

# **Localised and stable codes for goal and direction mix with a distributed control signal during multi-step spatial inference in monkey frontal cortex**

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## Abstract

The prefrontal cortex (PFC) of primates has long been associated with a diverse set of cognitive control and executive functions, governing decision making in complex situations. Neural recordings of isolated regions in PFC have revealed a similarly diverse set of neural codes, showing varying degrees of stability and temporal generalizability across studies, and hence leaving open the question of when and where PFC relies on each specific coding scheme. Here we use a novel multi-step maze task and large-scale recording arrays to record from 6 sub-regions of frontal cortex (FC) during complex planning behavior. We find that across regions FC seems to combine stable and localized codes with temporally-confined but spatially distributed codes. Instead of relying on one specific code, a multiplexed set of diverse codes is used to generate complex cognition.

**Keywords:** cognitive control; frontal cortex; multiplexed codes; population codes; planning; goal-directed behavior

## Introduction

The prefrontal cortex (PFC) of primates gives rise to complex cognition and especially contributes to tracking large-scale goals (Mushiake, Saito, Sakamoto, Itoyama, & Tanji, 2006) and understanding the abstract structure of tasks (Achterberg et al., 2022) involving multiple steps or variables. This is assumed to be true both in cognitive working-memory tasks and classical navigation tasks (Patai & Spiers, 2021). Whereas the general involvement of PFC in executive functions is clear, the data on the nature of its involvement has been varied, with some data showing continuous stable codes of cells to support working memory (Curtis & D’Esposito, 2003), and other data showing contrasting highly dynamical and unstable coding combined with activity-silent working memory (Sigala, Kusunoki, Nimmo-Smith, Gaffan, & Duncan, 2008; Chiang & Wallis, 2018; Stokes, 2015). Given that past primate electrophysiology recordings forced us to focus on small, isolated portions of FC, we wondered whether the seemingly contrasting codes observed in FC in the past could jointly be observed if we were able to record from multiple regions of FC. Here we use new large-scale recording arrays to record 2865 neurons from 6 sub-regions of FC (Table 1) in two macaque monkeys (*macaca mulatta*). During the recordings monkeys solve a task which requires holding goals in mind while solving multiple steps of spatial inference.

## Task

In our task, monkeys navigate a grid environment using saccades (Figure 1A). Monkeys always start in the middle of the grid. At the start of the trial, they see the current goal in one of four possible locations. After a delay, two choice options are shown, and they need to navigate over the grid by picking one of them after a go signal appears. Monkeys need to pick the option that is closer to the goal. Figure 1A shows an example of a first choice. Figure 1D shows how the monkey can

Table 1: Neurons recorded and analyzed across monkeys.

Region of frontal cortex	Neurons recorded
dorsal medial PFC (dmPFC)	360
dorsal PFC (dPFC)	684
Principal Sulcus (PS)	653
ventral PFC (vPFC)	469
Insula	358
dorsal lateral premotor cortex (dlPM)	341

complete this trial in two steps or four steps. Four step routes happen when the access to the goal is blocked at the second choice (‘Choice 2 (away)’). Importantly, the goal is only shown at the very beginning of the trial and not in-between consecutive choices within a trial. We do not allow monkeys to backtrack or take unnecessary detours, so all correct trials are either 2-step or 4-step routes, terminating in one of the four goal locations. Figure 1B shows all possible 2-step and 4-step routes of the task.

## Results & Discussion

After training monkeys on the described task, they can perform it with high accuracy (Figure 1C) across choices. The key variable in this task is the goal location which needs to be held in working memory across steps. So first, we want to investigate whether there is a stable code for the goal location which persists throughout trials. All following analyses are done by region. By calculating the average activity of each unit in each region for each goal location, we can extract a low-dimensional goal position subspace of the population activity using Principal Component Analysis (PCA). Here we use the first two principal components to visualize the structure of the population activity. To ensure this ‘Goal space’ is unconfounded by the move direction, we use data from the ‘Delay’ period before ‘Choice 2 (goal)’ and ‘Choice 4 (goal)’ to calculate unit mean activations. After extracting the 2D goal subspace we now want to see which shape the population activity takes in this space. For this we project data from different 200 millisecond windows from across the trial duration into the goal space in bootstrapped fashion. Colored ellipses in Figure 1E show the 95% confidence interval of the population activity of dmPFC by each goal. We can see that during the delay period before each choice, dmPFC codes for the target location in a geometrically structured way. This geometry is stable across choices. Further analyses (Figure 1G, top) show that this 2D subspace captures a relatively constant and significant portion of variance over the duration of the task. dmPFC is the only region showing such significant stable goal coding throughout the entire trial (other regions not depicted).

We now want to know whether the direction of the next move is also represented with a stable code. For this, we repeat the analysis from before but now using the mean activations of units for each movement direction during the ‘Choice presentation’ period of ‘Choice 2 (goal)’ and ‘Choice 4 (goal)’.

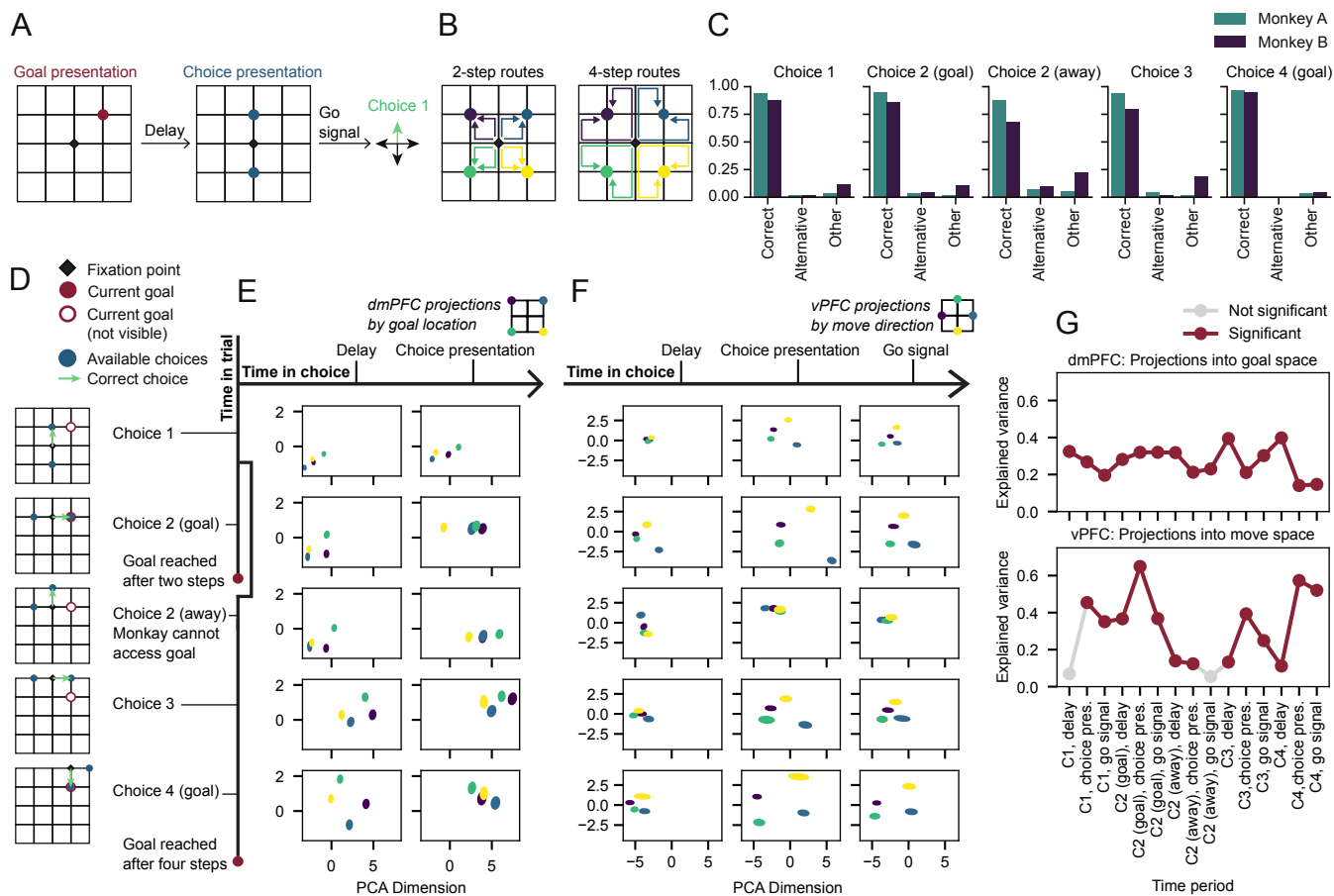


Figure 1: A, Maze grid shown to monkeys, depicting an example of the initial goal presentation period and the consecutive first choice. B, All 2-step and 4-step routes within the task. Colors are only for the purpose of visualization. C, Behavior of monkeys. 'Correct' stands for choosing the correct alternative, 'Alternative' for choosing the wrong alternative, and 'Other' for any other mistake. D, Example of how the trial started in (A) can be completed with a 2-step and a 4-step route. E, dmPFC goal space with 95% confidence interval projections via bootstrap. Colors relate to goal locations as depicted in inset. F, vPFC move space with 95% confidence interval projections via bootstrap. Colors relate to move directions as depicted in inset. G, Variance explained by spaces depicted in (E) and (F) throughout the trial. Significance tested with permutation test including FDR correction.

We find that vPFC (Figure 1F and 1G, bottom) shows a stable code for movement direction across choices, as shown by steady geometric order across 'Choice presentation' windows and significant variance explained across windows. Monkeys seem to already plan movements during 'Delay' periods, ahead of the choice presentation. Additionally, at choice 2 they seem to preplan the move towards the goal instead of the detour, shown by higher variance explained during the delay window of 'Choice 2 (goal)' and not 'Choice 2 (away)'. vPFC data is depicted but dPFC and dmPFC show similar patterns.

Only little variance of the movement direction of 'Choice 2 (away)' is explained within the otherwise generalizable movement space. By specifically comparing 'Choice 2 (goal)' and 'Choice 2 (away)' using paired t-tests on population activities during these choices shows that there is a widespread significant signal ( $p < 0.05$ ) across all recorded regions except for dPFC. This widespread signal could control the monkeys'

behavior to not approach the goal but instead take the detour over the outer ring of the maze and would hence implicitly code for the movement direction.

In conclusion, the data show that when recording across multiple regions of frontal cortex, we find that stable codes, like dmPFC's unique goal code, co-exist with more variable codes, like the movement code which is generally stable but is interrupted by a specific situational code to suppress accessing the goal prematurely. Instead of using one specific coding scheme for each variable, FC utilizes an entire set of multiplexed codes to solve the multi-step problem.

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