Figures and figure supplements

Posterior parietal cortex estimates the relationship between object and body location during locomotion

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Figure 1. Behavioral Measures. (A) Section of data illustrating, from top to bottom: the activity of the left and right brachialis (lBr and rBr); the distance-to-contact (DTC) and the time-to-contact (TTC) with respect to the obstacle. Solid vertical lines are aligned with the onset of each Br and the numerical values indicate measures of DTC and TTC for three steps before the step over the obstacle. (B) schematic representation of the relationship between DTC and TTC during the matched and visual dissociation tasks (see text). Steps –2 to 0 correspond to those in A. C,D: Box plots indicating the DTC (top panel) and the TTC (bottom panel) as measured at the onset of the lBr ('left') and rBr ('right') in the steps preceding the step over the obstacle for each limb during the matched (C) and visual dissociation (D) tasks. Pairs of steps (left/right) are shown in the same color. Steps –3 to 0 in the top row of C correspond to those in A. Boxes include 50% of the values and the vertical line inside the box indicates the median of the values. Horizontal lines (whiskers) enclose 1.5 * interquartile range. Values greater than 1.5 * interquartile range have been removed (see Materials and methods). The horizontal scale for time is kept constant in C and D, and therefore, the scale for distance is expanded in D because the obstacle moves relatively more slowly in the visual dissociation task. Vertical green and red lines (C,D) indicate the theoretical onset of a cell related to either DTC or TTC, respectively (see text). The curved (green) line indicates the limb stepping over the obstacle (blue vertical line). C and D compiled from 127 and 167 trials, respectively, taken from 14 experimental sessions in cat PCM7. (Figure 1—source data 1).

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Figure 2. Location of recording tracks. (A,B) Postmortem photographs of the rostral aspect of the brains of PCM7 (A) and PCM9 (B) (dorsal views). Circles superimposed on these photographs show the location of the recording tracks in each animal: filled white circles = penetrations; filled black
circles = location of step-advanced cells; blue circles = DTC-related cells; red circles = TTC-related cells; mixed red and blue circles = both DTC- and TTC-related cells recorded in the penetration. Horizontal bar indicates the approximate border between areas 5b and 7. (C-F) Tracings of the reconstructions of four penetrations (C,D from PCM7 and E,F from PCM9). The dotted line indicates the location of layer V and the filled circle indicates the recording site in the illustrated track. The medio-lateral location of each reconstruction is indicated by the black vertical lines on A,B; these lines originate from the penetration illustrated in each panel in C-F. Abbreviations: 5b, area 5b of the PPC; 7, area 7 of the PPC; ANS, ansate sulcus; LAT, lateral sulcus, COR, coronal sulcus; CRU, cruciate sulcus; SI, somatosensory cortex.

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Figure 3. Discharge of an example cell during the matched and visual dissociation tasks. (A,B) Cell discharge during left and right limb lead condition. For each task, we illustrate the average discharge in the form of peri-event histograms (PEHs), together with the raster of cell activity, the instantaneous
frequency during each trial, and the averaged activity of the coBr and iBr for the matched task (red), visual dissociation task (green), and for unobstructed walking (blue). Data are synchronized to the onset of activity (vertical black line) in the coBr (A) or the iBr (B) and displayed for 3200 ms prior to EMG onset and 2000 ms after. Vertical green and red lines and values indicate the average onset of cell activity during the visual dissociation and matched task, respectively, as calculated from the onset of the cell discharge in individual trials (see Figure 3—figure supplement 1). Insets between A and B show cell waveform during recordings of the matched (bottom trace) and visual dissociation (top trace) trials. (C) Schematic illustration showing selected temporal relationships tested between cell and muscle activity (see D). Shaded rectangle indicates the step over the obstacle by the left forelimb (LFL). RFL – right forelimb. (D) Linear regressions for cell onset vs. onset of the coBr during the step over the obstacle for the left and right limb lead condition (left), the relationship of cell onset to the onset of the flexor EMG in the lead limb in the step before the step over the obstacle (middle), and the end of cell discharge as a function of the onset of the activity in the Br of the lead limb during the step over the obstacle (right). Note that in the latter graph, measures are relative to the onset of activity in the Br in the preceding step. Data and linear regressions are shown for the left (red) and the right (cyan) limb lead conditions, together with the combined linear regression (black). (Figure 3—source data 1). Figure 3—figure supplement 1: Detection of bursts of unit activity in individual trials.

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Figure 3—figure supplement 1. Detection of bursts of unit activity in individual trials. From top to bottom: averaged peri-event histogram (PEH) of cell activity; individual trials in the form of rasters and instantaneous frequency; averaged activity of the coBr and iBr. Data trials include those from the matched, visual dissociation and acceleration tasks, explaining the difference in onset and duration of bursts. (A) Cell activity is aligned to the onset of the activity in the coBr (indicated by the vertical line). (B) Activity is aligned to the detected onset of the burst of unit activity in each trial (indicated by the vertical line). In A, data are rank-ordered according to the duration of the period of activity in the coBr. In B, they are rank-ordered according to the duration of the measured unit activity. Staggered red, vertical lines on the rasters in A, B indicate the end of the period of activity in the coBr and of the cell activity, respectively. Green and red circles in A indicate, respectively, the onset and offset of the burst of activity. Cell activity in the PEH and the individual trials is filtered at 25 Hz. Note that synchronization on the onset of the cell discharge results in substantial smearing of the EMG bursts supporting the data illustrated in Figure 3 showing that the onset of cell discharge is not time-locked to the onset of EMG activity.

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Figure 4. Relationship of cell discharge onset to distance and time (individual examples). A and C show two examples of cell discharge in the unobstructed (blue line), matched (red), and visual dissociation (green) task in the left limb leads condition, together with traces indicating DTC and TTC of the head from the obstacle. A is the same cell as in Figure 3. The vertical green and red lines are aligned with the average onset of cell discharge as calculated from individual trials (values indicated at the top of each line). Their intersection with the DTC and TTC traces is indicated with colored circles. The probability that the onset of cell activity during the matched and visual dissociation tasks is the same is indicated by the p-value. (B, D) Plots of the average DTC (top graph) and TTC (bottom graph) (± interval of confidence at p<0.05) for the matched and visual dissociation task in the lead and trail conditions. Results of an ANOVA are shown to the top right of each graph and asterisks indicate significant differences between left and right lead and matched (M) and visual dissociation (VD) tasks (Bonferroni correction, p<0.05). Plots for DTC and TTC in B,D are scaled to the same range (Figure 4—source data 1 and 2).

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Figure 5. Relationship of cell discharge onset to distance and time (population analysis). (A) Cells showing both a significant effect of TTC (left, cyan lines) and a non-significant effect of DTC (middle and right, cyan lines). (B) Cells showing a significant effect of DTC (left, red lines) and a non-significant effect of TTC (middle and right, red lines). Green lines in A, B (left) indicate cells showing a significant relationship to both DTC and TTC. Gray lines (middle and right) indicate cells showing a non-significant relationship with each. Magnitude of the response is plotted as a Z score in the left and middle plots and as absolute values on the right. (C) Probability of a significant relationship with TTC as a function of the probability of a significant relationship to DTC (log scales). Cyan rectangle illustrates the 14 DTC-related cells and the red rectangle illustrates the 15 TTC-related cells. Cells that had no relationship to either are clustered in the top right, whereas those with a significant relationship to both are in the bottom left. (D) Modulation index (see Materials and methods) for the DTC and TTC cells; green symbols indicate cells with a significant relationship to both. Asterisks in C and D indicate the two cells illustrated in Figure 4. (E) Histograms illustrating the distribution of values for TTC- and DTC-related cells. (Figure 5—source data 1 and 2). Figure 5—figure supplement 1: Bootstrapped data for index of TTC- and DTC-related cells. DOI: https://doi.org/10.7554/eLife.28143.015
Figure 5—figure supplement 1. Bootstrapped data for index of TTC- and DTC-related cells. For each cell, we used a replacement protocol to create 1000 datasets for each DTC- and TTC-related cell included in Figure 5D. We treated data for the matched and visual dissociation tasks separately but combined data for the left and right lead conditions. The number of points in each condition equaled the original dataset. A and B show the bootstrapped indexes for the two cells illustrated in Figure 4 and indicated by the asterisk in Figure 5D. The ellipse indicates the 95% confidence level. The ellipses for all the cells included in Figure 5D are illustrated in (C); D illustrates the centroids of these ellipses. Although there is some overlap of the two ellipses, the bootstrapped data separate into two groups in the same way as the original datasets.

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**Figure 6.** Relationship of cell discharge onset to distance and time (population averages). (A,D) Five example cells illustrating that the changes in cell discharge in the different populations begin at staggered times preceding the step over the obstacle. Cell discharge patterns taken from the matched condition and aligned to the onset of the Br. Cells scaled to the cell with the highest discharge rate in each illustrated group of cells. (B,C) Average discharge activity of the 14 DTC cells during left (B) and right (C) lead conditions. (E,F) Average discharge activity of the 15 TTC cells during left (E) and right (F) lead conditions. Data in B,C,E,F are shown for the matched (red traces) and visual dissociation (green traces) task. All traces are scaled identically in (B,C) and (E,F). **Figure 6—figure supplement 1:** Additional Population Averages. DOI: https://doi.org/10.7554/eLife.28143.020
Figure 6—figure supplement 1. Additional population averages. (A,B) Two examples of distance-related cells during left limb lead condition. Both examples show an earlier onset of activity during the visual dissociation task (green trace) than in the matched task (red trace). Moreover, in both examples, the discharge is also increased for several seconds before the abrupt increase in discharge related to the step over the obstacle, as illustrated in the population averages of Figure 6B,C. (C,D) Population discharge of all 51 cells included in Figure 5, indicating that the ramp discharge of cell activity as the obstacle moves toward the cat is also reflected in the total population of cells that we recorded.

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**Figure 7.** Effect of obstacle acceleration on behavior and cell discharge. A and B illustrate the distance of the cat from the obstacle at the onset of flexor muscle activity in the left and right limb lead condition (same representation as in Figure 1). The filled box indicates the step in which we applied  

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The steps are color-coded to identify each step before the step over the obstacle together with the pairs of steps, organized in a right/left manner in A and left/right in B. The red vertical line indicates the approximate expected location of the obstacle in the absence of acceleration. The blue vertical line indicates the approximate position of the obstacle at the end of the acceleration. Note that the sequence of the steps reverses during the acceleration. Details are in the text. (C, D) organized as for Figures 3–4, with the bottom trace indicating the speed of the obstacle; note we applied the acceleration 200 ms after the onset of activity in the coBr. Data are shown for the matched (red), visual dissociation (green), and acceleration (purple, 1L or cyan, 2R) task. In C, accelerations correspond to those illustrated in the middle trace of A (1L condition) while in D they correspond to those illustrated in the bottom trace of B (2R condition). Small orange rectangles indicate the coBr burst used to trigger the acceleration and correspond to the colored boxes in A, B. Similarly, numbers beside the Br bursts correspond to the numbers identifying steps in A, B. Same cell as illustrated in Figure 3. (Figure 7—source data 1 and 2). Figure 7—figure supplement 1: Effect of acceleration on gait pattern. Figure 7—figure supplement 2: Relationship between time and distance for the visual dissociation and the 1L acceleration task. Figure 7—figure supplement 3: Relationship between time and distance for the visual dissociation and the 2R acceleration task.

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Figure 7—figure supplement 1. Effect of acceleration on gait pattern. The figure repeats the data from the top part of Figure 7A with the addition of cat figurines to better illustrate the change in the gait pattern produced by the acceleration in the 1L condition. (A) Unperturbed situation in the right limb lead condition. The gait before the step over the obstacle is regular and the cat steps smoothly over the obstacle with the right forelimb. (B) The acceleration during step $-3$ (filled orange box) quickly closes the gap between the cat and the obstacle. As a result, instead of placing the left forelimb in front of the obstacle, as in the top illustration (top dark blue cat figurine), the cat instead, lifts this left limb over the obstacle. Note that the distance of the cat from the obstacle is always measured with respect to the step over the obstacle.

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Figure 7—figure supplement 2. Relationship between time and distance for the visual dissociation and the 1L acceleration task. The two traces at the top repeat the display of cell activity from Figure 7C during the visual dissociation task (green) and during acceleration (purple). The graph shows the relationship between distance and time with respect to the step over the obstacle (time = 0). During the visual dissociation task, there is a linear relationship between the two variables (green line and symbols). In the acceleration task (purple line and symbols), there is a linear relationship until the acceleration begins and then the distance between the obstacle and the cat decreases more rapidly. The text indicates the distance of the obstacle from the cat for exemplar times for the visual dissociation (green values) and the acceleration (purple values). We concentrate on three times indicated by arrows. (1) The green arrow indicates the distance of the obstacle (30.6 cm) at the onset of the cell discharge during the visual dissociation task (745 ms). (2) The black arrow indicates the time at which we applied the acceleration. At that time, the obstacle was 39.4 cm from the cat, but, because of the acceleration, took only 611 ms to close the gap to the cat. (3) In the acceleration condition, cell onset occurred 403 ms before the step over the obstacle. At this time, the obstacle was 30.2 cm from the cat, almost the same distance as when the cell fired in the unperturbed condition. Other values provide the distance of the obstacle from the cat in the two conditions for selected times before the step over the obstacle.

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Figure 7—figure supplement 3. Relationship between time and distance for the visual dissociation and the 2R acceleration task. Figure organized as for Figure 7—figure supplement 2. The green arrow indicates the distance of the obstacle (29.7 cm) at the onset of the cell discharge during the unperturbed visual dissociation task (723 ms). The black arrow indicates the time at which the acceleration was applied (1134 ms before the step over the obstacle). At that time, the obstacle was 56.0 cm from the cat. Cell onset during the acceleration occurred 733 ms before the step over the obstacle (blue arrow). At this time, the obstacle was 36.4 cm from the cat, slightly farther away than when the cell fired in the unperturbed condition.

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Figure 8. Examples and summary of effects of acceleration. (A,B) Example discharge of two DTC-related cells to acceleration of the obstacle in the 1L condition. (C) Example of a TTC-related cell to acceleration in the 1L and the 2L conditions. Figures organized as for Figure 7C. (D,E) Onset of cell discharge during accelerations as a function of the onset during the unperturbed visual dissociation task. Values are relative to the onset of the coBr during the step over the obstacle. (D), accelerations 1 step before (1L, 1R); (E), 2 steps before (2L, 2R). Filled circles in (D,E) indicate cells showing a significant change in the two conditions as determined by a t-test (p<0.05); open circles indicate non-significant values. (F) Slope of the cell discharge during the acceleration as a function of the slope during the unperturbed visual dissociation task. Slopes from all four acceleration conditions are

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illustrated (see key). Stars indicate the examples illustrated in Figures 7C and 8A,B (see text). Slopes were calculated from averaged traces as (max discharge– discharge at cell onset)/\Delta t. Boxes on the coBr trace in A-C indicate the burst used to trigger the acceleration. (Figure 8—source data 1 and 2).

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Figure 9. Population activity during obstacle acceleration. (A,B) Population discharge activity is shown for all cells for which we applied the 1L and 2R protocols. Green traces show averaged activity in the visual dissociation task; the purple trace indicates the 1L acceleration condition; and the cyan trace indicates 2R condition. Data aligned to the onset of activity in the Br during the step over the obstacle. Boxes on the coBr trace in A,B indicate the burst used to trigger the acceleration (Figure 9—figure supplement 1: Population averages during Acceleration Task).
Figure 9—figure supplement 1. Population averages during acceleration task. (A) 1R condition. (B) 2L condition. Data are organized as for Figure 9.
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Figure 10. Conceptual model illustrating a possible mechanism for limb selection. Left (A) and right (B) limb lead conditions. The top parts of A,B show activity on the left side of the brain and the bottom parts of A,B, show activity on the right side of the brain. In each part of the figure, the traces represent, from top to bottom, the population neuronal activity in the PPC, EMG activity from the left or right Br, a signal representing limb state, and the integrated (summed) activity of these two traces. We suggest that the signal from the PPC, providing information on gap closure, is integrated with a second signal providing information on limb state, on each side of the brain. Whichever integrated signal crosses a threshold level first determines which limb will be selected to be the first to negotiate the obstacle. The population neuronal activity in this illustration is assumed to start 60 cm before the step over the obstacle in both the left and right limb leads conditions. Whether the animal steps over with the left or right limb depends on when cell activity begins with respect to the ongoing locomotor activity of the animal. In A, a threshold level is achieved first on the left side (top illustration), whereas in B, the threshold level is achieved first on the right side (bottom illustration). Note that the integrated value will only cross the threshold level when the signal from the moving limb shows it to be in a state that is appropriate to negotiate the obstacle (e.g. the end of stance).

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