Neural correlates of biased competition in premotor cortex

Alexandre Pastor-Bernier and Paul Cisek

Département de physiologie and Groupe de recherche sur le système nerveux central
Université de Montréal, Montréal, Québec, Canada

SUPPLEMENTAL MATERIALS

Task apparatus and recording sites

The task involved moving a cursor from a central circle (2cm radius) to one of six possible targets (2.4cm radius) spaced at 60° intervals around a 12.6cm radius circle. The monkey performed movements using a cordless stylus whose position was recorded (125Hz) by a digitizing tablet (*CalComp*). Target stimuli and continuous cursor feedback were projected onto a mirror suspended between the monkey's gaze and the tablet, creating the illusion that they are in the plane of the tablet. Oculomotor behavior was unconstrained as eye movements do not strongly influence arm-related PMd activity (Cisek and Kalaska, 2002). Neural activity was recorded with 3-4 independently moveable microelectrodes (*NAN microdrive*) and data acquisition was performed with AlphaLab (*Alpha-Omega*). On-line spike discrimination was used to estimate cell preferred directions for choosing target locations. All analog waveforms were stored on disk for offline sorting using principal components (*Plexon*). All task events, trajectory data and spike times were stored in a database (*Microsoft SQL Server 2005*) accessed through custom scripts for data analysis (*Matlab*). After completing training, the animal was implanted under general anesthesia with a titanium head post and a recording chamber placed using MRI images (*Brainsight primate*). The chamber was centered on the arm area of PMd, between the precentral dimple and the junction of the arcuate sulcus and spur (Supplemental Fig 1). All procedures followed university and national guidelines for animal care.

Calculation of directional tuning

We calculated directional tuning preferences of each cell during each behavioral epoch (DELAY, MT, and THT) in the 1T block, and assessed significance with a non-parametric bootstrap test (1000 shuffles, $p<0.05$; Cisek et al., 2003). The PT of each cell was based on its activity in the DELAY period. For cells that did not have trials in the 1T block (e.g. cells which were found while the monkey was performing the 2T block) the PT was based on the delay period activity for FREE trials in which a high-valued target (PT selected) and a low-value target (OT non-selected) was presented to the monkey, who selected the high-value target. The tuning obtained with this method was readily comparable with the tuning obtained in the 1T task, with very few exceptions (N=2 cells, which were not tuned in 1T and became tuned in the 2T task). A possible confound with this tuning method is that it assumes that cells have value effects in the 2T block. To investigate the impact of such an assumption, we calculated the tuning of DELAY cells

with 1T trials (N=86/112, 77%) and DELAY cells without 1T trials (N=26/112, 23%) and treated them as two separate groups. Similar proportions of cells had statistically significant effects using t-tests ($p<0.05$): 42 out of 86 (49%) DELAY-tuned cells with 1T trials had value effects in 2T and 12 out of 26 (46%) DELAY-tuned cells without 1T trials had value effects in 2T. Comparable results were obtained using ANOVA and a post-hoc Tukey-Kramer test ($p<0.05$): 37 out of 86 (43%) DELAY tuned cells with 1T trials had value effects and 12 out of 26 (46%) DELAY tuned cells without 1T trials had value effects. A population analysis limited to cells with both 1T and 2T trials (Supplemental Fig 3) exhibited similar trends as an analysis of the total population (including cells without 1T trials). As in the full data, no significant effects were found during the DELAY in the 1T task (Wilcoxon signed-rank test, $p=1$) and value and distance effects were observed in the 2T task ($p<10^{-4}$ in 2T for all comparisons). This suggests that both groups of cells (with and without 1T trials) belong to the same population and were therefore analyzed together in the main text.

Additional repetitions in single-cell recordings

A typical 2T block had 90 trials with targets 120° apart, and the PT of an isolated cell was one of the targets in 60 of these trials. In an additional 60 trials the PT appeared with an OT 60° away, and in 30 the PT appeared with an OT 180° away. Thus, in each 2T block the trials in which the targets are 180° apart were slightly under-represented with respect to trials with the other two angular distances (60° and 120°). For cells that were held isolated long enough (Distance-complete cells) a comparable number of trials across angular distances were obtained through block repetition.

Statistics for the assessment of value and distance effects

To assess the statistical significance of value and/or distance effects at the individual cell level, we compared the DELAY period activity of each cell using two-tailed t-tests ($p<0.05$) and an analysis of variance (ANOVA) with post-hoc Tukey-Kramer tests ($p<0.05$). For example, the delay period activity for trials in any of the three values tested in 1T (L, M or H) were compared using ANOVA to assess whether there was a statistical difference within any value combination: low *vs.* high, low *vs.* medium and medium *vs.* high. Two-tailed t-tests and Tukey-Kramer tests were used to determine whether there was a statistically significant difference in a particular value combination (Criteria for a cell with value effects). In the 1T task there was no statistical significance for any cell with either of these two methods. In the 2T condition where the value in OT was varied (L, M, H) and the value in PT was held constant (M), the possible combinations were OT:low *vs.* OT:medium, OT:low *vs.* OT:high and OT:medium *vs.* OT:high. Both t-tests and ANOVA with Tukey-Kramer tests were in close agreement qualitatively and quantitatively (t-test: N=49 with $p<0.05$; ANOVA: N=42 with $p<0.05$). Similar numbers were obtained in the 2T condition in which the PT value was varied (L, M, H) and the OT value was held constant (M). The analysis of DELAY period activity for the three angular distances in 2T (60°, 120° and 180°) was performed with t-tests and ANOVA in a similar way as with value comparisons (t-test N=22 with $p<0.05$ and ANOVA N=18 with $p<0.05$). In general, both t-test and ANOVA methods were found to be in close

agreement, yielding N=52 cells with reward or value effect with t-tests and 47 cells with ANOVA and Tukey-Kramer tests.

In addition, we performed 2-way ANOVAs to compare reward value in PT and angular distance as well as reward value in OT and angular distance. Fourteen out of 38 distance-complete cells (37%) showed a significant interaction between relative value and angular distance. This is in good agreement with the proportion of cells obtained with the t-test method 19/38 (50%). The interactions between relative value and angular distance were also quite similar for the distance-complete cells that had both 1T and 2T trials 12/31 (39%, 2-way ANOVAS) and 17/31 (54%, t-tests).

Determination of a unique value for latency of effects

The latency for relative reward or distance effects was taken as the earliest discrimination time for value effects. For example, in the 2T condition where the value in OT was varied (L, M, H) and the value in PT was held constant (M), the latency of relative value effects was chosen as the earliest among the combinations OT:L *vs*. OT:M, OT:L *vs.* OT:H and OT:M *vs*. OT:H. The earliest latency for angular distance was chosen among the earliest discrimination time among the following combinations: 60° *vs.* 120°, 60° *vs.* 180°, or 120° *vs.* 180°.

Supplemental Table 1.
Classification of delay activity according to observed effects

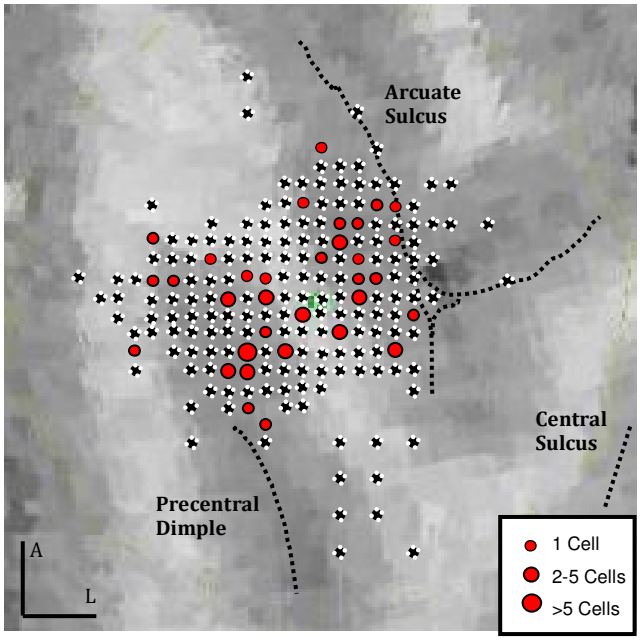
	N	N (1T & 2T)*
Cells tuned during delay (Delay-tuned)	**112**[1]	**89**
Delay-tuned with any effect of value or distance	**52**[2]	**41**[2]
Delay-tuned with value effect in 1T	0	0
Delay-tuned with value effect only (in 2T)	30	22
Delay-tuned with distance effect only	3	2
Delay-tuned with both value and distance effects	19	17
Delay-tuned with any value effect	49 (30+19)	39 (22+17)
Delay-tuned with any distance effect	22 (3+19)	19 (2+17)
Distance-complete delay-tuned cells	**50**	**41**
Distance-complete with any effect	**38**[3]	**31**[3]
Distance-complete with value effect in 1T	0	0
Distance-complete with value effect only (in 2T)	16	12
Distance-complete with distance effect only	3	2
Distance-complete with both value and distance effect	19	17
Distance-complete with any value effect	35 (16+19)	29 (12+17)
Distance-complete with any distance effect	22 (3+19)	19 (2+17)

(1T & 2T)* : Cells that have trials collected in both the 1T and 2T conditions
[1, 2] Cells used for general population analyses.
[3] Cells used for distance-and-value interaction effect (gain effect) and latency analyses.

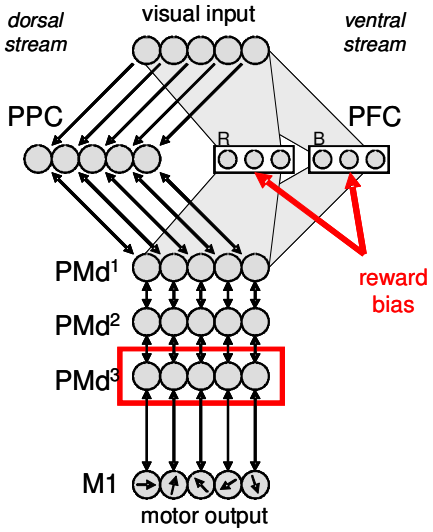
Supplemental References

Cisek P, Kalaska JF (2002) Modest gaze-related discharge modulation in monkey dorsal premotor cortex during a reaching task performed with free fixation. J Neurophysiol 88:1064-1072.

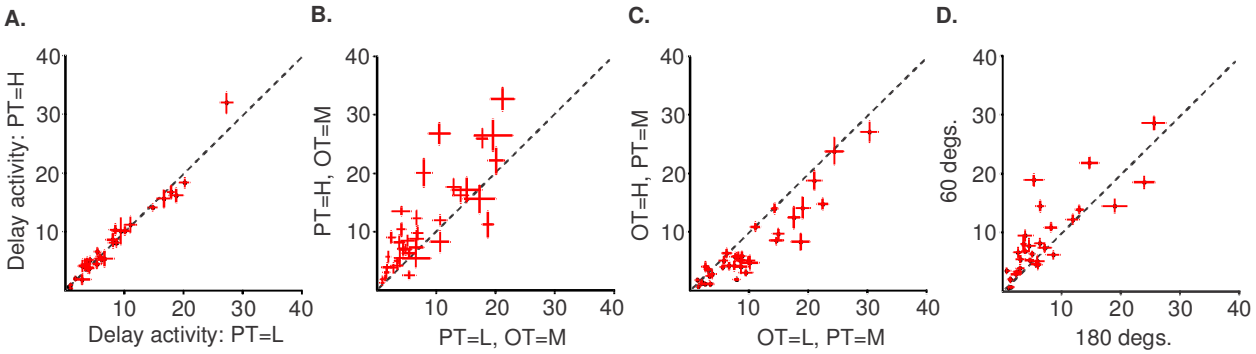
Cisek P, Crammond DJ, Kalaska JF (2003) Neural activity in primary motor and dorsal premotor cortex in reaching tasks with the contralateral versus ipsilateral arm. J Neurophysiol 89:922-942.



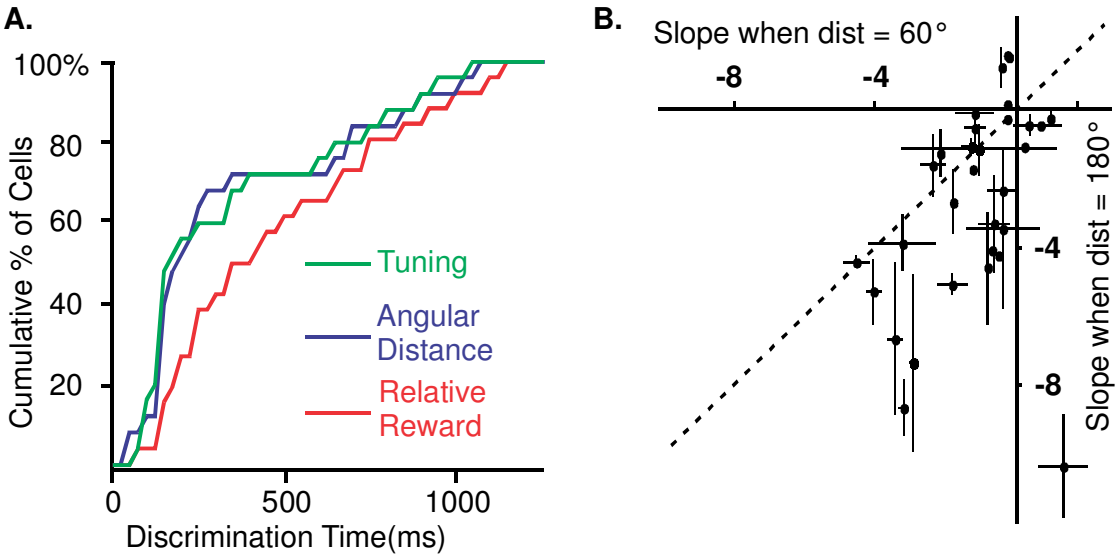
Supplemental Figure 1. Recording locations in PMd. Black crosses indicate recording sites. The locations for tuned cells with effects are shown with red circles (N = 52).



Supplemental Figure 2. Model of action selection, in which populations of cells along the dorsal stream implement a distributed representation of potential actions that compete against each other through lateral inhibition. Each population is modeled as a set of tuned neurons with "on-center-off-surround" recurrent connectivity. The model includes posterior parietal cortex (PPC), prefrontal cortex (PFC), three layers of PMd (rostral to caudal) and primary motor cortex (M1). Biasing signals related to absolute reward value enter as input to the PFC layer. Figure 4 in the main text shows activity from the caudal PMd population (red box).



Supplemental Figure 3. Population analyses limited to cells that had trials both in 1T and 2T blocks. **A.** Mean firing rate of individual cells in the 1T task when the PT was low-valued (x-axis) versus high-valued (y-axis). Each cross indicates mean and standard error of the mean. **B.** Firing rates comparing 2T trials in which the OT is medium-valued and the PT is low-valued (x) versus high-valued (y). **C.** Comparison of 2T trials in which the PT is medium-valued and the OT is low-valued (x) versus high-valued (y). **D.** Comparison of 2T trials in which both the PT and OT are medium-valued and are 60° (x) versus 180° apart (y).



Supplemental Figure 4. Latency and gain effect analysis limited to cells that had trials in both 1T and 2T. **A.** Cumulative distribution of latencies with which the cells (Distance-complete cells, N=31) exhibit tuning in the 1T task (green), and discriminate angular distance (blue) and relative value (red) in the 2T task. **B.** Comparison of the mean (and s.e.m.) of the slopes in the 60° versus 180° conditions, for all distance complete cells, N=31).