Heterogeneous representations in the superior parietal lobule are common across reaches to visual and proprioceptive targets

**Supplementary Figures and Table**

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Supplemental Figures 1-2: Alternate coordinate frames for analyses

In the main text, spatial variables are principally quantified in terms of angles along the arc of targets in the horizontal workspace, i.e. relative to a body-centered reference frame with the origin at the center of the target-arc (Supplemental Figure 1A, left column). However, the true tuning function of the cells could depend on angles defined with respect to other origins, for example, the starting location for the reaching hand (a hand-centered origin; Supplemental Figure 1A, center column) or the fixation point (a gaze-centered origin; Supplemental Figure 1A, right column). The spatial layout of the targets is quite different across reference frames. Most importantly, with the hand/body-centered origin target positions vary primarily in target angle, while with the eye-centered origin target positions vary primarily in eccentricity from the fixation point. Since the sampling of these reference frames is quite different, there could be differences in the power of our analysis to discriminate between these potential reference frames. Additionally, for the hand/body-centered origin the target distance varies with target angle, and for the gaze-centered origin the target elevation (z-axis) varies with target angle. These differences lead to potential mismatches between target locations that are nominally matched in the $\delta = 1$ condition (bottom row of Supplemental Figure 1A). This could lead to an interaction between fixation location and the neurally encoded target distance or elevation, again potentially biasing our results.

To determine the potential consequence of sampling biases or a mismatch in reference frame origin between the true neural tuning and that assumed in our analyses, we performed the
Supplemental Figure 1: A. Alternate reference frame origins. Each panel shows the layout of targets and fixation points with respect to a different potential reference frame. The reference frame origin is different for each column. For body- and hand-centered origins, the view is from the top (y-axis along sagittal line). For the gaze-centered origin, the view is from the cyclopean eye (y-axis is line from eye to fixation point; z-axis is visual elevation). The top row illustrates reference-frames that are independent of fixation (δ=0); the bottom row shows reference frames that shift with fixation (δ=1). As noted in the text, it is not possible to have a gaze-centered origin with δ=0. B-D. Histograms of best-fit shift values for artificially generated datasets with a known reference frame origin and shift value. Fit shift values were obtained using the analysis and inclusion criteria described in the Methods of the main text. For each true shift δ, the mean and standard deviation (std) of the best-fit values are indicated. A) Body-centered origin: the true origin matches that used in the analysis. B) Hand-centered origin: fixation location and target distance are potentially confounded. C) Gaze-centered origin: fixation location and the y-component of target location are potentially confounded.

tuning curve analyses on artificial datasets with known reference frame origins and shift values. First, for each reference frame origin and δ = 0, 0.5, or 1, target locations were defined as three-dimensional vectors in that reference frame. Supplemental Figure 1A illustrates these vectors for the cases where δ = 0 and 1. Note that for the gaze-centered origin, the fixation point lies at the origin by definition, so the shift value δ is always effectively unity. For each reference frame origin and δ, we then generated artificial datasets for 5000 cells using randomly generated three-
dimensional cosine tuning curves (Georgopoulos et al., 1986). For each artificial dataset, we randomly selected a three-dimensional preferred direction, baseline rate (0-50 Hz), modulation (5-50 Hz), and level of variability (0.5-1.5 Fano factor). Firing rates were then generated for six repetitions of each target and fixation point (the average repetitions in our data). Finally, we determined the best-fit shift value for the artificial firing rates using the same procedures we followed for the real data (see Methods). This allowed us to estimate both the precision and bias of our fits.

The goal of this analysis is to determine how sampling differences across reference frames and the true reference frame origin affect our estimate of the shift value, \( \delta \). (In contrast, the main text is primarily concerned with the shift value, independent of reference frame origin.) When artificial data were generated using a body-centered origin for target locations, there was no bias in the estimated tuning curve shift \( \delta \) (Supplemental Figure 1B). For the other two reference frame origins, however, small but highly significant biases were observed. When targets were defined with respect to a hand-centered origin, a small positive bias was observed, with a mean estimate of \( \delta = 1.09 \) when the true value was unity (Supplemental Figure 1C). When targets were defined with respect to a gaze-centered origin, a larger negative bias was observed, with a mean estimate of \( \delta = 0.81 \) when the true value was unity (Supplemental Figure 1D). Note however that these biases are small in the context of our results. In particular, the distribution of shift values obtained for the cells recorded in Area 5 and MIP appear to be unimodal (Figure 7, main text) with means of 0.25 and 0.51, respectively. This indicates a predominance of “intermediate” representations in these areas, even when the potential for biases is considered.

Supplemental Figure 1 also provides an estimate of the variability of best-fit shift values due to both variability in neural tuning and sampling noise. Notably, this level of variability is much smaller than that observed in the real data (compare Supplemental Figure 1 and Figure 7 main text). While the artificial datasets have standard deviations ranging from 0.18 to 0.24, the average standard deviation in shift values is 0.41 in Area 5 and 0.47 in MIP (standard deviation computed separately for each epoch and then averaged). Thus, the population of neurons in these
areas exhibits a greater range of shift values than can be explained simply by experimental variability.

In summary, Supplemental Figure 1 shows that our best-fit estimates of tuning shift are variable and potentially biased. Nonetheless, these simulations support the conclusion that the neural representations in Area 5 and MIP truly are heterogeneous, with a large number of cells having intermediate tuning curve shifts.

Supplemental Figure 2: Example reach trajectories and velocity profiles

Supplemental Figure 2: Examples of reach trajectories and velocity profiles from one day of recording for each animal. Monkey C made reaches using the right hand. Monkey E made reaches using the left hand. Colors indicate different reach targets and eye positions: cool colors indicate reaches with fixation to the left, warm colors indicate reaches with fixation to the right.
Supplemental Figure 3: Modulation of population responses in Area 5 and MIP

MIP cells had a tendency to show greater differences in firing rate modulation across modalities than Area 5 cells. This tendency is illustrated by a plot of mean firing rate modulation across the trial timeline for each area and target modality (Supplemental Figure 3). The difference in mean modulation is due in large part to inter-area differences in the number of cells tuned for each task type (see Figure 4, main text), however greater differences are still seen in MIP when only cells with significant tuning are included in the mean.

Supplemental Figure 3: Average neural responses for Area 5 and MIP cells, as a function of target modality and trial time. For each cell and trial condition (target and fixation), mean firing rates were computed in 100 ms time windows at 50 ms steps, with trials aligned on the Go-Tone (mean reaction time is 370 ms). For each cell and target modality, modulation is then defined as the difference in mean rate between the trial condition with maximum mean rate and the trial condition with the minimum mean rate.
**Supplemental Figure 4: R² of tuning curve fits**

Though R² statistics are not a true measure of goodness of fit for nonlinear models (Zar, 1974) such as the tuning curve models in this paper (Methods equations 1-3), we computed the R² of our fits to provide a heuristic evaluation of the tuning fits. We found a wide range of R² values across epochs and modalities in both Area 5 and MIP (Supplemental Figure 4). This range likely reflects the wide range of firing rate modulations and variability seen in our cells, rather than a deficiency in the tuning model for some cells, as visual inspection of fits suggest that the model captures the general shape of the target and eye position effects for all cells (see example tuning fits below and in Figure 5 of the main text). We found no significant differences in R² values as a function of target modality or epoch in Area 5 or MIP (p>0.05/2=0.025, ANOVA, Bonferroni correction for multiple comparisons).

![Supplemental Figure 4: Histograms of R² values for shift tuning curve fits (Equations 1 or 3).](image)

**Supplemental Figures 5-7: Additional example cells**

Here we provide additional examples of representative cells from Area 5 (Supplemental Figure 5) and MIP (Supplemental Figure 6) as well as some examples of cells with atypical responses (Supplemental Figure 7).
Supplemental Figure 5: Additional examples of Area 5 tuning curves. Each panel shows a different cell, and panel subplots show mean tuning (standard error) separated by target modality. Left subplots within each panel show responses aligned in a body/hand-centered reference frame. Right subplots within each panel show responses aligned in an eye-centered reference frame. Shift values (δ) above each row show the best-fit tuning shift and bootstrapped 95% confidence intervals (CI) for each modality. The dashed lines show the tuning curve model fits for each modality-epoch-cell.
Supplemental Figure 6: Additional examples of MIP tuning curves. Each panel shows a different cell, and panel subplots show mean tuning (standard error) separated by target modality. Left subplots within each panel show responses aligned in a body/hand-centered reference frame. Right subplots within each panel show responses aligned in an eye-centered reference frame. Shift values (δ) above each row show the best-fit tuning shift and bootstrapped 95% confidence intervals (CI) for each modality. The dashed lines show the tuning curve model fits for each modality-epoch-cell.
Supplemental Figure 7: Additional examples of cells with atypical tuning curves. A) Cell with unusually large gain modulation by eye position. B) Cell with shift values significantly outside 0-1. C) Cell with different preferred directions of tuning across tasks. Other plot conventions as in Supplemental Figures 6-7.
Supplemental Table 1: Comparison of VIS and PROP shifts divided up by area and epoch

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Supplemental Table 1: Correlation between best-fit shift values obtained with VIS and PROP trials, separated by area and epoch. The $r$ values shown here are lower than those for the combined datasets (Figure 6, main text) due to systematic differences in shift across areas (Figure 7, main text). The table also shows $p$-values for tests of significant differences in the mean (paired permutation test) or distribution (Kolmogorov-Smirnov test) of shift values between target modalities. Differences would be significant if $p<0.05/6=0.008$, Bonferroni correction for multiple comparisons; no comparisons approach significance.

Supplemental Figure 8: Decoding movement parameters from mixed representations

Given that the distribution of shift values differs between Area 5 and MIP, we asked whether this difference had a meaningful affect on the information that can be decoded from the two areas. We addressed this question by performing a linear decode of target location from the two neural populations, and comparing performance when target is represented in hand/body- or eye-centered space.

The linear decode was performed with simple linear regression. The dependent variable was the target location in either hand/body-centered space or eye-centered space. The independent variables were the single-trial firing rates of a randomly selected subset of cells, although the cells were not actually recorded simultaneously. All cells had at least four repetitions of each trial condition, though most had more. To facilitate the combination of recordings, we discarded any repetitions beyond the first four. Due to similarity in tuning, the firing rates of many neuron pairs are correlated across conditions (see the baseline distribution of correlations in Figure 8 of the main text). Therefore, we first performed a Principle Components
Analysis of the single-trial firing rates across cells. The principal components were added into the regression one at a time and the regression performance was assessed using leave-one-out cross-validation. When the cross-validation $R^2$ failed to decrease by more than 1%, no additional components were added. We report this final cross-validation $R^2$. For each cortical area, this process was carried out for 1000 random subsets of neurons for each population size: 10, 20, 30, 40, and 50 cells. Supplemental Figure 8 shows the mean and standard deviation of these cross-validation $R^2$ values for each cortical area, sample size, and dependent variable.

For both Area 5 and MIP, the $R^2$ values rapidly asymptote as a function of cell number. For Area 5, the $R^2$ values obtained for the hand/body-centered target location were larger than those for the eye-centered target location. This indicates that Area 5 encodes more information in a hand/body-centered reference frame, consistent with the reference frame analyses presented in the main text. For MIP on the other hand, the $R^2$ values are nearly the same for the two dependent variables, indicating roughly equal amounts of information about these two variables in the population response of MIP. This is consistent with the average tuning shift value of $\delta = 0.51$ for MIP cells. Thus, the difference in reference frame distributions across areas appears to have an effect on the fidelity with which movement parameters in different reference frames can be decoded from these areas.
Supplemental Figure 9: Gain analysis of eye position effects

Describing eye position effects in terms of gain modulation (Supplemental Figure 9) yields results similar to those obtained with reference frame shift (Figure 6). There are no significant differences in mean (p>0.05, paired permutation test) or distribution (p>0.05, Kolmogorov-Smirnov) of gain values across modalities. The percentage of epoch-cells for which gain is significantly different across modalities is differs by at most 2.8% from the percentages observed with the shift analysis. The correlations in gain values between modalities are nearly identical to the correlations in shift values (differing by at most 0.07). The inter-area differences are also similar for the two analyses (data not shown): the distribution of gain values is significantly different between Area 5 and MIP (p=0.001, permutation test), with MIP showing a tendency to have larger absolute gain values. Note that for gain modulation, we had no pre-defined range of expected parameter values (unlike for the shift), and so all epoch-cells with significant tuning were included in Supplemental Figure 9. The inclusion of these additional epoch-cells had little effect on the results. Thus, our main conclusions are independent of the model use to account for eye position effects: for both analyses representations are modality-independent, but they differ between Area 5 and MIP, with larger eye position effects in MIP.

Supplemental Figure 9: Comparison of best-fit eye-gain (γ) values across modalities for combined Area 5 and MIP datasets. Data points represent fits for a single epoch-cell; error bars represent bootstrapped standard error of the mean. Filled points indicate epoch-cells with significantly different gains between modalities. Plots include all epoch-cells with significant tuning for both modalities being compared. Correlation coefficients (indicated on plots) were qualitatively unchanged when computed separately for each area or epoch. See Methods for details.
Supplemental Figure 10: Direct rate comparison of reference frame

To ensure that our conclusions are not dependent on the tuning curve fit, we compared the results of our reference frame shift analysis to those obtained by a direct rate comparison. We tested three candidate reference frames (Supplemental Figure 10A): hand/body-centered (shift = 0), intermediate (shift = 0.5), and eye-centered (shift = 1). Cells were categorized based on the reference frame or reference frames that could not be rejected based on significant differences between firing rates on spatially paired trials (see Methods). The results of the direct rate and shift analyses were in good agreement for the modality-epoch-cells where both analyses successfully assigned a reference frame (Supplemental Figure 10B). While there were many modality-epoch-cells where this analysis had insufficient power (“All Accepted” group in Figure 10B), in only a small fraction of cases was there significant evidence against all categories tested (“None Accepted” group in Figure 10B). Of those cases, 34% had shift values that were significantly outside the zero to one range, meaning that both analyses rejected a simple reference-frame model for these cases. However, these were only a small percentage of modality-epoch-cells, and most response patterns were well described by these simple models. This supports the idea that cells responses could be well-described with a model allowing for shift and gain modulation of firing rate by eye position. Furthermore, the agreement between the tuning curve shift fits and the direct rate comparisons illustrates that the heterogeneity of the reference frame representations we observed in Area 5 and MIP does not depend on the measure being used to determine reference frame.
Supplemental Figure 10: Comparison of reference frames determined by tuning-curve shift and direct rate comparison analyses. A) Shows targets that were paired for the direct rate comparison in each of the three reference frames tested. B) Shows reference frames determined with direct rate comparison versus reference frame shift from tuning curve shift analysis. Each row of the color-plot represents the modality-epoch-cells in a particular direct rate comparison category. Color-plots show the distribution of best-fit shift values within each category. The “All Accepted” category is for modality-epoch-cells with no significant differences in any of the direct rate comparisons (see Methods). The “None Accepted” category is for modality-epoch-cells that had significant differences for all direct rate comparisons. This analysis only included the 908 modality-epoch-cells for which a best tuning shift was obtained.
Supplemental Figure 11: Encoding multiple movement parameters

Supplemental Figure 11: Six-category reference frame analysis comparing target versus movement vector (MV) tuning by modality and epoch. Figure 3 in the main text shows schematic figures illustrating the variables encoded in each reference frame. A) Categorizations across tasks. No significant differences, p=0.932. B) Categorization across epochs. No significant differences, p=0.253. P-values were calculated with chi-square tests.

References