Distinct dynamics of ramping activity in the frontal cortex and caudate nucleus in monkeys

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Running head: Dynamics of FEF and caudate activity

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ABSTRACT

The prefronto-striatal network is involved in many cognitive functions, including perceptual decision making and reward-modulated behaviors. For well-trained subjects, neural responses frequently show similar patterns in the prefrontal cortex and striatum, making it difficult to tease apart distinct regional contributions. Here I show that, despite similar mean firing rate patterns, prefrontal and striatal responses differ in other temporal dynamics for both perceptual and reward-based tasks. Compared to simulation results, the temporal dynamics of prefrontal activity are consistent with an accumulation of sensory evidence used to solve a perceptual task but not with an accumulation of reward context-related information used for the development of a reward bias. In contrast, the dynamics of striatal activity is consistent with an accumulation of reward context-related information and with an accumulation of sensory evidence during early stimulus viewing. These results suggest that prefrontal and striatal neurons may have specialized functions for different tasks even with similar average activity.
INTRODUCTION

The prefrontal cortex-striatum network has been studied extensively for its roles in cognition. Anatomically, the prefrontal cortex projects heavily to the striatum (particularly the caudate nucleus) as part of a circuit that loops through the basal ganglia and thalamus, then back to the prefrontal cortex (Alexander et al. 1986; Parent and Hazrati 1995). Given their anatomical interconnections, it is not surprising that both the prefrontal cortex and caudate nucleus have been implicated in similar cognitive functions, including perceptual decision making (Gold and Shadlen 2007; Ding and Gold 2013), categorization (Miller and Buschman 2007; Seger and Miller 2010), reward-based reinforcement learning (Doya 2000; Dayan and Daw 2008; Frank et al. 2009), oculomotor control (Goldberg and Bushnell 1981; Bruce and Goldberg 1985; Hikosaka et al. 2000) and time estimation (Meck et al. 2008). These similarities extend to many common patterns of task-related modulation of single-unit activity in these brain regions, especially in well-trained animals (Pasupathy and Miller 2005; Ding and Hikosaka 2006; Kobayashi et al. 2007; Ding and Gold 2010; Antzoulatos and Miller 2011; Ding and Gold 2012; Seo et al. 2012).

For example, in monkeys performing an asymmetric reward saccade task (Figure 1A), some neurons in the dorsolateral prefrontal cortex, frontal eye field (FEF) and caudate nucleus exhibit context-dependent “ramping” activity (i.e., a gradual increase in average spike rate over several hundred milliseconds) before reward-predicting cues (Figure 1C; Lauwereyns et al. 2002; Itoh et al. 2003; Ding and Hikosaka 2006; Kobayashi et al. 2007). This activity has been hypothesized to contribute to reward-biased saccade latencies. Similarly, in monkeys performing a visual motion direction-discrimination task (Figure 1B), some FEF and caudate neurons show ramping activity while the monkey is viewing the stimulus and forming its perceptual decision (Figure 1D; Kim and Shadlen 1999; Ding and Gold 2010, 2012). Such activity has been hypothesized to reflect the accumulation of sensory evidence to form the decision.
One interpretation of the similarity between FEF and caudate neural responses under these conditions is that task-relevant signals are computed in cortex and then simply relayed to the basal ganglia to inform action selection or other functions. In fact, a number of network models of the prefrontal-basal ganglia pathway adopted this assumption (Bogacz et al. 2006; Lo and Wang 2006; Rao 2010; Cavanagh et al. 2011). Alternatively, the cortex and basal ganglia may make different computational contributions to different tasks but in a manner that is not readily apparent in simple measures of neural activity like average spike rate. Here my aim was to distinguish these possibilities in the contexts of reward-biased behavior and perceptual decision making, which require the brain to interpret different types of information, and of apparently similar buildup activity that relates directly to behavioral performance on these tasks. Using variance of conditional expectation (VarCE; Churchland et al. 2011) and temporal correlations, I show that these brain regions can exhibit quite different, task-dependent temporal dynamics, suggesting that informational flow in the fronto-striatal network is flexibly controlled to meet diverse task demands.

**METHODS**

*Data source and inclusion*

Two previously published data sets are used in this study. One set of data was obtained from two monkeys performing an asymmetric reward saccade task (Figure 1A and C; Ding and Hikosaka 2006). For this task, the monkey initiated a trial by looking at a visual fixation point presented at the center of the screen. One second after the monkey acquired fixation, a visual target was flashed at one of two peripheral locations and the monkey was required to make a delayed saccade to that location after the disappearance of the fixation point. Reward context was alternated in blocks such that in one block of trials, one target location was paired with a
large reward while the other location was paired with a small reward. Analyses were limited to
activity on correct trials during a 700 ms epoch before target presentation (Figure 1C, the epoch
is indicated by dashed vertical lines; the first 300 ms of the fixation period was excluded to avoid
contamination of visual/saccade-related responses while fixation was acquired). Neurons with
average activity in the epoch that differentiated between reward contexts were included for
further analyses (n = 50 and 38 for FEF and caudate, respectively). The reward context that
was associated with higher activity during the pre-target period is designated as the “preferred”
reward context and the other is designated as the “null” reward context.

The other set of data was obtained from two monkeys performing a visual motion direction-
discrimination task (Figure 1B and D; Ding and Gold 2010, 2012). For this task, the monkey
viewed a random-dot motion stimulus centered on the screen and indicated its decision about
the global motion direction of the stimulus by making a saccade toward the corresponding target.
Motion strength was controlled by varying the percentage of the dots moving in the same
direction (coherence). Viewing duration was controlled by the monkey: the motion stimulus was
extinguished as soon as the monkey’s gaze left a preset fixation window. The same reward was
given for correct decisions for both directions. Analyses were limited to activity on correct trials
during a motion-viewing epoch (from 250 ms after stimulus onset to 100 ms before saccade
onset; Figure 1D, the epoch is indicated by dashed vertical lines). Neurons with average activity
in the epoch that was modulated by choice and stimulus strength were included for further
analyses (n = 29 and 43 for FEF and caudate, respectively). The choice that was associated
with higher activity during motion viewing is designated as the “preferred” choice and the other
is designated as the “null” choice. Note that Figure 1D differed slightly from Figure 3 of the
original report (Ding and Gold 2010): For the original figure, the curve for each condition was
truncated at the median RT across all neurons for that condition. For Figure 1D, average firing
rate for each neuron and condition was truncated at the median RT for that neuron-condition
combination and then averaged across neurons without further truncation, to allow visualization of the mean firing rate trajectories over a longer period.

**Temporal dynamics measurements**

For each trial, spikes were counted in a 100-ms sliding window with 50-ms steps. A data point plotted at time \( t \) was based on spike count in the window \([t-100 \text{ ms}, t]\). Trials were grouped by types (reward contexts or motion strength-choice combinations for the asymmetric-reward and motion discrimination data sets, respectively). For each neuron and condition combination, the mean, variance and Fano factor for spike counts were estimated. Spike count residuals in a time bin were obtained by subtracting the mean spike count in the same time bin over all trials of the same neuron-condition combination.

The variance of conditional expectation (VarCE) of spike count residuals is the difference between the total variance and the estimated point-process variance, assuming that spike trains are generated with a doubly stochastic process. Following methods described by Churchland et al. (2011), the minimum Fano factor for all conditions of each neuron was denoted as \( \phi \) (Figure 2A). Point-process variance was estimated as the mean spike count multiplied by \( \phi \). VarCE was computed by subtracting the point-process variance from the total variance of the spike count residuals across all conditions.

Temporal correlation was estimated by computing a covariance matrix of the spike count residuals in non-overlapping 100-ms time bins. Correlation coefficients were obtained by normalizing the covariance matrix with values in the diagonal. The correlation coefficient between successive time bins (i.e., the first sub-diagonal values of the correlation matrix) was used to track the temporal correlation of neural activity over time.

**Statistical analysis**
To test for task-relevant modulation in the average firing rates ($FR$), linear regressions were performed using:

$$FR_{i,j} = b_0 + b_1 C_j + b_2 I_i,$$

where $FR_{i,j}$ is the value for the $i^{th}$ neuron ($I_i$) and the $j^{th}$ condition ($C_j$). For the motion discrimination data, the conditions were the signed coherence (positive and negative for preferred and null choices, respectively). For the asymmetric reward data, the conditions were the preferred and null reward contexts, respectively.

For each region-task combination, two methods were used to test the null hypothesis that the slope value is zero for VarCE/correlation values over time. In the “population-based” method, linear regression coefficients were obtained from VarCE and correlation values measured from spike count residuals pooled from all cells. $T$-tests were performed to test against the null hypothesis that the slope was zero. Error bar values shown in figures were bootstrapped by randomly selecting trials (with replacements) from each condition for each neuron and then pooling spike count residuals across cells. In the “single-cell” method, linear regression coefficients were obtained from VarCE/correlation values measured from each neuron. Sign tests were performed to test against the null hypothesis that the median slope across cells was zero. To test for the brain region/task dependence of VarCE and temporal correlation, two-way ANOVAs with interaction were performed on single-cell slope estimates, with brain region and task as factors. For comparisons of VarCE between FEF and caudate neurons within shorter time spans, Wilcoxon rank sum and Chi-square tests were used for the slope values and proportion of positive values, respectively.

Simulation

Spike trains were simulated with doubly stochastic Poisson processes. The time-dependent rate
parameter $\lambda(t)$ for the Poisson processes (rectified at zero) was governed by four models. In a model with accumulation (drift-diffusion model, or DD), $\lambda(t)$ was proportional to the time accumulation of a normally distributed random variable $x(t) \sim N(m, \sigma_{DD})$, where $m$ and $\sigma_{DD}$, the mean and standard deviation of the normal distribution, respectively, were constant values for a given trial. To simulate the asymmetric reward task, the preferred and null reward contexts have different values for $m$ ($m_{\text{PREF}} > m_{\text{NULL}}$) and the same $\sigma_{DD}$. The rate parameter $\lambda(t) = \sum_0^t x(t) + \beta_{\text{PREF or NULL}}$, where $\beta_{\text{PREF or NULL}}$ approximated the baseline firing rate for the two reward contexts, respectively. To simulate the motion discrimination task, $m$ varied with signed motion coherence ($C$), i.e., $m = kC$, and $\sigma_{DD}$ was set at 1. Accumulation stopped if either of the two choice bounds ($+A, -B$) was crossed and the choice was assigned by the first crossed bound (i.e., if $+A$ was reached first, the trial ended with a PREF choice; if $-B$ was reached first, the trial ended with a NULL choice). Trials that did not reach a bound within 4000 steps (i.e., 4000 ms) were discarded. As the firing rate dispersion is usually asymmetric between PREF and NULL choices, the rate parameter $\lambda(t)$ was scaled differently for the two choices: $\lambda(t) = \alpha_{\text{PREF or NULL}} \sum_0^t x(t) + \beta_{\text{base}}$, where $\beta_{\text{base}}$ approximated the baseline firing rate.

In three models that do not implement accumulation but displays the same mean and same average variance over the simulated period of the rate parameter as the DD model, $\lambda(t)$ was proportional to independent samples from normal distributions with time-varying mean: for the “varT” model, $x(t) \sim N(m * t, \sigma_{DD} * \sqrt{t})$; for the “stdT” model, $x(t) \sim N(m * t, \sigma_{T} * t)$; and for the “fixedV” model, $x(t) \sim N(m * t, \sigma_{V})$. The particular values of $\sigma_{T}$ and $\sigma_{V}$ were set to match the average variance over 700 ms (the duration of the epochs of interest) to that of the “DD” and “varT” models. To simulate the asymmetric reward task, the rate parameter $\lambda(t) = x(t) + \beta_{\text{PREF or NULL}}$. Parameters $m_{\text{PREF or NULL}}$, $\sigma_{DD}$, and $\beta_{\text{PREF or NULL}}$ are the same as in the DD model. To simulate the motion discrimination task, the rate parameter $\lambda(t) = \alpha_{\text{PREF or NULL}} x(t) + \beta_{\text{base}}$. 
and parameters $m = kC, \sigma_{DD}, \alpha_{\text{PREF or NULL}}$ and $\beta_{\text{base}}$ are the same as in the DD model. Choice
outcome, trial truncation, and baseline period were determined by the DD model. For example, if a trial from the DD model was terminated at $t$ with a $\text{PREF}$ choice, the corresponding trials for the other three models were simulated with $\alpha_{\text{PREF}}$ and truncated at time $t$.

To approximate the ranges of firing rate for neural data, cell-matched simulations were performed using parameters extracted from neural data. For each neuron on the motion discrimination task, 10 parameters were extracted: 1) the average number of trials across all coherence; 2) the onset time of choice-selectivity was used to simulate the sensory delay ($T_{\text{choice}}$); 3) the baseline firing rate 100 ms before $T_{\text{choice}}$ was used to specify $\beta_{\text{base}}$; 4) the average slope of the ramping activity during 200 ms after $T_{\text{choice}}$ across coherence levels, separately for the preferred and null choices, were used to specify $\alpha_{\text{PREF}}$ and $\alpha_{\text{NULL}}$, respectively; and 5) $A, B, k$ and non-decision times were obtained by fitting the behavioral psychometric and chronometric functions obtained from the same session to a drift-diffusion model using maximum likelihood methods (Palmer et al. 2005; Hanks et al. 2006; Ding and Gold 2010, 2012).

For each neuron on the asymmetric reward task, five parameters were extracted: the number of trials, the average slope in firing rate over the epoch for the two reward contexts (used as $m_{\text{PREF}}$ and $m_{\text{NULL}}$, respectively) and the intercepts (used as $\beta_{\text{PREF}}$ and $\beta_{\text{NULL}}$, respectively). Because there is no constraint from behavioral data on the asymmetric reward task, multiple values of $\sigma_{DD}$ was tested for how well the simulated VarCE and correlation trajectories approximate the experimental ones (see Results).

A likelihood measure was used to assess how well a model captures the temporal dynamics patterns of the experimental data. Specifically, trajectories from 20 iterations of simulations were used to estimate the mean and standard deviation at each time bin. The log likelihood of
obtaining the experimental value at a given time bin was computed assuming a normal distribution and summed across bins. As the focus was on the time course of each trajectory, instead of its baseline value, a simulated trajectory was vertically shifted to match its value for the first time bin to that of the experimental trajectory. This first time bin was excluded from likelihood summation.

RESULTS

I analyzed data previously obtained from two monkeys performing an asymmetric reward saccade task (Ding and Hikosaka 2006) and two different monkeys performing a visual motion direction-discrimination task (Ding and Gold 2010, 2012). As reported previously, subsets of caudate and FEF neurons showed similar task-relevant modulation of mean firing rates. For the asymmetric reward task, during a “pre-target” period while the monkey waited for the visual target, the visual environment remained constant, but the reward context differed between blocks. Both regions exhibited pre-target activity that differentiated between reward contexts (Figure 1C; \( n = 50 \) and 38; linear regressions, test for \( H_0: \) no dependence on reward context before target appearance, \( p = 0.0001 \) and 0.009, respectively, for caudate and FEF). In addition, the average firing rate for the preferred reward context increased with time for both regions.

For the motion-discrimination task, during motion stimulus viewing, the reward context remained constant, but the sensory evidence differed between trials. Neural activity in both regions was modulated by the strength of sensory evidence used to form the direction decision and the decision itself (Figure 1D; \( n = 29 \) and 43; linear regressions, test for \( H_0: \) no dependence on choice or signed motion coherence during motion viewing, \( p < 0.0001 \) for both choice and signed coherence for caudate neurons; \( p < 0.0001 \) and \( p = 0.0004 \), respectively, for FEF neurons). The similarity was especially strong for the early motion viewing period. Later in the
motion viewing period, caudate activity for the PREF choice decreased, whereas FEF activity largely maintained a rising pattern (Ding and Gold 2010, 2012). In addition, the average firing rate for the preferred choice increased with viewing time for both regions. These results from analyzing average firing rate thus appear to support the assumption that, for both tasks, the cortex simply relays asymmetric-reward and visual-motion information to the basal ganglia. However, as detailed below, analyses of higher-order statistical structure in the responses challenge this assumption.

**VarCE**

The measurement of VarCE assumes that a neuron’s spike trains can be generated by a doubly stochastic Poisson process (Churchland et al. 2011). In such a process, the rate parameter for the Poisson process is itself stochastic. VarCE measures the portion of the spike-count variance that can be attributed to the stochastic rate parameter and complements more commonly used measures of total spike count variability, such as Fano factor, coefficient of variation, etc. (Brostek et al. 2013). It has been especially useful as a signature of neural computations related to temporal accumulation in the context of decision making (Churchland et al. 2011; Marcos et al. 2013; de Lafuente et al. 2015). Specifically, a doubly stochastic Poisson process can generate different patterns of VarCE and temporal correlation, depending on whether or not the underlying rate parameter is a direct product of temporal accumulation (Churchland et al. 2011): accumulation results in upward-ramping mean spike count, VarCE and correlation, whereas time-independent samples with the same upward-ramping mean spike count produce much dampened VarCE and flat correlation. I therefore examined if and how VarCE for the ramping activity in FEF and caudate neurons differed under the two task conditions and, more specifically, whether the VarCE trajectories follow a upward-ramping pattern indicative of temporal accumulation.
Operationally, VarCE is computed as the difference between the total spike-count variance and the estimated variance for a Poisson process with the mean rate parameter. Computing VarCE thus requires estimating a proportionality factor that transforms mean firing rate to point-process variance, \( \phi \) (Figure 2A; also see Methods). I found that this factor was not different between FEF and caudate for both tasks (Figure 2B and C; Wilcoxon rank sum test, \( p = 0.863 \) and 0.142, respectively). Moreover, scaling \( \phi \) artificially by 1.4, 1.2, 0.8 or 0.6 did not qualitatively change the VarCE patterns (data not shown). I therefore consider the estimation of \( \phi \) to be reasonably reliable for identifying potential differences in VarCE between FEF and caudate neurons for the two tasks.

I found several differences in VarCE computed for the caudate and FEF data from the two tasks. First, the overall magnitude of VarCE was greater for the FEF population than for the caudate population, for both tasks (Figure 2D and F, compare the ranges on the ordinates). Second, for the motion-discrimination task, the VarCE for the caudate population exhibited a sharp early increase, peaked near 400 ms after motion onset, and then gradually decreased until the end of motion viewing (Figure 2D, left; slope from linear regression with 100-ms time bins: 0.0077 bin\(^{-1}\), t-test for H\(_0\): zero slope, \( p = 0.231 \)). In contrast, the VarCE for the FEF population maintained an increasing trajectory for the majority of the motion viewing period (Figure 2D, right; slope: 0.029 bin\(^{-1}\), \( p = 0.0016 \)). Third, for the asymmetric reward task, the VarCE for the caudate population maintained an increasing trajectory throughout most of the fixation period in anticipation of reward-predicting targets (Figure 2F, left; slope: 0.018 bin\(^{-1}\), \( p < 0.0001 \)). In contrast, the VarCE for the FEF population followed a decrease-increase-decrease trajectory instead of a monotonic ramp (Figure 2F, right; slope: -0.0016 bin\(^{-1}\), \( p = 0.82 \)).

I also observed differences in the VarCE measured from FEF versus caudate data for separate task-specific conditions (Table 1). For the motion discrimination task, the VarCE for FEF neurons had consistently positive slopes (i.e., ramped up) for the preferred choice at all
coherence levels and more varied slope values for the null choice. In contrast, the VarCE for caudate neurons did not have reliably non-zero slopes for most conditions. For the asymmetric reward task, the slope in VarCE for FEF neurons was not different from zero for the preferred reward context, whereas the slope for caudate neurons was positive.

These population results were consistent with linear regression results from the VarCE computed for single neurons from the two brain regions. For the motion discrimination task, the median slope of VarCE as a function of time for individual caudate neurons was 0.0017 bin\(^{-1}\), which was not significantly different from zero (Figure 2E, left; sign test, \(p = 0.38\)). In contrast, the median slope for individual FEF neurons was 0.032 bin\(^{-1}\), which was significantly greater than zero (Figure 2E, right; \(p = 0.0011\)) and greater than those computed for caudate neurons (Wilcoxon rank-sum test, \(p = 0.019\)). For the asymmetric reward task, the median slope for caudate neurons was 0.0098 bin\(^{-1}\) for caudate neurons, which was significantly greater than zero (Figure 2G, left; \(p = 0.0031\)) and greater than those computed for FEF neurons (\(p = 0.0007\)). The median slope for FEF neurons was not different from zero (Figure 2G, right; \(p = 0.20\)). A two-way ANOVA with brain region and task as factors indicated modulation by task (\(d.f. = 1, F = 5.64, p = 0.019\)) and region-task interaction (\(d.f. = 1, F = 7.73, p = 0.006\)), but not by brain region alone (\(F = 1.62, p = 0.206\)).

The slope estimates from the entire viewing period so far indicated that the VarCE patterns were different between FEF and caudate neurons for the two tasks: the VarCE patterns for FEF neurons on the motion discrimination task and for caudate neurons on the asymmetric reward task seemed consistent with accumulation processes operating throughout the time epoch of interest, whereas other VarCE showed non-monotonic patterns inconsistent with continuous accumulation. To better characterize the temporal characteristics of these latter patterns, I estimated slope values for individual neurons within shorter epochs (300-ms sliding windows).

As shown in Figure 2H-K, this piece-wise analysis provided further support for brain region- and
task-dependent differences in VarCE. For the motion discrimination task, during the early
motion-viewing period VarCE slopes were similar in FEF and caudate, with similar median slope
values (Figure 2H) and proportion of neurons with positive slope values (Figure 2I). However, at
~350 ms after motion onset, the median slope of VarCE and the proportion of neurons with
positive slopes were significantly larger for FEF neurons than for caudate neurons (Wilcoxon
rank sum test, $p = 0.018$ and Chi-square test, $p = 0.046$, respectively). Afterward, both regions
showed a decreasing trend in median slope value and proportion of positive slopes,
although >50% of FEF neurons showed positive slopes throughout the epoch, whereas in
caudate a slight majority of neurons had negative slopes by the end of the epoch. These results
suggested that VarCE for caudate neurons was consistent with an accumulation process only
during early motion viewing. For the asymmetric reward task, the median slope value was
consistently positive throughout the epoch for caudate neurons, but more varied for FEF
neurons (Figure 2J). Similarly, the proportion of positive slopes was >50% throughout the epoch
for caudate neurons but more varied for FEF neurons (Figure 2K). The largest differences
between brain regions were observed at the beginning of the epoch, where caudate neurons
had relatively strong positive slopes and FEF neurons had relatively negative slopes (Wilcoxon
rank sum test, $p = 0.006$ and Chi-square test, $p = 0.0009$, respectively). Compared to values for
the motion discrimination task, the peak median slope value for the asymmetric reward task was
smaller for both regions (Figure 2L, triangles). However, the average value was similar for
caudate neurons between tasks (Figure 2L, filled circles), whereas the average value was much
smaller for FEF neurons for the asymmetric reward task (open circles), suggesting that caudate
neurons may be involved in accumulation-like processes for both tasks, whereas FEF neurons
may only be involved for the motion discrimination task.

Collectively, these results revealed task-specific regional differences in VarCE between FEF
and caudate neurons. Within the framework of a doubly stochastic Poisson process, VarCE is
sensitive to task-relevant computations underlying the rate parameter. The regional differences
in VarCE trajectories therefore suggest that, instead of constituting a general relay, FEF and
caudate neurons may be involved in distinct computations depending on task context.

**Temporal correlation**

The measurement of temporal correlation quantifies the relationship of spike-count residuals
between two neighboring time bins. Similar to VarCE, a process with temporal accumulation
generates correlation that increases with time (Churchland et al. 2011). Unlike VarCE, this
measure is agnostic about the underlying spike-generation process and thus is complementary
to the analyses presented above.

Similar to the regional differences observed in the VarCE, I observed substantial task-
dependent regional differences in temporal correlations measured from ramping activity of
caudate and FEF neurons. The first sub-diagonal correlation coefficients (correlation in short)
reflect spike-count correlations between neighboring time bins. As shown in Figure 3, correlation
values tended to be slightly higher for FEF activity than caudate activity for both tasks (brighter
pixels for the FEF matrices, Figure 3A and D; also compare traces in Figure 3B and E). For the
motion discrimination task, correlation values tended to ramp up as a function of time within a
trial for both caudate (albeit with a slight decrease after ~600 ms, as seen in Figure 3B, left;
slope of linear regression = 0.017 bin$^{-1}$, $p = 0.044$) and FEF activity (Figure 3B, right; slope =
0.027 bin$^{-1}$, $p = 0.0083$). In contrast, for the asymmetric reward task, correlation values tended
to ramp up over time in caudate but not FEF activity (Figure 3E; caudate slope = 0.025 bin$^{-1}$, $p =
0.0052$; FEF slope = -0.0001 bin$^{-1}$, $p = 0.99$).

I also observed differences in temporal correlations measured from FEF versus caudate data for
separate task-specific conditions (Table 1). For the motion discrimination task, mean
correlations ramped up over time (i.e., have positive slopes computed via linear regression) for
trials with the preferred choice for FEF, but less consistently for caudate, neurons. In contrast, for the asymmetric reward task, positive slopes were observed for both reward contexts in caudate neurons, but not FEF neurons.

These patterns of correlation dynamics as a function of time, measured from the pooled population data, were consistent with results from single-neuron analysis. For the motion-discrimination task, the median slope of correlation values versus time across cells was 0.013 bin\(^{-1}\) (sign test, \(p = 0.0011\)) for caudate neurons and 0.024 bin\(^{-1}\) (\(< 0.0001\)) for FEF neurons, respectively (Figure 3C). These slope values were larger for FEF neurons than for caudate neurons (Wilcoxon rank-sum test, \(p = 0.033\)). For the asymmetric reward task, the median slope from single-neuron analysis was 0.013 bin\(^{-1}\) (\(p = 0.0031\)) for caudate neurons and -0.0058 bin\(^{-1}\) (\(p = 0.32\)) for FEF neurons (Figure 3F). These slope values were significantly larger for caudate neurons than for FEF neurons (Wilcoxon rank-sum test, \(p = 0.005\)). A two-way ANOVA with brain region and task as factors indicated modulation by task (\(d.f. = 1, F = 19.68, p < 0.0001\)) and region-task interaction (\(d.f. = 1, F = 19.38, p < 0.0001\)), but not by brain region alone (\(F = 0.0038, p = 0.951\)). Piece-wise estimation of the slope values was not performed because the computation of temporal correlation resulted in too few time samples.

The region- and task-dependent VarCE and correlation patterns were robust with respect to choices of bin size. I repeated the analyses using different bin sizes (60, 80, 100 and 120 ms). As shown in Table 2, for all bin sizes tested, median VarCE slope was significantly different from zero only for FEF neurons for the motion discrimination task and for caudate neurons for the asymmetric reward task, not for other region-task combinations. Similarly, for all bin sizes tested, median correlation slope was significantly different from zero for the FEF neurons for the motion discrimination task. A similar pattern of results was evident in the caudate-asymmetric reward combination, except for the 60-ms bin size. For all bin sizes tested, two-way ANOVAs also consistently indicated modulation by the region-task interaction for the slopes of VarCE and
Collectively, these results indicate that, despite similar mean firing rate patterns, caudate and FEF spike trains showed distinct VarCE and temporal correlation patterns for the two tasks. The FEF population shows increasing VarCE and temporal correlation during motion viewing on the perceptual decision task, but not in anticipation of reward-predictive targets on the asymmetric reward task. In contrast, the caudate population shows increasing VarCE and temporal correlation in anticipation of reward-predictive targets on the asymmetric reward task and during early motion viewing on the perceptual decision task.

**Cell-matched simulations**

To examine whether an accumulation-like computation can account for the observed VarCE and correlation time courses in caudate and FEF neurons, I next performed simulations with four doubly stochastic Poisson processes that differ in whether temporal accumulation is directly involved. In the “DD” model, the rate parameter was directly governed by an accumulation-to-bound process. In the other models, the rate parameter was determined by independent samples from stochastic processes with ramping mean values (e.g., reflecting accumulation that occurs elsewhere) and with variance increasing linearly with time (“varT” model), quadratically with time (“stdT” model) or staying constant (“fixedT” model).

I focused on four questions. First, for the motion discrimination task, given that the ramping activity in FEF and caudate neurons during motion viewing has been postulated to reflect temporal accumulation of visual motion evidence (Kim and Shadlen 1999; Ding and Gold 2010, 2012), can a temporal accumulation process with cell-matched and behaviorally constrained parameters approximate the observed VarCE and correlation patterns? Second, on the asymmetric reward task, although the reward context is known to the monkeys and constant during the pre-target period, the magnitude of reward-context modulation increases with time in
cortical activity, caudate activity and saccade latency (Lauwereyns et al. 2002; Takikawa et al. 2002; Thompson et al. 2005; Ding and Hikosaka 2006, 2007; Kobayashi et al. 2007). These observations are consistent with an accumulation-like underlying computation. In relation to our dataset, can a temporal accumulation process with cell-matched parameters approximate the observed VarCE and correlation patterns in FEF and/or caudate activity? Third, for each task, can a common process capture the patterns for both FEF and caudate neurons? In other words, are the observed regional differences in VarCE and correlation due to differences in basic firing properties or differences in the computations performed by the two brain regions? Fourth, for each brain region, can a common process capture the VarCE and correlation patterns on both tasks? In other words, can a brain region be involved in a general-purpose computation to meet different task demands?

As detailed in Methods, for the motion discrimination dataset, simulation parameters were fully specified by the experimental data. With these parameters, all four models produced mean firing rates that were modulated by choice and motion coherence (Figure 4A and B). Because the DD model used bounded accumulation, while the rate parameter for the other models was not bounded, the excursion of the mean firing rate was larger in the non-DD models. As my focus was on comparing experimental and simulation results in terms of the time course of the VarCE and correlation curves and not their absolute average values (the latter of which may be influenced by task-independent factors), I shifted the simulated VarCE and correlation coefficient values vertically to match the corresponding experimentally measured values at the first time bin.

Overall, the model with accumulation (Figure 4C-H; “DD”, red) was better at capturing the patterns of VarCE and correlation than the models without accumulation (“varT”, blue; “stdT”, green and “fixedV”, magenta). VarCE trajectories from the DD model were similar to experimental curves during the early motion viewing period for caudate neurons (Figure 4C) and
throughout the motion period for FEF neurons (Figure 4F). Only the DD model produced the rising temporal correlation patterns seen in experimental results, while the other models produced flat trajectories for both regions (Figure 4D and G). To quantify these visual impressions, I computed the log₁₀ likelihood (LL) of observing the experimental results for the four models (Figure 4E and H; values were truncated at -10 for better visualization). I considered a positive sum of log(LL) as indication of a good match and a >1 difference in the mean log(LL) between two models as strong evidence for one model prevailing over the other (Kass and Raftery 1995). Based on these criteria, for the full motion viewing epoch, the DD model provided good approximation for FEF neurons (Figure 4H, open red bars), but not caudate neurons (Figure 4E, open red bars), although the match was significantly improved if only the early motion viewing epoch was considered (Figure 4E, solid red bars). For either the full or early motion viewing epoch, the DD model consistently outperformed other models for both brain regions: the differences in mean log(LL) between the DD model and the other three models were all greater than 1.6. Scaling down the mean firing rate excursion of the non-DD models, by applying a single scale factor for all neurons, resulted in a slight decrease in VarCE and no significant change in the time course of correlation (data not shown), which worsened the match to experimental results for these models. These results suggest that the temporal dynamics of FEF and caudate activity is more consistent with an underlying computation that accumulates motion evidence. Furthermore, because the DD model used parameters that were fitted to behavioral data and produced continuously increasing VarCE for both FEF and caudate datasets, the simulation results suggest that the plateau-decrease VarCE pattern for caudate neurons during late motion viewing was likely not an artifact of early decision termination in those recording sessions, but rather reflected disengagement of those neurons from ongoing, behaviorally relevant accumulation process.

For simulations of the motion discrimination dataset, the relationship between mean firing rate
and $\sigma_{DD}$ was constrained by behavioral performance. The asymmetric-reward dataset, however, only specified the simulation parameters that are related to the mean firing rates, leaving $\sigma_{DD}$ as an unconstrained guess parameter in simulations. As expected, using the cell-matched parameters, all models produced qualitatively similar reward context-modulated ramping mean firing rates for both brain regions (Figure 5A and B; data not shown for non-DD models). The accompanying VarCE and correlation patterns, on the other hand, depended on the particular values of $\sigma_{DD}$ and the model identity. I therefore performed simulations using different $\sigma_{DD}$ values to examine if any $\sigma_{DD}$-model combination can approximate the observed VarCE and correlation patterns.

Figure 5C-F illustrates the simulated VarCE and correlation curves with the DD and varT models using two $\sigma_{DD}$ values. With $\sigma_{DD} = 0.02$, the DD model generated VarCE and correlation curves that were similar to the experimental curves for caudate neurons (Figure 5C), but failed to do so for FEF neurons (Figure 5E). With $\sigma_{DD} = 0.04$, the varT model generated a VarCE curve that was similar to the experimental curve for caudate neurons, but with a flat correlation curve that deviated far from the experimental curve (Figure 5D). With the same $\sigma_{DD}$ value, the varT model failed to match VarCE and correlation curves to the corresponding experimental curves for FEF neurons (Figure 5F), although it was better than the DD model in Figure 5E. In my sample of $\sigma_{DD}$ values, only the DD model with $\sigma_{DD}$ values in the range of 0.016~0.024 produced positive sum log$_{10}$LL values for caudate activity (Figure 5G). No combination produced positive sum log$_{10}$LL values for FEF activity, although the non-DD models outperformed the DD model at most $\sigma_{DD}$ values (Figure 5H). These results suggest that, for the asymmetric reward task, a temporal accumulation process can account for the observed VarCE and correlation patterns in caudate neurons, but not for FEF neurons.

Combining all simulation results, for the motion discrimination task, temporal accumulation can capture the patterns of VarCE and correlation for FEF neurons during the full motion viewing...
epoch and for caudate neurons during the early motion viewing epoch. For the asymmetric
reward task, none of the models simulated here can account for the VarCE and correlation
patterns of both FEF and caudate neurons, suggesting that the two regions have different
functional roles on this task. When considered across tasks, the temporal dynamics of caudate
activity is consistent with a general-purpose accumulation-like computation for both tasks,
whereas the temporal dynamics of FEF activity does not reflect similar underlying computations
on the two tasks, despite similar task-relevant ramping mean firing rates. These results further
suggest that the regional differences in VarCE and correlation are more likely due to task-
specific presence/absence of temporal accumulation-like underlying computations than
differences in basic firing properties.

DISCUSSION

To better understand functional differences between the prefrontal cortex and striatum, I
analyzed spike-count properties of subsets of neurons previously recorded in monkeys
performing two decision tasks: a motion discrimination task used extensively for studying
perceptual decisions and an asymmetric reward task used extensively for studying reward-
based behaviors. These neurons showed gradually increasing (ramping up) mean firing rates
for the preferred condition (preferred choice or reward context). Despite the similarities in mean
firing rate, my analyses of spike count variability and temporal correlation patterns revealed
task-specific regional differences. The FEF population showed increasing VarCE and temporal
correlation throughout the motion viewing period on the perceptual decision task, but not in
anticipation of reward-predictive targets on the asymmetric reward task. In contrast, the caudate
population showed increasing VarCE and temporal correlation in anticipation of reward-
predictive targets on the asymmetric reward task and during early motion viewing on the
perceptual decision task. Compared to simulation results of models with and without temporal accumulation, these patterns suggest that FEF and caudate neurons are more involved in temporal accumulation of visual motion information to reach a perceptual decision and temporal accumulation of reward context-related information to modulate saccade behavior, respectively.

Before discussing the functional implications of these results, I note a potential caveat. As acknowledged before, the partition of spike count variability for VarCE estimation relies on the assumptions that spike trains can be characterized as a doubly stochastic process and the appropriate portion of point-process variance can be reliably estimated (Churchland et al. 2011). These assumptions have been examined and applied in analyses of cortical activity (Geisler and Albrecht 1995; Nawrot et al. 2008; Churchland et al. 2011; Lee and Seo 2011; Goris et al. 2014). In contrast, the validity of these assumptions for striatal activity remains to be more rigorously tested. Nevertheless, several considerations suggest that the observed regional differences are robust and interpretable. First, corticostriatal and striatal neurons show similar firing properties in anesthetized rats, in terms of the dependence on state transitions of membrane potential, the shape of interspike interval distribution and spike train variability (Stern et al. 1997). Consistent with these findings from intracellular neuron recordings, estimates of \( \phi \) in this study, which were based on extracellular neuron recordings and controlled the point-process variance estimation, did not differ between FEF and caudate neurons. In addition, doubly stochastic processes with cell-specific parameters can capture the temporal patterns of VarCE and correlation of caudate neurons during early motion viewing on the perceptual task and before target onset on the asymmetric reward task. These results suggest that the first assumption is a reasonable approximation for the purpose of this study. Second, artificially scaling \( \phi \) did not change the patterns of region- and task-specific difference, suggesting that these patterns are robust with respect to the precision of estimating the portion of point-process variance. Third, the differences in VarCE were also accompanied by congruent differences in
correlation patterns. As the measurement of correlation did not rely on the validity of the above assumptions, these results thus gave me confidence that the observed regional differences reflect functionally important modulation of spike count statistics.

What can we infer from these task-dependent patterns of VarCE and temporal correlation? In line with a previous report, simulations based on an accumulation model predicted a gradual increase of VarCE and temporal correlation (Churchland et al. 2011). For the motion discrimination task, although both caudate and FEF activity show patterns of mean firing rate consistent with motion evidence accumulation (Kim and Shadlen 1999; Ding and Gold 2010, 2012), FEF activity was more robust in exhibiting the predicted patterns of VarCE and temporal correlation, similar to LIP activity (Churchland et al. 2011), and caudate activity exhibited rising patterns only during early motion viewing. These observations suggest that cortical neurons are more intimately involved in the temporal accumulation of motion evidence to form the final decision. During the early accumulation phase, the rate of rise in VarCE of caudate activity was approximated by the DD model, but the rise in correlation was less than predicted. The varT and stdT models, with ramping mean and independent samples that may be thought of as products of pooling, produced increasing VarCE and flat correlation. These results thus suggest a pooling-relay scheme, where caudate neurons inherit accumulated signals from cortical areas through convergent corticostriatal projections (Zheng and Wilson 2002; Lo and Wang 2006; Bogacz and Gurney 2007; Rao 2010). During the late motion viewing phase, mean firing rate, VarCE and correlation all deviate from predictions of continued accumulation. Why and how caudate neurons transition out of the accumulation process remain to be examined. It is interesting to speculate whether these caudate neurons participate in an initial assessment of trial difficulty for online adjustment of decision formation and how the transition times of these caudate neurons influences behavioral performance.

For the asymmetric reward task, despite a similar prevalence of caudate and FEF neurons
demonstrating reward-context modulation of activity before target presentation (Ding and Hikosaka 2006), caudate neurons showed the rising VarCE and temporal correlation patterns as predicted by the DD model, while the non-monotonic time courses for FEF neurons do not conform to predictions of any of the models studied here. These observed regional differences are inconsistent with a simple FEF-caudate feedforward relay scheme as for the motion discrimination task. It remains to be tested whether a DD model incorporating information multiplexing as observed in other high-order cortical neurons could approximate the temporal dynamics of FEF activity (Meister et al. 2013; Park et al. 2014). A systematic application of temporal dynamics analyses to other brain regions involved in reward-biased behavior may provide insights into the underlying functional circuitry.

It has been proposed that, similar to sensory evidence, the value of different stimuli may also be accumulated over time to support value-based decisions in human subjects (Krajbich et al. 2010; Krajbich et al. 2012; Towal et al. 2013). My results further extend the idea that accumulation is a general brain computation that can be applied to a broad range of information. The rising mean firing rates, VarCE and correlation in caudate activity before target onset suggest that, even in the absence of stimuli, an accumulation-like computation is involved to support asymmetric reward-biased behavior. Furthermore, because all of these characteristics in caudate activity can be well approximated by the DD model, which accumulates a noisy, reward context-related quantity, the accumulation-like computation may operate on an internal reward context-related signal. This interpretation may appear puzzling: for the asymmetric reward task, reward context was altered in blocks of trials such that the current reward context was known to the monkeys and constant during the pre-target period. In other words, unlike for the motion discrimination or value-based decision tasks, where accumulation is needed to identify the stimulus or the higher-valued option, here the monkeys do not need to accumulate information to determine the identity of current reward context. It is thus unclear why an accumulation-like computation is
required. I speculate that the accumulation-like computation is a part of the process that incorporates the identity of current reward context into a behavioral bias. For example, biases in saccade latency have been consistently observed on asymmetric reward saccade tasks: for the same saccade target, latency is shorter if the larger reward is expected (Lauwereyns et al. 2002). Consistent with the idea of temporal accumulation, the magnitude of such a bias depends on the duration of the pre-target period, with larger bias corresponding to longer pre-target duration (Ding and Hikosaka 2007). The behavioral benefits of the time-dependent bias remain to be identified, but caudate neurons may accumulate a noisy neural representation of the fixed reward context information to contribute to the saccade latency bias. Alternatively, caudate neurons may contribute to time estimation, which has also been proposed to use accumulation as the underlying computation (Treisman 1963; Merchant et al. 2013), and the pre-target activity reflects reward-context modulation of the accumulated timing information. Under the current task conditions, these two schemes are mathematically equivalent. It awaits further investigation how the reward context-dependent accumulation process relates to other accumulation-like computations for time estimation and/or preparation for self-initiated movement (Schurger et al. 2012).

In summary, focusing on neurons with similar task-relevant modulation in mean firing rates, analyses of spike count variability and temporal correlations suggest that the subpopulations of neurons in FEF and the caudate nucleus have different functional roles in the accumulation of reward context and sensory information. Because caudate neurons appear to be directly involved in the accumulation of reward-context information and to inherit signals reflecting accumulated sensory evidence from FEF, they may serve strategic roles in forming decisions that must appropriately combine sensory and reward context information. Combined with differences in mean firing rate patterns observed in the larger population of the two regions, these results suggest that, instead of serving as a simple relay, the inner workings of the fronto-
striatal network are flexibly controlled to meet diverse task demands. Future efforts to understand computations underlying the fronto-striatal interaction and the functional roles of the larger cortico-basal ganglia network will likely benefit from analyses of VarCE, correlations, and other response properties beyond mean firing rates.

Acknowledgements

I thank Anne Churchland and Michael Shadlen for generous sharing of source code and tips for the VarCE analysis, and Joshua Gold, Yin Li and Takahiro Doi for providing valuable comments and suggestions. This work was supported by NIH 1R01EY022411 from the National Eye Institute.
References


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**Figure Legends**

**Figure 1.** Task designs and average responses of caudate and FEF neurons.

A, Asymmetric reward task. During the fixation period, the visual environment was the same, but reward context alternated between blocks of trials. See Methods for more task details.

B, Motion discrimination task. During the motion period, motion strength (%coherence) was randomly selected for each trial. Only correct trials were rewarded, with equal reward size for both choices. See Methods for more task details.

C, Average firing rates of caudate (n = 38) and FEF (n = 50) neurons showed similar reward context-modulated ramping activity during the pre-target fixation period of the asymmetric reward task. Vertical dashed lines denote the epoch used for analyses of temporal dynamics.

D, Average firing rates of caudate (n = 43) and FEF (n = 29) neurons showed similar coherence and choice-modulated ramping activity during the motion viewing period of the motion discrimination task. Note that the average caudate activity was less truncated in time here than in the original report (Ding and Gold 2010). Gray scales indicate coherence levels. Vertical dashed lines denote the epoch used for analyses of temporal dynamics.

**Figure 2.** Comparison of VarCE between caudate and FEF neurons.

A. Illustration of \( \phi \) estimation. Gray traces are Fano factor computed from a neuron for different coherence-choice combinations (solid: preferred choice; dashed: null choice). \( \phi \) denotes the minimum Fano factor for all combinations (horizontal line with arrow), which was used to compute point-process variance for the neuron.

B and C, Histograms of \( \phi \) estimate for neurons recorded on the motion discrimination (B) and asymmetric reward (C) task. Cd: caudate.

D, VarCE (mean ± s.e.m estimated with resampling) computed from pooling the population data. Dashed lines indicate the start time of the epoch for regression analyses (same as in Figure 1D).
E, Histograms of slope values from linear regression of VarCE computed for individual neurons. Filled bars indicate cells with significant non-zero slopes (t-test, p < 0.05). Triangles indicate median values for each population.

F-G, Same conventions as D-E, for the asymmetric reward task.

H, Median slope values of VarCE estimated using a sliding window of 6 consecutive points (300 ms) for the motion discrimination task. A data point at time t represents the value obtained for the t ~ t+300 ms epoch. Asterisks indicate bins with significant regional difference (p < 0.05).

I, Percentage of cells showing positive slope values. Asterisks indicate bins with significant regional difference (p < 0.05).

J and K, Same conventions as H and I, for the asymmetric reward task.

L, Peak (triangles) and average (circles) median slope values across all sub-epochs in H and J.

Figure 3. Comparison of temporal correlation between caudate and FEF neurons.

A, Correlation matrices obtained from pooling each population for the motion discrimination data set.

B, The first sub-diagonal correlation curves from A (i.e., correlation between the i'th and (i + 1)'th bins; mean ± s.e.m. estimated with resampling).

C, Histograms of slope values from linear regression of the first sub-diagonal correlation as a function of time bins for individual neurons. Filled bars indicate neurons with significant non-zero slope (t-test, p < 0.05). Triangles indicate median slope values for each population.

D-F, Correlation results for the asymmetric reward data set. Same conventions as A-C.

Abbreviation: Cd: caudate.

Figure 4. Cell-matched simulation results for the motion discrimination datasets.

A and B, Mean firing rates from the caudate (A) and FEF (B) datasets for the experimental (left) and simulation data (four right panels).
C, VarCE computed from experimental (black, mean only) and simulation data (red: DD; blue: varT; green: stdT; magenta: fixedV; mean ± s.e.m.) for caudate neurons. The simulated curves were shifted vertically to match the experimental values at the first time bin.

D, Correlation curves computed from experimental and simulation data. Same conventions as C. The simulated curves were shifted vertically to match the experimental values at the first time bin.

E, sum of log likelihood for VarCE and correlation trajectories of different models, for the caudate dataset. Values below -10 were truncated. Open bars: the sum of log_{10}(LL) for all time bins; solid bars: the sum of log_{10}(LL) for bins 2-8 for VarCE and for bins 2-4 for correlation.

F-H, same conventions as C-E, for the FEF dataset.
Figure 1

A. Asymmetric Reward Task

- Fixation
- Reward Context 1
- Reward Context 2

B. Motion Discrimination Task

- Fixation
- Choice targets
- Motion
- Saccade

C. Caudate

- Firing rate (Hz)
- Time from target onset (ms)

D. FEF

- Time from motion onset (ms)

- %Coh
  - 51.2
  - 25.6
  - 12.8
  - 6.4
  - 3.2

- Choice
  - PREF
  - NULL
Figure 3

A. Caudate and FEF correlation map from motion onset (ms) to time from target onset (ms).

B. Correlation plots for motion: Cd and FEF vs. time from motion onset (ms).

C. % cells histogram for Cd and FEF slopes (bin^-1).

D. Caudate and FEF correlation map from target onset (ms) to time from target onset (ms).

E. Correlation plots for reward: Cd and FEF vs. time from target onset (ms).

F. % cells histogram for Cd and FEF slopes (bin^-1).
Figure 4

A Caudate DD varT stdT fixedV
Rate (Hz)

200 600 200 600 200 600 200 600

Time from motion onset (ms)

B FEF DD varT stdT fixedV
Rate (Hz)

200 600 200 600 200 600 200 600

Choice
- PREF - NULL

C D Caudate Caudate
VarCE VarCE

Time from motion onset (ms)

0.1 0.3 0.5 0.7 0.9

VarCE

0.6 0.8 1.0 1.2 1.4 1.6 1.8

D E F G H

Sum log(LL)

-10 -5 0 5

VarCE Corr

0 0.3 0.5 0.7 0.9 1.1 1.3 1.5

Sum log(LL)

-10 -5 0 5

DD varT stdT fixedV DD varT stdT fixedV

Table 1. Condition-specific results. VarCE and temporal correlation were estimated by pooling data from all neurons for each condition. The slope was measured by linear regression with time bin as the regressor. Coh: motion coherence. \( P \) values < 0.05 (t-test) are indicated as bold.

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Table 2. Statistical results from analyses using different bin sizes. Slope values are in s^{-1}. P values less than 0.05 are indicated in bold.

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