

Neural biases in PMd and M1 during a two-target reaching task

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When the motor system is presented with multiple potential actions, it weighs information about relevant task-related variables (e.g. movement complexity, potential for reward, time constraints) to arrive at a final decision. If these differ significantly for some action choice (e.g., if a leftward reach is likely to result in a much larger reward than a rightward reach), the final decision may be predictable. However, when all options are equal, the decision must be driven by internal biases or stochastic processes within the involved brain areas. By recording simultaneously from many neurons, we were able to observe the dynamics of decision making on single trials. We found that when presented with two equipotential reach targets, both dorsal premotor cortex (PMd) and primary motor cortex (M1) displayed a wide range of biases in representation. When one of the movement options subsequently disappeared, both areas either maintained (if initial bias was correct) or switched (if initial bias was incorrect) to a representation of the remaining target. The observed magnitudes and dynamics of these processes suggest that movement planning and decision-making is quickly influenced by both internal and external factors.

Methods

In order to probe movement planning on single trials, we recorded from chronically implanted 96-channel electrode arrays in both PMd and M1 as a Rhesus macaque performed two blocks of center-out reaches (Fig. 1). On each trial of the first block (one-target trials), we presented a single target (in one of eight locations) with two instructed delays, separated by a brief memory period. In the subsequent block (two-target trials), we instead presented two targets separated by 180 degrees during the first delay period, but removed one prior to the second delay.

We analyzed single trial activity by first reducing the recorded activity to ten dimensions using principal component analysis (PCA; calculated from single-target activity). Throughout each two-target trial, we calculated the Mahalanobis distance between the instantaneous 10-D neural state and the neural state corresponding to each of the eight single-targets (Fig. 2). This provided, on each trial, an estimate of the neural state with respect to each target axis. We identified biases in neural representation of simultaneous targets by comparing these distances as the trial progressed.

Results

Averages over all trials appeared to suggest that the appearance of two targets lead to an immediate and equal representation in PMd that persisted throughout the entirety of delay period (Fig. 3A). Similarly, M1 appeared to be almost completely uninvolved until the monkey received the single target cue (Fig. 3B). However, by analyzing activity on single trials, we found that PMd activity during the memory period was significantly biased toward one or the other of the two targets on about 83% of trials. On many of these trials, it appeared that the monkey was not only biased, but had actually disregarded one of the targets altogether (Fig. 3C, negative values during memory period). In general, we found a wide range of biases in PMd representation throughout the first delay period, often originating about 200 ms after cue onset (Fig. 4A). The biases identified in PMd were also observed in M1, suggesting that they did not result from non-uniform neural sampling or a similar artifact from the analysis. Additionally, the biases were not fixed for a given target pair, with a seemingly random distribution of biases across trials.

In addition to early-phase biases, we also observed significant differences in the neural state at the time of movement for one- and two-target trials. Even though we found no differences in reach kinematics for the two trial types, the relative strength of the selected target representation (compared to non-selected target) at the time of movement initiation was weaker in both PMd and M1. This effect also appeared to be slightly affected by the early trial bias in PMd, with the lowest relative representation observed during “switch” trials. Thus, not only do strong biases in neural representation exist despite equivalent potential reach targets, but the effects also persist throughout movement planning and execution.

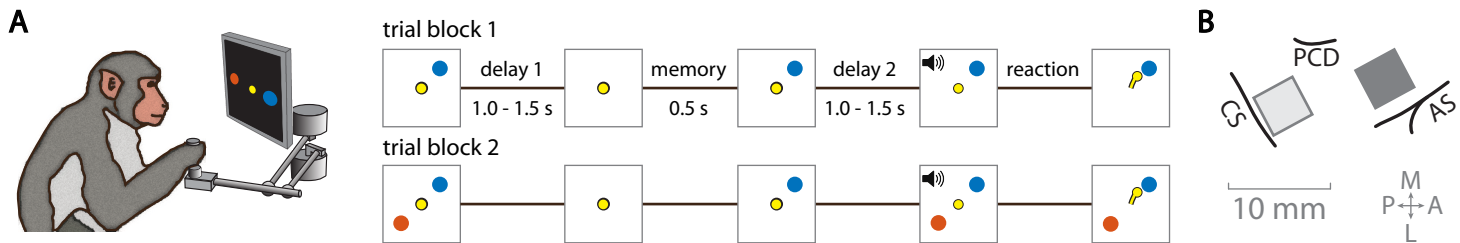


Figure 1. Experimental setup. **A.** A monkey performed center-out reaches using a planar robotic manipulandum to control a cursor on a vertical monitor. During each trial in the first block, the monkey was presented with a single target in one of eight locations. After two instructed delay periods separated by a short memory period, the monkey received an audible go cue. In the second block of trials, the monkey was presented with two targets separated by 180 degrees. Following the memory period, one of the targets was removed for the entirety of the second delay period. **B.** Throughout the experiment we recorded from two chronically implanted 96-electrode arrays (Blackrock Microsystems Inc.) implanted in dorsal premotor (PMd) and primary motor (M1) cortex.

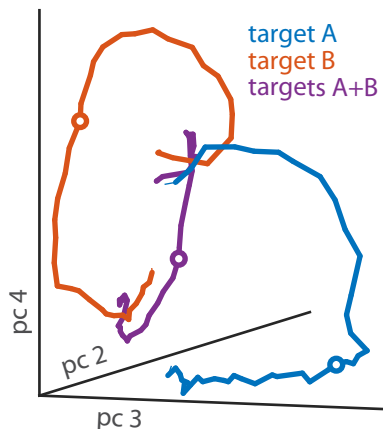


Figure 2. Example low-dimensional trajectories of delay-period PMd activity during trials with one (blue, orange) or two (purple) targets. We computed the representation during each two-target trial by calculating the Mahalanobis distances between the instantaneous 10-D neural state and the neural states observed during trials to each of the eight targets in the first trial block.

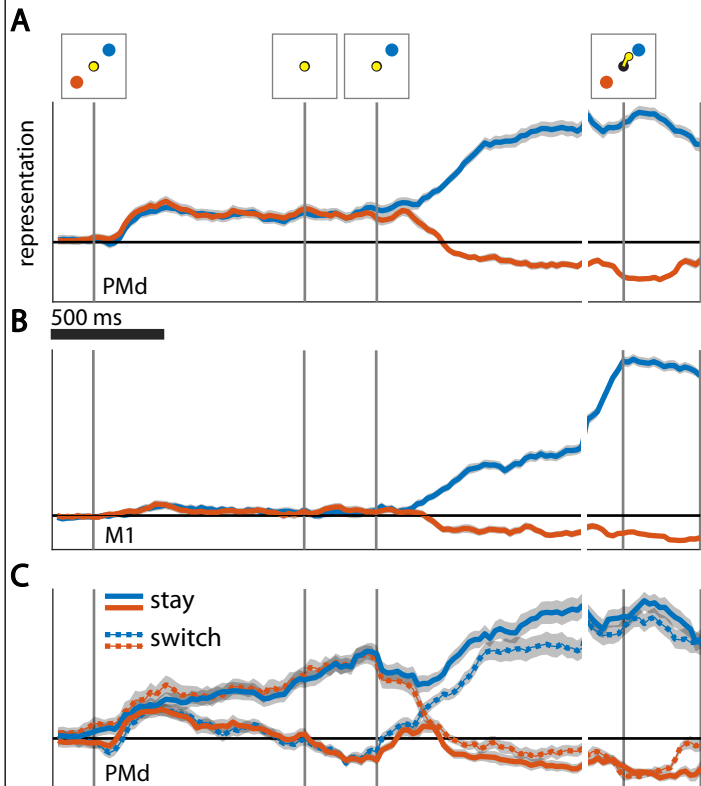


Figure 3. Two-target representations from low-dimensional neural trajectories. **A.** PMd representations of both presented targets, averaged over all trials. Representations for both targets appear quickly after presentation, and remain until the single target cue. **B.** Same as A but for M1. Representations appear only after presentation of single target cue. **C.** Same data as in A, but split into 'stay' and 'swap' trials. Stay trials correspond to those in which the memory-period representation in PMd was significantly biased toward the target that was ultimately cued. Swap trials correspond to trials with a significant bias toward the other (non-cued) target. Stay and swap trials accounted for 83% of all trials.

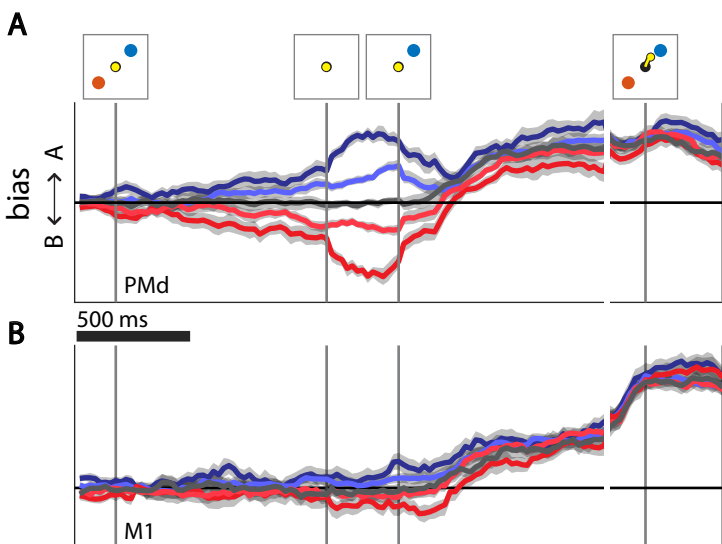


Figure 5. Bias in representation of presented targets. **A.** Biases in the representation of the two targets for all trials, split by magnitude of bias. Trials were categorized as either strongly biased (dark blue/red; 30%), weakly biased (light blue/red; 53%) or not biased (grey; 17%). The cued (correct) target was always labeled 'Target A'. **B.** Biases calculated in M1 activity using the trial groupings defined in A. Although much less pronounced, memory-period biases in M1 matched those of PMd.

Figure 4. Traces of non-selected target representation persist throughout movement initiation. Despite there being no difference in reach kinematics (reach speed, reaction time, etc.), in the two-target task, both PMd and M1 represented the chosen target more weakly than the non-selected target. This effect persisted throughout movement initiation, suggesting that motor areas maintain residual representations of available but non-selected movement options.

