Distributed coding of evidence accumulation across the mouse brain using microcircuits with a diversity of timescales

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Abstract

The gradual accumulation of noisy evidence for or against options is the main step in the perceptual decision-making process. Using brain-wide electrophysiological recording in mice (Steinmetz et al., 2019), we examined neural correlates of evidence accumulation across multiple brain areas. We demonstrated that the neurons across the brain exhibited ramping-like firing rate activity that was modulated by the strength of evidence. These neurons had distinct properties in their intrinsic timescale, which were organized hierarchically across the brain. Our findings support the existence of evidence accumulation over multiple timescales. Besides variability across brain regions, a heterogeneity of intrinsic timescales was observed within each brain region as well. We demonstrated that this variability reflected the heterogeneity of microcircuit accumulation parameters, such that populations with longer timescales had higher recurrent excitation strength.

1- Introduction

Decision-making, the process of choosing between options, is a fundamental cognitive function. Different types of decision-making, including perceptual (Gold & Shadlen, 2007) and value-based decision-making (Hunt et al., 2012), are thought to be characterized by a gradual accumulation of noisy evidence for or against options until a threshold is reached and a decision is made. The study of the evidence accumulation process started within cognitive psychology, where researchers explored sequential sampling models, i.e., the drift-diffusion model (DDM), using behavioral data (Ratcliff & McKoon, 2008). In these models, noisy information is accumulated over time from a starting point toward a decision boundary.

Later studies on the neural basis of decision-making developed computational models for the accumulation process using neurons showing signatures of the drift-diffusion model, referred to as DDM-like neurons (Mazurek et al., 2003; Wang, 2002). These studies explored some brain regions containing DDM-like neurons, such as the posterior parietal cortex (PPC) (Roitman & Shadlen, 2002; Shadlen & Newsome, 2001), frontal eye field (FEF) (Ding & Gold, 2012; Kim & Shadlen, 1999), striatum (Ding & Gold, 2010), and superior colliculus (Horwitz & Newsome, 1999) in monkeys, as well as the frontal orienting field (FOF) and PPC (Hanks et al., 2015) in rats.

Although previous studies on the neural basis of decision-making explored a few brain regions showing the neural correlate of evidence accumulation, the distribution of DDM-like neurons across the brain is still unknown. Recent brain-wide electrophysiological and calcium imaging studies in mice revealed that neurons involved in decision-making are distributed across the brain (Steinmetz et al., 2019; Zatka-Haas et al., 2021). These findings motivated us to explore the existence of choice-selective neurons that have DDM-like firing rate activity across the brain. Similar to the drift-diffusion process, these neurons have ramping-like firing rates associated with the strength of stimulus evidence, such that stronger evidence levels lead to a faster ramping of firing rate and vice versa. However, these patterns of activity can be explained by different accumulation mechanisms, i.e., single (DDM) and dual (Race) accumulators (Bogacz et al., 2006).

Therefore, to fully characterize the subpopulation of neurons involved in decision-making, we need to distinguish between these two mechanisms.

Moreover, the distributed coding of evidence accumulation suggests multiple timescales over this cognitive process (Chen et al., 2015). This property stems from the fact that each brain area exhibits a distinct intrinsic timescale leading to a hierarchical organization that largely follows the anatomical hierarchy (Chen et al., 2015; Honey et al., 2012; Murray et al., 2014; Pinto et al., 2022; Rossi-Pool et al., 2021). In addition to the between-area differences in intrinsic timescales, single-neuron timescales are heterogeneous within each brain area as well (Cavanagh et al., 2016; Fascianelli et al., 2019). The observed heterogeneity may be due to differences in local microcircuits, which lead to functional differences in neural populations (Soltani et al., 2021). As such, we used the brain-wide electrophysiological recording data recently published by (Steinmetz et al., 2019) to investigate the distribution of DDM-like neurons across the brain. We demonstrate that these neurons are distributed across the brain and exhibit distinct intrinsic timescales. Our findings support the hypothesis that evidence accumulation is a distributed process across the brain over multiple hierarchically-organized intrinsic timescales.

In addition to the overall intrinsic timescale across brain regions, we found a heterogeneity of neural timescale within brain regions. Therefore, we further examined whether the observed intrinsic variability within these brain areas corresponded to the heterogeneity of the neural integrator parameters. Our results support the hypothesis that a longer intrinsic timescale subpopulation of neurons had a stronger recurrent connection strength in some regions. We have also examined two popular accumulation mechanisms to test whether neurons within each brain area were better described by single or race accumulation mechanisms. Our results demonstrated that most areas are better characterized by the single accumulation mechanism compared to the race model.

2- Results

Distributed evidence accumulation across the mice's brain

To investigate whether or not the evidence accumulation process is distributed across the brain, we used the brain-wide neural recording in mice during a visual discrimination task (Steinmetz et al., 2019) (see Methods). In each trial, a visual stimulus of varying contrast (Gabor patch with sigma 9 and 45° direction) appeared on the right, left, both, or neither side screens. In order to get a reward, the mice had to turn the wheel to move the stimulus with the higher contrast into the center screen (Figure 1 – A). During the visual discrimination task, the neural activity of approximately 30,000 neurons in 42 brain areas was recorded using Neuropixel probes. We focused our analysis on the seven groups of brain areas demonstrated in Table 1 and Figure 1 - B, according to the Allen Common Coordinate Framework (CCF) (Wang et al., 2020).

To detect the neurons with DDM-like firing rate activity, we first determined the choice-selective neurons within each group of regions. Preliminary analyses showed that most neurons simultaneously encode different task variables, especially in higher cortical areas. Therefore, we first used demixed principal component analysis (dPCA) (Kobak et al., 2016) to decompose the population neural activity into a few principal components representing specific task variables (Figure 1 - C). We then determined whether a neuron responded more strongly to the stimulus or decision by measuring the reconstructed neural activity's explained variance (R-squared) using each set of stimulus and decision-related components (Supp-Figure 1 - A). The results revealed that neurons across the brain regions belong to one of three clusters: those best represented by the stimulus-related components, the decision-related components, or their interaction components (Figure 1 – D, Supp-Figure 1 - B). We excluded the hippocampus region from further analyses because of poor performance in the clustering analysis.

We evaluated dPCA results using the standard auROC metric to measure how well a neuron encodes the stimulus or decision variables. This metric is commonly used to calculate the differences between spike count distributions across different conditions (Britten et al., 1996). There is a strong correlation between the stimulus and animal choice by design. So we used the combined condition auROC metric to reduce the

effect of other task variables on the decoding performance (see Methods). For the stimulus decoding, we measured the differences between the spike count distribution of trials with contralateral stimulus higher than zero and trials with zero contra stimulus contrast level for all 12 conditions.

Table 1 - Brain regions within each group of areas according to the Allen CCF

Group name	**Regions within each group**
Hippocampus	POST, SUB, DG, CA1, CA3
Thalamus	LP, LD, RT, MD, MG, LGd, VPM, VPL, PO, POL
Visual	VISp, VISrl, VISam, VISpm, VISl, VISa
Striatum	CP, GPe, ACB, LS
Frontal	MOs, ACA, PL, ILA, ORB
MOpSSp	MOp, SSp
Midbrain	MRN, SCm, SCs, APN, PAG, SNr

Similarly, decision decoding was evaluated by measuring the differences between Hit and Missed trials within 12 conditions referred to as 'Detect Probability' (DP) (Hashemi et al., 2018). Our results showed that the stimulus-selective neurons detected by dPCA, indeed encoded the stimulus more strongly than the decision. Similarly, the decision-selective neurons encoded the decision better than the stimulus (Supp-Figure 1 - C).

Finally, we found the DDM-like neurons within the decision-related clusters across the brain. Previous studies on the neural basis of evidence accumulation have discovered that DDM-like neurons in the posterior parietal cortex (LIP area) had a ramping-like firing rate activity associated with the strength of a motion stimulus (Roitman & Shadlen, 2002; Shadlen & Newsome, 2001). Similar properties were also found in the mouse's PPC (Hanks et al., 2015) and anterior dorsal striatum (ADS) in rats (Yartsev et al., 2018). According to the properties of DDM-like neurons, we found the choice-selective neurons that additionally encoded the strength of the input evidence (difference between Right and Left stimulus

contrasts). We used the combined condition auROC metric to measure each neuron's choice probability (CP) and evidence selectivity. Accordingly, we calculated the differences between trials with right and left choices within 12 groups to measure the CP. For measuring evidence selectivity, we evaluated whether or not the trials within a group with the higher evidence level had greater neural activity than those within all the groups having lower evidence (Figure 2 - B) (See Methods).

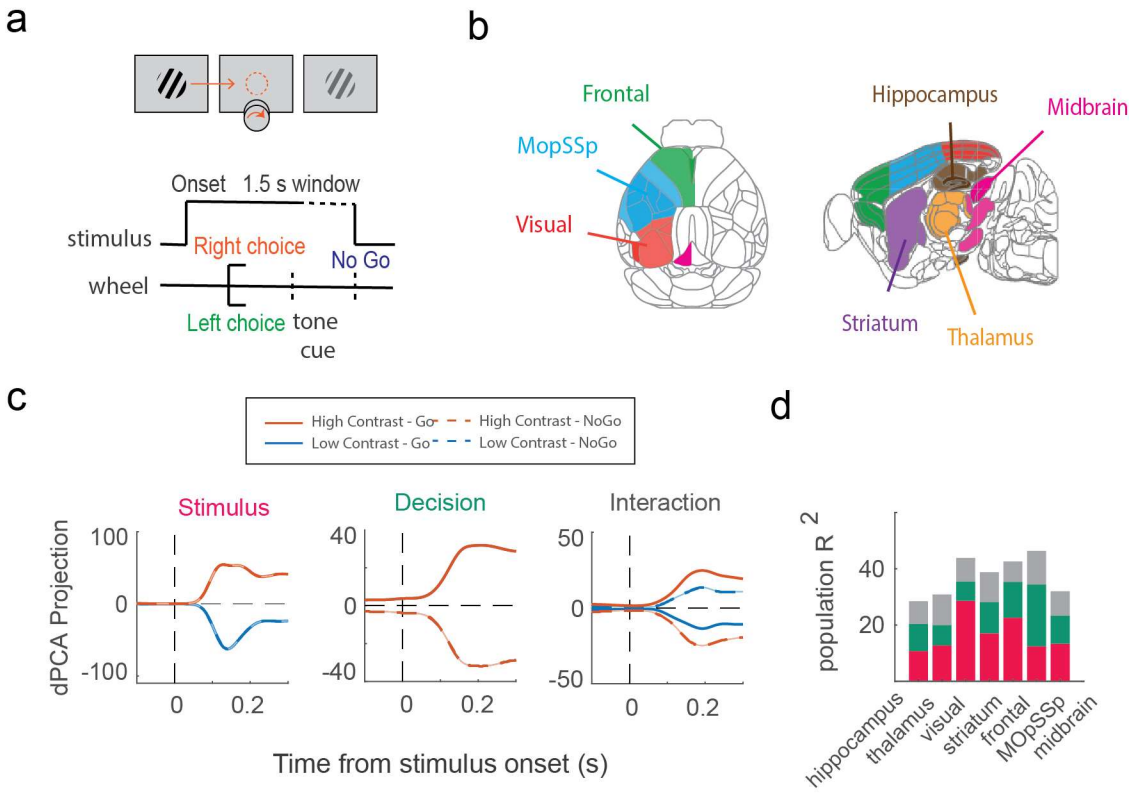


Figure 1 - Decomposing brain-wide electrophysiological data into the task-related components using dPCA. A) task protocol, B) grouping the brain-wide electrophysiological data into the seven regions according to the Allen CCF. C) projecting the population firing rate into the stimulus, decision, and interaction components. D) R-squared values of the reconstructed population neural activity using the task-related dPCA components.

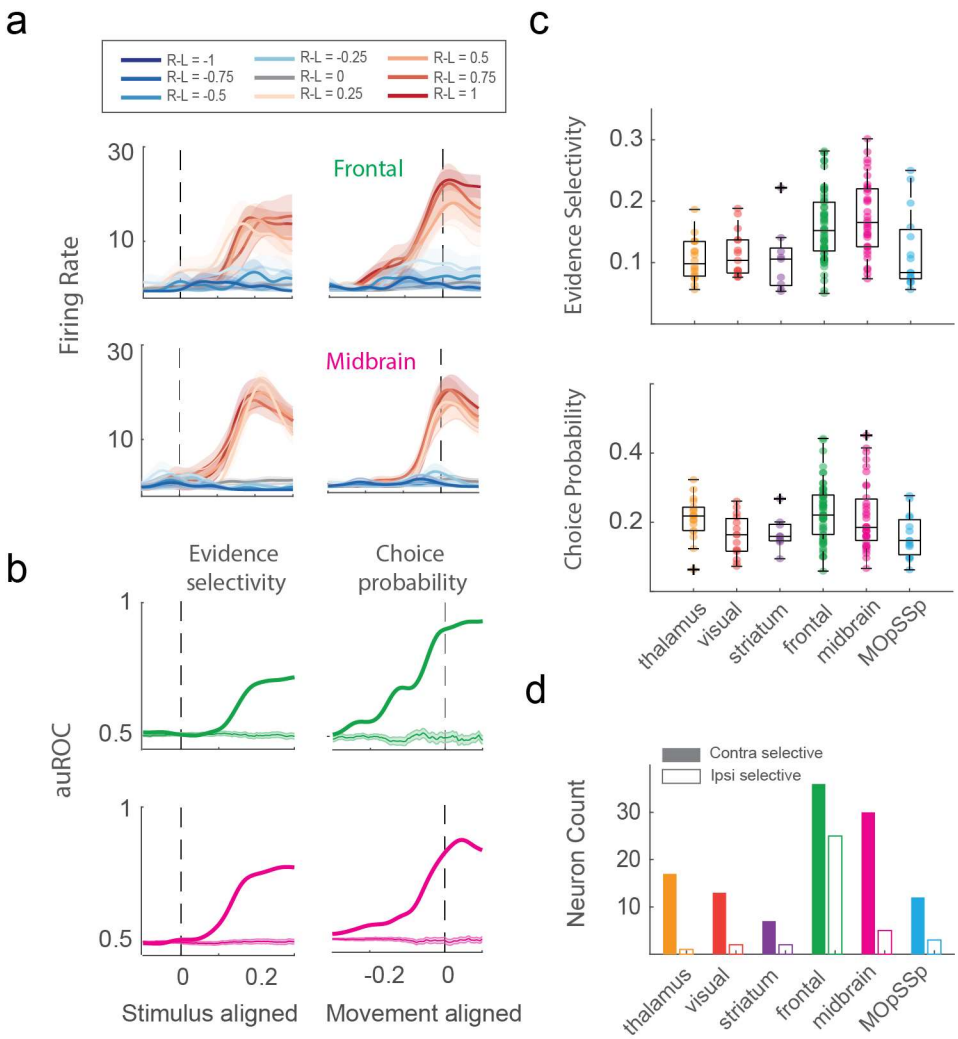


Figure 2 - DDM-like neurons across the mice's brain. A) Example neurons with DDM-like firing rate activity. The curves represent neurons' average firing rate activity across trials with a specific evidence level. The strength of the color indicates the strength of the evidence level. Shaded areas represent the confidence interval. B) Evidence selectivity and choice probability of the sample neurons across time in the frontal and midbrain region. C) maximum values of evidence selectivity and choice probability of the DDM-like neurons. D) the total number of DDM-like neurons within each group region. Filled and empty bars represent the number of neurons with contralateral and ipsilateral choice preferences, respectively.

Moreover, to determine whether or not a neuron significantly encoded choice and evidence, we measured decoding performance at the chance level by randomizing the trial labels (Figure 2 - B). The selective neurons were further visually inspected to exclude those without a ramping-like firing rate activity. The results revealed that the surviving selective neurons have DDM-like firing rate activity (Figure 2 - A, Supp-Figure 2 - A) distributed across the brain regions groups (Figure 2 – C & D, Supp-Figure 2 – B & C). Most

DDM-like neurons were found in the frontal (MOs, PL, ACA, ILA, and ORB) and midbrain (MRN, SNr, SCm, and SCs) regions. A lower percentage of these neurons were located in the striatum (CP and ACB) and visual pathway (VISam, VISI, and VISp), thalamus (VPL, VPM, LP, PO, LD), and MOpSSp (Supp-Figure 2 – B & C). Some of the discovered DDM-like sub-areas within the frontal, the striatum, and visual regions were consistent with the previous studies on the neural basis of evidence accumulation in rodents (Hanks et al., 2015; Scott et al., 2017; Yartsev et al., 2018). A single hemisphere contained neurons with both ipsilateral and contralateral choice preferences in most grouped regions (Figure 2 - D), consistent with the previous studies (Scott et al., 2017). The frontal region was mostly bilateral since the number of the ipsilateral and contralateral DDM-like neurons were similar. In contrast, other brain regions were mostly unilateral.

Multiple accumulation mechanisms across the brain

Previous studies on the neural mechanisms of evidence accumulation proposed different architectures for evidence integration (Bogacz et al., 2006). The drift-diffusion model (DDM) is the most commonly used approach, with one decision variable accumulating the difference between the two input streams. The decision is made when the accumulator reaches the top or the bottom decision boundaries. Race accumulator is the other popular accumulation mechanism with separate accumulators that independently integrate the evidence for each option. In this accumulation mechanism, an option is chosen when the integrator associated with that option reaches the decision boundary sooner than the others (Bogacz et al., 2006).

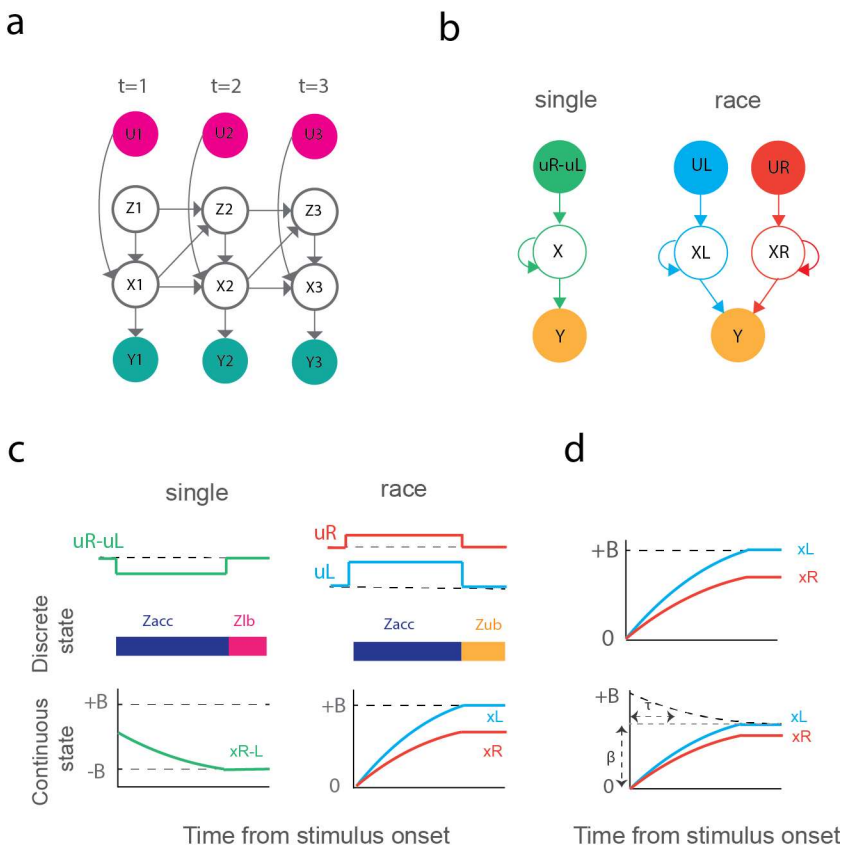


Figure 3 - The recurrent switching linear dynamical system (rSLDS) framework to model the single and race accumulation mechanisms. A) schematic of the rSLDS containing the hidden discrete variable Z, hidden continuous variable X, and observed variables U related to the stimulus strength and neuron spike data Y. B) single and race accumulator models implemented in rSLDS. C) discrete and continuous states of single and race accumulation mechanisms within sample trials. D) constant (top row) and collapsing (bottom row) decision boundaries. Collapsing boundary contains two parameters β and τ, for the boundary offset and the rate of exponential decay.

To investigate whether the DDM-like neurons across the mice brain integrate evidence through a single or race accumulation mechanism, we used a general framework for the accumulation modeling based on the recurrent switching linear dynamical system (rSLDS) (Zoltowski et al., 2020) (Figure 3). Using rSLDS, the high-dimensional population neural activity can be described as the dynamics of a few continuous latent variables in a low-dimensional state space, evolving through time according to state-dependent dynamic models (Figure 3 - A). The rSLDS was reformulated to implement the single and race accumulation mechanisms by considering the accumulators as the continuous latent variables of the model (Figure 3 – B & C) (Zoltowski et al., 2020).

We first generated subpopulations of neural activity by resampling the neurons within each region. Several bilateral (including neurons with contralateral and ipsilateral choice preference) and unilateral (including neurons with contralateral choice preference) subpopulations were generated during the resampling process (Figure 4 - E) (See Methods). We fit the single and race accumulators to the bilateral subpopulations since these subpopulations contain neurons with both contralateral and ipsilateral choice preferences. On the other hand, the unilateral subpopulations contain neurons with only contralateral choice preference, so we fit the single accumulator to them. The best initial parameters of the dynamic models and the optimal boundary type (Figure 3 - D) were selected through a greedy search approach (See Methods).

Since we only modeled the evidence accumulation phase of the decision-making process, we excluded the neural activity during the visual encoding phase from the accumulator modeling by estimating the accumulation latency using the auROC metric. The evolution of the single and race variables in sample trials is illustrated in Figure 4 – A. As shown in this figure, the discrete state switches to the wheel movement state when the continuous variables reach the decision boundary.

The best model for bilateral subpopulations was determined using the AIC differences between single and race models (Figure 4 - C) (See Methods). The results demonstrate that most regions contained single and race accumulator subpopulations (Figure 4 - F). However, the number of single accumulator preferences is higher than the race model in most areas which can be due to the single hemisphere neural recording. We have also computed the explained variance (R-squared) of the models in both bilateral and unilateral subpopulations (Figure 4 – D and Supp-Figure 3).

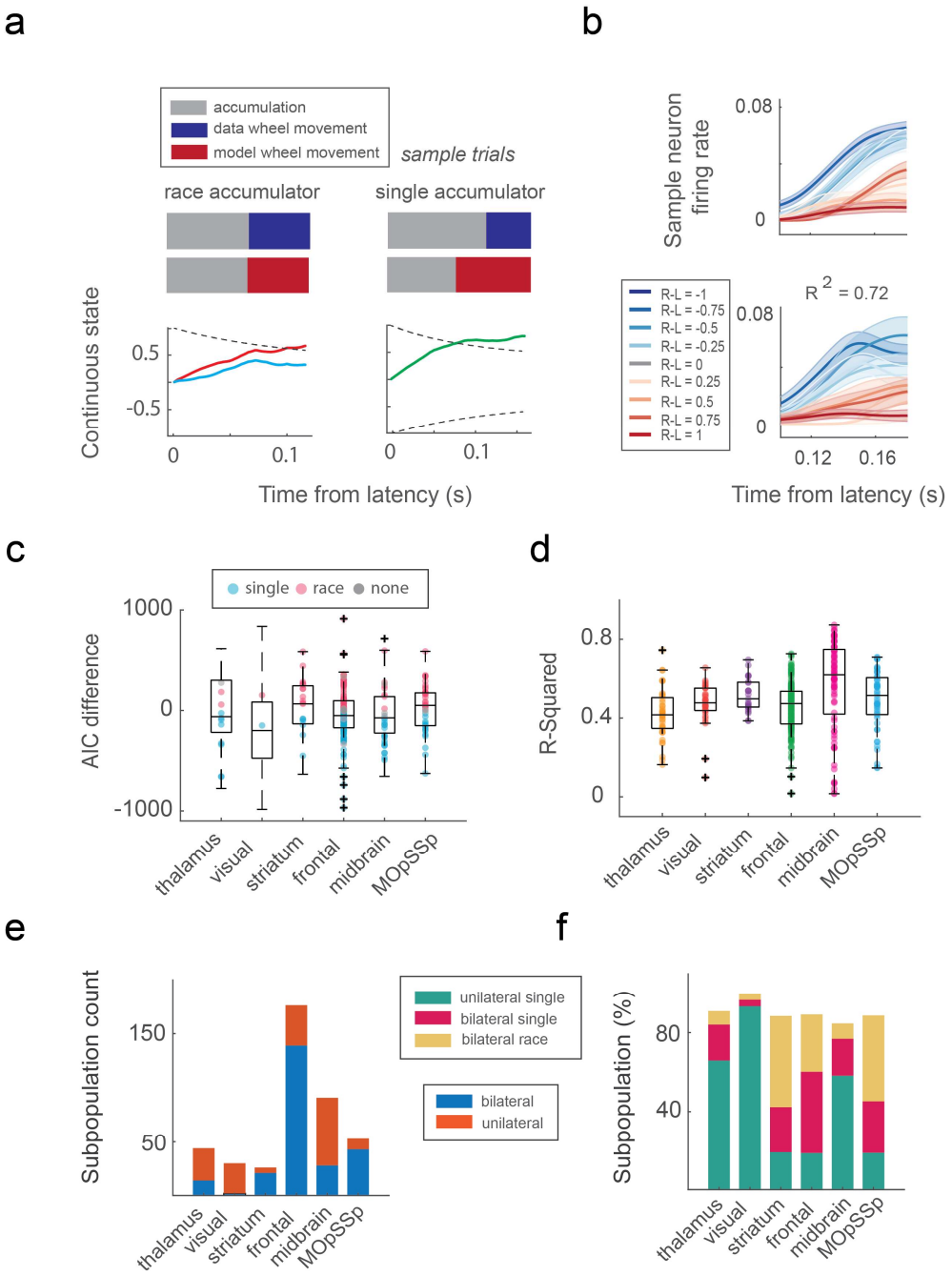


Figure 4 - Evaluation of the single and race accumulator models. A) continuous and discrete variables in the single and race models, the discrete state switches to the right choice state when the continuous variable reaches the collapsing boundary. B) The firing rate of the sample neuron and the fitted model. The explained variance (R-squared) between the data and model firing rate is depicted above the figure. C) model comparison using the AIC difference on bilateral subpopulations. D) explained variance (R-squared) values for each brain region's bilateral and unilateral subpopulations. R-squared values were computed between data and the best model selected using the AIC difference for the bilateral subpopulations. For the unilateral subpopulations, this metric was computed using the single accumulator. E) the number of bilateral and unilateral subpopulations within the brain regions. F) the percentage of bilateral and unilateral subpopulations preferring single and race accumulators.

Distributed evidence accumulation over multiple intrinsic timescales

The distributed coding of evidence accumulation across the brain suggests that the accumulation process is happening over multiple timescales, which can be organized hierarchically across the brain (Murray et al., 2014; Pinto et al., 2022). The ability of the brain to function in different timescales stems from the heterogeneity of local microcircuits and their long-range connectivity (Chaudhuri et al., 2015). Here, we examined whether DDM-like neurons across the brain had distinct intrinsic properties in terms of the timescale.

Accordingly, the intrinsic timescale of the neurons was estimated using the autocorrelation structure of the baseline neural activity (Murray et al., 2014), both at the single neuron and population levels within each brain region (Figure 5 - A). The estimated population-level intrinsic timescale displayed a hierarchical organization across the brain, starting from the visual to the MOpSSp in the cortical regions and the thalamus to the midbrain in the subcortical ones (Figure 5 - B), which is consistent with previous studies (Chaudhuri et al., 2015; Pinto et al., 2022). The resulting hierarchy demonstrates that thalamic and visual areas integrated the information in a shorter timescale than the midbrain and the MOpSSp regions.

Although the brain regions show a hierarchical organization in terms of their global intrinsic timescale, the neurons' timescales within each brain region show substantial heterogeneity (Figure 5 - C). Recent studies suggested that intrinsic timescales are predictive of neurons' functional roles within brain areas (Cavanagh et al., 2018; Cavanagh et al., 2016). Therefore, we next sought to investigate the relationship between the intrinsic properties of neural subpopulations and their functional role as evidence accumulators, i.e., the accumulation parameters.

We explored whether the diversity of DDM-like neurons' timescale within brain regions reflects differences in the local accumulation circuit. To address this hypothesis, we estimated the intrinsic timescale of neural subpopulations. Therefore, Pearson's correlation between the recurrent connection strength of the accumulators (Figure 3 - B) and the timescale of subpopulations was computed for the best accumulators that were chosen by the AIC model comparison (Figure 5 – D to F).

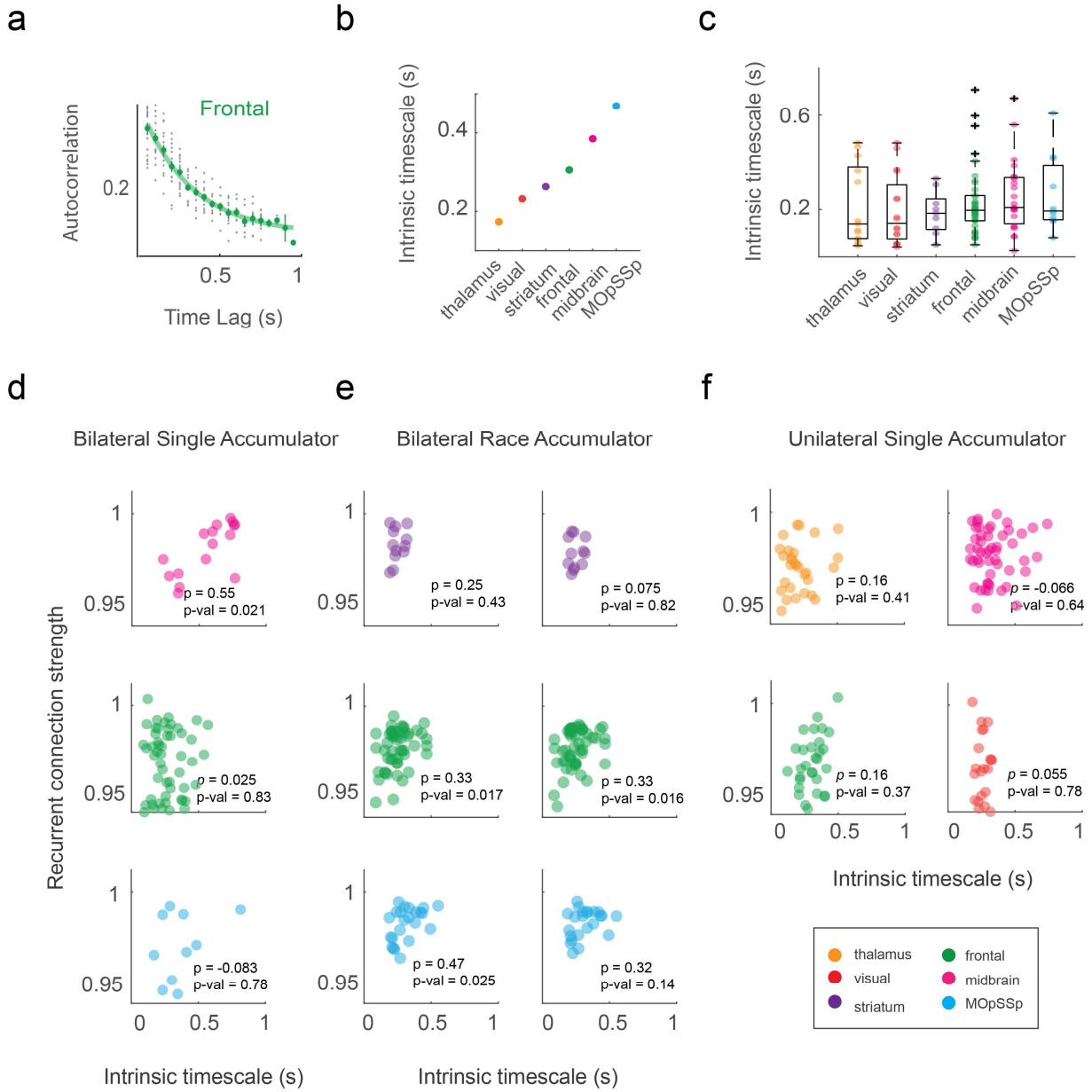


Figure 5 - relationships between the recurrent excitation connection and neuron's intrinsic timescale within each brain region. A) Estimating the timescale of sample neuron using the autocorrelation structure within baseline neural activity that follows an exponential decay. B) The hierarchy of overall intrinsic timescale across the brain areas. C) The timescale of single neurons within brain regions. Neurons having poor-fitting performance were excluded from this figure. D-F) Pearson's correlation between the recurrent connection strength and the intrinsic timescale. Panel D corresponds to the bilateral subpopulations with a single accumulator preference. Panel E corresponds to the bilateral subpopulations with race accumulator preference, first and second columns represent the right and left accumulator nodes, respectively. Panel F corresponds to the unilateral subpopulations. The areas with lower than ten samples within their single or race accumulator preferences were removed from this analysis.

Our results revealed a significant positive relationship between recurrent connection strength and the timescale of bilateral subpopulations preferring the single accumulator within the midbrain region ($p = 0.55$, p-value = 0.021) (Figure 5 - D). For the race accumulator preferences, we observed a significant correlation between the connection strength of the right accumulator and the intrinsic timescale within the frontal ($p = 0.33$, p-value = 0.017) and MOpSSp ($p = 0.47$, p-value = 0.025) regions. A similar relationship was observed for the left accumulator within the frontal region (p = 0.33, p-value = 0.016) (Figure 5 - E). However, we did not find any significant relationship between the recurrent connection strength of the single accumulator and the timescale within unilateral subpopulations.

The results support the hypothesis that the heterogeneity in the intrinsic neural timescale reflects the differences in the local accumulator circuits in some regions. Such that the subpopulations with the longer intrinsic timescale have stronger recurrent excitation connections in some of the regions, consistent with the previous studies (Cavanagh et al., 2020; Cavanagh et al., 2018; Chaudhuri et al., 2015; Murray et al., 2014; Soltani et al., 2021).

3- Discussion

Using brain-wide electrophysiological recording in mice (Steinmetz et al., 2019), we showed that evidence accumulation during perceptual decision-making is a distributed process across the brain. We found different cortical and subcortical areas, i.e., visual and frontal cortices, MOp, striatum, midbrain, and thalamus, contain neurons with Drift-Diffusion-Model-like (i.e., evidence-sensitive ramping firing rate) activity. We showed that these regions consist of subpopulations that accumulate evidence through both single and race accumulation mechanisms. We further characterized the DDM-like neurons by their intrinsic timescale. The brain regions containing these neurons showed different intrinsic timescales, which were organized hierarchically consistent with the anatomical hierarchy of these regions. In addition to the variability of timescales across the brain regions, there was a heterogeneity of intrinsic timescales within

each brain region. We showed that the observed diversity of timescales is linked to the accumulator circuit parameters, i.e., the strength of the recurrent connections, in a subset of brain regions. More specifically, the neurons with longer intrinsic timescale had stronger recurrent connectivity.

The identified brain regions in this study are consistent with and complement the existing findings on the neural substrates of evidence accumulation. Prior work has demonstrated the contribution of a subset of these areas i.e., PPC (Roitman & Shadlen, 2002; Shadlen & Newsome, 2001), FEF (Ding & Gold, 2012; Kim & Shadlen, 1999), striatum (Ding & Gold, 2010), superior colliculus (Horwitz & Newsome, 1999) and FOF (Hanks et al., 2015) in the evidence accumulation process.

The neurons with DDM-like firing rate activity across the brain could integrate the information through single or dual accumulation mechanisms (Bogacz et al., 2006). However, the dual accumulator needs the neural populations supporting each choice alternative. The brain regions we examined contain neurons with both contralateral and ipsilateral choice preferences in the left hemisphere, which were mostly observed in the frontal area. The bilateral behavior of the regions suggested the existence of the dual accumulation mechanism within a single hemisphere, consistent with the previous studies (Mante et al., 2013; Ratcliff et al., 2007; Wong et al., 2007). We tried to investigate whether DDM-like neurons in the brain were best represented using single or dual accumulators. Our results revealed that most areas contained mostly subpopulations with a single accumulation mechanism. This preference could be partly due to the dataset's scarcity of neurons with ipsilateral choice preferences. However, the number of dual accumulator preferences in the frontal and MOpSSp regions was relatively high.

We sought to address whether the distributed nature of evidence accumulation processes was related to how neurons in different brain regions represent information at different timescales. The estimated neuron's intrinsic timescale at the population level revealed hierarchical organization across the brain regions. According to this hierarchy, the intrinsic timescale increases from visual to MOpSSp in the cortical regions and from the thalamus to the midbrain in the subcortical ones, which is consistent with the previous studies

(Chaudhuri et al., 2015; Honey et al., 2012; Pinto et al., 2022). This hierarchical organization could be an essential component of the distributed evidence accumulation process across the brain (Pinto et al., 2022), which may be due to the variability in the level of recurrent excitation connections within areas (Chen et al., 2015; Gao et al., 2020), and their long-range connectivity profile (Chaudhuri et al., 2015). Our findings lend further support to previous claims that different brain areas in humans, primates, and rodents display a hierarchical organization in terms of their timescale (Demirtaş et al., 2019; Gao et al., 2020; Honey et al., 2012; Murray et al., 2014; Pinto et al., 2022; Rossi-Pool et al., 2021).

In addition to the variability of timescale across the brain, we observed heterogeneity of timescale within each brain region. This heterogeneity could arise from the variation in the local neurons' microcircuits. Thus, we investigated the relationship between the intrinsic timescale of neuron subpopulations and the parameters of the accumulator circuit they form. Our findings support the hypothesis that subpopulations with a longer intrinsic timescale had stronger recurrent connections in the frontal, MOpSSp, and midbrain regions. The results are in accordance with previous research that revealed the association between recurrent connection strength and the intrinsic neural timescale (Chaudhuri et al., 2015; Kim & Sejnowski, 2021; Zeraati et al., 2021).

In summary, we have investigated the neural correlate of evidence accumulation across the brain. We identified that DDM-like neurons are distributed across the brain, which can integrate the information through single or dual accumulation mechanisms. These neurons were characterized using distinct intrinsic and task-related timescales. We further revealed that the brain regions containing these neurons displayed hierarchical organizations in terms of two types of timescales which were highly similar. Our findings support the hypothesis that evidence accumulation is a distributed process over multiple timescales. We also found that each brain region contains DDM-like neurons with diverse timescales. Our results support the hypothesis that the observed heterogeneity of timescales could arise from the variations in accumulator circuits. So that longer timescale neurons had a stronger recurrent connection.

4- Materials and Methods

4-1 Behavioral task

We used a publicly available dataset published recently by (Steinmetz et al., 2019). The dataset comprises behavioral and physiological data from ten mice over 39 sessions on a two-alternative unforced choice task. Mice sit on a plastic apparatus with their forepaws on a rotating wheel, surrounded by three computer monitors. At each trial that was started by briefly holding the wheel, visual stimuli (Gabor patch with sigma 9 and 45° direction) with four grading levels were displayed on the right, left, both, or neither screen (Figure 1 - A). The stimulus was presented in the mouse's central monocular zones, and the animal did not need to move its head to perceive it.

Mice earned water by turning the wheel to move the stimulus with the highest contrast to the center of the screen or by not turning the wheel if neither stimulus was displayed. Otherwise, they received a white noise sound for one second to indicate an improper wheel movement. Therefore, three types of trial outcomes (right turn, left turn, and no turn) lead to reward. After the stimulus presentation, a random delay interval of 0.5–1.2s was considered, during which the mouse could freely turn the wheel without incentive. At the end of the interval, an auditory tone cue (8 kHz pure tone for 0.2s) was played, at which point the visual stimulus position became coupled with the wheel movement.

4-2 Neural recording

Recordings were made in the left hemisphere using the Neuropixel electrode arrays from approximately 30,000 neurons in 42 brain areas in 39 sessions. Using the Neuropixel probes with the ability to record from multiple brain regions produced data simultaneously recorded from several regions in each session. The neural activity of the regions was divided into seven main groups according to the Allen Common Coordinate Framework (CCF) atlas (Wang et al., 2020) (Figure 1 - B). We performed all the analyses on these groups of regions.

4-3 Single neuron decoding analysis

We performed the single neuron decoding using the standard receiver operating characteristic (auROC) analysis using the Mann–Whitney U statistic (Britten et al., 1996). We can measure the differences between spike count distributions of two conditions using this approach. According to the task design, the stimulus and choice encoding are highly correlated and cause the decoding analysis. To overcome this limitation, we used combined condition auROC analysis to compute stimulus selectivity, choice probability, detect probability, and evidence selectivity. The trials were then divided into different groups according to the task conditions, and the weighted average of the auROC values across conditions was considered the final decoding result. For this analysis, the neuron's spikes were binned at 0.005s and smoothed using a causal half-Gaussian kernel with a standard deviation of 0.02s. We also z-scored the firing rate of the neurons by subtracting the mean and dividing by the standard deviation calculated during the baseline period (-0.9s to -0.1s, stimulus aligned) across all trials.

4-3-1 Stimulus selectivity

We computed the contra stimulus selectivity using the combined condition auROC metric. Accordingly, the trials were divided into 12 groups based on the different choice alternatives (right, left, NoGo) and stimulus contrast levels (0, 0.25, 0.5, 1) presented on the left screen. We then applied the Mann–Whitney U statistic to measure the stimulus selectivity by comparing the spike counts of a neuron within the trials with the right stimulus higher than zero with the trials having the right stimulus equal to zero. The final stimulus selectivity was measured using the weighted average across 12 conditions.

4-3-2 Choice probability

Using the combined condition auROC statistic, we tested whether the neurons encode the choice. To compensate for the effect of the stimulus conditions, we divided the trials into 12 groups based on different

combinations of right and left stimulus contrast levels, ignoring equal contrast conditions. Within each condition, we used the Mann–Whitney U statistic to compare the spike count of the trials with right/left choice with another choice in a window ranging from -0.3s to 0.1s (aligned with wheel movement). A weighted average was then utilized to compute the final choice probability over different conditions. The absolute deviation of auROC from the chance level was considered as the choice selectivity: $CP = |auROC - 0.5|$.

4-3-3 Detect probability

We also measured how well the neural activity encodes whether or not the animal turned the wheel correctly and referred to this measurement as 'Detect probability' (Hashemi et al., 2018). Accordingly, the trials were divided into 12 groups based on the different combinations of the right and left stimulus contrast levels, excluding the conditions with equal contrast levels. We then measured whether the Hit (correctly turning the wheel) trials had greater neural activity than the Missed trials using the Mann–Whitney U statistic during the stimulus epoch (-0.1s to 0.3s). The level of selectivity for this measurement was calculated as the deviation of auROC from the chance level: $DP = auROC - 0.5$.

4-3-4 Evidence selectivity

We measured how a neuron can encode the evidence (difference of right and left stimulus contrast levels) and defined it as 'Evidence selectivity'. The trials were divided into nine groups according to the number of evidence levels (ranging from -1 to 1 with a step size of 0.25). We then tested to see whether the group of trials with the higher evidence level had greater neural activity than all those groups with lower evidence. Final evidence selectivity was calculated by taking the weighted average of auROC values across eight group comparisons. Absolute deviation of auROC from the chance level was considered as the measure of evidence selectivity: $ES = |auROC - 0.5|$.

4-3-5 Significant auROC selectivity

We also performed the auROC analysis on the shuffled trial labels to identify significantly selective neurons. We created the distribution of the auROC on the shuffled trials by repeating the shuffling process 100 times. The selectivity of a neuron at time *t* was considered significant if the value of the true auROC was outside the confidence interval of the shuffled auROC values. We restricted our analysis to the time points with at least two significant neighbors to correct the multiple comparisons.

4-4 Neuron latency

Evidence accumulation usually starts after a latency, mainly related to the visual encoding state (Roitman & Shadlen, 2002). In this study, we restricted the evidence accumulation analysis to the neural activity within the window starting at the end of latency until 50ms after wheel movement. We used auROC analysis to compute latency which appears like the time of significant change in neural activity compared with the baseline activity.

Accordingly, the spike counts of the Go trials having reaction times within the range (0.15s to 0.5s) were smoothed using a causal boxcar filter of size 100ms during (-0.5s to 0.5s) aligned to stimulus onset. We then computed the average firing rate across neurons within each trial, followed by the Mann–Whitney U statistic to compare the neural activity of trials within the stimulus (0s to 0.5s) and a point in the baseline (-0.1s) epochs. The significance level (p-value < 0.05) was employed to detect the samples with significant neural activity changes. We restricted our analysis to the significant points with at least two significant neighbors to correct for multiple comparisons. The latency was then selected as the first time point with significant changes in neural activity.

4-5 Demixed principal component analysis (dPCA)

Most neurons, especially in the higher cortical areas, encode different types of task information and display a mixed selectivity (Kobak et al., 2016). This complexity in response selectivity of the neurons can conceal their expressed information. To overcome this limitation, we exploited the advantage of demixed principal component analysis (dPCA) to decompose the population neural activity into a few latent components, each capturing a specific aspect of the task (Kobak et al., 2016). The resulting dPCA subspace captures most variation in the data and decouples different task-related components.

According to the dPCA analysis, we prepared a matrix $X_{N\times4\times2\times T}$ containing marginalized activity of N neurons over four stimulus contrast levels (1, 0.5, 0.25, 0) and two decision alternatives (Hit and Missed) during T time points within the stimulus epoch (-0.1s to 0.3s). We excluded the neurons having an average spike count lower than 1Hz during the reaction time boundary (from stimulus onset until wheel movement). We first divided trials into four groups to construct the matrix based on the contralateral stimulus contrast levels. Within each group, the average trial activity of each neuron was then computed based on whether or not the animal turned the wheel. The dPCA algorithm was applied to the neural population matrix to construct a latent subspace with 20 task-related principal components. The resulting components characterized the decision (X_{dt}), stimulus (X_{st}), stimulus-decision interaction (X_{sdt}), and condition-independent (X_t) information by estimating task-specific decoders F_α and encoders D_α using the following loss function (Kobak et al., 2016):

$$L_{dPCA} = \sum_{\alpha} \|X_\alpha - F_\alpha D_\alpha X\|^2 \quad , \qquad \alpha \in \{t, st, dt, sdt\} \tag{1}$$

We computed the stimulus and decision explained variances R_α^2 (R-squared) of the neurons by projecting the neural activity to the task-specific principal components using the decoder matrices D_α and reconstructing the neural activity with the decoder matrices F_α as follows:

$$\bar{X} = \frac{1}{4}\frac{1}{2}\frac{1}{T}\sum_{s=1}^{4}\sum_{d=1}^{2}\sum_{t=1}^{T} X_{sdt} \tag{2}$$

$$R_{\alpha}^{2} = 1 - \frac{\sum_{s=1}^{4}\sum_{d=1}^{2}\sum_{t=1}^{T}(F_{\alpha}D_{\alpha}X_{sdt} - X_{sdt})^{2}}{\sum_{s=1}^{4}\sum_{d=1}^{2}\sum_{t=1}^{T}(X_{sdt} - \bar{X})^{2}} \quad , \quad \alpha \in \{st,\ dt\}$$

We then separated the neurons into stimulus, decision, and interaction groups within each brain region using their task-related R-squared values (R_{st}^{2} , R_{dt}^{2}) and fuzzy C-means clustering algorithm (Bezdek, 2013). We excluded the neurons within the stimulus and interaction clusters from further analysis.

4-6 Intrinsic timescale

We measured the timescale of the neurons using the spike count autocorrelation of neural activity during the baseline period proposed by (Murray et al., 2014). Accordingly, we computed the Pearson's correlation of binned spike counts between each pair of time bins $i\Delta$ and $j\Delta$ ($j > i, \Delta = 0.05s$) across trials within the baseline period (-1s before stimulus onset). The resulting autocorrelation values follow an exponential decay which can be explained using the following equation (Murray et al., 2014):

$$R(k\Delta) = A \times (exp(-\frac{k\Delta}{\tau}) + B) \tag{3}$$

Where A is the amplitude, B indicates the contribution of timescales longer than the observation window, $k\Delta$ is the time lag, and τ denotes the timescale.

We fitted equation (3) to the average autocorrelation values of the neurons using the Levenberg-Marquardt method. The time lag with the greatest autocorrelation reduction was selected as the starting point for overcoming the negative adaptation (Murray et al., 2014). We tried five different initial parameter values to select the best model having the lowest mean square error (MSE) value.

4-7 Recurrent switching linear dynamical system (rSLDS)

We employed a general framework proposed by (Zoltowski et al., 2020) for modeling the evidence accumulation process. Different evidence accumulation models are formulated in this framework as a recurrent switching linear dynamical system (rSLDS). The rSLDS contains multiple discrete states $z_t \in \{1, \dots, K\}$ and each state is associated with specific linear dynamics (Figure 3 - A) as follows:

$$x_t \sim N(A^{z_t} x_{t-1} + V^{z_t} u_t + b^{z_t}, Q^{z_t}) \tag{4}$$

Where $x_t \in R^D$ is the continuous state, $u_t \in R^M$ represents input streams, $Q^{z_t} \in R^{D \times D}$ is the noise covariance matrix, and the matrices $A^{z_t} \in R^{D \times D}$ and $V^{z_t} \in R^{D \times M}$, and vector $b^{z_t} \in R^D$ denote the state-specific dynamic parameters. Transition probabilities between discrete states are parameterized as follows:

$$p(z_{t-1}, x_{t-1}) \propto exp\{\gamma(R_{z_{t-1}} x_{t-1} + r_{z_{t-1}})\} \tag{5}$$

Where $R_{z_{t-1}} \in R^{K \times D}$ and $r_{z_{t-1}} \in R^K$ parameterize the influence of the continuous state on the discrete state transitions. The parameter γ determines the sharpness of transition. The observed activity of data was modeled using the Poisson distribution of a generalized linear model as follows:

$$y_t \sim Poisson(f(Cx_t + d)\Delta_t) \tag{6}$$

where $C \epsilon R^{D \times N}$ and $d \epsilon R^D$ is the linear mapping parameters, $f(x) = log(1 + exp\,(x))$ is the Softplus function, and Δ_t denotes the size of time bins.

Zoltowski et al., 2020 introduced a variational Laplace-EM algorithm to estimate the model parameters. Briefly, the posterior over the discrete and continuous states were calculated using variational and Laplace approximations. The model parameters were also updated by sampling from the discrete and continuous posteriors followed by an Expectation-Maximization (EM) approach (Zoltowski et al., 2020).

4-7-1 Single accumulator

A single accumulator model, which is commonly referred to as the drift-diffusion model (DDM), is described with a single decision variable that accumulates the differences in the input streams (Bogacz et al., 2006). This accumulation mechanism has two decision boundaries, one for each choice alternative. When the decision variable reaches one of the boundaries, the decision is made.

To reformulate the rSLDS framework to a single accumulator, we considered three discrete states for the accumulation ($z_t = acc$) phase, right wheel movement ($z_t = rwm$), and left wheel movement ($z_t = lwm$) (Figure 3 - C). During the evidence accumulation state, the one-dimensional continuous variable $x_t \in R^1$ accumulates the differences between right and left input streams $u_t \in R^1$. The state transition was also parameterized such that when the continuous variable x_t reaches one of the decision boundaries (±B), the discrete state switches from the accumulation state ($z_t = acc$) to the right wheel movement ($z_t = rwm$) or left wheel movement ($z_t = lwm$) states. Therefore, the transition parameters were set as follows:

$$R_{z_{t-1}} = \begin{bmatrix} 0 \\ 1 \\ -1 \end{bmatrix}, \qquad r_{z_{t-1}} = \begin{bmatrix} 0 \\ -B \\ -B \end{bmatrix}, \qquad \gamma = 1 \ , \ B = 1 \tag{7}$$

According to the settings, by increasing the value of x_t toward B, the probability of transition from the $z_t = acc$ to $z_t = rwm$ increases. On the other hand, decreasing the value of x_t toward -B, increases the probability of transition to $z_t = lwm$ (Zoltowski et al., 2020).

In equation (4), the term $A \in R$, denotes the recurrent connection strength, and the term $V \in R$ determines the weight of the received input stream (Figure 3 - B). We excluded the term $b \in R$ from our analysis. In the accumulation state ($z_t = acc$), we only trained the term A^{acc} and the noise Q^{acc}, and set the term V^{acc} constant. In the other states ($z_t = rwm, lwm$), we just trained the noise variance Q and considered $A^{rwm} = A^{lwm} = 1$ and $V^{rwm} = V^{lwm} = 0$. We tried different initial values for the parameters $A^{acc} \in \{0.95, 1\}$, $V^{acc} \in \{0.004, 0.008, 0.01, 0.02, 0.03, 0.04, 0.05\}, Q \in \{0.005, 0.01\}$ to select the best combination of parameters that produced maximum log-likelihood.

4-7-2 Race accumulator

A race accumulator model contains a decision boundary and two independent integrators for the input streams supporting each choice alternative. In this accumulation mechanism, a decision is made favoring the integrator that reaches the decision boundary sooner (Bogacz et al., 2006).

To reformulate the rSLDS into a Race accumulator mechanism, we considered a two-dimensional continuous variable $x_t \in R^2$ for two accumulators. Each of these variables accumulated the right/left input streams $u_t \in R^2$. We set the parameters of the dynamic model $(A_{acc}, V_{acc}, Q_{acc})$ to be diagonal such that the decision variables integrate the input streams independently. Similar to the single accumulator, we considered three discrete states for the accumulation ($z_t = acc$) phase, right wheel movement ($z_t = rwm$), and left wheel movement ($z_t = lwm$) (Figure 3 - C).

We also set the transition parameters such that the probability of switching from the accumulation state to one of the wheel movement states increases by approaching x_t to decision boundary B. Accordingly, the transition parameters were set as follows:

$$R_{z_{t-1}} = \begin{bmatrix} 0 & 0 \\ 1 & 0 \\ 0 & 1 \end{bmatrix}, \qquad r_{z_{t-1}} = \begin{bmatrix} 0 \\ -B \\ -B \end{bmatrix}, \qquad \gamma = 1 \ , \ B = 1 \tag{8}$$

In equation (4), diagonal matrix $A \in R^2$ determines the excitatory connection strength for two accumulators, and diagonal matrix $V \in R^2$ denotes the weight of the received input stream for each accumulator variable (Figure 3 - B). Similar to the single accumulator mechanism, we excluded term b from our analysis. In the accumulation state ($z_t = acc$), we only trained matrices A^{acc} and noise Q^{acc}, and set matrix V^{acc} constant. In the other states ($z_t = rwm, lwm$), we just trained the noise covariance matrix Q and considered $A^{rwm} = A^{lwm} = I$ and $V^{rwm} = V^{lwm} = [0\ 0\ \ 0\ 0\ ]$. We tried different initial values for the diagonal parameters $A^{acc} \in \{0.95, 1\}, V^{acc} \in \{0.004, 0.008, 0.01, 0.02, 0.03\}, Q \in \{0.005, 0.01\}$ to select the best combinations of parameters that produced maximum log-likelihood.

4-7-3 Collapsing boundary

In the accumulators with the collapsing boundary, less evidence is required to reach the boundary as time passes so that the boundaries collapse toward the center (Figure 3 - D). This mechanism is much like the urgency signal, magnifying the evidence as time passes (Ratcliff et al., 2016). Besides the constant decision boundaries, we also evaluated the collapsing boundary in single and race accumulators.

In the rSLDS framework, we can reformulate equation (*5*) to implement the linear collapsing boundary for a single accumulator as follows (Zoltowski et al., 2020):

$$p(z_{t-1}, x_{t-1}) \propto exp\{\gamma(R_{z_{t-1}} x_{t-1} + r_{z_{t-1}} + W\,\bar{u}_t)\}, \quad W = \begin{bmatrix} 0 & 0 \\ 0 & \beta \\ 0 & \beta \end{bmatrix}, \qquad \bar{u}_t = \begin{bmatrix} u_t \\ t \end{bmatrix} \tag{9}$$

Where $W\,\bar{u}_t$ is the linear function of time points *t* and vector $\bar{u}_t$ contains the input streams and the current time. This equation describes a linear collapsing boundary with the rate of β. We need to add another column to the matrix V in equation (4) and set it to zero with this new formulation. We further modified equation (*9*) to formulate a nonlinear collapsing boundary for a single accumulator as follows:

$$\begin{aligned} &p(z_{t-1}, x_{t-1}) \propto exp\,\{\gamma(Rx_{t-1} + r + Wf(\bar{u}_t))\} \\ &f(t) = \beta + (1-\beta) \times \exp\left(\frac{-t}{\tau}\right) \\ &W = \begin{bmatrix} 0 & 0 \\ 0 & -B \\ 0 & -B \end{bmatrix}, \qquad R = \begin{bmatrix} 0 \\ 1 \\ -1 \end{bmatrix}, \qquad r = \begin{bmatrix} 0 \\ 0 \\ 0 \end{bmatrix}, \qquad \bar{u}_t = \begin{bmatrix} u_t \\ t \end{bmatrix} \end{aligned} \tag{10}$$

Where β denotes the boundary offset and τ describes the decay rate of the exponential function. We can control the collapsing rate with these two parameters (Figure 3 - D). To implement the collapsing boundary for the race accumulator, we set the parameters of the transition model as follows:

$$W = \begin{bmatrix} 0 & 0 & 0 \\ 0 & 0 & -B \\ 0 & 0 & -B \end{bmatrix}, \qquad R = \begin{bmatrix} 0 & 0 \\ 1 & 0 \\ 0 & 1 \end{bmatrix}, \qquad r = \begin{bmatrix} 0 \\ 0 \\ 0 \end{bmatrix}, \qquad \bar{u}_t = \begin{bmatrix} u_t \\ t \end{bmatrix} \tag{11}$$

Similar to the previous model fitting processes, we tried different initial values for $\beta \in \{0.3, 0.4, 0.5\}$ and $\tau \in \{50, 100\}$ in addition to the dynamic parameters.

4-7-4 Model goodness of fit

4-7-4-1 Akaike Information Criterion (AIC)

We compared the model fitting to the data using the Akaike Information Criterion (AIC) goodness of fit, which is defined as follows (Anderson & Burnham, 2004):

$$AIC = 2k - 2E_{\theta|y_t}[\log p(y_t|x_t, z_t, \theta)] \tag{12}$$

Where k is the number of free parameters in the model and the expectation term $E_{\theta|y_t}$ can be estimated by sampling the fitted model 100 times as follows:

$$E_{\theta|y_t}[\log(y_t|x_t, z_t, \theta)] = \frac{1}{s}\sum_{s=1}^{100} \log p(y_t|x_t, z_t, \theta^s) \tag{13}$$

Where θ^s denotes sampling of the model using trained parameters. AIC measurement contains a penalty term for the number of parameters which is a correction for how much the model with k parameters will increase the log-likelihood.

4-7-4-2 R-Squared

We also measured how well a model can explain the data using the R-Squared explained variance. Accordingly, we simulated the spike counts from each model 100 times for each trial. The firing rate of the real and simulated spike counts of subpopulations was computed using a causal boxcar filter of size 50ms, and the average firing rate of trials within each evidence level (Right contrast level-Left contrast level) was computed. We then used the R-Squared explained variance metric on the subpopulations as follows (Latimer et al., 2015):

$$R^2 = 1 - \frac{\sum_{e\in S_e}\sum_{t\in S_t}\left(f_{ne}(t) - f_{me}(t)\right)^2}{\sum_{e\in S_e}\sum_{t\in S_t}\left(f_{ne}(t) - \overline{f_{ne}}\right)^2} \tag{14}$$

$$\overline{f_{ne}} = \frac{1}{9}\frac{1}{T}\sum_{e\in S_e}\sum_{t\in S_t} f_{ne}(t)$$

Where e is the evidence level from the set of evidence S_e, terms f_{ne} and f_{me} represent the average firing rate of the data and simulated spike counts across the trials with evidence level *e,* respectively. Set S_t denotes the time points within the window from the latency until the median reaction time of the session. The Term $\underline{f_{ne}}$ is the average firing rate of the data over all time points and coherence levels. $R^2 = 1$ demonstrates that the model firing rate perfectly matches the data, and lower values correspond to the worst fit.

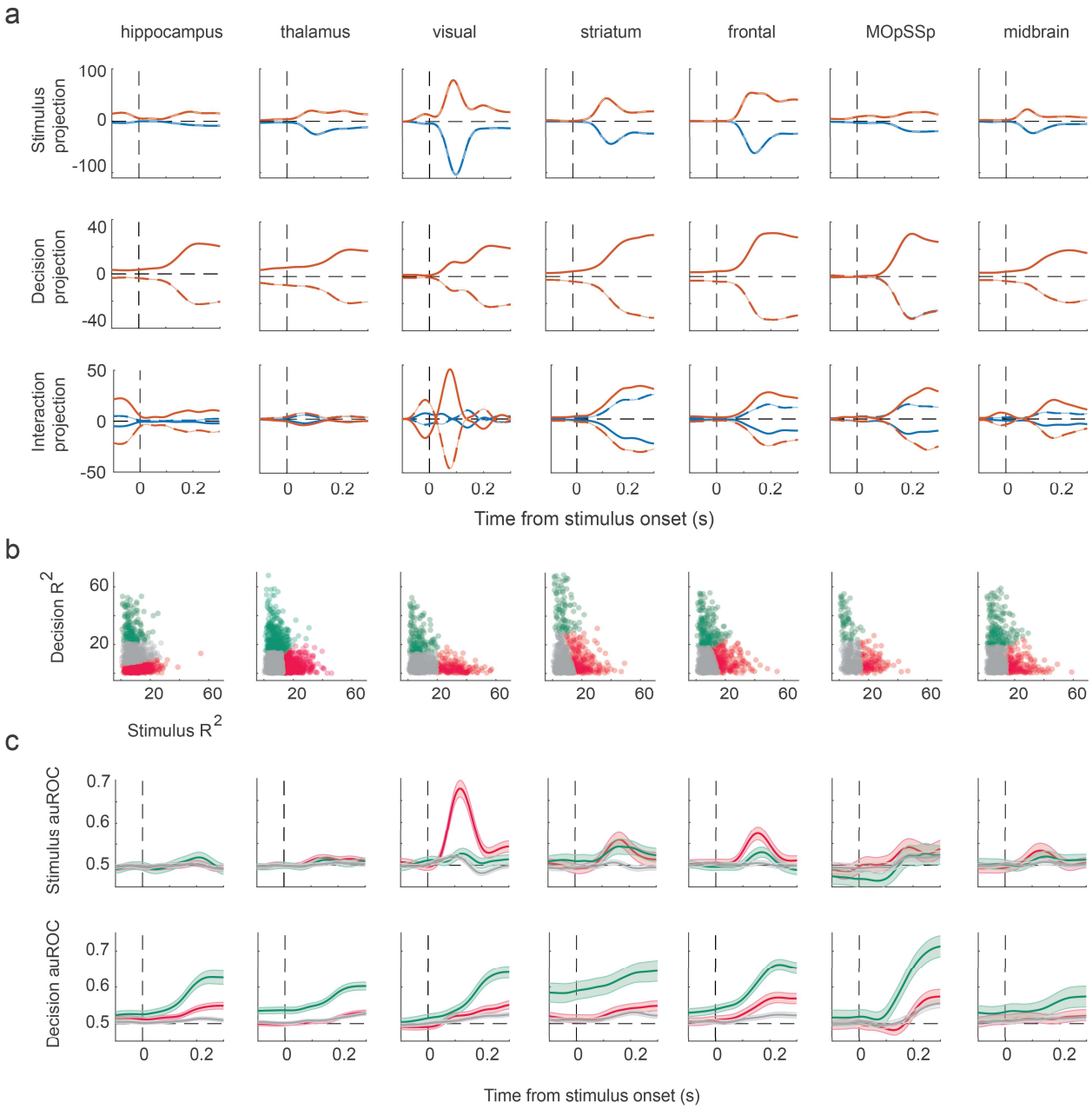
4-7-5 Model comparison

The preferred accumulator type among the single and race accumulators is selected using the AIC differences calculated between pairs of models (Figure 4 - C). We set the threshold value of ±10 to choose the preferred model, which provides strong support for one model over others (Anderson & Burnham, 2004). The preferred model is the one with an AIC difference lower than -10 (or higher than 10) (Figure 4 - C).

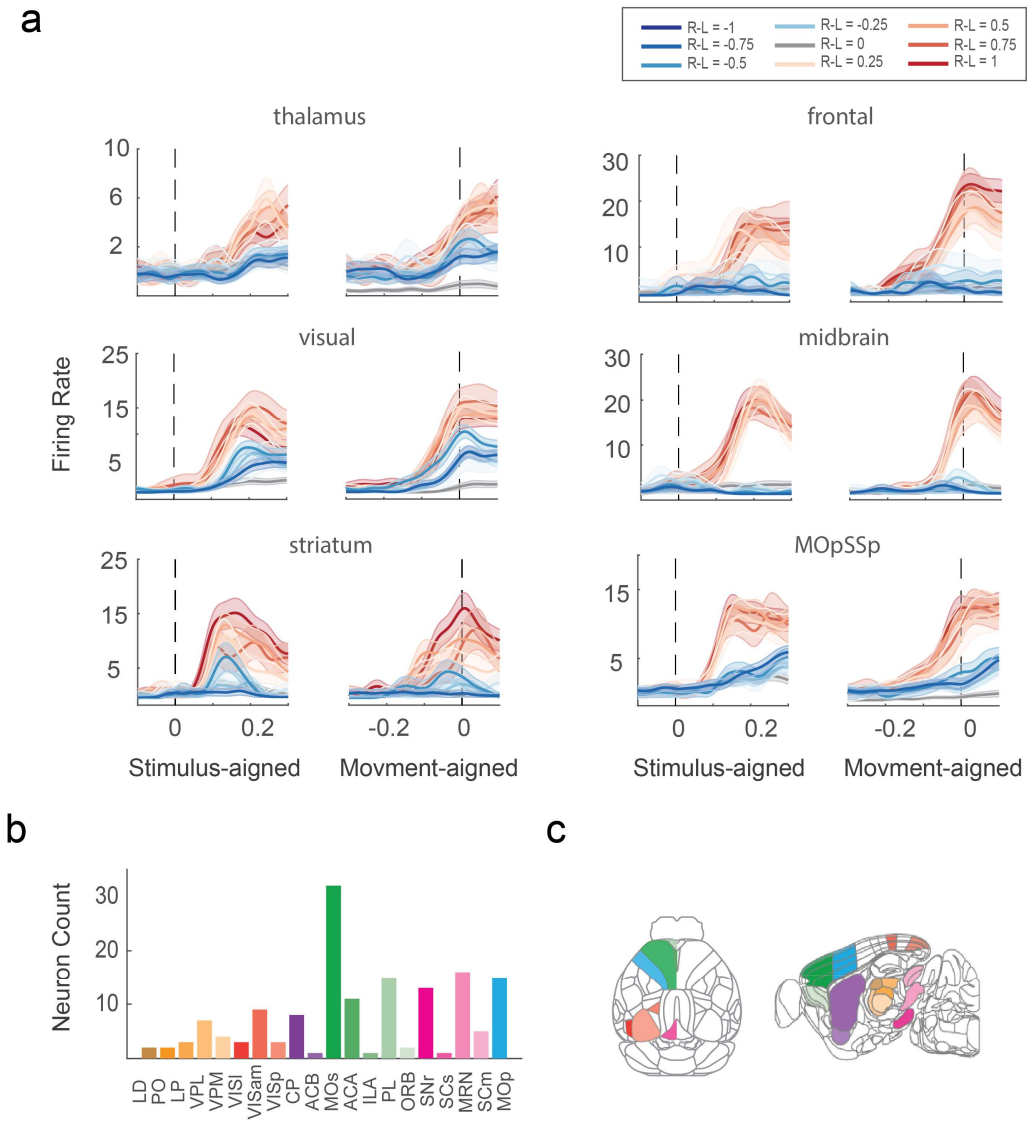
4-8 Data processing

All analyses were carried out using customized MATLAB and Python code. Statistical analyses and fuzzy C-means clustering were performed using MATLAB toolboxes. Decomposing neural activity into different task-related variables was carried out using the open-source dPCA toolbox (Kobak et al., 2016). The accumulator analysis was performed using the recurrent switching linear dynamical system (rSLDS) toolbox (Zoltowski et al., 2020), which was customized by the authors.

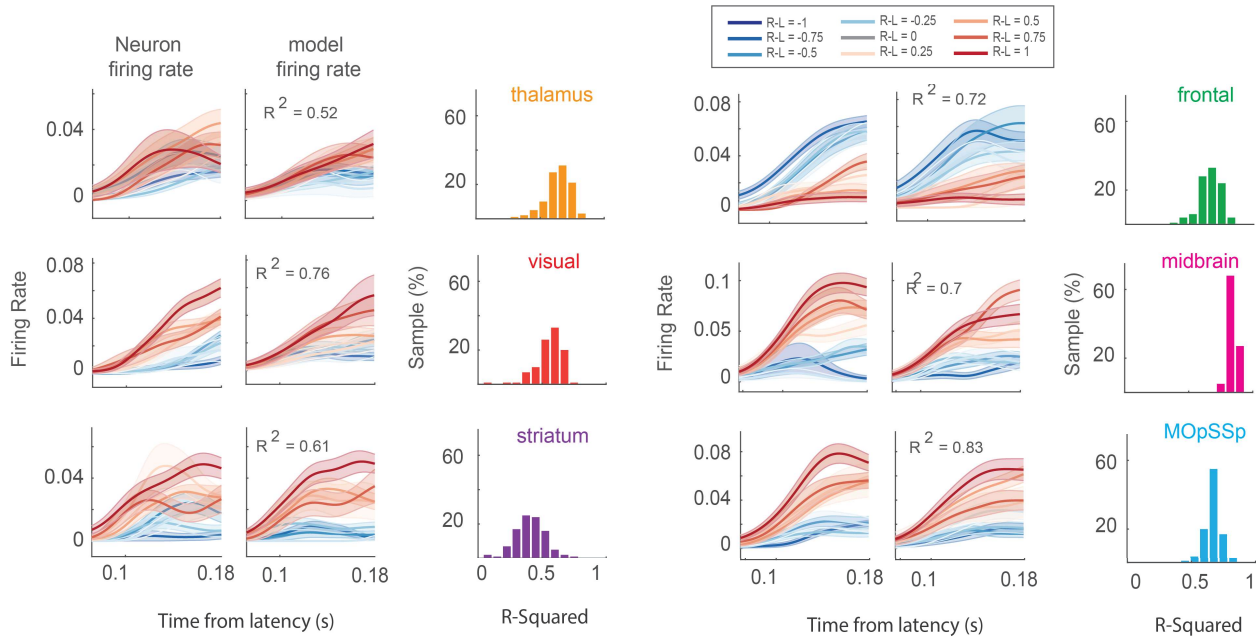
4- Supplemental information



Supp-Figure 1 - Separating neurons into the decision-selective and the stimulus-selective neurons. A) projection of the population neural activity into the task-related components. B) clustering the neurons based on their stimulus-related and decision-related R-squared values. C) performance of the stimulus and decision decoding using each group of neurons (stimulus, decision, and interaction).



Supp-Figure 2 - Distribution of DDM-like neurons across the brain. A) sample DDM-like neurons. The curves represent the average firing rate activity of the neuron across trials with a specific evidence level. The strength of the color indicates the strength of the evidence level. Shaded areas represent the confidence interval. B) the number of DDM-like neurons across different brain areas. C) distribution of DDM-like across the brain



Supp-Figure 3 - Results of the accumulator fitting. Data and model firing rate of sample neurons and their corresponding explained variance (R-Squared) value. The distribution of R-squared values for each neuron was generated by sampling the accumulator model 100 times. The curves represent the average firing rate activity of the neuron across trials with a specific evidence level. The strength of the color indicates the strength of the evidence level. Shaded areas represent the confidence interval.

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E.I., S.R., Ah.H., and M.M.G. performed conceptualization. E.I. and M.M.G. curated the data. E.I. performed the analyses. E.I., Ah.H., M.M.G. contributed to the methodology. E.I., S.R., Al.H., Ah.H., H.P., and M.M.G. wrote the paper. H.P., Ah.H., and M.M.G. supervised the project.

Competing interests

The authors declare no competing interests.