

Supplementary Information for

Mixed-Selective Organization of Reach and Grasp in the Primate Fronto-Parietal Network

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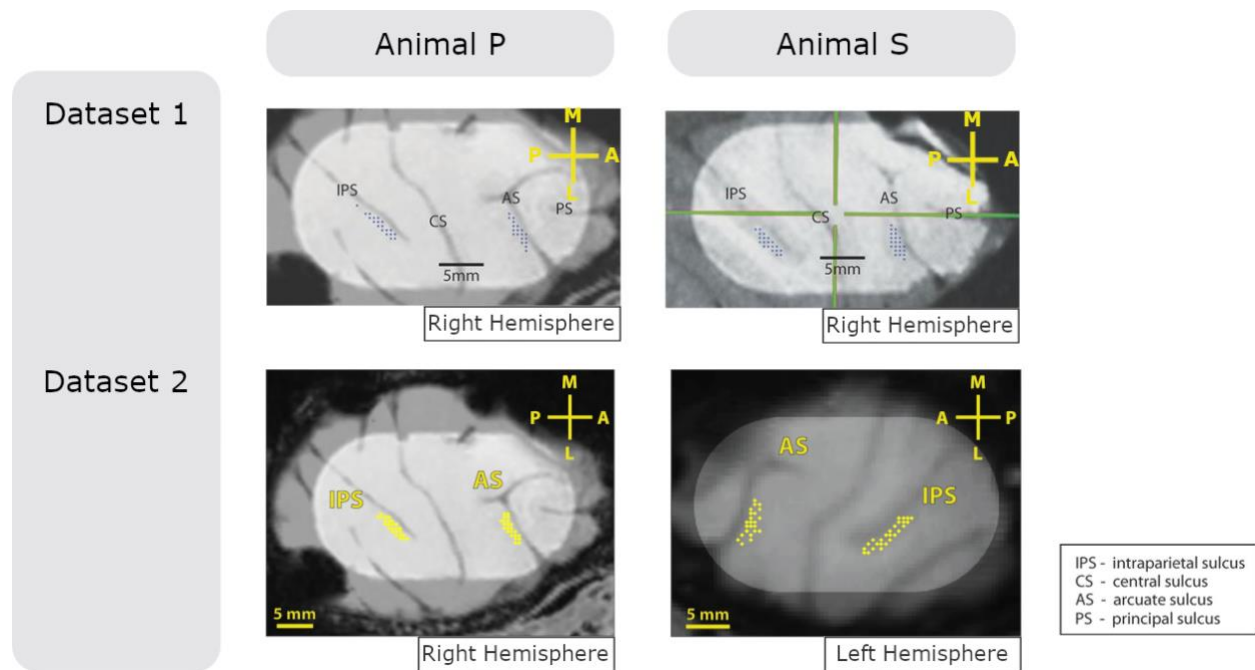


Figure S1. Recording locations for monkey P and S overlaid on a structural MRI. The illuminated oval marks the outline of the recording chamber. The cross shows the medial (M), lateral (L), anterior (A), and posterior (P) directions. Images for dataset 1 and dataset 2 are reproduced from Lehmann et al. (2013) and Michaels et al. (2018), respectively.

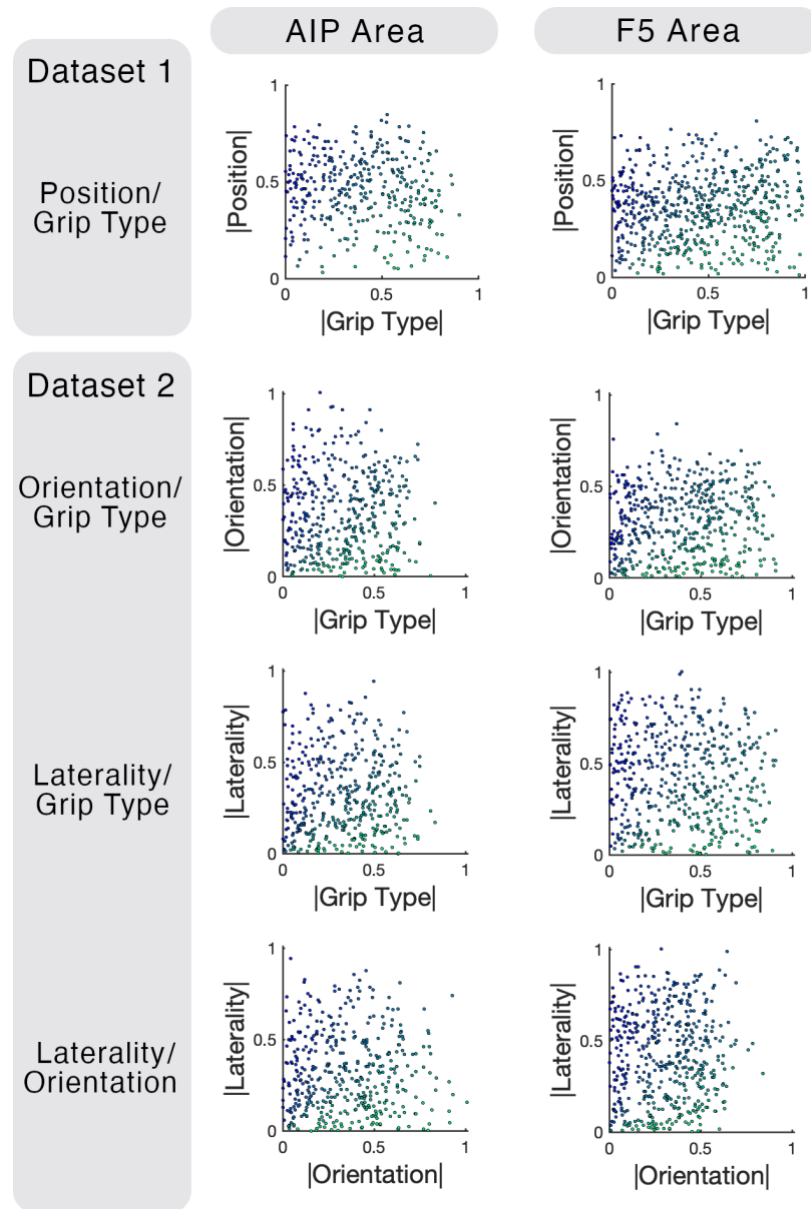


Figure S2. Neural activity cannot be categorized by selectivity. Scatter plots illustrate the contribution of AIP and F5 neurons, respectively, to different pairs of task parameters, with each point representing a neuron. The top row (Dataset 1) shows position vs. grip type, while the remaining rows (Dataset 2) depict orientation vs. grip type, laterality vs. grip type, and orientation vs. laterality, respectively.

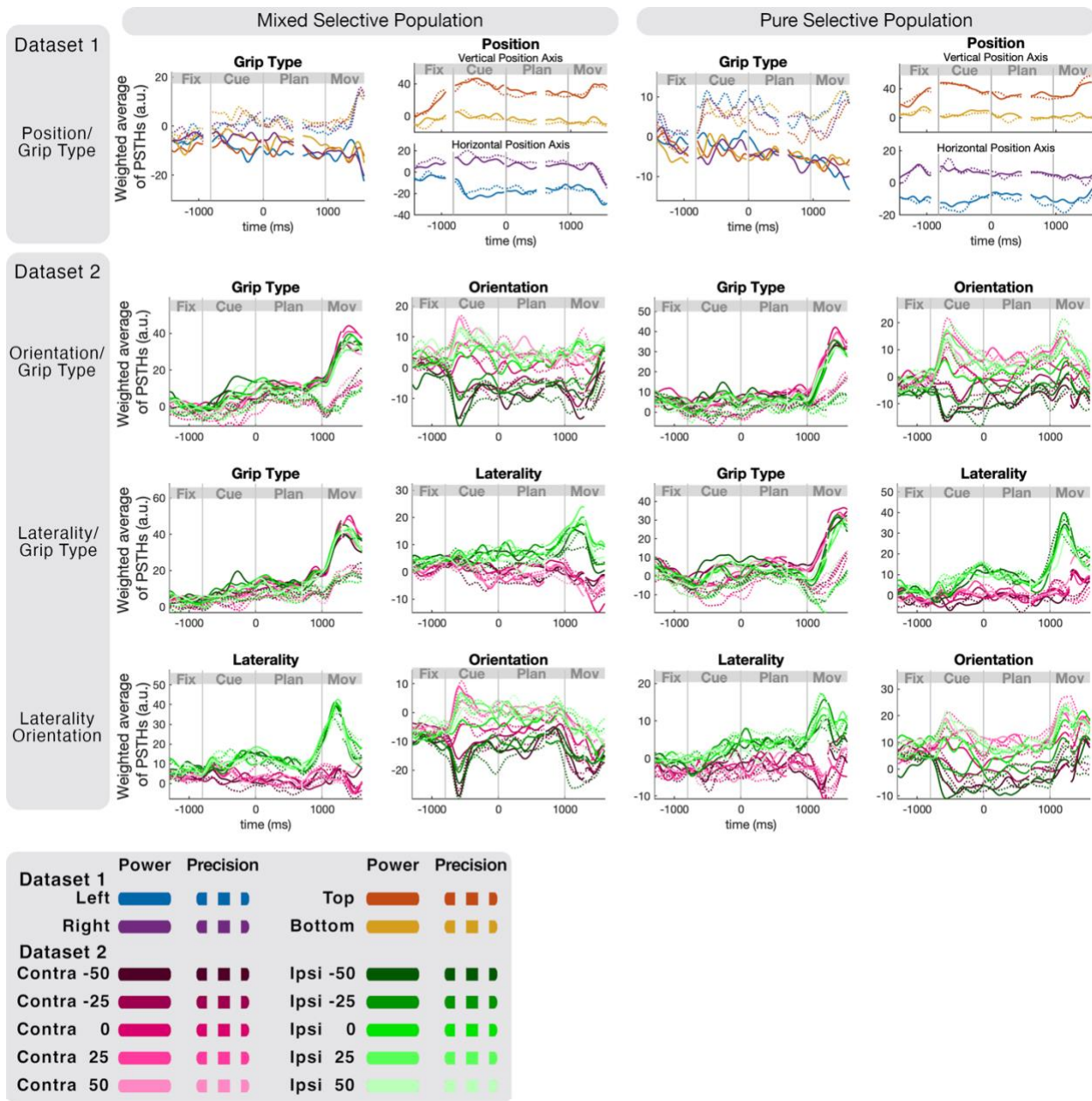


Figure S3. Task parameters are extractable from both mixed and pure selective populations in the AIP area. Weighted averages of peri-stimulus time histograms (PSTHs), using regression coefficients as weights, reveal parameter-specific population responses. Each row shows the population responses for two groups of pure and mixed selective neurons categorized based on the Mixed Selectivity Index (MSI) corresponding to a parameter pair. The top row (Dataset 1) shows position vs. grip type, while the remaining rows (Dataset 2) depict orientation vs. grip type, laterality vs. grip type, and orientation vs. laterality, respectively.

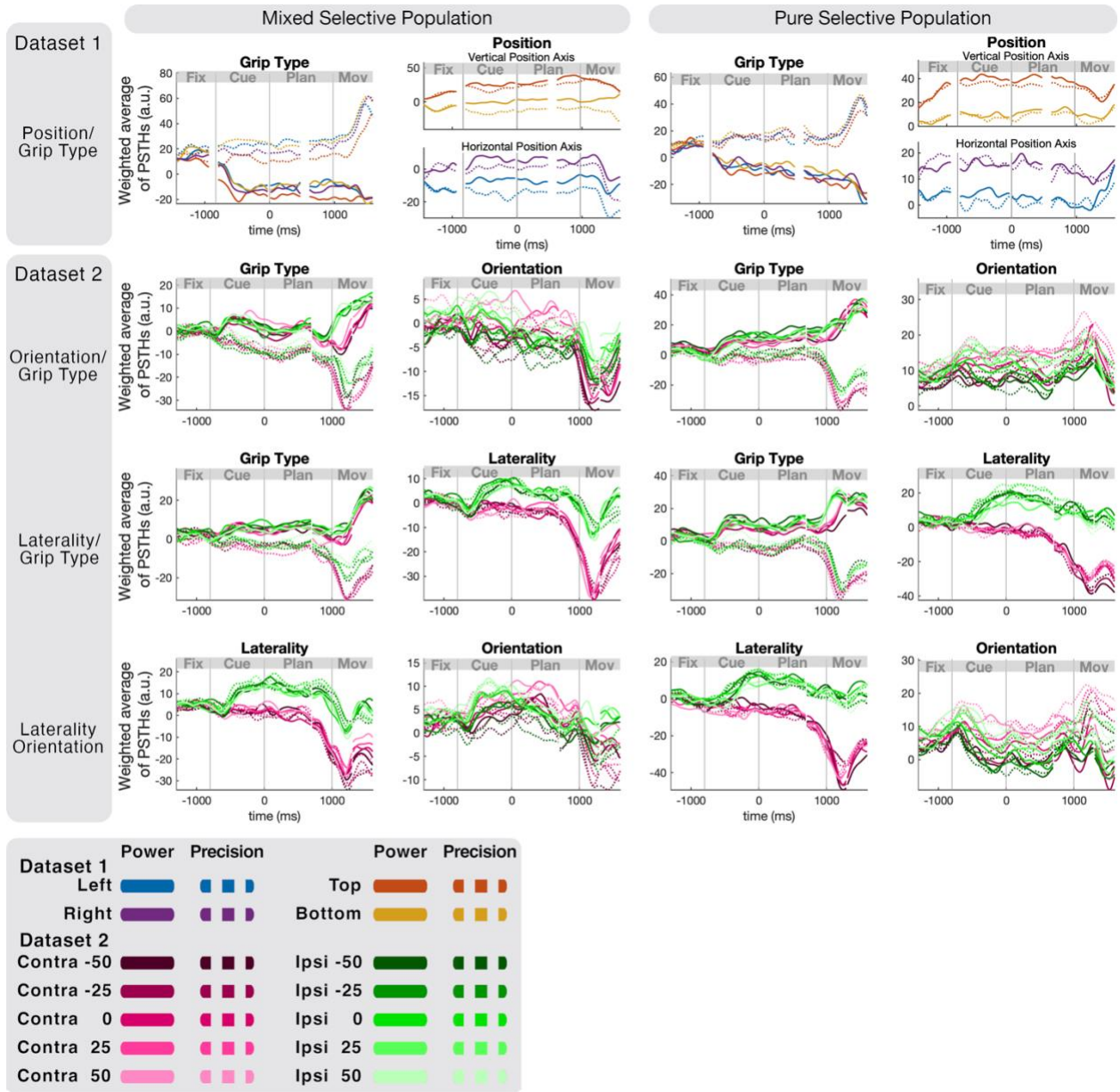


Figure S4. Task parameters are extractable from both mixed and pure selective populations in the F5 area. Weighted averages of peri-stimulus time histograms (PSTHs), using regression coefficients as weights, reveal parameter-specific population responses. Each row shows the population responses for two groups of pure and mixed selective neurons categorized based on the Mixed Selectivity Index (MSI) corresponding to a parameter pair. The top row (Dataset 1) shows position vs. grip type, while the remaining rows (Dataset 2) depict orientation vs. grip type, laterality vs. grip type, and orientation vs. laterality, respectively.

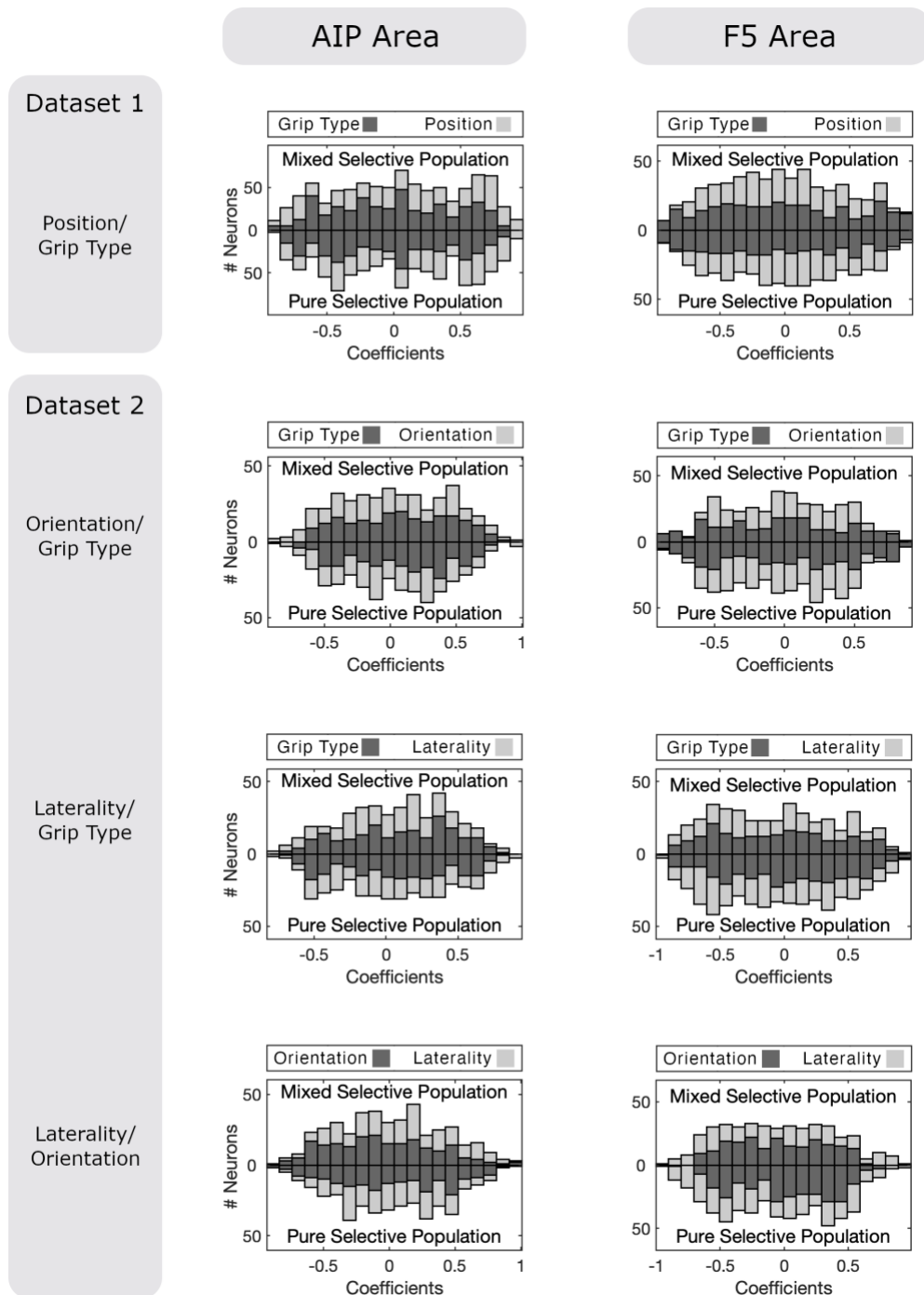


Figure S5. In each panel, the distributions of regression coefficients for a parameter pair are shown separately for mixed (top) and pure (bottom) selective subpopulations.

AIP Area

F5 Area

Dataset 2

Orientation/ Grip Type

MSI > 0:
Grip Type
MSI < 0:
Orientation

Laterality/ Grip Type

MSI > 0:
Grip Type
MSI < 0:
Laterality

Laterality/ Orientation

MSI > 0:
Orientation
MSI < 0:
Laterality

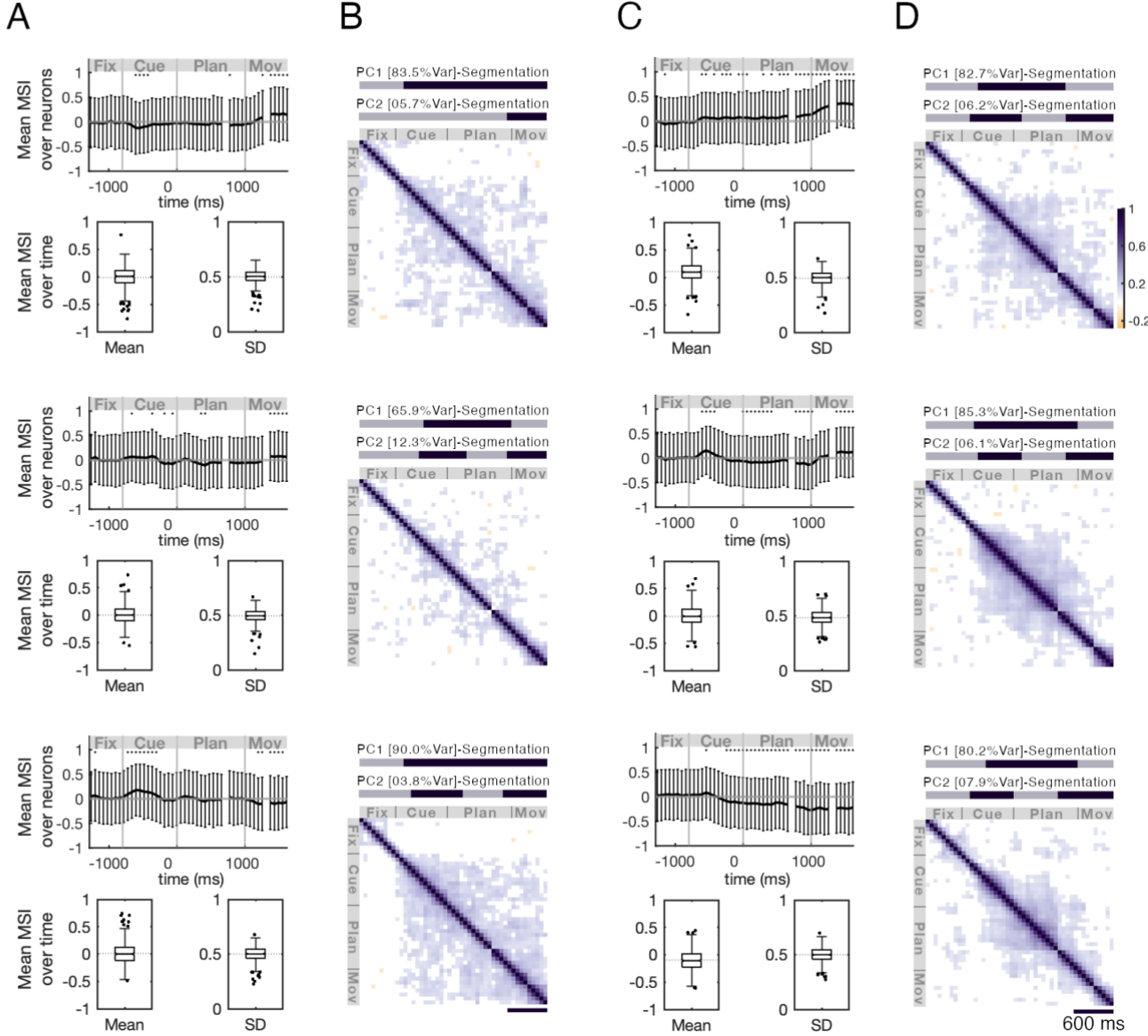


Figure S6. Dynamics of neural selectivity. Each row of panels represents a parameter pair from dataset 2. For each area, the top row shows orientation vs. grip type, and the remaining rows depict laterality vs. grip type and orientation vs. laterality, respectively. **A** and **C**: Single neurons' selectivity fluctuates substantially across the task. In each panel, the top plots show the time-dependent Mixed Selectivity Index (MSI), computed in 60-ms bins and averaged across neurons in AIP (**A**) and F5 (**C**). Error bars indicate the standard deviation across neurons within each time bin. Asterisks above the error bars mark time points at which the mean MSI differs significantly from zero (t-test, $p < 0.01$). The bottom plots summarize each neuron's temporal selectivity profile by displaying its mean (left) and the standard deviation (right) of its time-dependent MSI across all 60-ms bins. These measures reflect both the central tendency and variability of each neuron's selectivity over the course of the trial. **B** and **D**: Population-level selectivity is organized within a low-dimensional structure. Each panel shows a similarity matrix displaying the significant correlations of neuronal MSI values across all pairs of time bins. The bar plots indicate the time segmentation of the first two MSI principal components (PCs), obtained by detecting change points in their root-mean-square (RMS) values. Gray and black intervals indicate segments of stable PC activity.

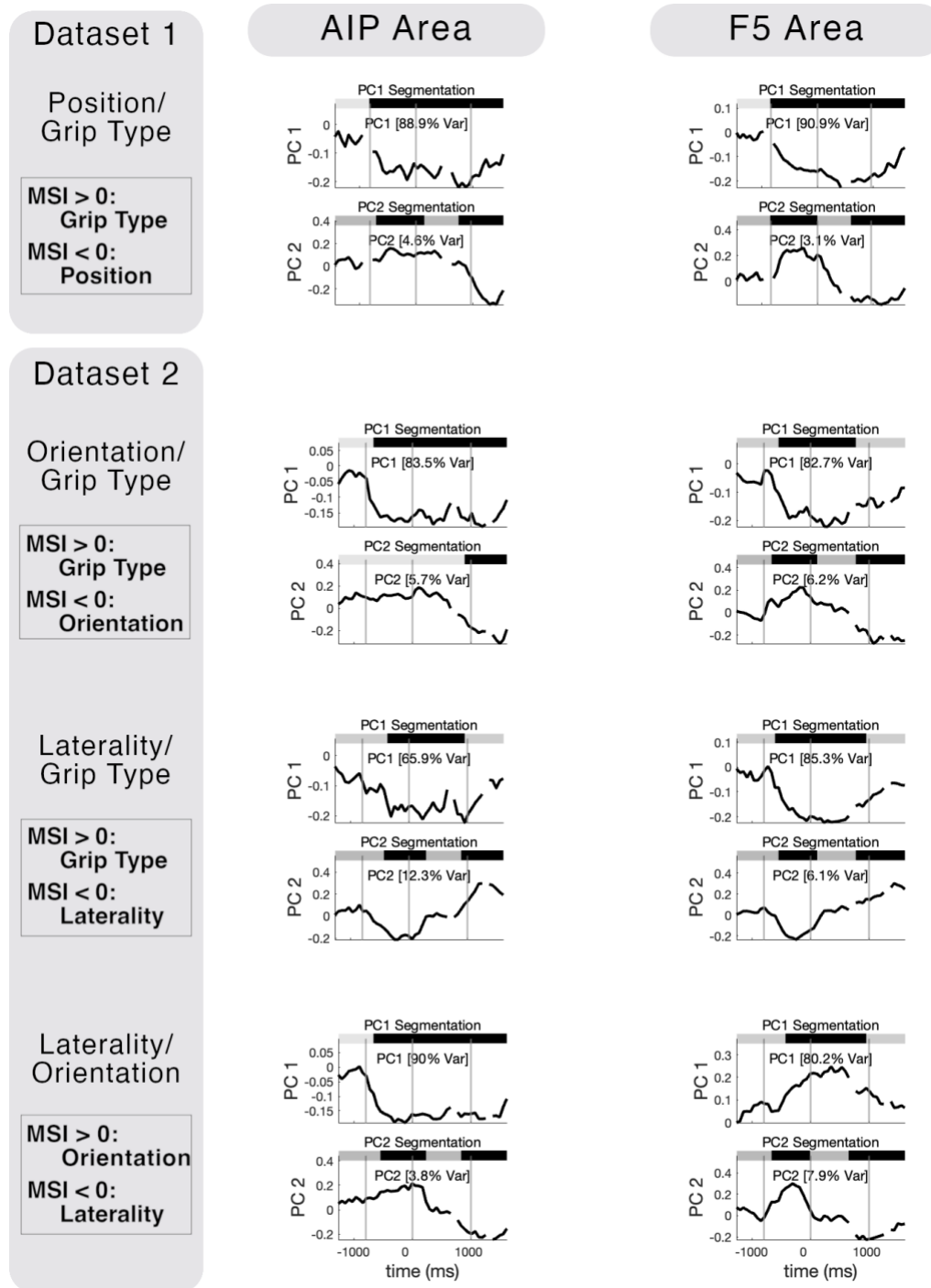


Figure S7. PCA analysis of the time-dependent MSI values. For each parameter pair, the panels show the loading vectors for the first two principal components (PC1 and PC2) computed from the MSI data. Each loading represents a set of weights across time points that defines a temporal pattern explaining a substantial portion of the variance across neurons. Together, PC1 and PC2 illustrate the primary temporal profiles driving population-level MSI variability. Vertical lines indicate different task epochs, and the variance explained by each component is noted in the plots. Similar to Fig. 5 and S6, the bar plots indicate the segmentation of the first two MSI PCs over time, obtained by detecting change points in their root-mean-square (RMS) values. Gray and black intervals indicate segments of stable PC activity.

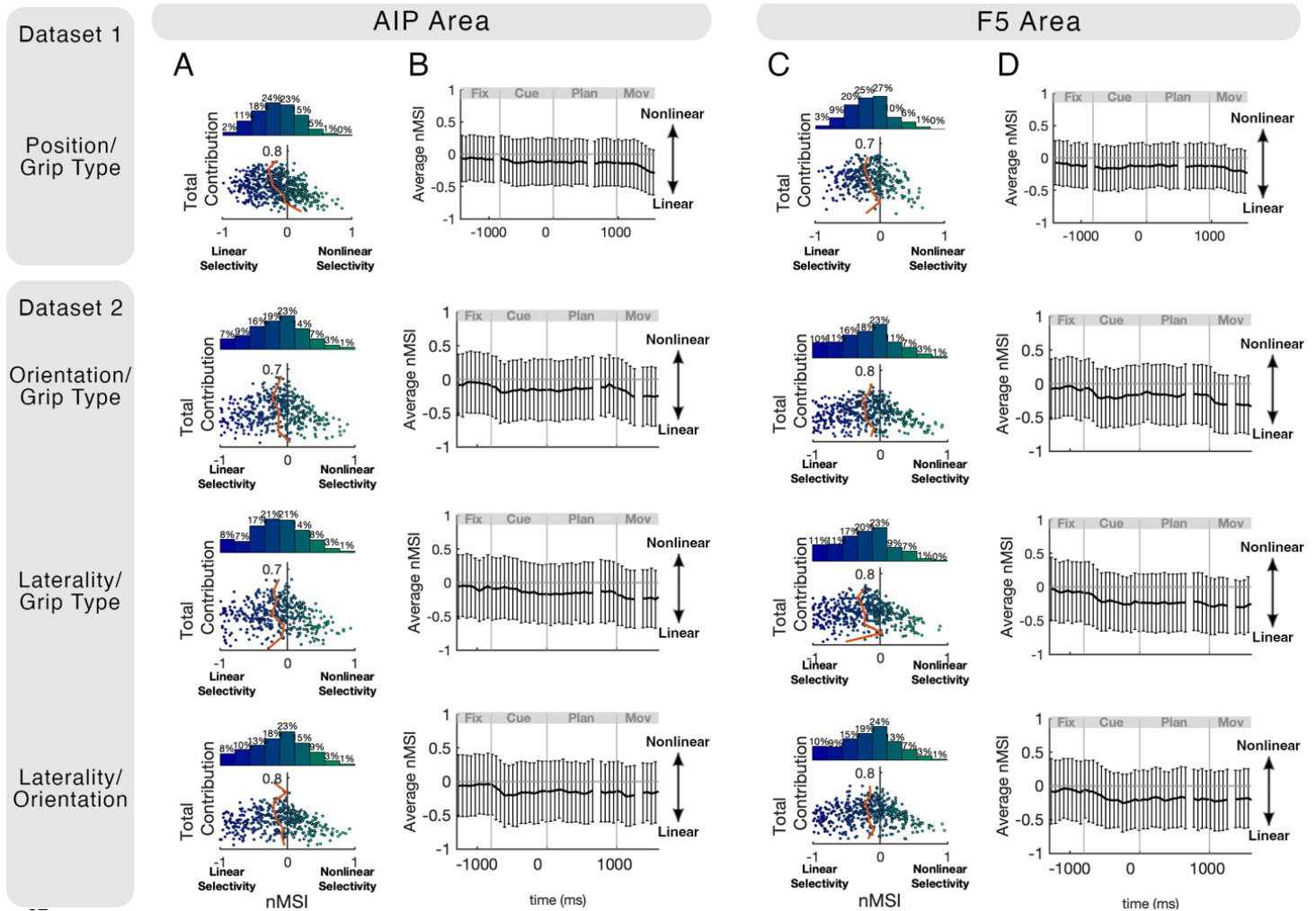


Figure S8. Interaction between task parameters. Each row of panels is dedicated to the nonlinear Mixed Selectivity Index (nMSI) of a task parameter pair. The top row (Dataset 1) shows position vs. grip type, while the remaining rows (Dataset 2) depict orientation vs. grip type, laterality vs. grip type, and orientation vs. laterality, respectively. **A** and **C**, Each figure displays nMSI distributions of a task parameter pair. The top histograms show the distribution of nMSI values, while the bottom scatter plots illustrate the total contribution strength of each neuron against the nMSI index. Red lines indicate moving bin averages of nMSI along the (vertical) total contribution strength axis. **B** and **D**, Average nMSI across neurons in 60-ms time bins for AIP (**B**) and F5 (**D**) areas. Error bars indicate standard deviation, and vertical lines separate task epochs.

Peer Review Overview

Manuscript Title: "Mixed-Selective Organization of Reach and Grasp in the Primate Fronto-Parietal Network"

Received	10-Aug-2025
1 st Decision	20-Oct-2025
1 st Revision Submitted	10-Dec-2025
2 nd Decision	16-Jan-2026
2 nd Revision Submitted	22-Jan-2026
Accepted	27-Jan-2026

1st Decision Letter

Dear Mr. Fathian,

Thank you for submitting your manuscript to Progress in Neurobiology.

We have completed our evaluation of your manuscript. The reviewers recommend reconsideration of your manuscript following major revision. We invite you to resubmit your manuscript after addressing the comments below. Please resubmit your revised manuscript by **Nov 19, 2025**.

When revising your manuscript, please consider all issues mentioned in the reviewers' comments carefully: please outline every change made in response to their comments and provide suitable rebuttals for any comments not addressed. Please note that your revised submission may need to be re-reviewed.

To submit your revised manuscript, please log in as an author at <https://www.editorialmanager.com/proneu/>, and navigate to the "Submissions Needing Revision" folder.

Research Elements (optional)

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Progress in Neurobiology values your contribution and we look forward to receiving your revised manuscript.

Kind regards,

Brett L. Foster
Associate Editor

Laura Colgin
Co-Editor-in-Chief
Progress in Neurobiology

Editor and Reviewer comments:

Reviewer #1: This manuscript presents convincing results showing mixed selectivity for reach and grasp parameters in both AIP and F5. While there was a minority of neurons that were largely tuned to one parameter such as grip type, position, orientation, or laterality, the majority of neurons were tuned to multiple parameters and also showed non-linear tuning. Despite this mixed selectivity, the authors showed how population activity could demix these parameters and accurately decode each of these parameters. Importantly, despite this mixed selectivity, the authors found similar neural responses between grip types and orientations regardless of position and laterality in AIP and similar responses between positions regardless of grip type in F5 which supports the idea that AIP is more concerned with high-level position and laterality information whereas F5 is more related with lower-level motor information, i.e. grip type.

Major comments

1. It would be useful to know where exactly you are recording in F5 (a relatively large area) without having to refer to previous papers. In particular, were the recordings done within the arcuate sulcus or on the gyrus. How deep were these recordings?
2. It's not clear to me how the regression models used for Figure 7 are different than those used in previous analyses. They seem identical.

Minor comments

1. In Figure 3, it is not clear to me what Total Contribution means on the scatter plots on B and D?
2. On line 271, "trials (see Methods section)..." should read "trial (see Methods section)..."
3. On line 307, "(Fig. 5 C and F)" should read "Fig. 5 B and D"
4. On lines 724-25, I don't see where the $\hat{x}$ values for linear parameters are depicted in Figure 3?

Reviewer #2: This is a summary study from a well-known group that has studied the representation of grasp within the frontal and posterior parietal cortices for many years. While the experiments and analyses are well conducted, and the writing for the most part is very clear, it is less clear what new ground is broken here.

A major theme is the mixed representation of different grasp parameters found in both AIP, and F5. Early in the introduction, the authors comment: "One possibility is that distinct neuron categories encode each parameter separately. 59 However, an equally plausible scenario is that individual neurons encode multiple parameters with mixed 60 selectivity (Rigotti et al., 2013)." Given the comment beginning the next paragraph, it seems even the authors acknowledge that this is largely a strawman hypothesis.

However, the authors further develop this theme in the results section, where they assert, "Considering the high dimensionality of the information and the mixed selectivity phenomenon that 227 causes complex co-representation of information, it is unlikely that single-neuron responses can be utilized 228 directly. Instead, these responses likely contribute to population-level readouts of downstream areas."

And

"...the population responses can effectively demix parameters, indicating that by 8 adjusting the linear combination weights, specific information can be extracted 239 from the neuronal population 240 that may not be readily apparent from single-neuron activities."

And

"Despite the high degree of mixing at the single-neuron level, our findings 425 suggest that relevant task information can still be effectively extracted at the population level."

These general statements and the analytical approaches they refer to are very well established at this point. Any decoding study accomplishes the separation of these mixed representations. It is not at all clear to me that these results and very general comments add much to these theoretical arguments.

At the same time, the novelty of the results this study contributes toward our understanding of higher

order grasp control is also somewhat limited. There is little in the analysis that distinguishes the two areas from one another, or which the task type reveals. Near the end of the results is the summary, "Various results of the current study have demonstrated a slight bias in neural representations, with grip 352 type being more prominent in F5, and position and orientation more in AIP." Is this really meant to be the take home of this complex study?

Figures get progressively smaller and more cluttered with virtually identical, repeated panels. Figure 5 is particularly bad. It, and the associated text are hard to interpret without reference to the supplement. Even so, it's difficult without captions for the latter. Many figures could be reduced to single examples with summary comments, taken from one area/task combination, and the remaining panels moved to supplement and simply summarized in the main text. This would allow those results which actually distinguish the function of these two areas to be highlighted, allowing whatever take home message the authors would like to leave us with to be reinforced. Fig 7 is a more interesting format for summarizing the roles of neurons in these two areas. I think all of the preceding detail dilutes, rather than enhances its impact.

Major (sort of)

"...position was more prevalent in AIP than in F5, grip type representation was stronger 210 in F5 than in AIP."

How are these comparisons being made quantitatively? I buy the latter; the former is rather more difficult to see.

"Further, based on the MSI scatter plots in B and C panels, 212 we found the selectivity preference to be independent of the magnitude of contributions..."

I don't get this. Why the reference to B and C, which differ in both area and analysis?

"...there is a slightly stronger selectivity for grip type in the movement epoch relative to other 279 parameters, which is most prominent in F5. Also, during the cue epoch in AIP, orientation selectivity is 280 slightly stronger than grip type."

It is hard to imagine that either of these differences reaches significance, given the large error bars. Was it tested?

"...linear 285 combinations of time points that maximize MSI variations..."

This sounds like you used PCA to collapse time over time, but I assume that's not the case. Even Fig S3 is hard to interpret without a caption. Clarify in the main text.

"A time segmentation analysis was performed..."

What is this?

"294 The bottom plots show each neuron's mean MSI value and standard deviation (SD) across time bins."

Which time bins, the entire trial? What do they reveal?

"...the fixation epoch was separated from the 300 remaining period in all parameter pairs."

Where do we see this? The confusion matrices? Bins within the fixation epoch do seem to be essentially uncorrelated with themselves. Is this the point you're making? I agree, that it is not terribly surprising. What do we learn?

Fig 5: as large and complicated as this figure is (with fonts that are too small to read), there is very little text devoted to it. Is there something of note besides the greater similarity for temporary proximate bins, and the lack of correlation during fixation? It is not clear to me what we learn of importance. One example here would suffice, with all the rest moved to the supplement. I do not understand the PC segmentation. Is this somehow derived from the confusion matrix (although the text seems to suggest the opposite relation)?

"In Dataset 1, positive correlations in AIP between precision and power grips at each handle position suggest 371 that grip type has minimal influence on the neural selectivity for position. In contrast, in F5, all but one 372 correlation between different positions within the same grip type was positive..."

Why is this, "in contrast"? It seems to be the same kind of observation, as is the following one, which is preceded by, "similarly".

"...we observed subtle shifts in selectivity at specific task epochs. For 435 instance, in F5, grip type selectivity became more pronounced during the movement epoch, while in AIP, 436 orientation selectivity increased during the cue epoch. Further analysis using PCA and pairwise time-point 437

correlations revealed that this single-neuron variability can be reduced to a stable, low-dimensional 438 subspace, enabling the extraction of multidimensional information at the population level." This is not particularly innovative, technically. What does it tell us about this part the brain?

"...linear mixed selectivity was far more prevalent than 445 nonlinear. Despite these differences, both linear and nonlinear selectivity parameters contributed similarly 446 to the decoding performance at the population level (Fig. 6 E)."

It's a bit difficult for me to reconcile the "far more prevalent" selectivity, with the similar contribution to decoding. Can this be clarified?

"It was unexpected that, in both areas, 454 hand laterality, a fundamental aspect of motor action, is positioned at a lower level in the hierarchical 455 clustering, relative to grip type or hand orientation. In line with the established role of AIP and F5 as high14 level planning areas..."

This strikes me as one of the more interesting results, although it is not clear to me why "planning" should necessarily ("in line with") begin with grasp type as opposed to limb. What is the logic here?

What was the relative timing of the tone and visual cues in task 2? Could this have anything to do with the hierarchy of representation of laterality and grasp type?

Minor

"...neurons based on their functions, such as grasping, holding, and tearing..." Possibly mean something other than "tearing"?

"...allowed the subjects to move their left hand (contralateral to the recording chamber) between four 117 locations—left, right, top, or bottom— using two electrical motors."

What do motors have to do with allowing the monkey to move their hand?

"The eye position was 119 located at the center of the workspace, while the target position was varied between the four locations. 2) 120 Gaze variation: The handle position was located at the center of the workspace, while the gaze position..."

Do eye and gaze positions really refer to different concepts, given that the head is fixed?

"...orientation is 269 relatively stronger during the cue epoch..." orientation is stronger during the cue epoch

"...we computed Pearson correlations between neural responses to each condition pairs." all condition pairs?

"The handle was illuminated during 628 the cue in the following, revealing its position..." Clarify

702 "...report the ePAIRS statistics. However, since [] is dependent on , we..." Missing variable.

"...(gaussian kernel 50-ms)...," Gaussian

1st Author Response Letter

Thank you for the opportunity to submit a revised version of our manuscript. We sincerely appreciate the time and effort the reviewers have invested in providing thoughtful and constructive feedback. We have carefully considered all comments and have incorporated changes to address the reviewers' suggestions. Our detailed responses are provided below in a point-by-point format. Revisions made to the manuscript are highlighted for clarity. Please note that all line numbers and figure references mentioned in the reviewers' comments have been updated to correspond to the correct locations in the revised manuscript.

Manuscript title: Mixed-Selective Organization of Reach and Grasp in the Primate Fronto-Parietal Network

Manuscript number: RONEU-D-25-00503

Revision Version: 1

Editor's Decision Received Date: 21.10.2025

Revision Submission Date: 10.12.2025

Comments from Reviewer 1

► **Comment 1.1:** This manuscript presents convincing results showing mixed selectivity for reach and grasp parameters in both AIP and F5. While there was a minority of neurons that were largely tuned to one parameter, such as grip type, position, orientation, or laterality, the majority of neurons were tuned to multiple parameters and also showed non-linear tuning. Despite this mixed selectivity, the authors showed how population activity could demix these parameters and accurately decode each of these parameters. Importantly, despite this mixed selectivity, the authors found similar neural responses between grip types and orientations regardless of position and laterality in AIP and similar responses between positions regardless of grip type in F5, which supports the idea that AIP is more concerned with high-level position and laterality information, whereas F5 is more related to lower-level motor information, i.e., grip type.

We thank the reviewer for her/his thoughtful summary, which precisely captures the main findings of our study. We appreciate the positive evaluation and the efforts to help improve the clarity and quality of our manuscript. We found all of the reviewer's comments highly constructive and have thoroughly addressed them in the manuscript.

Major comments from reviewer 1

► **Comment 1.2:** It would be useful to know where exactly you are recording in F5 (a relatively large area) without having to refer to previous papers. In particular, were the recordings done within the arcuate sulcus or on the gyrus? How deep were these recordings?

We agree with the reviewer that the recording locations are of importance. The recording was done at the transition from the gyrus to the arcuate sulcus. The recording depth was from the cortical surface to a maximum of ~10 mm below the dura mater. We added this information to our manuscript at lines 145 and 691-693. Further, we added supplementary Fig. S1 to illustrate the recording sites overlaid on structural MRIs of the animals' brains.

► **Comment 1.3:** It's not clear to me how the regression models used for Figure 7 are different than those used in previous analyses. They seem identical.

The regression model used to create Fig. 7 relies on a different set of independent variables. In the main regression model, the task parameters served as the independent variables: grip type and handle position in Dataset 1, and grip type, handle orientation, and hand laterality in Dataset 2. In contrast, the regression model for Fig. 7 treated each condition as an independent binary variable. Both models were based on data that underwent the same preprocessing, and this difference in independent variables is the only distinction between the two models.

We thank the reviewer for pointing out this lack of clarity. This difference was only mentioned in the methods section of the original manuscript. To improve clarity, we have now elaborated on our description (lines 741-745) and also briefly described the Fig. 7 model in the results section (lines 383-384).

Minor comments from reviewer 1

► **Comment 1.4:** In Fig. 3, it is not clear to me what Total Contribution means on the scatter plots?

The total contribution is a measure used to quantify the average response of each neuron to all task parameters. For each neuron, we defined the total contribution as the sum of the absolute values of its regression coefficients. Accordingly, using the terminology introduced in the Methods section (lines 725-728), the total contribution for neuron n is $|\beta_n^{max}(GripType)| + |\beta_n^{max}(Position)|$ in Dataset 1, and

$|\beta_n^{max}(GripType)| + |\beta_n^{max}(Orientation)| + |\beta_n^{max}(Laterality)|$ in Dataset 2. We described this measure in the method section (lines 735-739).

► **Comment 1.5:** On line 276, "*trials (see Methods section)...*" should read "trial (see Methods section)..."

We have corrected this mistake (line 276).

► **Comment 1.6:** On line 324, "*(Fig. 5 C and F)*" should read "Fig. 5 B and D"

Thank you for pointing this out. The text was indeed intended to refer to panels B and D of Fig. 5. The text now refers to the correct panels (line 324).

► **Comment 1.7:** On lines 782-784, I don't see where the $\hat{X}$ values for linear parameters are depicted in Figure 3?

We are grateful for your detailed review, and we apologize for the mistake, as we intended to refer to Fig. 4 A–D. The matrix $\hat{X}$ describes the population-level, parameter-specific responses to each condition across time. In Fig. 4, these responses are shown in panels A–D. Each panel corresponds to a specific task parameter, and within each panel, the population responses for the different conditions are displayed. We have corrected the manuscript accordingly and added a more detailed explanation in the revised text (lines 782-784).

Comments from Reviewer 2

► **Comment 2.1:** This is a summary study from a well-known group that has studied the representation of grasp within the frontal and posterior parietal cortices for many years. While the experiments and analyses are well conducted, and the writing for the most part is very clear, it is less clear what new ground is broken here.

We thank the reviewer for his/her thoughtful reading of our manuscript and the positive remarks regarding the quality of our experiments, analyses, and writing. We find the reviewer's comments very constructive and have made extensive changes to improve the clarity and conciseness of our manuscript.

We understand that one of the main concerns is about the clarity of the take-home messages and key findings, as the level of detail in the figures and the structure of the text made them difficult to discern. In response, and to incorporate the reviewer's advice, we moved some figure details to the supplementary material to better highlight the prominent findings of our paper. Furthermore, we revised the portions of the text that address the key findings, both in the Introduction (lines 77-89) and within each section (lines 204-206, 265-267, 328-330, 351, and 415-419). These findings are also discussed in our response to Comment 2.4.

We believe these revisions successfully address all of the reviewers' comments and substantially improve the manuscript's overall clarity and impact.

► **Comment 2.2:** A major theme is the mixed representation of different grasp parameters found in both AIP and F5. Early in the introduction, the authors comment: "[line 59] *One possibility is that distinct neuron categories encode each parameter separately. However, an equally plausible scenario is that individual neurons encode multiple parameters with mixed selectivity (Rigotti et al., 2013).*" Given the comment beginning the next paragraph, it seems even the authors acknowledge that this is largely a strawman hypothesis.

We sincerely thank the reviewer for highlighting this alternative reading of the section. We wish to clarify that the statement quoted was not intended as our main or key hypothesis but rather as a broad conceptual bridge to transition into the next paragraph, where we begin to address mixed selectivity. However, after considering the reviewer's perspective, we acknowledge that this section can be misleading.

While our work builds upon the concept of mixed selectivity, our primary focus is on advancing this concept and exploring its broader implications. Specifically, we examined the temporal and functional organization of the cortical areas AIP and F5, the nonlinearity of MS, and the impact of mixed selectivity on population-level responses.

We have rewritten the quoted sentence to clarify that it is not a core hypothesis and have placed less emphasis on it to prevent misinterpretation (lines 59-60). Additionally, we revised the Introduction section to better highlight the key questions and findings (lines 69-71 and 77-89).

► **Comment 2.3:** However, the authors further develop this theme in the results section, where they assert, "[line 224] *Considering the high dimensionality of the information and the mixed selectivity phenomenon that causes complex co-representation of information, it is unlikely that single-neuron responses can be utilized directly. Instead, these responses likely contribute to population-level readouts of downstream areas.*" And "[line 237] *...the population responses can effectively demix parameters, indicating that by adjusting the linear combination weights, specific information can be extracted from the neuronal population that may not be readily apparent from single-neuron activities.*"

And "[line 450] *Despite the high degree of mixing at the single-neuron level, our findings suggest that relevant task information can still be effectively extracted at the population level.*"

These general statements and the analytical approaches they refer to are very well established at this point. Any decoding study accomplishes the separation of these mixed representations. It is not at all clear to me that these results and very general comments add much to these theoretical arguments.

We thank the reviewer for this comment. We agree that parameter demixing has been frequently applied to various types of parameters and neural populations. The main question we address in this section is the impact of mixed and purely selective neurons on the demixing process. Although mixed selectivity enhances the computational capacity of neurons, its heterogeneous and seemingly disordered nature adds complexity to the readout process that must be assessed.

The core questions we asked are whether a linear method can decode condition information from a mixed population, and whether mixed populations could pose any challenges for linear decoding compared to purely selective populations. To assess this, we employed a dimensionality reduction method using the regression coefficients shown in Fig. S2 to identify parameter-specific population responses. As shown in Fig. S2, the regression coefficients are broadly distributed at the neural level without any condition-specific categories. By using these data in the dimensionality reduction method, we observed that, despite the absence of a categorical representation at the single-neuron level (Fig. 3 and S2), these mixed representations are capable of separating conditions at the population level using linear decoders (Fig. 4). This finding indicates that although decoding is not feasible from a single mixed neuron, a population of mixed neurons allows the decoding of various types of information using appropriate readout mechanisms.

Furthermore, we examined the possibility that the demixing method might be driven solely by purely selective neurons, with mixed-selective neurons contributing little to the decoding process. As shown in Figs. 4E–F and S3–S5, this was not the case, as both pure and mixed neurons contributed comparably to demixing and decoding processes.

We thank the reviewer for highlighting the need for clarification on this point. We have added this information to lines 228, 239–273, 265–267, and 454 of our manuscript.

► **Comment 2.4:** At the same time, the novelty of the results this study contributes toward our understanding of higher order grasp control is also somewhat limited. There is little in the analysis that distinguishes the two areas from one another, or which the task type reveals. Near the end of the results is the summary, "[line 369] *Various results of the current study have demonstrated a slight bias in neural representations, with grip type being more prominent in F5, and position and orientation more in AIP.*" Is this really meant to be the take-home of this complex study?

We thank the reviewer for this comment. We would like to clarify that the quoted sentence was not intended to convey the main take-home message of our study. Rather, it served as an introductory remark at the beginning of that section. The purpose of this section is to explore potential differences in the hierarchical organization of representations between AIP and F5, specifically, whether these areas show different tendencies in reflecting various task parameters. The sentence in question was meant to indicate that earlier results in the manuscript provide hints of such differences, thereby motivating the more detailed analysis presented in that section. We recognize that our phrasing may unintentionally suggest that this summary reflects the study's principal conclusion, and we apologize for the lack of clarity. We have revised the text at line 369 to better convey its intended role as a transition into the subsequent analyses and explicitly state the take-home message of this section at lines 415–519.

As discussed earlier, the central focus of our paper is to explore the structure and implications of mixed selectivity in the AIP and F5 areas. To provide a comprehensive investigation, we examined five distinct aspects: 1) The distribution of selectivity across neurons (results: section 4), 2) The impact of mixed selectivity on the read-out mechanism (results: section 5), 3) The temporal organization of mixed selectivity (results: section 6), 4) The non-linearity in mixed selectivity (results: section 7), and 5) The comparison between AIP and F5 areas (results: section 8). Respectively, the main findings of each aspect are as follows. Notably, these findings have not been published before from this laboratory or the datasets:

- The selectivity of individual neurons across the examined parameters is predominantly mixed.
- Although mixed selectivity can impede decoding at the single-neuron level, it does not inherently present challenges for decoding at the population level.
- Despite a high level of variation in mixed selectivity at the single-neuron level over time, populations of neurons provide temporally stable representations.
- The majority of mixed-selective neurons exhibit non-linear mixing.
- AIP is more concerned with position and orientation information, whereas F5 is more related to motor information (grip type).

We sincerely appreciate the reviewers' insights. We have made efforts to better highlight the key findings in the manuscript. Specifically, as noted in our previous responses, we updated the Introduction sections (lines 77-89) and now clearly state the key findings at each relevant section (lines 204-206, 265-267, 328-330, 351, and 415-419).

► **Comment 2.5:** Figures get progressively smaller and more cluttered with virtually identical, repeated panels. Figure 5 is particularly bad. It and the associated text are hard to interpret without reference to the supplement. Even so, it's difficult without captions for the latter. Many figures could be reduced to single examples with summary comments, taken from one area/task combination, and the remaining panels moved to supplement and simply summarized in the main text. This would allow those results which actually distinguish the function of these two areas to be highlighted, allowing whatever take-home message the authors would like to leave us with to be reinforced. Fig. 7 is a more interesting format for summarizing the roles of neurons in these two areas. I think all of the preceding detail dilutes, rather than enhances its impact.

We find the reviewer's points very insightful and believe they have significantly contributed to improving the quality of our paper. We agree that the findings presented in Fig. 7 are of particular interest. As noted in the following responses, we have updated the manuscript to provide more detailed descriptions and interpretations for Fig. 7.

Following the reviewer's suggestion and to highlight the main findings, we moved certain parts of the figures to the supplementary material file. Specifically, for Figs. 3 and 4, some panels were transferred to the supplementary document, while for Figs. 5 and 6, we retained only the results from dataset 1 in the main figures and moved dataset 2 results to the supplementary material. As a result, Fig. 3 in the original manuscript has been split into Figs. 3 and S2, Fig. 4 into Figs. 4 and S5, Fig. 5 into Figs. 5 and S6, and Fig. 6 into Figs. 6 and S8 as well as Table 1.

Major comments from reviewer 2

► **Comment 2.6:** "[line 209] ...position was more prevalent in AIP than in F5, grip type representation was stronger in F5 than in AIP." How are these comparisons being made quantitatively? I buy the latter; the former is rather more difficult to see.

The quoted statement is based on the statistical analysis of the MSI distributions shown in Fig. 3. As defined in the manuscript (eq. 4), for each pair of parameters, the MSI value ranges from -1 to +1, with positive values indicating stronger selectivity toward parameter 1, negative values indicating stronger selectivity toward parameter 2, and values near zero indicating mixed selectivity. To determine the significant tendencies of neural populations for each parameter pair, we performed a two-sided one-sample t-test on the MSI values. Specifically, we tested whether the mean MSI differed significantly from zero. If the mean was significantly non-zero, its sign indicated a tendency toward parameter 1 or 2; if not significant, no tendency was assigned. For each pair of task parameters, significant tendencies are marked by asterisks on the sides of the histogram plots in Fig. 3 (t-test, $p < 0.01$). This information has been added to the manuscript (lines 207-211).

► **Comment 2.7:** "[line 212] Further, based on the MSI scatter plots in B and C panels, we found the selectivity preference to be independent of the magnitude of contributions..." I don't get this. Why the reference to B and C, which differ in both area and analysis?

We apologize for the confusion caused by this citation error. The text was intended to refer to panels B and D of the manuscript, rather than B and C. The text has been revised and now references the correct figures (line 212).

► **Comment 2.8:** "[line 283] ...there is a slightly stronger selectivity for grip type in the movement epoch relative to other parameters, which is most prominent in F5. Also, during the cue epoch in AIP, orientation selectivity is slightly stronger than grip type." It is hard to imagine that either of these differences reaches significance, given the large error bars. Was it tested?

We thank the reviewer for this observation. To confirm the tendencies in the selectivity of neural populations, we performed a t-test analysis on the MSI distributions at each time point. The test is similar to the test introduced in comment 2.6. The results confirm that the shifts in the MSIs toward grip type during the movement epoch in F5 and towards orientation during the cue epoch in AIP are significant. The time points with significant tendencies are marked with asterisks at the top of each plot in Figs. 5 and S6. We included this information in lines 285-287 of the manuscript.

As the reviewer correctly notes, there is substantial MSI variability across neurons shown in Fig. 5 and S6, A and C. This variability was a central point of that section, as our aim was to highlight the substantial heterogeneity of MSI values at the single neuron level and over time, and to emphasize that any apparent tendencies are minor relative to this variability. We emphasized this in lines 288 and 296 of the manuscript.

► **Comment 2.9:** "[line 291] ...linear combinations of time points that maximize MSI variations..." This sounds like you used PCA to collapse time over time, but I assume that's not the case. Even Fig. S7 is hard to interpret without a caption. Clarify in the main text.

We thank the reviewer for pointing this out. We did not collapse time in our analysis. In our PCA, each observation corresponds to a neuron's MSI, and each feature corresponds to a time point. PCA was therefore applied across neurons to identify the major patterns of covariation in MSI over time. Consequently, the principal components reflect dominant temporal profiles in the MSI data rather than collapsing or averaging the time dimension. We have revised the main text to clarify this point (lines 291-293) and added a clearer caption to Fig. S7.

► **Comment 2.10:** "[line 312] A time segmentation analysis was performed..." What is this?

We thank the reviewer for this question. To identify stable phases of the principal components, we performed a time-segmentation analysis, as shown in the horizontal bar plots in Fig. 5. In this approach, abrupt changes in the PCs were detected based on shifts in the root mean square (RMS) values over time. The algorithm segments each PC into intervals by identifying change points that minimize the total within-segment RMS. This procedure is described in detail in the Methods section (lines 793-797), and we have added additional clarification in the results (lines 312-316) and the captions of Figs. 5, S6, and S7 to make this immediately clear.

► **Comment 2.11:** "[line 304] *The bottom plots show each neuron's mean MSI value and standard deviation (SD) across time bins.*" Which time bins, the entire trial? What do they reveal?

As defined in the Methods (lines 787-788), the time-dependent MSI values capture how selectivity for each parameter pair evolves throughout the trial. To obtain these values, we computed the MSI within each 60 ms time bin, providing a full temporal profile of each neuron's selectivity.

In this figure, each dot represents a single neuron and shows the mean (left panel) and standard deviation (right panel) of its time-dependent MSI values across all 60 ms bins. We update the caption of Fig. 5 to improve clarity (lines 304-306). These plots illustrate that MSI values are generally centered around zero and exhibit substantial variability over time. Together with the top plots, these plots demonstrate that individual neurons show considerable variation in their selectivity dynamics across both neural and temporal dimensions. We have added this clarification to lines 295-298 of the manuscript.

► **Comment 2.12:** "[line 316] *...the fixation epoch was separated from the remaining period in all parameter pairs.*" Where do we see this? The confusion matrices? Bins within the fixation epoch do seem to be essentially uncorrelated with themselves. Is this the point you're making? I agree that it is not terribly surprising. What do we learn?

Yes, the confusion matrices for each parameter pair show that the fixation time bins are uncorrelated both with one another and with the time bins of the other task epochs. This result is expected, as no task-specific information is presented during the fixation period; consequently, no selectivity is formed at those times. We have added this explanation to lines 316-317 of the manuscript.

► **Comment 2.13:** Fig 5: as large and complicated as this figure is (with fonts that are too small to read), there is very little text devoted to it. Is there something of note besides the greater similarity for temporary proximate bins and the lack of correlation during fixation? It is not clear to me what we learn of importance. One example here would suffice, with all the rest moved to the supplement. I do not understand the PC segmentation. Is this somehow derived from the confusion matrix (although the text seems to suggest the opposite relation)?

Thank you for pointing this out. We have improved the quality of Fig. 5 by enlarging key text elements and moving the dataset 2 panels to the supplementary materials.

This figure compares the dynamics of neural selectivity at both the single-neuron and population levels. At the single-neuron level, panels A and C show the mean MSI across neurons (top plots), and the mean MSI across time (bottom plots). Together, these panels demonstrate that individual neurons exhibit substantial variability in their selectivity dynamics across both neural and temporal dimensions. In contrast, panels B and D depict the population-level dynamics, showing that this highly variable single-neuron selectivity can be captured within a stable, low-dimensional subspace. We have revised the manuscript to make these findings clearer (lines 328-330).

As discussed in response to Comment 2.10, the segmentations are derived from the principal component values.

► **Comment 2.14:** "[line 391] *In Dataset 1, positive correlations in AIP between precision and power grips at each handle position suggest that grip type has minimal influence on the neural selectivity for position. In contrast, in F5, all but one correlation between different positions within the same grip type was positive...*" Why is this "in contrast"? It seems to be the same kind of observation as is the following one, which is preceded by "similarly".

The use of "in contrast" was intended to emphasize the functional difference between the AIP and F5 areas. In the quoted sentence regarding Dataset 1, the distinction is that:

- AIP: The positive correlations between precision and power grips at each handle position mean that grip type has minimal influence on the neural selectivity for position (object-related factor is stable).
- F5: The positive correlations between different positions within the same grip type mean that, conversely, position has minimal influence on the neural selectivity for grip type (motor-related factor is stable).

The subsequent use of "Similarly" for Dataset 2 was to highlight that this hierarchical pattern of stability is consistent across both datasets:

- AIP (Dataset 2): Grip type has minimal influence on the neural selectivity for orientation (object-related factor stable).
- F5 (Dataset 2): Orientation has minimal influence on the neural selectivity for grip type (motor-related factor stable).

We appreciate you pointing out this unclarity in the wording. We have updated our manuscript (lines 391-405) to clarify the functional distinction between the parameter representation in AIP and F5.

► **Comment 2.15:** "[line 460] *...we observed subtle shifts in selectivity at specific task epochs. For instance, in F5, grip type selectivity became more pronounced during the movement epoch, while in AIP, orientation selectivity increased during the cue epoch. Further analysis using PCA and pairwise time-point correlations revealed that this single-neuron variability can be reduced to a stable, low-dimensional subspace, enabling the extraction of multidimensional information at the population level.*" This is not particularly innovative, technically. What does it tell us about this part of the brain?

We appreciate the reviewer's comment and agree that dimensionality-reduction approaches such as PCA are not themselves technically novel. Our aim here was to use these tools to reveal an organizational principle. Specifically, our results show that despite the strong mixed selectivity and substantial temporal variability of individual neurons, the population-level representation in both AIP and F5 collapses onto a low-dimensional structure whose temporal organization is stable and aligned with behaviorally meaningful epochs.

Our data reveal subtle but meaningful shifts in feature selectivity across task epochs in AIP and F5, highlighting their complementary roles in the grasping network. Orientation selectivity in AIP peaked during the cue epoch, consistent with a role in early sensory analysis and the extraction of object affordances necessary for planning potential grasps. By contrast, grip-type selectivity in F5 became more pronounced during the movement epoch, suggesting that F5 increasingly represents the motor plan as the action is executed. This temporal dissociation aligns with the hierarchical representation in Fig. 7, as AIP emphasizes object-related computations, providing the sensory constraints for action, while F5 translates these constraints into specific motor commands. Such dynamics support the idea that the parieto-frontal network flexibly shifts its coding priorities to match the computational demands of different task stages.

We added these lines to the revised manuscript (lines 459-468).

► **Comment 2.16:** "[line 475] ...linear mixed selectivity was far more prevalent than nonlinear. Despite these differences, both linear and nonlinear selectivity parameters contributed similarly to the decoding performance at the population level (Table 1)." It's a bit difficult for me to reconcile the "far more prevalent" selectivity with the similar contribution to decoding. Can this be clarified?

We thank the reviewer for raising this important point. Linear mixed selectivity was indeed more prevalent at the single-neuron level. As illustrated in the histograms of Figs. 6 and S8, this pattern appeared across all parameter pairs as a shift in the mean nMSI values toward linear mixing. However, this shift was relatively small, and the majority of neurons exhibited both linear and nonlinear contributions. Thus, even though linear selectivity was somewhat more common, nonlinear selectivity was still widely present across the population.

Further, in our decoding analysis, each task parameter is represented by multiple variables in the classifier. As a result, removing one linear or nonlinear variable does not eliminate all information about that parameter, because related variables can still carry overlapping or redundant information. This redundancy moderates the impact of removing any single variable and contributes to the observed similarity in decoding performance when either linear or nonlinear components are removed.

More broadly, several factors can influence population-level decoding, such as the contribution of weakly selective neurons, the size of the neural population, differences in noise sensitivity across linear and nonlinear components, and the complexity of the task. While Table 1 demonstrates that both linear and nonlinear variables measurably affect decoding performance, a detailed analysis of these subtle factors was beyond the scope of our study.

We have now clarified this point in lines 475-482 of the revised manuscript.

► **Comment 2.17:** "[line 491] *It was unexpected that, in both areas, hand laterality, a fundamental aspect of motor action, is positioned at a lower level in the hierarchical clustering, relative to grip type or hand orientation. In line with the established role of AIP and F5 as high-level planning areas...*" This strikes me as one of the more interesting results, although it is not clear to me why "planning" should necessarily ("in line with") begin with grasp type as opposed to limb. What is the logic here? What was the relative timing of the tone and visual cues in task 2? Could this have anything to do with the hierarchy of representation of laterality and grasp type?

We thank the reviewer for this insightful observation. In both tasks, all cues occurred simultaneously (lines 679-680). Specifically, in Task 2, the audio tone indicating limb laterality was presented at the same time as the LED cue signaling grip type. Therefore, the observed hierarchy of representation is not attributable to differences in cue timing, but instead reflects the functional priorities of AIP and F5, which preferentially encode the action goal (grip type) over effector identity.

The stronger representation of grip type relative to limb laterality in both AIP and F5 can be interpreted in light of the functional roles of these regions. AIP is primarily involved in processing object-related information and planning grips, while F5, as part of the ventral premotor cortex, transforms object affordances into motor programs for hand actions. Both areas are therefore fundamentally concerned with how the hand interacts with an object rather than which hand executes the action, which likely explains the predominance of grip-type encoding.

This observation also aligns with the concept of motor equivalence, where similar action goals can be achieved with either limb. In this sense, both AIP and F5 appear to prioritize the functional aspect of the action (the grip) over limb identity. Limb laterality may be represented more subtly in contexts that require learning or explicit differentiations. In this task, in which the

subjects were trained with both hands equally and did not demand hand-specific distinctions, neural activity naturally emphasized grip type over limb.

This pattern is consistent with previous studies showing that some neurons encode grip type independently of which hand performs the action (Rizzolatti et al., 1988), as well as with observations that mirror neurons in F5 can encode observed actions regardless of the effector used (Ferrari et al., 2005). Together, these findings suggest that action representations in AIP and F5 are goal-centric: grip type encodes the core functional goal, while limb identity is secondary.

We added these lines to the revised manuscript (lines 491-504).

Minor comments from reviewer 2

► **Comment 2.18:** "[line 41] ...neurons based on their functions, such as grasping, holding, and tearing..." Possibly means something other than "tearing"?

The term "tearing" was taken directly from the original classification in Rizzolatti et al. (1988). In that study, tearing neurons were defined as neurons that became active during hand, finger, and wrist movements suitable for tearing or breaking objects. We agree that this term may be ambiguous, and to ensure clarity in the present study, we use the term 'pulling objects' instead (line 41).

► **Comment 2.19:** "[line 114] ...allowed the subjects to move their left hand (contralateral to the recording chamber) between four locations—left, right, top, or bottom— using two electrical motors." What do motors have to do with allowing the monkey to move their hand?

We apologize for the imprecise phrasing. The electrical motors are not involved in the movement of the monkey's hand, but rather are part of the mechanical setup used to change the positions of the grasp target (handle) and fixation light.

To clarify this in the manuscript, we have revised the sentence (lines 114-116). It now reads: "As depicted in Fig. 1 B, the handle and eye-fixation light were mounted on a board, which was moved electrically between four locations (left, right, top, or bottom), allowing the subjects to reach the target with their left hand (contralateral to the recording chamber)."

► **Comment 2.20:** "[line 117] The eye position was located at the center of the workspace, while the target position was varied between the four locations. 2) Gaze variation: The handle position was located at the center of the workspace, while the gaze position..." Do eye and gaze positions really refer to different concepts, given that the head is fixed?

We thank the reviewer for highlighting this inconsistency in terminology. You are correct; given that the monkey's head was fixed during the experiment, "eye position" and "gaze position" refer to the same concept: the position of the visual fixation point in the workspace. To ensure consistent terminology throughout the manuscript, we have revised the text to use "gaze position" exclusively when referring to the animal's point of visual fixation.

► **Comment 2.21:** "[line 273] ...orientation is relatively stronger during the cue epoch..." Orientation is stronger during the cue epoch

We have made this change in the manuscript (line 273).

► **Comment 2.22:** "[line 386] ...we computed Pearson correlations between neural responses to each condition pairs." All condition pairs?

Yes, for this analysis, we computed the Pearson correlation coefficient between neural responses for all pairs of the task conditions. We updated the manuscript (line 386) to clearly state "all task condition pairs".

► **Comment 2.23:** "[line 676] *The handle was illuminated during the cue in the following, revealing its position...*" Clarify

The phrase "in the following" is redundant and misleading and has been removed from the manuscript. The revised sentence (line 676) now reads: "During the cue epoch, the handle was illuminated, revealing its position (key information in task 1) and orientation (key information in task 2)".

► **Comment 2.24:** [line 760] "...report the ePAIRS statistics. However, since [] is dependent on, we..." Missing variable.

The variable θ was missing in this sentence. We have revised the manuscript (line 760) to include this variable.

► **Comment 2.25:** "[line 778] *...(gaussian kernel 50-ms)...*" Gaussian

Thank you for pointing this out. We have updated the text to correctly capitalize "Gaussian" (line 778).

References

- [1] Rizzolatti, G., Camarda, R., Fogassi, L., Gentilucci, M., Luppino, G., & Matelli, M. (1988). Functional organization of inferior area 6 in the macaque monkey: II. Area F5 and the control of distal movements. *Experimental brain research*, 71(3), 491-507.
- [2] Ferrari, P. F., Rozzi, S., & Fogassi, L. (2005). Mirror neurons responding to observation of actions made with tools in monkey ventral premotor cortex. *Journal of cognitive neuroscience*, 17(2), 212-226.

2nd Decision Letter

Dear Mr. Fathian,

Thank you for submitting your manuscript to Progress in Neurobiology. We have received comments from reviewers on your manuscript. Your paper should become acceptable for publication pending suitable minor revision and modification of the article in light of the appended reviewer comments.

When resubmitting your manuscript, please carefully consider all issues mentioned in the reviewers' comments, outline every change made point by point, and provide suitable rebuttals for any comments not addressed.

To submit your revised manuscript go to <https://www.editorialmanager.com/proneu/> and log in as an Author where you will see a menu item called 'Submission Needing Revision'.

Please resubmit your manuscript by **Feb 06, 2026**.

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We look forward to receiving your revised manuscript.

Kind regards,

Brett L. Foster
Associate Editor

Laura Colgin
Co-Editor-in-Chief
Progress in Neurobiology

Comments from the Editors and Reviewers:

Reviewer #1: The authors have addressed all my concerns.

Reviewer #2: The authors have responded nicely to nearly all of my concerns. In particular, the distracting figure complexity is much improved, as are most of the summary comments, which now emphasize particular results rather than more general observations. A lingering modest concern is that there remain a number of comments about basic decoding methods that still seem to suggest a degree of innovation that is simply not there. Placing clearer and emphasis on the results of those methods rather than the methods themselves would be less distracting. A couple of examples follow.

"although decoding is not feasible from a single mixed neuron, a population of mixed neurons allows the decoding of various types of information using appropriate readout mechanisms."
Perhaps make this very general point once but don't repeat it. This is the essence of any decoding study.

"despite the

242 absence of categorical representation at the single-neuron level (Figs. 3 and S2), these mixed
243 representations are capable of separating conditions at the population level using linear decoders
(Fig. 4)."
Likewise

These results confirm that a linear method can decode condition
266 information from a mixed population, and that mixed populations do not pose any challenges for
linear
267 decoding compared to purely selective populations.
Again...

"...individual neurons exhibit substantial variability in their selectivity dynamics across
329 both neural and temporal dimensions..."
What is meant by individual neurons varying across a neural dimension?

2nd Author Response Letter

Manuscript title: Mixed-Selective Organization of Reach and Grasp in the Primate Fronto-Parietal Network

Manuscript number: RONEU-D-25-00503; Revision 2

Comments from Reviewer 1

None.

Comments from Reviewer 2

The authors have responded nicely to nearly all of my concerns. In particular, the distracting figure complexity is much improved, as are most of the summary comments, which now emphasize particular results rather than more general observations.

We thank the reviewer for their positive assessment of our revision and the constructive feedback. We are pleased that these revisions have improved the clarity and readability of the manuscript.

► **Comment 1:** A lingering modest concern is that there remain a number of comments about basic decoding methods that still seem to suggest a degree of innovation that is simply not there. Placing clearer and emphasis on the results of those methods rather than the methods themselves would be less distracting. A couple of examples follow.

"[From the 1st revision's response document] *Although decoding is not feasible from a single mixed neuron, a population of mixed neurons allows the decoding of various types of information using appropriate readout mechanisms.*" Perhaps make this very general point once but don't repeat it. This is the essence of any decoding study.

"[line 240] *despite the absence of categorical representation at the single-neuron level (Figs. 3 and S2), these mixed representations are capable of separating conditions at the population level using linear decoders (Fig. 4).*" Likewise

"[line 265] *results confirm that a linear method can decode condition information from a mixed population, and that mixed populations do not pose any challenges for linear decoding compared to purely selective populations.*" Again...

We agree that multiple statements in the manuscript placed an unnecessary emphasis on the decodability of neural populations, which is a well-established result rather than a novel contribution. In this revision, we now make this point only once and have removed repeated statements that could be interpreted as emphasizing methodological innovation.

Specifically, we revised lines 240–243, which now read: *"Dimensionality reduction analysis revealed that population responses, utilizing mixed representations, can effectively separate conditions despite the lack of categorical representation at the single-neuron level"*. We also removed the repeated emphasis on linear decodability from lines 265–266, which now read: *"The results confirm that mixed populations do not pose any decoding challenges compared to purely selective populations"*, and we toned down the description of decodability at lines 354 and 450.

► **Comment 2:** "[line 328] *...individual neurons exhibit substantial variability in their selectivity dynamics across both neural and temporal dimensions...*" What is meant by individual neurons varying across a neural dimension?

We thank the reviewer for pointing out this lack of clarity. We meant to convey that neural selectivity varies substantially across neurons and over time. The revised text at lines 327–328 now reads: *"Together, although neural selectivity varies substantially across neurons and over time, the population-level analysis shows that this variability can be captured within a stable, low-dimensional subspace"*.