Task representation in the macaque posterior parietal cortex during virtual navigation

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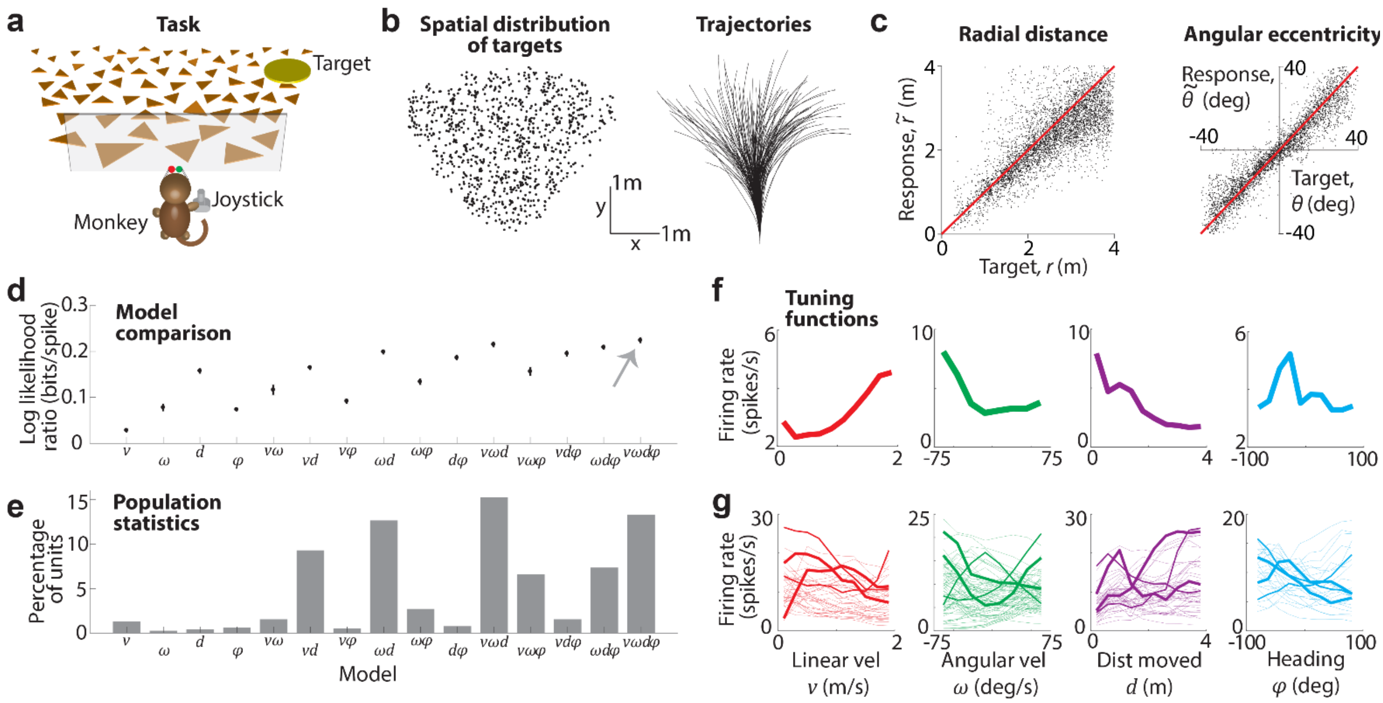
Summary

Much of what we know about how the brain computes comes from highly controlled tasks that use stimuli with stationary statistics and a limited set of actions (usually two). Such tasks may be inadequate to fully reveal the rich structure of neural representations and computations that mediate fluid behaviour. To understand dynamic neural processing underlying natural behaviour, we trained two macaque monkeys on a continuous-time foraging task in which they used a joystick to steer freely and catch targets in a two-dimensional virtual environment devoid of landmarks. Targets appeared briefly at a random location on the ground plane within the field of view. In order to solve the task, monkeys had to dynamically update their position estimates by integrating optic flow generated by self-motion. We implanted multi-electrode arrays to sample the activity of a large number of neurons in the posterior parietal cortex (PPC). Fitting a generalized additive model to the neural activity revealed that a majority of neurons encoded multiple task-relevant variables ranging from the monkeys' instantaneous linear and angular velocity to more abstract, integrated variables such as distance and direction of heading. We then inferred the structure of neural interactions by extending our model to include coupling between neurons. We found that there was sparse but indiscriminate flow of information between neurons encoding different task variables, and that the coupled model provided a better account of neural responses. To understand how task variables are represented at the population level, we used canonical correlation analysis and found that the dimensionality of task-relevant neural subspace was as high as possible. Similar analyses on uncoupled and coupled model populations showed that coupling between neurons was responsible for decompressing the task representation. These results demonstrate that recurrent connections in the primate PPC facilitate processing and integration of sensory inputs in dynamic environments.

Supporting Materials

Behaviour: At the beginning of each trial, a circular target blinked briefly (~300ms) and monkeys had to use a joystick to steer to the target by integrating optic flow generated by their own movements (**Fig. 1a**). The ground plane was composed of transient elements to prevent them from serving as landmarks. Distance and angular eccentricity of the targets varied randomly across trials, prompting monkeys to use a variety of trajectories (**Fig. 1b**). Monkeys successfully learned to steer and stop close to the target, as seen by comparing the radial distance and angular eccentricity of the stopping location ('response') against the target location across several trials (**Fig. 1c**).

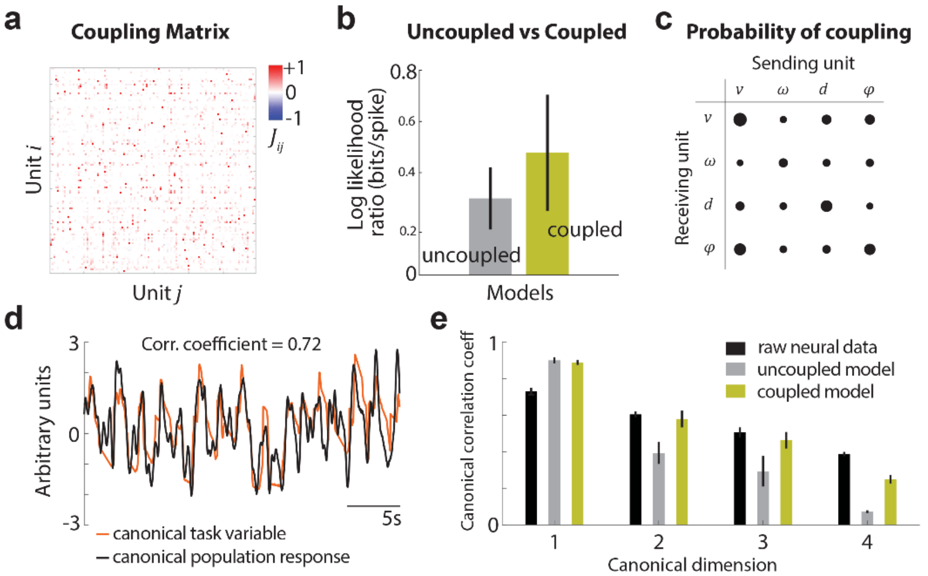


Single neurons: To investigate whether single neurons encode task-relevant variables, we fit the response of each neuron to a generalized additive model with exponential nonlinearity and Poisson noise according to:

$$E(y) \sim \exp(\sum_k f_k(x_k))$$

where $E(y)$ denotes the mean response of the neuron, $f_k(.)$ denotes any arbitrary nonlinear function of the task variable x_k. We considered four key task variables – linear velocity (v), angular velocity (ω), distance moved (d), and direction of heading (φ) – and fit several combinations by selecting one, two, three, or four variables resulting in a total of fifteen models per neuron. For each model, we fit f_k by maximising the likelihood of the model given data, subject to a constraint that functions f_k vary smoothly. We verified the resulting fits by performing a 10-fold cross-validation. **Fig. 1d** shows the log likelihood ratio of all models relative to a null model that assumed constant firing rate, for one example neuron. The response of this neuron was best explained by the model that included all four task parameters (grey arrow). Most neurons in the population were best explained by multivariable, rather than single-variable models (**Fig. 1e**). We used estimates $\widehat{f_k}$ of the best model to reconstruct model-based tuning curves to each variable x_k by computing the conditional expectation of response $E(y|x_k) \propto \exp(\widehat{f_k}(x_k))$, where the constant of proportionality is obtained by marginalizing over all other variables (**Fig. 1f**). Across all neurons, we observed diverse tuning ranging from increasing to decreasing to non-monotonic (**Fig. 1g** – highlighted in bold).

Neural interactions: To quantify the structure of pairwise neural interactions, we extended the above model by adding a coupling term $\sum_{j \neq i} J_{ij} y_j$ to the task-dependent term $\sum_k f_k(x_k)$ in the above equation, where J_{ij} denotes strength of coupling from neuron j to neuron i, and y_j denotes the response of neuron j. We fit the model as described above, now under an additional constraint that $\beta \sum_j |J_{ij}|$ be small for each neuron i, where β is a hyper-parameter that enforces sparseness. We systematically varied β and found that the best model had sparse connectivity. To visualise the coupling matrix, we normalised the set of couplings for each neuron (rows of the matrix) by the largest coupling (**Fig. 2a**). Across all neurons, incorporating the coupling term increased model likelihoods (**Fig. 2b**, cross-validated) without altering selectivity or tuning to task variables. To test whether couplings were limited to neurons carrying similar signals, we labelled each neuron by the dominant task variable that drove its response and found that the probability of receiving inputs was independent of this label (**Fig. 2c**, disc radii encode probability P[receiving unit|sending unit]).



Population: To understand how the population as a whole represents task variables, we performed canonical correlation analysis (CCA) between population response and the task variables. CCA identifies the set of orthogonal directions in the response space that is maximally correlated with task variables, thereby revealing the number of task-relevant dimensions in the population response. We applied CCA on the neural data and found four dimensions (maximum possible given four task variables) along which responses were highly correlated with task variables (**Fig. 2d** shows a short segment along leading dimension; Corr. coeffs. in **Fig. 2e** – black). In contrast, CCA on simulated population based on the uncoupled model revealed only three dimensions with appreciable correlation with task (**Fig. 2e** – grey). Remarkably, adding couplings restored the dimensionality (**Fig. 2e** – dusty gold) suggesting that coupling between neurons helps decompress the task representation.