Neuron
Article

Deliberation and Commitment in the Premotor and Primary Motor Cortex during Dynamic Decision Making

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http://dx.doi.org/10.1016/j.neuron.2014.01.031

SUMMARY

Neurophysiological studies of decision making have primarily focused on decisions about information that is stable over time. However, during natural behavior, animals make decisions in a constantly changing environment. To investigate the neural mechanisms of such dynamic choices, we recorded activity in dorsal premotor (PMd) and primary motor cortex (M1) while monkeys performed a two-choice reaching task in which sensory information about the correct choice was changing within each trial and the decision could be made at any time. During deliberation, activity in both areas did not integrate sensory information but instead tracked it and combined it with a growing urgency signal. Approximately 280 ms before movement onset, PMd activity tuned to the selected target reached a consistent peak while M1 activity tuned to the unselected target was suppressed. We propose that this reflects the resolution of a competition between the potential responses and constitutes the volitional commitment to an action choice.

INTRODUCTION

When buying a house, one is motivated to first collect relevant information and then take time to think about the best choice. Because careful deliberation is important to human behavior, studies of the neural mechanisms of decision making have largely focused on scenarios in which subjects decide about information that is stable over time. For example, perceptual decisions are usually studied using stimuli whose informational content is constant in each trial (Britten et al., 1992; Romo et al., 2004), leading to models of deliberation as the integration of sensory evidence to a threshold (Gold and Shadlen, 2007; Ratcliff, 1978). Likewise, studies of value-based decisions focus on conditions in which the value of options is stable (Padoa-Schioppa, 2011; Platt and Glimcher, 1999), leading to serial models in which the costs and benefits are converted into a "common currency," the decision is made, and the chosen action is then prepared (Padoa-Schioppa, 2011). However, the vertebrate brain evolved to guide behavior in a dynamic world, in which decisions are made during ongoing activity, action options and their payoffs are continuously changing, and animals are free to decide when to take time to deliberate and when to commit quickly to their current best guess. Here, we investigate such "embodied" decisions and ask which conclusions from static scenarios generalize to real-time dynamic decisions.

In particular, studies of static tasks have suggested that the brain gradually integrates repeated samples of the stimulus, causing neural activity to build up to a threshold (Gold and Shadlen, 2007; Ratcliff, 1978). However, if the sensory information can suddenly change, such a process is suboptimal, because integrators are sluggish to respond to changes in input. Recent human studies of dynamic tasks have suggested that instead of integrating the sensory state, the brain quickly tracks it, and activity buildup is caused by a growing urgency to act (Cisek et al., 2009; Thura et al., 2012). These models can only be distinguished with dynamic tasks, because they make identical predictions for any static task, at both the behavioral and neural level.

Furthermore, many neurophysiological studies have shown that decision making influences activity in the sensorimotor system (Gold and Shadlen, 2000; Platt and Glimcher, 1999; Salinas and Romo, 1998; Wallis and Miller, 2003). In particular, when animals are faced with multiple response options, the brain represents them in parallel within sensorimotor regions (Baumann et al., 2009; Cisek and Kalaska, 2005; McPeek et al., 2003), and these representations are modulated by decision variables (Basso and Wurtz, 1998; Dorris and Glimcher, 2004; Pastor-Bernier and Cisek, 2011; Roitman and Shadlen, 2002; Yang and Shadlen, 2007). For example, information for deciding between manual actions influences neural activity in premotor and parietal regions (Hernández et al., 2010; Klaes et al., 2011; Pastor-Bernier and Cisek, 2011), modulates corticospinal excitability (Klein-Flügge and Bestmann, 2012; Michelet et al., 2010), and even influences reflexes (Selen et al., 2012). Such results have led to the proposal that decisions between actions involve processes within the sensorimotor system (Cisek, 2007; Hernández et al., 2010; Shadlen et al., 2008). However, it is also possible that they simply reflect information that spills in from upstream regions that are actually responsible for deliberation and commitment. To establish whether the sensorimotor system

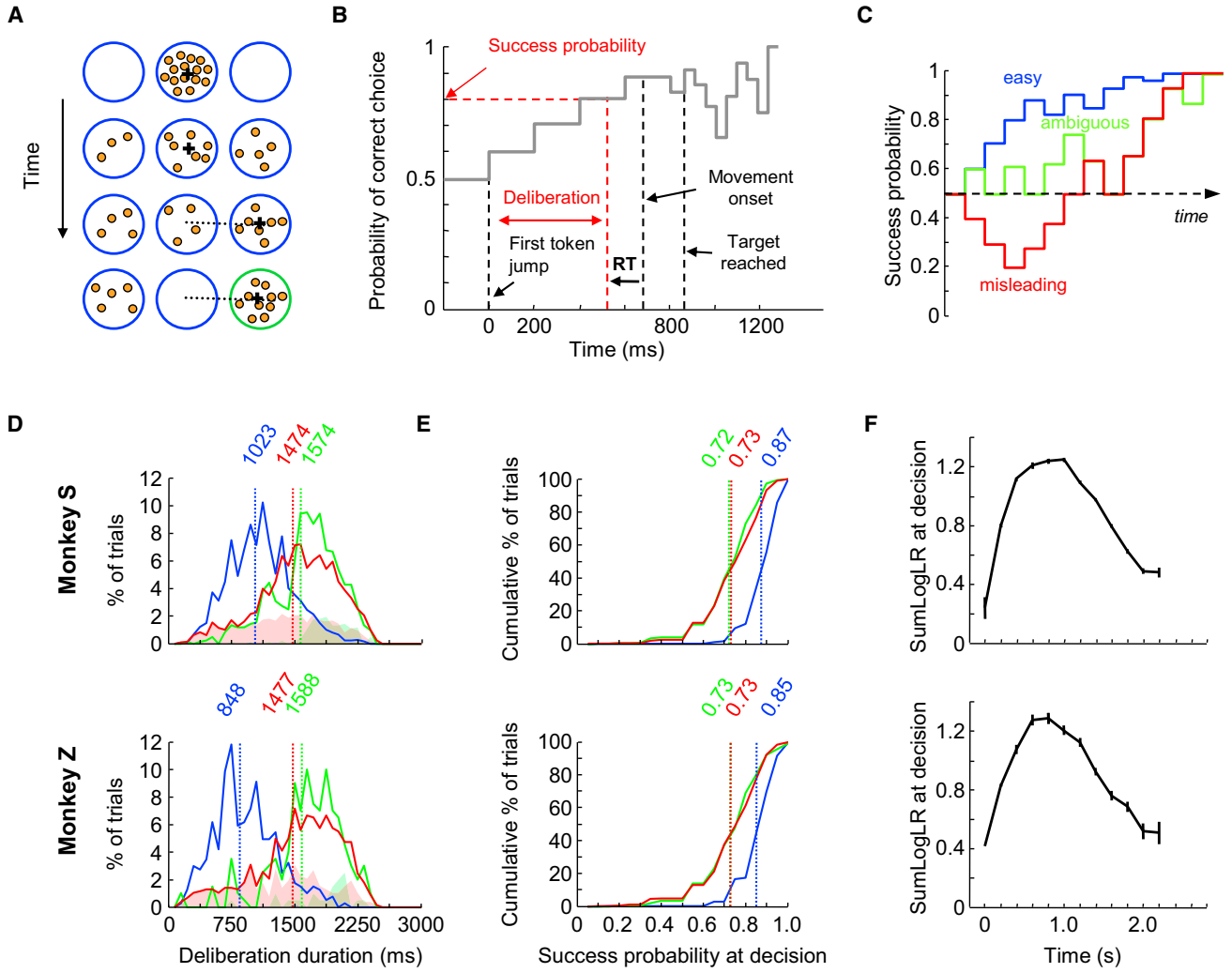

Figure 1. Task and Behavior

(A) The token task (see text).

(B) Temporal profile (thick gray line) of the probability that a given target is correct, computed using Equation 1. The vertical, dashed red line indicates the estimated time of the decision (see text), allowing estimation of the success probability at that moment (horizontal, dashed red line).

(C) Profiles of success probability of one easy (blue), one ambiguous (green), and one misleading trial (red). A trial is considered easy if the SP exceeds 0.6 after two token jumps and 0.75 after five. A trial is ambiguous if SP is 0.5 after two jumps, between 0.4 and 0.65 after three, and then between 0.55 and 0.66 after five and seven jumps. A trial is misleading if SP is below 0.4 after three jumps.

(D) Distributions of decision durations in easy (blue), ambiguous (green), and misleading (red) trials for monkey S (top) and Z (bottom). Shaded regions indicate error trials. Vertical dotted lines indicate the mean (in ms) for each trial type.

(E) Cumulative distributions of success probabilities at decision time in the same trial types. Vertical dotted lines indicate mean success probability.

(F) Mean (±SE) of the estimated confidence (SumLogLR) at which the decision was made, averaged across all trials grouped as a function of decision duration.

plays an active role in deliberation, neural activity must be examined well before commitment is made, and this can be accomplished with dynamic tasks.

Here, we investigate these questions through neurophysiological recordings in the dorsal premotor (PMd) and primary motor cortex (M1) of monkeys trained to perform two reaching tasks. In the "tokens" task (Figure 1A), monkeys watch a set of 15 tokens jumping every 200 ms from a central target to one of two peripheral targets and must guess which target will ultimately receive the majority of the tokens. Importantly, the decision can be taken at any time, and when a target is reached, the token jumps accelerate, allowing the monkey to save time by taking an early guess. In the "delayed response" (DR) task, only a single peripheral target is presented, and the monkey must withhold movement until the 15 tokens jump into the target simultaneously (GO signal).

Our paradigm has two critical properties. First, the sensory evidence in the tokens task is continuously changing, allowing us to dissociate different models of how sensory information is treated. Second, in the tokens task, the monkeys are free to

respond at any time, allowing us to distinguish processes related to deliberation from those related to commitment. In particular, by comparing activity during the tokens task with activity during the DR task, in which both the choice and its timing are externally instructed, we can identify the neural phenomena specifically associated with volitional commitment to action.

RESULTS

The Decision Criterion Decreases over Time

In the tokens task, monkeys' success rate varied between 64%–87% (mean: 77%; SD: 5%, SE: 0.5%). To analyze how behavior depended upon the specific pattern of token jumps in each trial, we first estimated the total sensory and motor delays using the mean reaction time (mRT) from the DR task (Monkey S: 291 ± 40 ms; Monkey Z: 335 ± 93 ms) and then subtracted this from the reaction time (RT) in the tokens task to estimate the decision time (DT) (Figure 1B). Next, we estimated the success probability at decision time (SPD) using Equation 1 below. We compared these variables in three trial types: easy, ambiguous, and misleading (Figure 1C), classified post hoc from the fully random trials. As expected, both monkeys made decisions significantly earlier in easy than in ambiguous or misleading trials (Kolmogorov-Smirnov [KS] test, $p < 0.01$) (Figure 1D). They also made decisions at a significantly lower level of success probability in ambiguous and misleading trials than in easy trials (KS test, $p < 0.05$) (Figure 1E). This is consistent with the hypothesis that to solve the task, monkeys use an accuracy criterion that decreases over time. To test this across all trials, we grouped data according to the number of tokens that moved before DT and calculated an estimate of the accuracy criterion (or "confidence") for the selected target at that time. This estimate was based on the sum of the log likelihood ratios of individual token jumps (SumLogLR; see Experimental Procedures), which is related to the difference in the number of tokens in the two targets. The result is shown in Figure 1F. Except for fast guesses (<1 s), there is a trend for decisions to be made at a lower level of accuracy as time passes. This demonstrates that both monkeys use a similar strategy as humans to solve the task (Cisek et al., 2009)—they decrease their accuracy criterion over time. Previous studies have suggested that this can be implemented by combining sensory information with a growing "urgency signal" (Churchland et al., 2008; Cisek et al., 2009; Standage et al., 2011; Thura et al., 2012).

Neural Activity in PMd and M1 Reflects the Time Course of Sensory Evidence

While monkeys performed the tokens task, neural activity was recorded from 178 cells in the arm area of PMd (135 in monkey S) and 74 cells in M1 (55 in monkey S) excluding the most caudal region in the central sulcus (Figure S1 available online). Among these, 99 cells (68 in PMd and 31 in M1) had a significant directional preference before DT (see Experimental Procedures) and thus reliably predicted whether an arm movement would be made toward or away from the cell's preferred target (PT).

Figure 2A shows the activity of an example PMd neuron, aligned on the start of token jumps and plotted until 300 ms before movement onset, during easy, ambiguous, and misleading trials in which the monkey chose the cell's PT or the opposite target (OT). In easy trials, activity strongly and quickly increases when the monkey selects the PT and is quickly suppressed when the OT is chosen. In ambiguous trials, activity fluctuates and gradually increases during the first seven token jumps (~1.4 s), and the cell discriminates between PT and OT only late in the trial. The pattern of activity is again very different in misleading trials. When the PT is ultimately selected, activity is initially low while the first few tokens favor the OT and later switches to predict the PT choice. In contrast, in OT trials the early activity is strong, while tokens favor the PT, and later decreases.

Interestingly, we found very similar phenomena in M1, as shown in Figure 2B for an example cell. Like the PMd cell in Figure 2A, this M1 neuron quickly reflected the choice in easy trials, fluctuated during ambiguous trials, and reflected the switch of evidence in misleading trials.

Figure 2C illustrates the average activity of all 68 PMd and 31 M1 decision-related neurons. The top panel shows the profile of success probability for each cell's PT for easy (blue), ambiguous (green), and misleading (red) trials in which the monkey correctly chose the PT (solid) or OT (dashed). Below that, we show the average neural activity of the 68 PMd and 31 M1 cells aligned on the first token jump and plotted until 300 ms before movement initiation (diamonds) during those same trials. About 150 ms after the first token jump, activity increases or decreases in a manner that reflects the sensory evidence and the monkey's ultimate choice, especially in PMd. In addition to the influence of the changing sensory evidence, there is a trend for activity to increase over time, and this is especially pronounced in M1.

To further quantify these observations, we calculated the latency at which activity discriminates between PT and OT for all PMd and M1 decision-related cells in easy or ambiguous trials. The mean discrimination time was significantly shorter in easy than in ambiguous trials both in PMd (280 versus 624 ms; KS test; $p < 0.01$) and in M1 (341 versus 807 ms; KS test; $p < 0.01$). Moreover, in both easy and ambiguous trials, discrimination times were shorter in PMd than in M1, although this did not reach significance (KS test; $p > 0.05$).

To quantify the effect of sensory evidence on neural activity across all trials (not just the three types shown in Figure 2), we measured each cell's firing rate in successive 200 ms epochs following the first token jump. We then plotted this as a function of the sensory evidence (SumLogLR) present during the previous token jump (to allow for sensory delays). The result for example PMd and M1 cells is shown in Figures 3A and 3C, respectively. Both neurons exhibited a clear modulation of activity as a function of the evidence, increasing their firing rate as the evidence in favor of their PT increased (Spearman's rank test; mean $r = 0.93$ for the PMd neuron and 0.75 for the M1 neuron). Moreover, this relationship changed as time was passing. In particular, both the baseline and the slope (calculated at the equal evidence point; vertical dashed line) tended to grow over time. These effects also held at the population level in both PMd and M1 (Figures 3B and 3D). Notably, at the population level, the increase of activity over time was primarily due to a baseline shift (Figure S2).

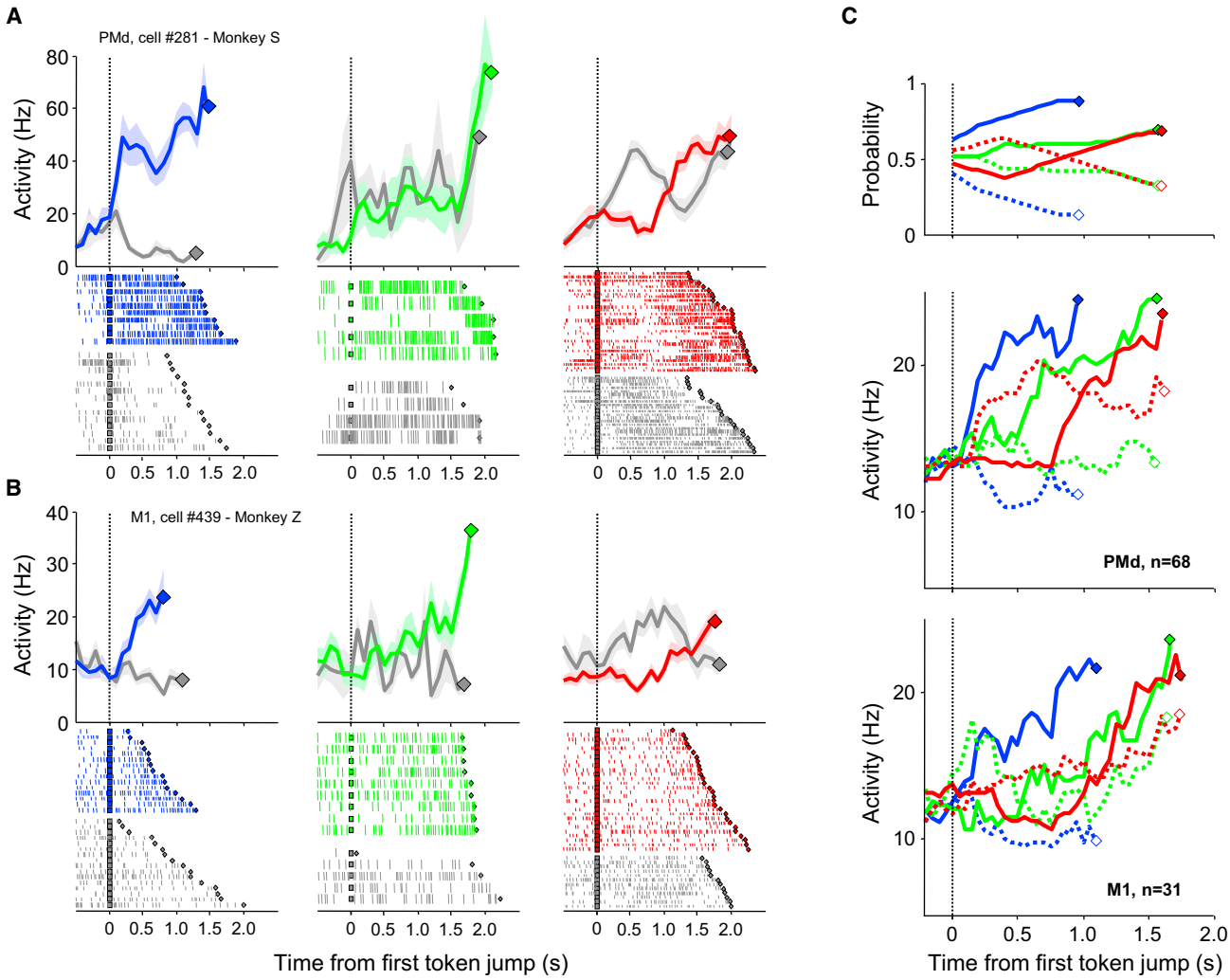

Figure 2. Neural Activity Tracks the Changing Evidence

(A) Response of a decision-related PMd neuron in the tokens task during easy (left), ambiguous (middle), and misleading (right) trials in which the monkey correctly chose the cell's PT (colored) or OT (gray). Activity is aligned on the first token jump (squares) and truncated 300 ms before movement onset (diamonds) to avoid averaging artifacts. Rasters are sorted by decision duration.

(B) Same as A for an example M1 neuron.

(C) Top shows the success probability of the PT during easy (blue), ambiguous (green), and misleading (red) trials, in which the monkey correctly chose the PT (solid lines) or OT (dotted lines). Middle shows the average activity of 68 spatially tuned PMd neurons during those same trials. Bottom shows the average activity of 31 spatially tuned M1 cells.

PMd and M1 Track the State of Sensory Information without Integrating It

The above results raise the question of what computational mechanism transforms sensory information into neural activity and what is responsible for the activity buildup. It has been suggested that during perceptual discrimination, such as deciding about the direction of noisy motion, the sensory signal is integrated over time by repeatedly resampling the stimulus (Bogacz et al., 2006; Gold and Shadlen, 2007). Does a similar mechanism operate during the tokens task? In particular, does the brain temporally integrate the state of the sensory information about which the decision is made (i.e., the distribution of tokens), or does it simply track that sensory state? To distinguish between these two mechanisms, we examined additional trial types, classified post hoc from the fully random set. For example, during "bias-up/down" (BUD) trials (Figure 4A, top, green line) the first three tokens move to the PT, then the next two move toward the OT, and then the rest of the trial resembles an easy trial toward the PT (which is the correct target). In contrast, during "bias-down/up" (BDU) trials, the first two tokens move to the OT and the next three to the PT, and the rest of the trial is similar to BUD. Comparison between these two trial types is critical, because if the sensory state is integrated, then after the fifth token neural activity related to the PT will be higher in BUD than in BDU trials (because an integrator retains a "memory" of previous states). In contrast, if the sensory state is simply

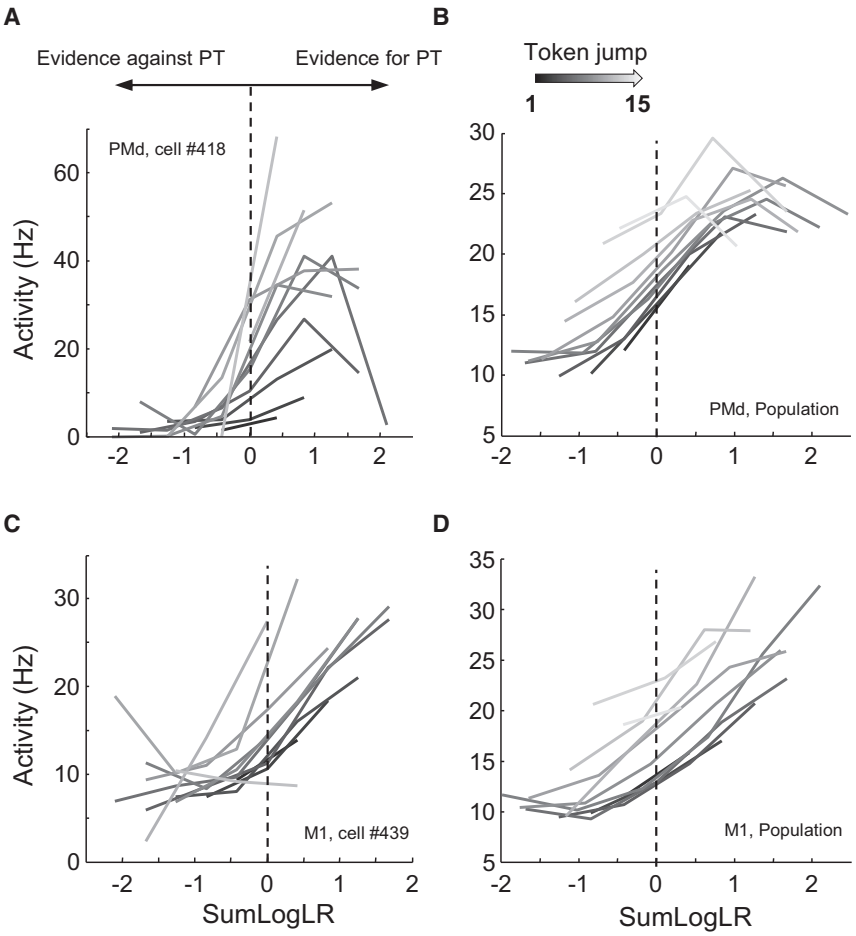

Figure 3. Evolution of the Relationship between Neural Firing and Sensory Evidence

(A) Analysis for one example PMd neuron. Each line illustrates the relationship between the SumLogLR with respect to the PT and the mean neural activity calculated 200 ms later in a 200 ms epoch, color coded from the darkest (first token jump) to the lightest. Only epochs preceding our estimate of DT are included.

(B) Same analysis averaged across 68 PMd cells.

(C) Same as (A) for an example M1 cell.

(D) Same analysis averaged across 31 M1 cells.

tracked, then one would not predict a significant difference between the trial types.

Figure 4A illustrates the activity of one PMd neuron recorded during BUD and BDU trials. Importantly, we include only trials in which the monkey made decisions after the initial bias (>800 ms) and truncate activity 300 ms before movement onset. About 200 ms after the first token jump, activity begins to reflect the bias in the two trial types, becoming stronger in BUD than BDU trials. After 800 ms, as sensory evidence converges in both trials, neural activity likewise becomes similar. Therefore, this neuron did not integrate the sensory state during the bias, but instead tracked it quickly (note the rapid increase of activity after 800 ms in BDU trials, clearly visible in the rasters). This observation holds true when activity is averaged across PMd and M1 cells (Figure 4B). To test whether this effect is robust across individual cells, we compared the mean activity of each PMd and M1 decision-related cell in BUD and BDU trials in two epochs: during and after the bias. As predicted by both mechanisms, during the bias, the response is usually stronger in BUD than BDU trials. However, after the bias, most of the cells no longer discharge differently in the two trial types, consistent with a system that simply tracks the sensory state (Figures 4C and 4D).

The integration and tracking mechanisms also make very distinct predictions at a behavioral level. In particular, integration predicts faster decisions in BUD than BDU trials, whereas tracking predicts no difference. In agreement with the latter, we found no statistical difference between decision durations in BUD versus BDU trials in both monkeys (Figure 5A, top row). Similar analyses on two other pairs of trial types (Figure 5A, middle and bottom rows) yielded the same conclusion—that choices were not biased by the early evidence, consistent with fast tracking of the sensory state and not with integration. In Figure S3 we show that neural activity in both PMd and M1 also tracks the sensory state in these trial types and exhibits no memory of the sensory state after the initial bias has ended.

The observations above suggest that the sensory information is quickly tracked, perhaps through a low-pass filter with a very short time window (i.e., less than the duration between two token jumps [200 ms]). To test this explicitly, we computed the mean neural activity during two 200 ms epochs, from 200–400 ms and from 400–600 ms after the first token jump, and sorted trials according to the pattern of the two first token jumps: in step-for trials, the first token jumps to the cells' PT, and the second token jumps to the OT. In step-against trials, this pattern is reversed. Accounting for sensory delays, the first epoch of analysis reflects the consequences of the first token jump. Comparison between step-for and step-against trials shows that activity in PMd is significantly higher (KS test; $p < 0.05$) and shows a similar trend in M1 during that first epoch in step-for than in step-against trials (Figure 5B). However, 200 ms later in the trial, activity is similar between the two conditions, in agreement with fast tracking of sensory information.

PMd and M1 Activity Signals the Commitment to a Decision

Because monkeys are allowed to make their decision at any time during the tokens task, we can examine cortical activity for the neural signature of the moment at which commitment to a choice is made. To this end, we aligned activity on movement onset, as shown on Figures 6A and 6B, for one PMd and one M1 neuron. Note that approximately 300 ms before the monkey chooses the

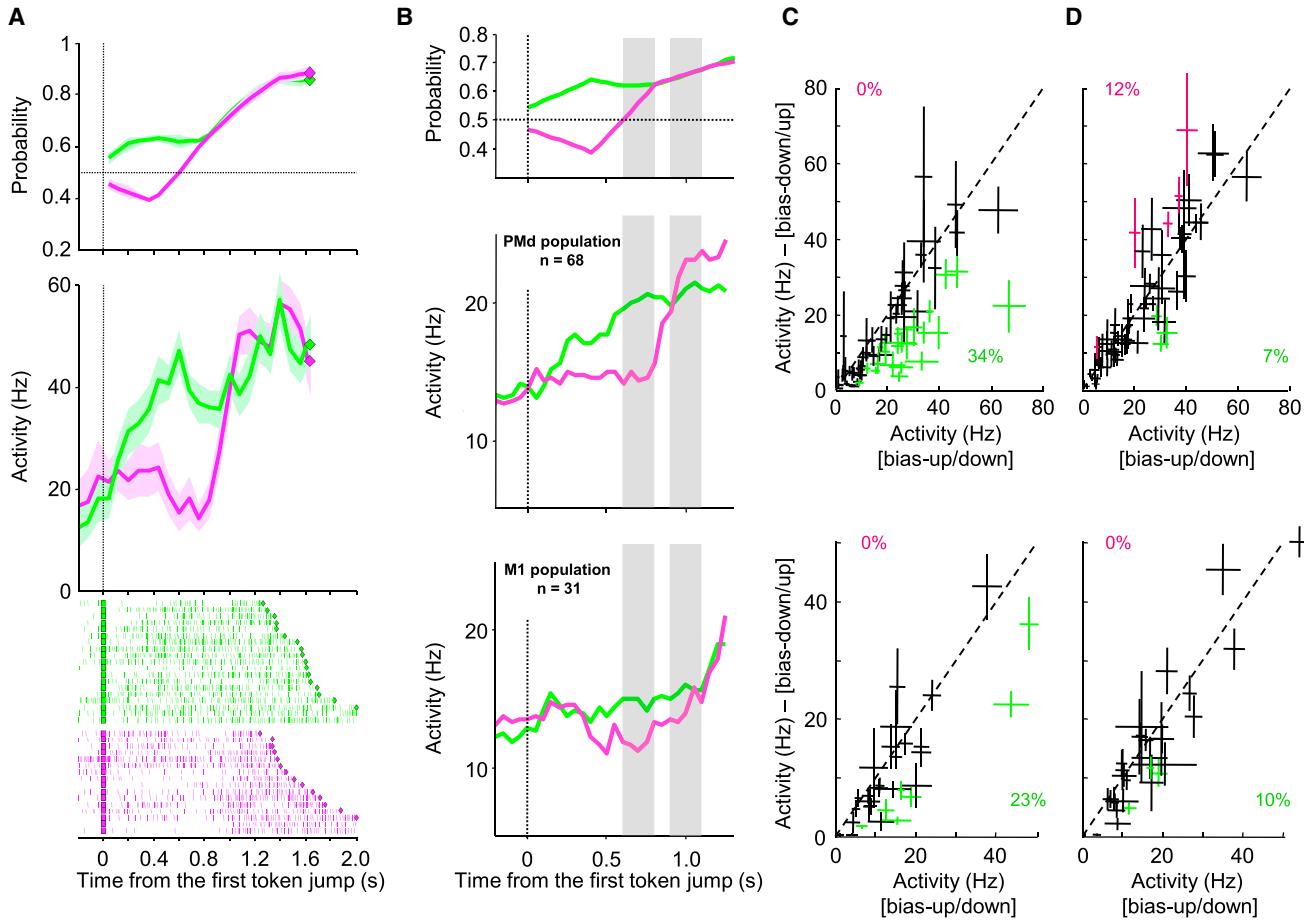

Figure 4. Neural Activity Does Not Integrate the Sensory State

(A) Top shows the success probability with respect to PT during bias-up/down (green) and bias-down/up trials (magenta). Bottom shows the activity of a PMd neuron during the two trial types. Only trials in which DT ≥800 ms are included.

(B) Top shows the mean success probability during bias-up/down (green) and bias-down/up trials (magenta). Middle shows the average activity of 68 decision-related PMd neurons during the two trial types. Bottom shows the average activity of 31 M1 neurons.

(C) Comparison of mean neural activity (±SE) of 68 PMd (top) and 31 M1 neurons (bottom) recorded during bias-up/down versus bias-down/up trials from 600–800 ms after the first token jump (left shaded area in [B]). Colored crosses illustrate neurons with a significant modulation of activity (green indicates stronger activity in bias-up/down; magenta indicates stronger activity in bias-down/up). Percentages denote the proportion of significantly modulated cells.

(D) Same as (C), but showing activity from 900–1,100 ms after the first token jump (right shaded area in [B]).

cell's PT, there is a clear peak of activity in both cells, and the amplitude and timing of this peak are similar across the different trial types. As shown in Figure S4, this phenomenon exists at the level of individual trials and is not an artifact of averaging over trials of different lengths. It is also not related to saccades: although analysis of oculomotor behavior in our task will be described in a future publication, it is important to mention here that in most trials (74%–79%), the monkeys were already fixating the chosen target well before the peak in PMd activity.

Figure 6C shows the average activity of the 68 PMd and 31 M1 neurons aligned on movement onset. In both areas, neural activity related to the PT shows a striking characteristic regardless of the trial type: between the start of token jumps and movement onset, activity first shows the influence of the mounting sensory evidence, then reaches a peak, and finally decreases prior to movement onset. The approximate timing of that peak (vertical gray line in Figure 6C) as well as its amplitude is very similar across trial types, appearing earlier in PMd than in M1. Importantly, at approximately the same time, activity in M1 related to the unselected OT target becomes rapidly suppressed. This is seen most clearly in ambiguous and misleading trials, in which there was some evidence favoring the OT choice. To further quantify the timing of these phenomena, we first averaged the activity of PMd and M1 neurons across all trials in which the PT was chosen and detected the peak firing rate across 10 ms bins. In PMd, this peak was reached 280 ms before movement onset, whereas in M1 it occurred 140 ms later (Figures 7A and 7D, left). To assess the robustness of this observation, we also calculated the peak timing for each cell separately and computed its mean and median latency across the population (Figures 7A and 7D, right). Except for a few cells whose maximum activity occurs very early, there is a clear trend for

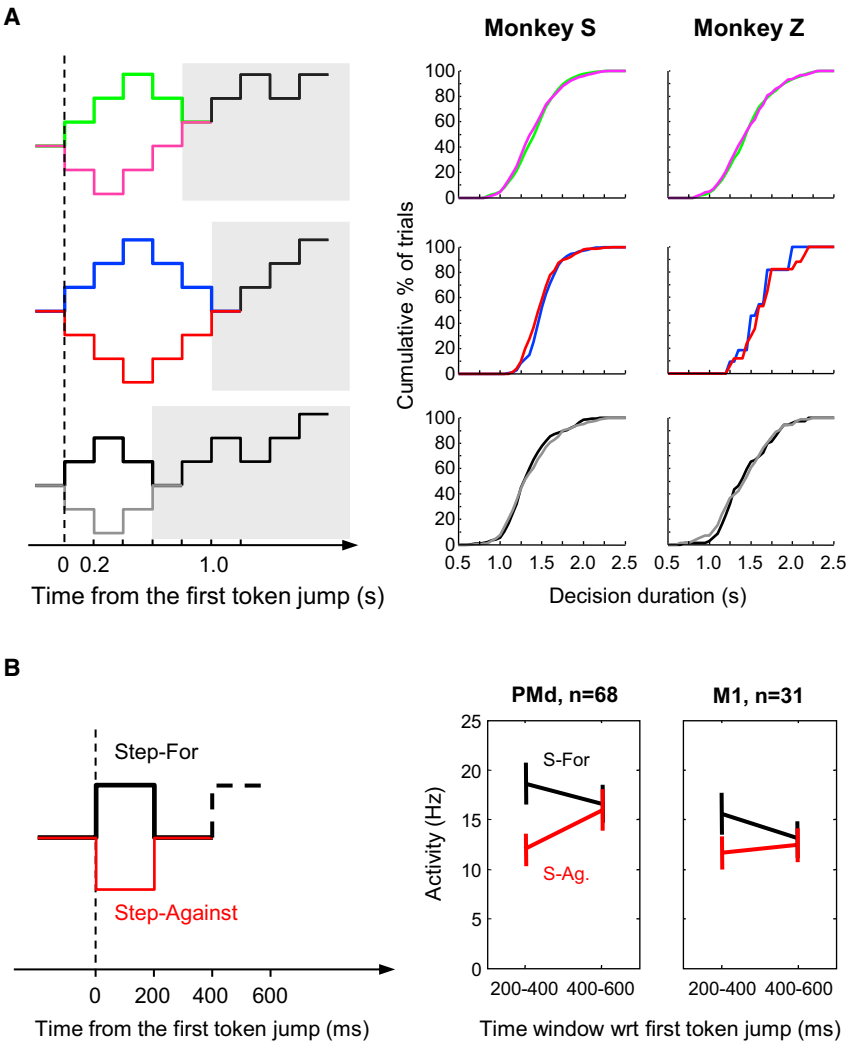

Figure 5. The Sensory State Is Quickly Tracked

(A) Left shows the following six trials for testing integration versus tracking: bias-up/down (green) and bias-down/up (magenta), long bias-for (blue), long bias-against (red), short bias-for (black), and short bias-against (gray). Right shows the cumulative DT distributions in these six trial types, including only trials in which the decision was made after the bias (gray areas in the left panel).

(B) Left shows step-for trials (black), in which the first token jumps to the PT and the second to the OT, and step-against trials (red), in which the pattern is reversed. Right shows average (±SE) neural activity in PMd and M1 from 200–400 ms and 400–600 ms after the first token jump.

the peak to occur approximately 260 ms before movement onset in PMd and 179 ms in M1. Next, we sought to determine whether the latencies of neural activity peaks correlate with RTs and are consistent across trial types. For each cell, we calculated the mean latency of the peak in easy and misleading trials and then plotted these against the RT in those same trials (Figures 7B and 7E). In almost all PMd and M1 neurons, there is a strong relationship with a slope near unity, suggesting that regardless of the history of sensory information during a trial, the timing of PMd and M1 peaks is consistent relative to movement initiation.

Here, we will use the earliest of these latency values as our estimate of the timing of commitment: 280 ms before movement onset. Figure 7C shows that the amplitude of the PMd activity at this moment in PT trials is very consistent across trial types, although there is a slight trend for it to be lower in easy trials, in which decisions are shorter.

Most interestingly, at this same moment, M1 activity tuned to the unselected target becomes rapidly suppressed (Figure 6C). For each PMd and M1 cell, we quantified the timing of this suppression by examining how activity changed between two consecutive 50 ms bins at different latencies with respect to movement onset (see Figure S5). The distribution of the time of the greatest change between bins is quite broad for PMd, suggesting that there is no specific moment of suppression of cells tuned to the unselected target. In M1, however, the distribution is narrower, and the mean timing across cells (275 ms) roughly corresponds to our estimate of commitment time.

Comparison of Volitional Commitment versus Instructed Movement

In the tokens task, monkeys are free to decide both which target to choose and the time at which they commit to that choice. Figures 6 and 7 suggest that the neural peak in PMd and suppression in M1 signals this moment of free commitment. However, are these phenomena simply the correlates of movement initiation? To address this, we examined the activity of the same cells during the DR task, in which both the target and the time to respond are externally instructed. Most of the cells recorded in the tokens task (58/68 in PMd; 25/31 in M1) were also recorded in the DR task. Using the same PT and OT as in the tokens task, we found that 30/58 PMd cells tuned in the tokens task before DT were also significantly tuned in the DR task (for the same targets) during the last 200 ms before the GO signal. Figures 8A and 8B illustrate the activity of one of these tuned cells. Likewise, most M1 cells (18/25) tuned in the tokens task were also tuned in the DR task (e.g., Figures 8E and 8F). In both cells, activity increased shortly after target onset (~160ms) and then stabilized well before the GO signal. Notably, at the time of the GO signal there was no obvious change in neural activity, which began to decrease only just before movement onset. This observation held true at the population level, as shown in Figures 8C and 8G, for the 30 PMd cells significantly tuned in the delayed reach (DR) task, the 28 other PMd cells, as well as the 18 tuned M1 cells. Note that when

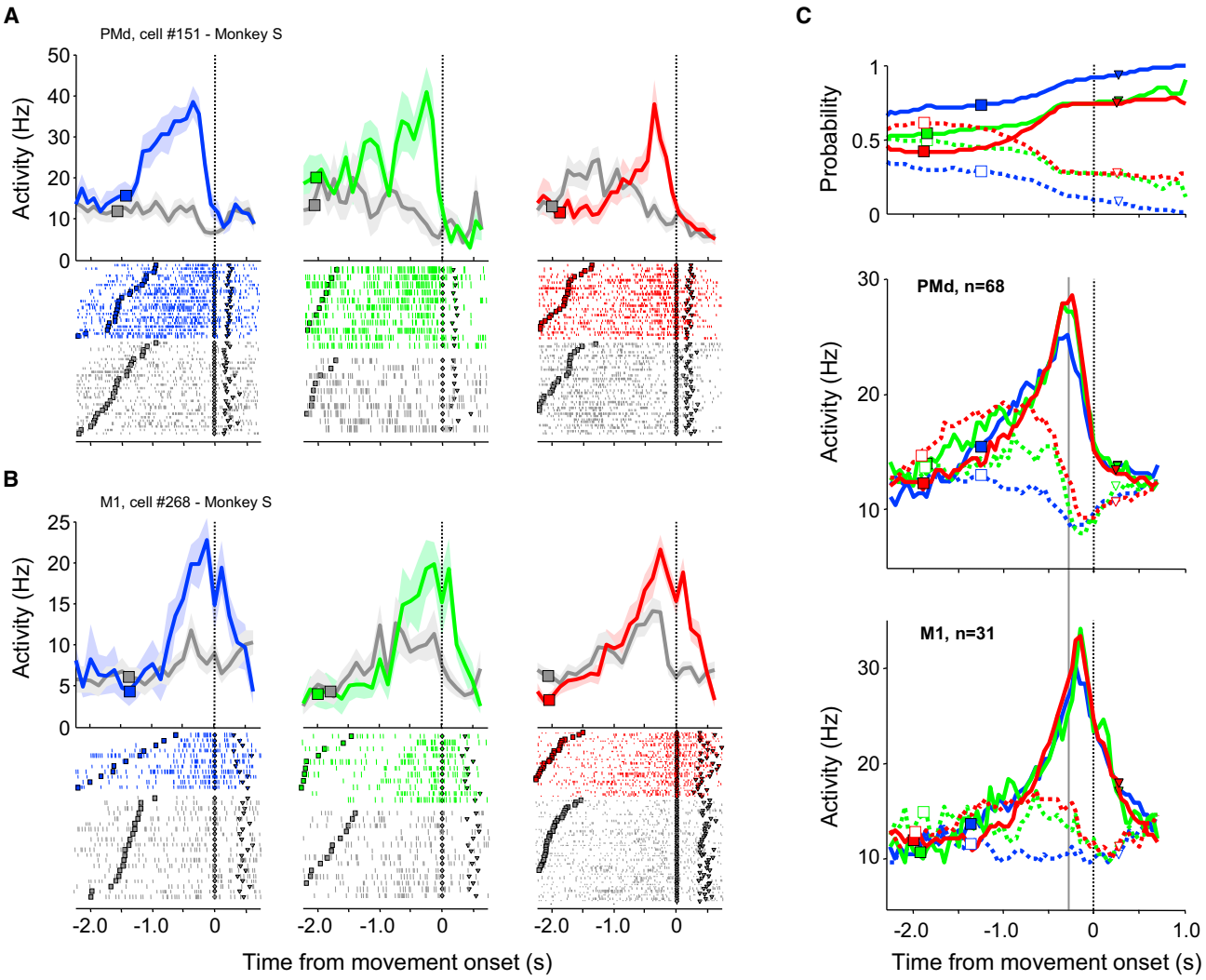

Figure 6. Neural Correlates of the Moment of Commitment

(A) Response of a tuned PMd neuron in easy (left), ambiguous (middle), and misleading (right) trials. Same convention as in Figure 2A except that here activity is aligned on movement onset (diamonds). Triangles mark movement offset.

(B) Same as (A) for an example M1 neuron.

(C) Success probability (top) and average activity of 68 PMd (middle) and 31 M1 (bottom) neurons, aligned on movement onset. The vertical gray line indicates our estimate of commitment time (see Figure 7 and text for details).

activity is aligned on the GO signal (middle plots of [A], [C], [E], and [G]), there is no clear change in neural activity in any of the cell groups. In contrast, in the tokens task all three groups exhibit a clear peak well before movement onset.

To further test whether the activity peak before movement is particular to volitional commitment as opposed to movement initiation, we also examined a group of cells in M1 that were more closely related to the kinematic or dynamic aspects of the movement itself (Kalaska et al., 1989). In particular, we chose cells (n = 19) whose predecision activity in the tokens task did not correlate with success probability, but whose premovement activity in the tokens task was significantly correlated with movement speed. None of these were among the 31 cells described above. In contrast to the decision-related cells, in both tasks these cells exhibit a similar peak of activity shortly before movement onset (tokens task: ~100 ms; DR task: ~40 ms) and do not exhibit any particular response in the tokens task at our estimated moment of commitment (Figure S6). We propose that the activation of such cells is what determines movement initiation, but the PMd peak that occurs about 180 ms earlier is related to volitional commitment.

In summary, the PMd and M1 cells described here appear to be involved in both deliberation and commitment. These processes are most clearly dissociable in misleading trials, which include an initial bias toward the wrong target that is visible in neural activity (Figure 2). If the monkey correctly withholds commitment at this time, activity related to the misleading target should not exceed the level of activity reached at commitment

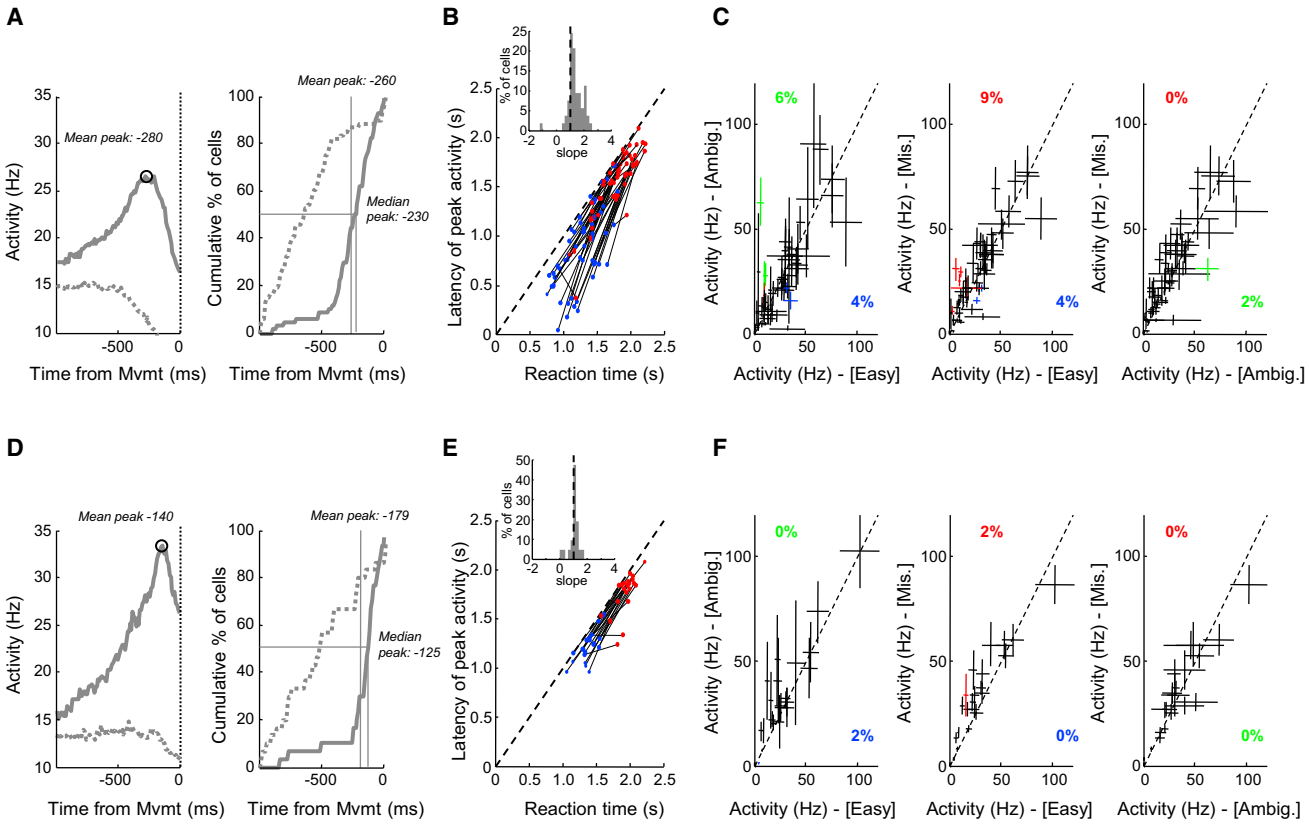

Figure 7. Timing and Robustness of the Neural Activity Peak

(A) Left shows average activity of the 68 decision-related PMd cells across all trials (in 10ms bins) for PT (solid) and OT choices (dotted). The peak of the average PT-related activity is indicated and its timing defined relative to movement onset. Right shows cumulative distribution of PT- (solid) and OT- related (dotted) peak activity timing relative to movement onset, calculated individually in each of the 68 PMd cells.

(B) Relationship between latencies of peak activity of the 68 PMd cells and reaction time. For each cell (black lines), the mean peak activity latencies are calculated in easy (blue) and misleading (red) trials for the cell's PT and plotted against the mean RTs in these same trials. The inset shows the distribution of slopes of the black lines (dashed line is unity slope).

(C) Comparison of the mean firing rate ±SE at commitment time (280 ms before movement onset) of each of the 68 PMd cells during easy-versus-ambiguous (left), easy-versus-misleading (middle), and ambiguous-versus-misleading trials (right). Colored crosses illustrate neurons for which the difference is significant (KS test, $p < 0.05$). Percentages denote the proportion of neurons whose activity is significantly different in each comparison.

(D) Same as (A) for a population of 31 decision-related M1 neurons.

(E) Same as (B) for the 31 M1 neurons.

(F) Same as (C) for the 31 M1 cells (note that the mean firing rate ±SE of M1 cells is calculated 280 ms before movement onset).

time. To test this, we performed an additional analysis of each cell (recorded during at least four trials) to see if neural activity during the bias ever reaches a level higher than that reached at commitment (Figure S7). Results show that, in both PMd and M1, there is a clear trend for misleading-related activity to be weaker than correct-target-related activity around decision commitment. We also show that when the monkey makes an error during misleading trials, the activity tends to be higher than in correct trials, suggesting that the errors occur when neural activity is strong enough to reach the level for commitment, leading the monkey to make an overly hasty guess.

DISCUSSION

Decisions about action are arguably the most fundamental kinds of decisions that animals face in the natural world. For such decisions, the choices themselves are defined by the immediate environment and are constantly changing during ongoing activity. This motivates the hypothesis that multiple potential actions are specified simultaneously and compete against each other within the sensorimotor system (Cisek, 2007) and that this competition is biased by a continuous flow of sensory information (Coles et al., 1985; Kim and Shadlen, 1999). Our results support this hypothesis and suggest a mechanism for how sensory information brings the system to commit to one action versus another. In particular, we show that information pertinent to reach selection is continuously influencing activity in reach-related regions of PMd and M1 (Figures 2–5). This information is combined with a nonspecific urgency signal that gradually builds up tension between the options until one of them gets strong enough to suppress the other (Figures 6 and 7). We propose that this moment, when the competition

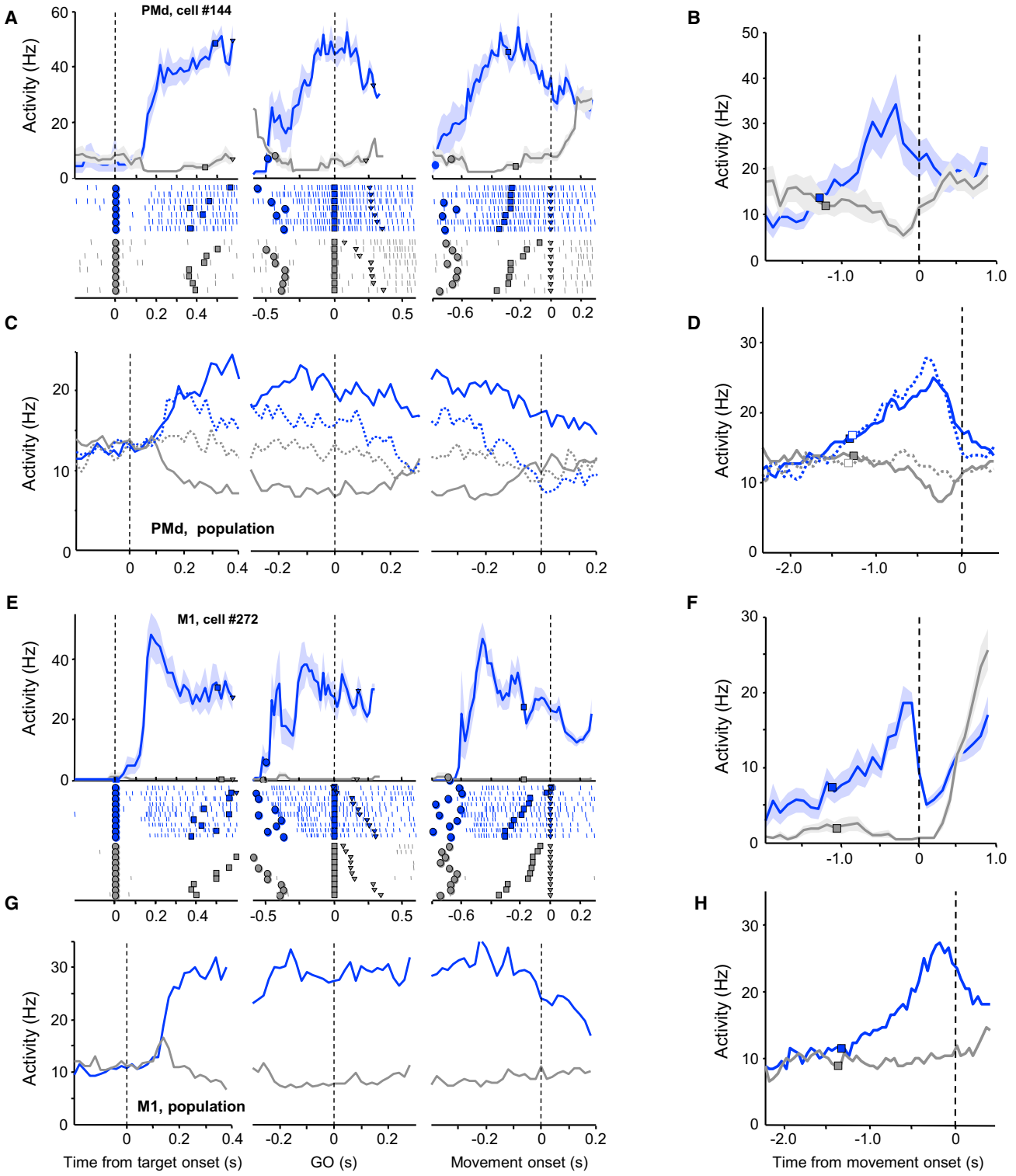

Figure 8. Comparison of Volitional Commitment versus Instructed Movement

(A) Activity of a PMd decision-related neuron during the delayed reach task, in trials to the PT (blue) or OT (gray), aligned on target onset (left), GO signal (middle), and movement onset (right).

(B) Activity of the same neuron during easy trials in the tokens task and aligned on movement onset.

(C) Average activity of 58 PMd neurons recorded during the DR task, in trials to the PT (blue) or OT (gray). Among these, 30 are significantly tuned in the DR task (solid) whereas 28 are not (dotted).

(legend continued on next page)

between actions is resolved within the motor system, constitutes the voluntary commitment to an action choice.

The proposal that the motor system is involved in decision making is based on the observation that decision-related variables modulate activity in many regions implicated in sensorimotor control (Basso and Wurtz, 1998; Cisek and Kalaska, 2005; Gold and Shadlen, 2000; Platt and Glimcher, 1999; Salinas and Romo, 1998; Wallis and Miller, 2003). However, the presence of such modulation does not prove that the motor system participates in the decision process, because it could be argued that the modulation is related to other variables such as arousal (Leathers and Olson, 2012; Roesch and Olson, 2003) or is merely reflecting decision-making processes occurring upstream. Padoa-Schioppa (2011) suggests that to truly establish that motor regions contribute to the decision process, it is necessary to show that (a) decision-related activity is indeed within the motor system, (b) it reflects subjective variables, and (c) it is not downstream of the decision process. Here, we satisfy these criteria by showing neural correlates of deliberation within M1 (criterion a), reflecting not just the sensory information but also the animal's subjective urgency to act (criterion b), and occurring prior to the moment of commitment (criterion c). Because our recordings were limited to PMd and M1, it is conceivable that another region, such as lateral or medial prefrontal cortex (PFC), may be the site of commitment and simply relay its results downstream. However, it is hard to imagine neural events that are more consistent across conditions than what we observed in PMd and M1. Indeed, preliminary recordings in dorsolateral PFC showed that the peak of activity in that region does not remain consistent across easy, ambiguous, and misleading trials in terms of its timing and amplitude (Thura and Cisek, 2010). We thus conclude that PMd and M1 are part of the circuit responsible for the commitment to a choice between reaching actions.

Continuous Flow and Competition between Actions in Premotor and Motor Cortex

Our results demonstrate that the sensory information provided by the token movements continuously influences neural activity in PMd and even M1. In particular, Figure 2 shows that neural activity in both regions quickly predicts the choice in trials classified as easy, remains uncommitted longer in ambiguous trials, and reflects when the bias switches in misleading trials. These phenomena are clearer in PMd than in M1, and in both regions there is an overall tendency for activity to increase over time. In Figure 3 we show that similar results hold across all trials and that neural activity in both regions appears to be a gradually rising sigmoidal function of the log evidence for a choice.

Many studies have shown that information pertinent to decisions can influence the sensorimotor system (for reviews, see Cisek and Kalaska, 2010; Glimcher, 2003; Gold and Shadlen, 2007; Hernández et al., 2010). For example, electromyographic responses to transcranial magnetic stimulation of M1 correlate with the potential value of movements (Klein-Flügge and Bestmann, 2012) and reflect when subjects change their mind between conflicting choices (Michelet et al., 2010). Even at the periphery, reflex gains change with the evidence in favor of a given response (Selen et al., 2012), demonstrating a continuous flow of sensory information into the motor system (Coles et al., 1985). The influence of decision variables on neural activity is well-documented in many parts of the oculomotor (Platt and Glimcher, 1999; Roitman and Shadlen, 2002) and reaching system (Donner et al., 2009; Klaes et al., 2011; Pastor-Bernier and Cisek, 2011; Romo et al., 2004). For example, PMd cells appear to engage in a biased competition between potential actions represented in a sensorimotor map (Pastor-Bernier and Cisek, 2011), and the same cells continue to reflect when a monkey changes his mind even after movement onset (Pastor-Bernier et al., 2012).

Here, we characterize how the bias between potential actions unfolds over time. Although the bias is surely subject to many factors, in our experiment we can clearly identify two: the evidence in favor of each option and the growing urgency to act. This finding was predicted by a previous study with humans (Cisek et al., 2009), which showed that behavior in the tokens task could be explained by a model ("urgency-gating") in which a filtered estimate of sensory evidence was combined with a growing urgency signal. Our present results with monkeys are in good agreement with that study. In particular, decisions are made more quickly in easy than in ambiguous trials but at a higher level of success probability (Figures 1D and 1E), DTs are similar in any tested pair of trial types that differ only in the initial sensory state (Figure 5A), and the overall criterion of information for committing to a choice decreases over time (Figure 1F). Furthermore, here we confirm that evidence and urgency influence the time course of activity in directionally tuned PMd and M1 neurons, at both a single-cell and population level (Figures 2 and 3).

Importantly, in a human study using the tokens task (Cisek et al., 2009) as well as the present study, the sensory information was not integrated over time, as predicted by the widely accepted drift-diffusion model (Mazurek et al., 2003; Ratcliff, 1978). Any integrator predicts that even after the state of sensory information became identical in two trials, neural activity would continue to reflect the within-trial history of that state. However, here we saw no effects of within-trial history differences (Figures 4 and 5), as if the sensory information was not integrated but instead simply low-pass filtered with a short time constant (less than 200 ms) (Figure 5B). Although a leaky integrator (Usher and McClelland, 2001) could potentially explain this result, the leak would have to be so strong that the time constant of the system would be very short, and it would effectively be equivalent to a low-pass filter.

It is possible that fast tracking of sensory information is specific to the tokens task but that the brain integrates information with a longer time constant when the stimulus is noisy or

(D) Average activity of the same PMd neurons during easy trials in the tokens task.
(E) Same as (A) for an example M1 neuron.
(F) Same as (B) for the same M1 neuron as (E).
(G) Same as (C) for 18 M1 neurons tuned in the DR task.
(H) Same as (D) for the same 18 M1 neurons.

when a memory of sensory events is necessary. However, a recent study using a variant of the classic motion discrimination task in which the coherence was changing during each trial (Thura et al., 2012) found results similar to those reported here, inconsistent with a long-time constant of integration. Indeed, slow integration does not make good sense during natural behavior (Chittka et al., 2009), because it is too sluggish to respond to sudden changes. It is more useful for the brain to emphasize only novel information, thus remaining sensitive to the current sensory state without integrating redundant samples. Furthermore, we have shown that a decreasing decision criterion (Figure 1F), which may be implemented using an urgency signal, yields a higher reward rate than any setting of a constant criterion (Thura et al., 2012). Thus, we conclude that during natural, dynamic decision making, the brain does not integrate sensory samples but instead quickly tracks sensory information and combines it with a growing urgency signal. It remains to be seen whether a longer time constant of integration is used when making decisions in static tasks.

The results shown on Figures 2–4 are compatible with two recent studies using tasks in which evidence changed over time. In the monkey, Yang and Shadlen (2007) showed that LIP activity reflects the sequential information provided by stimulus cues about which of two saccade targets was the most likely to yield a reward. Similar to what we found in PMd and M1 (Figure 3), LIP activity resembled a sigmoidal function of the log evidence for a choice. Some buildup over time was also observed, but it was much weaker than what we found here. This may be due to differences in recording sites and effector systems or due to the fact that in their study the monkeys were not allowed to make decisions until the end of the trial, motivating them to keep the urgency signal low.

In the human, Gluth et al. (2012) showed that when subjects were given sequential information about the value of a hand response choice, the BOLD signal in motor output regions combined value information with a signal related to the growing urgency to respond. The effect of growing urgency was strong, perhaps because subjects were allowed to respond at any time, as in our study. This agrees with the proposal (Ditterich, 2006; Standage et al., 2011; Thura et al., 2012) that when an agent is free to decide at any time, the policy that maximizes reward rate is to have a decreasing decision criterion, which can be implemented through a growing urgency signal. Some studies have suggested that urgency is multiplicatively combined with sensory information (Cisek et al., 2009; Ditterich, 2006; Stanford et al., 2010; Thura et al., 2012), while others suggest an additive process (Churchland et al., 2008; Gluth et al., 2012). Here, we found that while some cells showed a change in both the slope and baseline of their neural response function over time (Figures 3 and S2), the average population response was dominated by a baseline shift (Figures 3B and 3D), consistent with an additive urgency.

The proposal of a biased competition in the sensorimotor system raises the question of what the source of the relevant biases is. Previous studies implicate the lateral prefrontal cortex (lPFC) as a major source of task-specific information for action selection (Kim and Shadlen, 1999; Tanji and Hoshi, 2001; Wallis and Miller, 2003), and it is likely that, in our task, that is the region contributing information about token movements. Indeed, pilot recordings in lPFC of monkey S showed an effect of sensory evidence on cell activity (Thura and Cisek, 2010). Buildup activity resembling our urgency signal has been reported in the supplementary motor areas (Casini and Vidal, 2011; Fried et al., 2011; Mita et al., 2009) and for oculomotor tasks in LIP (Churchland et al., 2008; Janssen and Shadlen, 2005; Maimon and Assad, 2006). It is also plausible that all of these regions receive a common urgency signal from the basal ganglia, which may control both the timing of action selection as well as the vigor of the selected movement (Desmurget and Turner, 2010).

Decision Commitment Occurs when the Competition between Actions Is Resolved

Our results are consistent with a model in which a competition between movement options is continuously biased by evolving sensory and urgency signals. In Figures 6 and 7, we observe the moment at which this competition is resolved, approximately 280 ms prior to movement onset. Here, we refer to this as the ''moment of commitment,'' although we recognize that such labels are perforce tentative. At this moment, the activity of PMd cells tuned to the selected target reaches a peak, while the activity of M1 cells tuned to the OT is suppressed (Figure 6C). Approximately 140 ms later, M1 cells tuned to the selected target also reach their peak of activity. Finally, approximately another 40 ms later, a peak occurs among M1 cells that are not significantly tuned during decisions (Figure S6), but which reflect kinematics of movement and may be involved in initiation and execution (Kalaska et al., 1989).

The timing of these events is remarkably consistent across trial types and clearly predicts movement initiation (Figures 6C and 7B). However, the peak of PMd activity is not simply related to movement initiation itself. First, it is very early, about 280 ms before the cursor begins to move, and thus at least 200 ms before any voluntary muscle contractions. This is close to the monkey's total RT in the DR task, a point we will return to later. Second, when movement is externally instructed in the DR task, there is no evidence for similar events taking place around the GO signal (Figure 8). During the DR task, the delay-tuned PMd population becomes strongly active shortly after cue presentation (Figure 8C, solid lines), reaching a discharge rate comparable to its activity at the moment of commitment in the tokens task (about 25 Hz) (Figure 8D, solid lines). However, unlike in the tokens task, this activity is sustained throughout the delay period, and at the time of movement onset, it falls to a level comparable to onset-time activity in the tokens task (16 Hz) (Figure S8). Similar phenomena are seen in the delay-tuned M1 population. However, when activity is aligned at the time of the GO signal (middle panels in Figure 8A, 8C, 8E, and 8G), we see no evidence of task-related activity changes in either area. Interestingly, PMd cells that do not meet the criteria for significant tuning in the DR task still show similar trends (Figures 8C and 8D, dashed lines), although their activities at movement onset are not consistent across the tasks.

We propose the following interpretation of these results: To initiate a movement, the motor system must have committed to a given option and must not be actively inhibited. In the DR task (as in previous studies with static decision tasks), the

commitment presumably occurs shortly after the presentation of the cue, but the system is actively inhibited from initiating movement by a mechanism that does not involve the cells we recorded here. Previous studies have suggested that there are no "omnipause" neurons in M1 (Kaufman et al., 2013) and that active inhibition of movement initiation may involve spinal mechanisms (Duque et al., 2010; Prut and Fetz, 1999). In the tokens task, such active inhibition is not necessary because the monkey is allowed to respond at any time. Therefore, all that is necessary to meet the conditions for movement initiation is that commitment to a given option is reached. For this reason, in the tokens task we observe a buildup of activity with a clear and brief PMd peak that predicts movement onset time approximately 280 ms later.

We now return to the question of the timing of this "moment of commitment." It precedes movement onset by approximately 280 ms, which is remarkably close to the average RTs in the DR task (Monkey S: 291 ± 40 ms; Monkey Z: 335 ± 93 ms). This raises an intriguing quandary: how can the time interval between the GO signal and movement onset, which presumably includes both sensory and motor delays, be similar to the interval between an internal commitment and movement onset, which presumably only includes a motor delay? We considered two possibilities. The first is that in the DR task the monkeys may have learned to anticipate the timing of the GO signal so well that, on average, movement initiation begins before the sensory cue, and so the mean RT is entirely accounted for by pure motor delays. However, monkeys' behavior is not consistent with this explanation. For instance, in monkey S, the distribution of RTs in the DR task was narrower (SD = 71.2 ms) than the distribution of latencies between target and movement onsets (SD = 140.6 ms), and there was no trend for the latter to decrease during training. An alternative explanation is that the motor delay is longer when commitment is volitional than when it is externally instructed, as suggested by previous studies. For example, van Donkelaar et al. (1999) found that the latency between activity in the motor thalamus and movement onset was often 50–150 ms longer when actions were internally generated than when they were visually triggered. Earlier studies by Romo et al. (Romo et al., 1992; Romo and Schultz, 1992) comparing striatal and SMA activity during visually versus internally triggered tasks found that activity in both regions begins long before self-initiated movements. Those authors suggested that self-initiated movements require reverberating activity within the cortico-striatal circuit, whose total loop time was estimated at 35–50 ms. Our findings are in good agreement with this proposal. If total RT in the DR task is approximately 300 ms and the visual latency in PMd is approximately 50–80 ms (Cisek and Kalaska, 2005; Ledberg et al., 2007), then the motor delay is about 220–250 ms. If volitional commitment requires an additional pass through a cortico-striatal loop, then the delay between commitment in PMd/M1 and movement should be about 255–300ms, compatible with our estimate of 280 ms. Further research would be necessary, of course, to test this conjecture.

A Mechanism for Action Choice Formation and Commitment

All of the results summarized above may be parsimoniously explained in terms of a class of simple dynamic "attractor" models of recurrent competitive networks (Cisek, 2007; Grossberg, 1973; Standage et al., 2011; Wang, 2002). In such models, cells tuned to different options compete through mutual inhibition, and this competition is biased by various factors. A decision is said to be made when the activity of one group of cells becomes strong enough to suppress the others, and the system exhibits a phase transition. This event need not involve any explicit threshold detection mechanism but instead emerges from the dynamics of the system (Grossberg, 1973). Nevertheless, the activity of the winning cells at that moment may be similar across task conditions and thus appear as a consistent peak of activity, as in our data.

While our findings contradict the traditional view that all decision making is a cognitive process taking place in terms of abstract outcome-related variables (Padoa-Schioppa, 2011), it should be emphasized that not all decisions are the same. Obviously, the challenges faced by an animal moving around its environment are very different from those faced by an economist selecting a stock portfolio or a radiologist looking for a tumor. In particular, during action selection, the choices themselves are defined by sensory information about the geometric layout of the environment around the animal, which may be continuously changing, especially if the animal is moving. That information influences not just the reward and costs of the potential actions but also determines whether the decision between them must be all-or-none or whether a mixture is also an option (Pastor-Bernier and Cisek, 2011). Because opportunities may be lost over time, there is no preset level of desired performance but instead a trade-off between speed and accuracy that may be achieved through a growing urgency signal (Thura et al., 2012). Finally, regardless of how the decision unfolds over time, its consequences only begin to play out after an action is taken. Thus, commitment is only meaningful insofar as an action is initiated. In summary, when deciding between actions, there are many reasons why the processes of deliberation and commitment should take place within the sensorimotor system itself.

EXPERIMENTAL PROCEDURES

Subjects and Apparatus

Two male monkeys (Macaca *mulatta*; S was 6 years old and 6 kg; Z was 4 years old and 4 kg) were implanted, under anesthesia and aseptic conditions, with a titanium head-fixation post and recording chambers. Surgery, testing procedure, and animal care were approved by the local animal ethics committee. Monkeys sat head-fixed in a custom primate chair and performed two planar reaching tasks using a vertically oriented cordless stylus whose position was recorded by a digitizing tablet (CalComp, 125 Hz). Their nonacting hand (for S, left hand for ~2 years then right hand for 6 months; for Z, left hand) was restrained on an arm rest with Velcro bands. In some sessions, unconstrained eye movements were recorded using an infrared camera (*ASL*, 120Hz). 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. Neural activity was recorded with one to four independently moveable (NAN microdrive) microelectrodes (FHC), and data was acquired with the AlphaLab system (Alpha-Omega Eng.).

Behavioral Tasks

In the "tokens" task (Figure 1A), the monkey is presented with one central starting circle (1.75 cm radius) and two peripheral target circles (1.75 cm radius, 180° apart, and 5 cm from the center). Each trial begins when the cursor is placed in the central circle, in which 15 small tokens are randomly arranged.

The tokens then begin to jump, one-by-one every 200 ms ("predecision" interval), from the center to one of the two targets. The monkey's task is to move the cursor to the target that he guesses will ultimately receive the majority of tokens, and he is allowed to make the decision at any time. When the cursor reaches a target, the remaining tokens move more quickly to their final targets ("postdecision interval," which was either 50 ms or 150 ms in separate "fast" and "slow" blocks of trials). In the present report, we primarily use data from the slow blocks (although we also include some fast blocks from monkey Z early in his experience, while his behavior was statistically indistinguishable in the two blocks). Once all tokens have jumped, visual feedback is provided (the chosen target turns green for correct or red for error choices), and a drop of fruit juice delivered after correct choices.

In the DR task (usually 30–48 trials per session), the monkey again begins by placing the cursor in the central circle containing the 15 tokens. Next, one of six peripheral targets is presented (1.75 cm radius, spaced at 60° intervals around a 5 cm radius circle), and after a variable delay (500 ± 100 ms), the 15 tokens simultaneously jump into that target. This "GO signal" instructs the monkey to move the handle to the target to receive a drop of juice.

Neural Recordings

Recording chambers were centered near the arcuate sulcus of the hemisphere contralateral to the performing hand. Placement was guided using anatomical MR images (Siemens 3T) coupled with neuro-navigation software (Rogue Research Inc.). Within each chamber, we used the frontal eye field as a landmark, localized as the region where saccades could be evoked by intracortical microstimulation (40 ms train of 0.2 ms monophasic pulses at 500 Hz) with current ranging from 50–100 μA (Bruce et al., 1985). During recordings in PMd and M1, the extracellular signal was amplified (×1000) and band-pass filtered (0.3–3 kHz), and action potentials were isolated on-line using template matching. This was used to identify task-related cells and estimate their spatial tuning for target placement. However, all analog waveforms were stored on disk for subsequent offline sorting using principal components (Plexon), and all results presented here are based on the offline sorted data. All tasks events, kinematics, gaze position, and spike times were stored in a database (Microsoft SQL) accessed for data analysis via custom-written scripts (Matlab, Mathworks).

During recording sessions, we focused on cells showing a change of activity in the tokens task, and monkeys were usually performing the task while we were searching for cells. When one or more task-related cells were isolated, we ran a block of 30 to 48 trials of the DR task to determine spatial tuning and select a PT for each cell (i.e., the target associated with the highest firing rate during one or more task epochs). Next, we ran blocks of tokens task trials using the PT of an isolated cell and the 180° OT. We sometimes simultaneously recorded several task-related cells showing different spatial preferences, and since we always selected a single pair of targets, the actual best direction for each of the recorded cells was not always one of these two. Nevertheless, when comparing activity between the tokens and DR tasks, we always chose a cell's "PT" from among the two targets used in the tokens task.

Behavioral Data Analysis

In the tokens task we can calculate, at each moment in time, the success probability $p_i(t)$ associated with choosing each target *i*. For instance, if at a particular moment in time the right target contains N_R tokens, whereas the left contains N_L tokens, and there are N_C tokens remaining in the center, then the probability that the target on the right will ultimately be the correct one (i.e., the success probability of guessing right) is the following:

$$p(R|N_R,N_L,N_C)=\frac{N_C!}{2^{N_C}}\sum_{k=0}^{\min(N_C,7-N_L)}\frac{1}{k!(N_C-k)!}. \quad \text{(Equation 1)}$$

Calculating this quantity for the 15 token jumps allows us to construct the success probability profile $p_i(t)$ associated with each trial (Figure 1B). Although each token jump and each trial was completely random, we could classify a posteriori some specific classes of trials embedded in the fully random sequence (e.g., "easy," "ambiguous," and "misleading" trials) (Figure 1C).

We focus behavioral analyses on three variables: DT, SPD, and "confidence" at DT. To estimate the DT, we first detect the time of movement onset (based on analysis of kinematics; see Pastor-Bernier et al., 2012) and subtract from this the monkey's mRT in the DR task on the same day. We then use Equation 1 to compute for each trial the SPD (Figure 1B).

Calculation of the monkey's confidence at DT is based on the available sensory evidence favoring the chosen target at the time of the decision. We do not believe that monkeys can calculate Equation 1, but we expect that they can make a reasonable estimate. We thus computed a simple approximation of sensory evidence as the sum of log likelihood ratios (SumLogLR) of individual token movements (see Cisek et al., 2009 for more details), which is proportional to the difference in the number of tokens present in each target.

Neural Data Analysis

All neurophysiological data reported here were acquired from correct or error trials in which the monkeys completed the tokens task by choosing one of the two targets. Neurons were selected according to their anatomical location and physiological properties. Among all cells recorded in PMd and M1, we focus here on those showing a significant spatial preference for one of the targets during the deliberation process (i.e., between the first token jump and our estimate of DT). For each cell, we calculated the mean activity for each target choice during the 200 ms preceding DT in the tokens task and assessed the significance using a receiver-operating characteristic analysis with a criterion of 0.65.

Instantaneous firing rate was assessed via a partial interspike interval method. When analyzing data with respect to the start of the trial (first token jump), we usually exclude all spikes occurring after our estimate of DT, thus precluding any activity associated with movement initiation and/or execution. This is important in order to prevent averaging artifacts due to the very wide range of DTs in the tokens task. KS tests were used to compare activity distributions. Spearman's rank test was used to assess significance of the relationship between SumLogLR and neural activity. We determined the moment that a cell discriminated between PT and OT when the difference of activity exceeded two SDs (computed from baseline) in a 10 ms sliding window with a 2 ms step size (Sato and Schall, 2003). To be included in our analyses, cells had to have been recorded during at least four trials in each tested condition. The significance level of all statistical tests was set at 0.05.

SUPPLEMENTAL INFORMATION

Supplemental Information includes eight figures and can be found with this article online at http://dx.doi.org/10.1016/j.neuron.2014.01.031.

AUTHOR CONTRIBUTIONS

P.C. designed the experiment, D.T. collected and analyzed data, and D.T. and P.C. wrote the manuscript.

ACKNOWLEDGMENTS

This research was supported by CIHR (MOP-102662), CFI, FRSQ, and EJLB Foundation (to P.C.) and FYSSEN Foundation and GRSNC (to D.T.). We thank Marie-Claude Labonté for technical support and John F. Kalaska for valuable comments.

Accepted: January 15, 2014
Published: March 19, 2014

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