cells with increased firing and for none of the cells with decreased firing.

Neuronal Responses to Gait Modifications Induced by Visual Occlusion
In the situation in which the occlusion was applied in the step cycle before the step over the obstacle in the lead condition the cat had to initiate the gait modification in the absence of visual feedback of the relative position of the limb and the obstacle (Fig 1). However, in some cases, full visual input was restored while the cat was just beginning to step over the obstacle and while the obstacle was still visible to the cat (i.e., had not yet passed under the body). In this situation we frequently observed significant changes in cell discharge that occurred shortly after the end of the period of occlusion. We suggest that these changes in activity are related to corrective changes in limb trajectory that are triggered by the visual input.

An example of this type of response pattern can be seen in Fig. 4C in which the cell discharge was significantly increased shortly after the end of the occlusion as the cat stepped over the obstacle, despite the lack of significant effect during the occlusion itself. Two individual trials during occlusion (red and green traces) from the same cell are illustrated in Fig. 8A. In both trials the occlusion (green rectangle) began just prior to the gait modification and continued until the cat had begun the modification of gait required to step over the obstacle (gray rectangle). As in the average traces of Fig. 4C, there was a significant increase in the discharge frequency of the cell, in both trials, that began just after the end of the occlusion and that continued for 100 - 200
ms. Associated with this increase in cell discharge there was an increase in the magnitude of the activity in the coBr (arrow). Both the time of the onset of the deviation from the interval of confidence and the time of the peak of the change in cell activity clearly preceded the time of the onset and the peak, respectively, of the change in EMG activity (change in cell activity preceded the change in EMG activity by 117 and 120 ms in the two traces). Inspection of the video recordings showed that upon restoration of vision, the paw was in a position where it would have hit the obstacle had the cat not made a rapid correction of its trajectory. This is illustrated schematically in Fig. 8B (ii) and may be compared to the situation in an unoccluded step (Fig. 8B, i). The two limb trajectories are compared in the schematic illustration in Fig. 8B, iii where the red trace illustrates that in the occluded condition there was a rapid increase in limb flexion as the cat modified the trajectory of the limb over the obstacle.

Two other examples, from different cells, are illustrated in Figs. 8C, D. The example in Fig. 8D is particularly striking as there is a substantial increase in cell discharge that clearly deviates from the background and occurs at a time at which the cell was normally inactive. Cell activity preceded the change in EMG activity by 94 and 136 ms in the 2 examples in Fig. 8C and by 77 and 160 ms in the two examples in Fig. 8D. Altogether, we examined 62 cycles from 22 cells in which visual occlusion occurred in the step cycle before the gait modification, and in which vision was restored just before, or just after the onset of the step over the obstacle (as in Fig. 8). We observed changed activity, similar to that illustrated, in 24/62 (39%) steps from 9 cells. In all of the 24 cases with modified activity there were also clear modifications of limb trajectory. Similarly, trials with no clear change in cell activity showed no clear changes in limb trajectory. In all except 2/24 of the steps showing significant changes, the onset of the change in cell discharge preceded that of the change in EMG activity in the Br or ClB by an average of 103 ms.

Substantial changes in cell activity and behavior were also occasionally observed when the occlusion ended just prior to the step over the obstacle. In some steps we observed large changes in cell activity subsequent to the end of the occlusion that were significantly different from the overall average of the responses in the same condition. For example, in Fig. 9 (same example as in Fig. 5A) we illustrate the average responses when occlusion was applied two steps before a step over the obstacle in the lead condition (Fig. 9A) and the same situation in the trail
condition (Fig 9B). The average response is a decrease in cell discharge during the occlusion, with the cell returning to the level that it showed in the absence of occlusion when the lights came back on. However, in each condition, examination of the individual trials showed one trial with a quite different response in which the discharge activity at the end of the occlusion was substantially larger than in the unoccluded situation (Figs. 9C, D).

Examination of the behavior of the cat from the video recordings in these trials showed that the cat made substantial modifications of its gait as illustrated by the cartoons of Fig. 9E. The top series of cartoons illustrate the sequence of activity in a normal sequence of locomotion when the cat stepped over the obstacle with the lead, left, limb. The right paw was placed at an appropriate location in front of the advancing obstacle and the cat stepped over the obstacle smoothly with the left forelimb. The bottom series in Fig. 9E shows the situation during the individual trace illustrated in Fig. 9D. The cat started the sequence during the occlusion in the same manner as in the top series. The right paw was planted prior to the end of the occlusion and the gait modification initiated. However, when the room was again illuminated the cat aborted the gait modification, placed the left forelimb on the treadmill, and instead stepped over the obstacle with the right forelimb (i.e. a trail condition). The large increase in cell discharge observed in Fig. 9D began prior to the curtailment of activity in the coBr and continued until the onset of activity in the iBr (right forelimb).

In the example in Fig. 9C, a more complex change in gait accompanied the large increase in activity as the cat made a large swing with the left forelimb (evident in the increased activity in the coBr), and then a very short step with the right forelimb before ultimately stepping over the obstacle with the left forelimb.
As detailed in the Introduction, we have recently reported the discharge characteristics of a population of cells in area 5 of the posterior parietal cortex of the cat whose activity increased 2-3 steps before the step over an obstacle (Andujar et al. 2010). We suggested that these cells contribute to the planning of the gait modification and raised the question of the extent to which continuous visual input influenced this early discharge. The present experiments have provided some insight into this issue. There were three important findings in this study. The first was that the cat continued to successfully perform the task, despite the fact that the occlusion caused a loss of visual information regarding the speed of the obstacle and the position of the cat with respect to the obstacle for an entire step cycle (equivalent to nearly two complete steps). Furthermore, the occlusion occurred during a critical point in time when the cat was either preparing to, or was in the process of, placing the paw in front of the obstacle in order to ensure that the subsequent step cleared the obstacle (a property that has been shown to be dependent on an intact PPC, Lajoie and Drew 2007). This suggests that the cat retains a neural estimate of the projected position of the obstacle relative to its own position during the visual occlusion. The second important finding was that the discharge pattern of fully 57% of the PPC neurons that discharged in advance of the obstacle showed no significant change when the visual occlusion was applied during the period of modified activity. In addition, a second group of PPC neurons demonstrated either a long latency increase or decrease in discharge activity during the visual occlusion. The third important finding was that we found cells that modified their discharge activity in situations in which gait was altered when vision was restored. Together, these three findings support our view (Andujar et al. 2010) that many PPC neurons that discharge in advance of the step over an obstacle are related to the higher level processing (i.e., motor planning) of the gait modification to step over an obstacle rather than being driven primarily by continuous visual input. Moreover, the finding that many cells showed no change in activity during visual occlusion shows that this motor plan may be maintained even in the absence of visual information.

The suggestion that motor planning is a key function of the PPC is supported by several of our findings in addition to the lack of change in discharge activity during occlusion. For
example, changes in cell discharge in the unoccluded condition only began shortly before the
gait modification whereas the obstacle was visible to the cat for several seconds prior to this (see
also Andujar et al. 2010). This finding is reminiscent of the PPC cells recorded in the primate
that only begin to discharge when an object is brought into immediate extrapersonal space
(Mountcastle et al. 1975). Furthermore, if cell firing reflected primarily visual responses,
changes in discharge frequency following visual occlusion would be expected at latencies of less
than 100 ms (Dubner and Rutledge 1964). In contrast, however, we found that most of the cells
that showed a change in discharge activity did so at latencies substantially greater than 100 ms
following the onset of visual occlusion (see Fig. 7B). Moreover, several cells altered their
discharge when the cat modified its gait when the lights came back on. This finding (discussed
below) implies that a change in PPC discharge activity coincides with a change in motor plan.
The preparation of a motor plan that is not dependent on continuous visual input is compatible
with reports from several different investigators studying related questions in the PPC (Eskandar
and Assad 1999; Gnadt and Andersen 1988; Murata et al. 1996). Although the emphasis in this
paper is on the contribution of visual information to the activity of the PPC cells, it should also
be noted that the PPC receives proprioceptive inputs that will also influence discharge. However,
the similarity of the EMG activity preceding the modified step to the EMG activity during
unobstructed steps (control activity) suggests that proprioceptive activity is probably largely
unchanged in the period in which the discharge activity of the step-advanced cells is modified. It
is also possible that the PPC discharge may reflect an efference copy signal related to a motor
plan sent from other cortical regions. Unfortunately, our experiments were not designed to
address this possibility.

The fact that the cats are able to step over the obstacle even when the occlusion occurs in the
step cycle preceding the step over the obstacle suggests that the cat is able to retain a
representation (or memory) of the motor plan. We suggest that discharge activity of the
population of PPC cells that maintain their discharge activity during such occlusions contribute
to this maintained motor plan. Such PPC neurons might provide the neural substrate for the
ability to step over or around obstacles on the basis of only intermittent visual sampling of the
environment (Hollands and Marple-Horvat 1996; Patla et al. 1996; Wilkinson and Sherk 2005).
The ability to maneuver in an environment with obstacles and/or varying ground terrain without
the need for continual visual input is imperative for survival. For example, if objects immediately
in the path of progress only need to be periodically checked, the animal may scan other regions of the surroundings to identify secondary or subsequent goals or to spot predators or prey. The PPC may thus have a built-in storage capacity, which requires only periodic updating from visual input. These properties are similar to those of PPC neurons in area 5b that increase their discharge when the obstacle crosses between the forelimbs and hindlimbs where no direct visual input is available once the obstacle passes under the head of the cat (Lajoie et al. 2010; see also McVea et al. 2009).

While some cells maintained their discharge activity unchanged during the occlusion, others showed long latency increases or decreases in activity. The fact that both increases and decreases in activity were observed suggests that visual input modulates activity in these PPC cells by inhibitory sculpting as well as by more direct excitatory inputs. Overall, the presence of cells showing either changed or unchanged activity to occlusion makes it likely that the cells detailed in this paper are representative of a population that is able to retain information over varying periods of time. The long latency modification of activity in some of these cells may be related to the eventual decay and degradation of the motor plan. This decay of a motor plan may explain why the cats occasionally hit the obstacle or, more frequently, needed to make online corrections of gait when vision was restored (see below). Such a slow and progressive decay of the signal in the PPC may also accord with the decrease in accuracy when humans take multiple steps without vision and are required to walk to a target, avoid a series of obstacles, or step over an obstacle (Patla and Greig 2006; Pham and Hicheur, 2009; Thomson 1980, 1983). In this respect it is also interesting that Wolpert et al. (1998) have reported on a patient with damage to the PPC who was unable to maintain an internal estimate of limb position without continuous visual input.

It is tempting to speculate that the group of step-advanced PPC neurons unaffected by visual occlusion forms part of an internal model within the cortex. There are several reasons why this may be the case. For example, the neurons do not appear to be related to specific muscle activity (i.e., they demonstrate limb-independent discharge). In addition, they are not driven purely by visual input since visual occlusion does not alter their normal increase in discharge prior to the step over the obstacle. As such, it is possible that the discharge activity relates to an estimate of the obstacle position in relation to body/limb position (i.e., state estimation) and is used to form the motor plan for a gait modification. It is also pertinent that many of these cells...
showed discharge activity preceding the gait modification but stopped discharging at the moment that the cat began to step over the obstacle (e.g. Figs. 3A,C). This is similar to the recent findings of Cerminara et al. (2009) who found Purkinje cells in the cerebellum that discharged during visual occlusion as cats tracked a moving cursor. The fact that these cells were related to neither limb nor eye movements led the authors to suggest that they may provide the neuronal basis for an internal model predicting movement and allowing for interception. Similarly, Mulliken et al. (2008) have recently demonstrated evidence that PPC neurons in the monkey provide a real-time update or estimate of the current state of a cursor (representing hand position during a reach) moving to a target. Alternatively, or complementarily, the discharge of our PPC neurons may reflect the integration of this information with obstacle velocity to plan when to initiate the gait modification and monitor paw placement and/or limb trajectory in front of and over the obstacle. Indeed, increased PPC discharge of area 5 neurons has been shown to trigger self-initiated arm movements (Maimom and Assad 2006b).

One striking finding was the fact that cell discharge was modified in several cells when the cat altered its locomotor pattern following visual occlusion. These modifications, which may be considered as online corrections of the motor plan took two forms. In one case, when the gait modification had already begun, the cat sometimes had to rapidly modify limb trajectory to clear the obstacle (Fig. 8). In other cases, when the lights came back on prior to the step over the obstacle, the cats modified the gait pattern in order to facilitate the following step over the obstacle (Fig. 9). In both cases, these corrections to the movement were preceded by significant changes in cell discharge activity, suggesting a possible causal contribution of the PPC to these online corrections. This would be compatible with experiments in humans in which transcranial magnetic stimulation over the PPC has been shown to modify subjects’ ability to perform online corrections of a planned reaching movement (Desmurget et al. 1999; Rice et al. 2006; Tunik et al. 2005). It is also compatible with recent findings in human locomotion showing that visual information can be used to make fast online corrections of limb trajectory during swing to improve the accuracy of foot placement (Reynolds and Day 2005).

In summary, our results extend our previous findings (Andujar et al. 2010) by demonstrating that the discharge activity preceding the step over the obstacle may be independent of continuous
visual input. This supports our previous suggestions that this early discharge contributes to a motor plan that assures that the limbs are placed appropriately in front of the obstacle and that the gait modification is initiated and executed at the appropriate time. Moreover, the rapid changes in discharge preceding the corrections of gait support a contribution of cells in the PPC to both the planning and the execution of the gait modifications. Together, our results provide strong evidence of the importance of the PPC for the planning and execution of visually guided locomotion.

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References


Figure Legends

**Fig. 1. Task conditions** Visual occlusion was produced by switching off a series of LED lights (providing the only illumination in the laboratory during this part of the experiment) at different times during the approach of the obstacle. Occlusions of 900ms duration were triggered shortly after the onset of the contralateral (left) brachialis (coBr) EMG, as in this example, or the contralateral cleidobrachialis (coClB) EMG, 1 (green rectangle), 2 (pink) or 3 (blue) step cycles before the step over the obstacle. Note that as these occlusions were triggered on the activity of the coClB or coBr, they are displaced by 0.5 step cycle with respect to the activity of the ipsilateral cleidobrachialis (iClB) and the ipsilateral brachialis (iBr) for stimuli applied in the trail condition. The shaded gray rectangles in this and all other figures indicate when the lead limb steps over the obstacle. Note that the obstacle was visible to the cat for ~2 m before the gait modifications as represented by the break in the treadmill belt. The arrow indicates the direction of movement of the obstacle.

**Fig. 2. Behavioral effects of the occlusion.** A-C, duration of the step cycle prior to the step over the obstacle in the lead condition. A: Representative average EMG traces during the task. We measured the duration of each of the two step cycles preceding the step over the obstacle when occlusion was applied 1 (green horizontal bar) or 2 (pink horizontal bar) step cycles before the step over the obstacle. Step cycle duration was measured as the time of onset of one burst of activity in the coBr EMG until the time of onset in the subsequent burst (horizontal arrows). B,C: histograms of the average (± standard deviation, SD) step cycle durations identified on A from cats PCM7 (B) and PCM9 (C) for the unoccluded condition (black bars) and when occlusion was applied 1 (green) or 2 (pink) step cycles prior to the step over the obstacle. Asterisks indicate significant differences (p< 0.05). D-F: distance of the paw from the obstacle 1, 2 and 3 steps (not step cycles) before the step over the obstacle in the lead condition. D: The distance of the paw at each step was measured as the distance between the reflecting points placed on the tip of the toe and on the obstacle at the moment of paw contact with the treadmill at the end of swing. The three horizontal arrows superimposed on the EMG traces show the three measured steps. Pink and green horizontal bars indicate the time of the occlusions, as in A. E: For each step, we illustrate the mean distance ± SD in the unoccluded condition (black) and when occlusion was
applied, 1 (green) or 2 (pink) step cycles before the step over the obstacle (see part D). F: the SD of the data plotted in Fig. 2E (the arrow highlights data that are detailed in the text). Note that as the SD was calculated from the entire database, we have no index of variability for this measure. The key between B and E is valid for B, C, E and F. Values of N in B and C indicate the number of measures included in each average in each condition. Similarly, the values for N in E indicate the number of values for each condition and for each step in front of the obstacle: data on each line refer, respectively, to the averages made 3, 2 and 1 steps before the obstacle. Data in F are taken from E. Data in B, C, E and F are taken from a minimum of 4 experimental sessions and a maximum of 30.

**Fig 3: Cells showing no significant change in activity during the occlusion.** A-C show examples of 3 different cells, two from cat PCM7 (A, B) and one from cat PCM9 (C). All three examples show data from trials in which the contralateral (left) limb was the second to step over the obstacle (trail condition). A, B, C (left column): post-event histogram (PEH), raster display of cell activity and averaged EMG activity of selected muscles in the absence of occlusion. The raster is synchronized on the onset of the burst of activity in the coBr (A, B) or the coCIB (C) occurring two step cycles before the step over the obstacle and used to trigger the occlusion. In this figure and in Figs. 4-6, the EMG burst used to trigger the occlusion is indicated by a vertical black line and the step over the obstacle by a shaded gray rectangle. Trials are rank-ordered according to the duration of the EMG burst in the triggering muscle. The subsequent, staggered ticks in this and the other figures indicate the end of the period of activity in the Br. Data are not normalized and are displayed for 1500ms prior to the trigger muscle and for 3200ms subsequent to this event: binwidth = 2ms. A, B, C (middle column): PEHs, rasters and averaged EMG activity during occlusion applied 2 step cycles before the step over the obstacle. The period of the occlusion in this and all other figures is indicated by the colored vertical and horizontal bars using the same code as in Fig. 1; in this example the pink bars indicate the occlusion occurred 2 step cycles before the step over the obstacle. A, B, C (right column): averaged and superimposed activity of the cell in the absence of occlusion (thicker black line) and during occlusion (red line). The thinner black lines indicate the interval of confidence (p < 0.05) of the standard error of the mean of the unoccluded cycles.
Fig. 4. Examples of cells when occlusion was initiated just before the step over the obstacle.
Data are displayed as in Fig. 3 with the following exceptions. In A, B and C the occlusion occurs only 1 step cycle before the step over the obstacle as opposed to 2 step cycles in Fig. 3. Moreover, in C, data are shown for a cell when occlusion was applied in the lead condition.

Fig 5: Cells showing a significant increase or decrease in activity to occlusion. A: Example of a cell in which occlusion produced a decrease in activity. Data are shown for occlusions applied in the lead (left column) and in the trail condition (right column). In all 4 traces we show the PEHs of cell activity and averages of the coBr and iBr activity both in the absence of occlusion (black traces) and in its presence (red traces). The raster displays likewise show activity in the control and occluded conditions (same color code). Arrows indicate the decreases in activity. B: example of a cell showing increased cell discharge to the occlusion; organized as for A. Arrows indicate increase in activity.

Fig. 6: Additional examples of cells showing an increase or decrease in activity during occlusion. A, B: two cells showing decreased activity. C, D: two cells showing increased activity. Organization as in previous figures.

Fig 7: Magnitude and latency of the changes in discharge frequency evoked by occlusion. A: Magnitude of the changes in discharge frequency. Discharge frequency was calculated for all cells and for all periods of occlusion, regardless of when the occlusion was applied. Responses are classified based on whether they showed significant increases, decreases or no change according to the criteria supplied in the Methods. Values are plotted as a percentage of control (100%). B: similar display for the latencies of those responses classified as significant. Latencies were measured as the point at which the trace exceeded the interval of confidence (p < 0.05) of the SE of the mean of the control responses. Note that data were measured from all occlusions applied to each cell (cases) during both lead and trail conditions. The number of cases therefore exceeds the number of cells.

Fig. 8: Changes in discharge activity related to corrections of gait during the step over the obstacle. A: two individual trials (red and green traces) during occlusion showing activity
changes in the cell and the coBr (arrows) when the cat corrected its gait during the step over the obstacle (same cell as in Fig. 4C). The black traces show the unoccluded situation. B: i) schematic representation taken from tracings of video images showing the position of the limb during the step over the obstacle during unoccluded locomotion. ii, change in trajectory during one of the steps illustrated in A. iii, schematic representation of limb trajectory in the unoccluded (black dashed line) and occluded (red solid line) situation. C, D: two additional cells, each showing the averaged activity during the step over the obstacle and the activity of two selected trials during the occlusion. Note that as we are examining single trials in these examples, the thinner lines indicate the interval of confidence (p <0.05) of the SD of the mean, and not the SE as in the previous figures. In addition, the traces are normalized and synchronized on the onset of activity in the coBr during the step over the obstacle.

Fig. 9: Changes in discharge activity related to corrections of gait occurring before the step over the obstacle. A, B: cell discharge activity in the unoccluded (black traces) and occluded (red traces) situations during the lead (A,C) and trail (B,D) conditions. Occlusion was applied 2 step cycles before the step over the obstacle in each case. A,B show averaged activity and C, D an individual trial in each situation. Thin arrows in C, D indicate changes in cell and coBr activity that are described in the text. Same cell as in Fig. 5A. E: cartoons showing sequence of events during an unmodified and a modified step over the obstacle (see text). The shaded figurine indicates the period of occlusion.
Table 1: The effect of visual occlusion on PPC neuron discharge activity.

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<thead>
<tr>
<th></th>
<th>All Occlusions</th>
<th>Full Overlap</th>
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<tbody>
<tr>
<td>No Δ</td>
<td>17 (41%)</td>
<td>16 (57%)</td>
</tr>
<tr>
<td>↓</td>
<td>9 (22%)</td>
<td>5 (18%)</td>
</tr>
<tr>
<td>↑</td>
<td>14 (34%)</td>
<td>6 (21%)</td>
</tr>
<tr>
<td>Other</td>
<td>1 (2%)</td>
<td>1 (4%)</td>
</tr>
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</table>

The table shows the number and percentage of cells in which we determined the effect of occlusion on cell discharge: either no change (no Δ), an increase (↑) or a decrease (↓). Numbers and percentages are provided for occlusion occurring at any time with respect to the cell discharge (All Occlusions) and then for conditions in which at least one period of occlusion completely overlapped with the modified cell discharge (Full Overlap).
Fig. 1
Fig. 2
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