Encoding the Past, Present, and Future of Self-motion in the Rat Posterior Parietal Cortex

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Abstract

Navigation is critical among different species such as rodents, monkeys, and humans because the brain is capable of taking in information of directional actions and projects into a distributed spatial navigational network. Parietal cortex neurons, which are a part of the network, are able to map our location on a route based on directional actions (linear and angular speeds). By taking into account the current LS and AS, some parietal cortex neurons can determine what direction the rat was going at that time, as well as the rat's location along the route. Additionally, rather than only reflecting the rats' behavior at the present time, neurons in the parietal cortex can encode information across a short period of time referred to as an integration window. To explore how the integration window could potentially change when the rat was trained on a complex setting which replicate the real world environment, we examined the self-motion tuning in the parietal cortex of rats when they performed a Triple-T spatial working memory task. The parietal cortex neurons are tuned to angular and/or linear speeds. Many self-motion sensitive neurons in the parietal cortex are able to integrate information through a longer temporal window on the given task. Thus some neurons are able to encode the past, present, and future of self-motion in the rat posterior parietal cortex.

Introduction

Navigation is a critical cognitive ability for almost any species. It requires spatial cognition in the form of awareness of location and orientation of oneself relative to the environment. Furthermore, the available pathways through an environment are constrained by obstacles and/or are dictated by pathways such as roads.

The hippocampus (HPC), entorhinal cortex (EC), and anterior thalamus have been proposed to encode location and orientation. The posterior parietal cortex (PPC) has been proposed to encode both self-motion (linear and angular velocity) and route position.

The Hippocampus and the Place Cells

In 1976, John O'Keefe discovered that place cells in the HPC of an animal can specifically fire for a certain location of the animal in an environment. The firing activity of a place cell will not change even in specific conditions such as: the platform where the animal is located on within a room is rotated, or the light is off during the experiment (O'Keefe, 1976). The specific location where the neuron shows a maximal firing activity or tuning is called a "place field." Different place cells have different firing activity and different place fields. The place field of a single place cell will change if the environment is changed. For example, if the rat is moved from one room to another room, the original place field which the neuron was tuned to will change to another location. The finding of place cells in the HPC supported the proposed theory of a "cognitive map" and spatial mapping in the brain. The "cognitive map" was originally proposed by Edward Tolman in 1951. Tolman stated that the way rats or humans navigate through different environments was related to the spatial map in the brain being used as an internal system guiding our behavior when navigating through the external environment (Tolman, 1951).

The Head Direction Cells

Another type of cell that contributes to the idea of spatial mapping are the head direction cells. The head direction cells were first discovered by James B. Ranck Jr in the postsubiculum, (the output region of the HPC) which encodes the animal's head direction, irrespective of the animal's location, behavior, and their trunk position (Taube, J. S. el al., 1990). Later on, the head direction cells were also found in several other brain regions including the medial entorhinal cortex (MEC), the anterior thalamus, and the retrosplenial cortex (RSC) (Fyhn et al., 2004, Hafting et al., 2005, JS Taube, 1995, Cho, J., 2001).

The Entorhinal Cortex

In addition to the HPC, the EC also contributes to the “cognitive map”. In the medial entorhinal cortex (MEC), information on position, direction, and self-motion integrates together as revealed by a grid pattern (Fyhn et al., 2004, Hafting et al., 2005). Each grid cell has multiple firing fields that together are able to form a special grid pattern; with each firing field having equal distance to another. Some grid and head direction cells in the MEC show overlapping firing activity; specifically, certain grid cells are also tuned to certain head directions, and they both are modulated by the animal's speed (Sargolini, F., 2006).

There is another type of cell in the MEC that interacts with the grid and head direction cells: the border cells. The border cells have firing fields along the edge of walls (Solstad, T. 2008). The firing field of the border cells is also maintained and will stretch along with the edge of the wall if it were to be stretched. Unlike the place cell, the firing field of the border cell will not change its location if the environment is changed (Solstad, T. 2008). Thus, the border cell could serve as a reference to the external environment and integrate the information from place cells, head direction cells, and the grid cells together to form the cognitive map in the brain.

The Parietal Cortex

The parietal cortex is another region involved in spatial navigation. The neurons in the PPC have action correlates to the animal’s locomotion (left turn, right turn, or straight motion). It was first discovered by McNaughton, B. L., et al., (1994). The evidence in their study demonstrated that action correlates can be modulated by different spatial contexts or the internal body representation of self motion through the space (McNaughton, B. L., et al., 1994). Nitz, D.A., (2006) found a different pattern of the firing activity in the PPC neurons observed through an experiment. The firing activity of the PPC neurons is related to how the route is ordered, not taking into account the place or direction of the animal relative to its environment. Before diving into these “route” cells, there are few ways I will define a route. It can be simply defined by the overall shape of the route. A route can also be defined as a series of set locations or a series of direction actions along the route. The firing activity of these PPC neurons, or “route” cells, is aligned with the shape and the space defined by the route. That is, there is a population of neurons that seem to be encoding the shape of the route itself (Nitz, D.A., 2006).

Frames of Reference

When referring to the firing activity of the above-mentioned types of neurons, there are several frames of reference generally used by neuroscientists: the abstract frame of reference such as the “egocentric” frame of reference, and arbitrary frame of reference, which includes “allocentric,” “object-centered” , and “route-centered” frames of reference. In the “egocentric” frame of reference, we usually process the stimulus relative to our own body such as the retina, hands, or the trunk. The term “allocentric” refers to anything else other than self. The “object-centered” frame of reference is usually used to describe parts of the object relative to its whole. When we refer to an object or one’s location relative to the route, we use the “route-centered” frame of reference. In general, neurons in the HPC take an allocentric frame of reference. That means that the firing activity of the HPC neurons is more sensitive to where in the environment an animal is rather than what the self is doing.

PPC is positioned anatomically to regions of the brain with neural responses in both egocentric frames of reference (Mohan et al., 2018) and allocentric frames of reference (Whitlock, J. R., et al., 2018; LaChance, P. A. et al., 2022; Sugar, J., et al., 2011). PPC is also known to integrate information over time (Whitlock, Jonathan R., et al. 2011; Alexander, A. S., et al., 2022). PPC neurons have shown to be action-correlated in some studies in which they encode specific self-motion (left or right turns) or acceleration at present and up to 500ms in advance (Chen et al., 1994; Whitlock et al., 2012). Additionally, PPC neurons have been proposed to integrate past, present, and future of an animal's self-motion for up to 2 seconds in the past and 2 seconds in the future in unstructured environments (Alexander et al., 2022). The PPC neurons are able to respond to more complicated tasks by encoding self-motion of the rat for a longer period of time.

Integration of Self-Motion

In the most recent study on PPC neurons, Alexander et al. (2022) found that neurons in the PPC can encode the past, present, and future of self-motion within a certain temporal window. The setting of the study has two conditions. The first condition is free foraging. The data was collected when the animal was freely running in an open arena in search of rewards. In another condition (i.e. pursuit condition), the data was collected when the animal was chasing a laser pointer. The laser always followed a certain shape so the rat could learn through training.

Results show that under both conditions, certain PPC neurons are tuned to encode the rats' past route behavior. For instance, if the rat made a left turn up to 2 seconds in the past, the tuned PPC neuron would encode that information. Other specialized PPC neurons will encode information if, for example, the rat would make a right turn in the next 2 seconds. Assuming that the rat is currently running straight, specialized PPC neurons will fire for the route in present time, however the above mentioned PPC neurons will fire for the past and future respectively at the same time. This means that these three types of PPC neurons work together to encode for the whole time frame for past, present, and future of self-motion. In addition, the time frame is larger under the laser-light chasing condition when the animal was trained to follow a certain shape.

The setting for the experiment done by Alexander et al. (2022) was an open arena, but this provides an insight into the route-specific firing activity of the PPC neurons. A possible explanation is that all the neurons together encode route positions from past to future. Knowing this, a neuron will not fire for all right or left turns because the past or future of the turning action is different even within one route.

Therefore, the purpose of this research is to seek the explanation regarding the route-specific firing activity of neurons in the PPC. Our world is well-structured, the path we walk everyday is formed by barriers and obstacles. We are able to navigate through this complex environment and memorize the whole structure with little to no difficulty. Therefore, in this study we used a well-structured environment - a Triple-T maze to assess the similarity and difference of neural firing activity when the animal performed spatial working memory tasks with different environmental contexts. In addition, we will also be looking at the integration window when the PPC neuron encodes the past, present, and future of the rat's self-motion under this condition. We hypothesize that the integration window will be larger than when the animal was trained on the unstructured environment, which means that the PPC neurons are able to integrate more information over a longer time when the animal was trained on a well-designed maze. Therefore studying PPC in this environment, and analyzing these data in this way should reveal interesting results with regard to frames of reference and integration of self-motion from past to the near future.

Results

Rats performed a spatial working memory task on a Triple-T maze

5 rats were trained to perform a spatial working memory task on a "Triple-T" maze (Figure 1). In each trail, the rat is trained to navigate through 1 of 4 internal paths to collect its reward at the reward site. Along the internal paths, there are 3 sequential turning points that the rat could freely choose to either turn left or right. The rewards at the reward sites were 1/4 cheerios each. The rat was required to complete a find-all-four task before the reward sites got reset by researchers. After collecting the reward, the rat could freely choose either one of the two external paths that surrounded the internal paths to return back to the starting point.

This task would require the rat to remember for longer durations of time where they have been and where they plan to go. Through the training, the rats were able to navigate the maze with high speeds going in one direction.

The whole experiment consisted of 67 recording sessions. In order to better understand the neuron firing activity regarding rats behavior on the maze, we selected the behavioral data where the rat was on internal paths (from start point to the reward site) or external paths (from reward sites back to the starting point).

Rats displayed high proficiency on the spatial working memory task as they are able to navigate through the maze without any stop or hesitation in the middle of the track. Rats Also regularly display perfect blocks (Figure 2, median perfect blocks percentage = 0.5625, IQR = 0.4534 – 0.6799). This demonstrates that they were able to create a sense of the structure of the maze as well as the history and future plan of their actions.

The firing activity of some parietal cortex is modulated by the sequence of actions

Based on the finding from Alexander et al. (2022), the firing activity of some populations of parietal cortex neurons can be modulated by the sequence of actions. That is, the neuron not only responds to the rat's current behavior, but also reflects its past or future behavior. We assessed if the finding from Alexander et al. (2022) is also applicable to the Triple-T task.

First we looked at the rate map of each neuron, which shows how each neuron responded to the rat's behavior when it navigated on the Triple-T task (Figure 3, left). Additionally, for each neuron we also plotted linearized activity for each path (Figure 3, right).

Based on the rate map and linearized rate map of each neuron, we found expected firing activity of each neuron regarding the rat's actions (linear and angular speeds). The firing fields of PPC neurons are not consistent or stereotyped to certain actions, such as firing strongly for turning L or turning R or firing strongly for running straight. We observed that some neurons exhibited high firing rate for some left/right turning actions but not every single turning L or turning R.

Self-motion tuning curve of PPC neurons

Self-motion tuning curves were made for each PPC neuron recorded. In order to assess the neuron firing activity when the animals performed the spatial working memory task, we recorded 5 rats using in vivo electrophysiology when the animals performed the task on the maze. 236 neurons were recorded from the posterior parietal cortex (n = 5 rats, n = 67 extracellular recording sessions). We calculated the linear and angular velocity tuning curves for all PPC neurons (n = 236 cells).

Each recorded neuron in the parietal cortex displayed slightly different tunings to linear and/or angular speeds. Some neurons that are tuned to high linear speed also displayed tuning to low angular speed as the rat was running straight with high speed on the maze. Neurons that are tuned to high angular speed also display tuning to medium to low linear speed. (Figure 4, n = 236 cells).

PPC neurons display heterogeneous tunings to angular velocity

In order to understand the tuning of linear and angular speeds among the neuron population in the parietal cortex, we sorted 236 cells by their maximum firing rate in responding to angular and linear speed. The angular speed tuning curves of all neurons were sorted from the farthest left turn action to the farthest right turn action. The population of linear speed tuning curves were sorted from 0 to 60 cm/s (Figure 4).

Based on the population tuning curve, the feature of the population linear speed tuning curve is similar to the graph from Alexander et al. (2022). These graphs demonstrate that one parietal neuron is usually tuned to a certain linear speed. Additionally, within the population, those neurons together can reflect rats' linear speed from lowest to highest.

However, the population angular speed tuning curve is different from what Alexander et al. (2022) proposed in their study. The population of PPC neurons displays an unexpected heterogeneous firing activity to self-motion. Remarkably, while performing the triple-T task, many individual PPC neurons encoded angular velocity for turning L and for turning R.

By comparing the tuning curve and linearized activity profile for each neuron, we noticed a discrepancy between the tuning of the neurons and where in space they fired on the Triple-T maze. This result aligned with the finding from Alexander et al. (2022), which indicated that PPC neurons are able to integrate self-motion across time. Therefore, instead of only assessing PPC neurons' firing activity based on present behavior, we also considered the past and future behavior of the animals and its impact on the neural firing activity of the PPC.

The PPC neuron maintains a relatively consistent tuning across seconds

In order to test the temporal integrative properties, we followed the method Alexander et al. (2022) used in their paper by shifting the spike train relative to the fixed angular and linear velocity. This shifted tuning curve would reveal if the neurons were preferentially tuned to self-motion that occurred in the past or future.

If the spike train is shifted retrospectively, or back in time with a better tuning, it would suggest that the neuron is tuned to the rat’s past (retrospective) behavior. If the neuron displays a better tuning when the spike train is shifted forward relative to the fixed angular or linear speeds, it suggests that the neuron is tuned to the rat’s anticipatory behavior.

In the study done by Alexander et al. (2022), they shifted the spike train 2 s backward and forward. However, in our study we shifted the spike-train for 15 seconds into the past and 15 seconds into the future. The reason we choose 15 seconds in particular is because it takes a rat about 8-10 seconds to run a traversal. With a 15 seconds shifted spike train, we are able to cover more than one traversal in order to cover the entire route. After generating time-lagged tuning curves for all neurons (n = 236), we found that some neurons surprisingly maintained a relatively consistent tuning across seconds with history and future dependent firing (Figure 7. Linear speed: mean = 4.35 seconds; Angular speed: mean = 3.69 seconds).

Dbscan

After we generated time-lagged tuning curves, we noticed that the tuning was consistent across seconds. Therefore, we assessed the temporal window of the tuning of linear and angular speed by using Dbscan in order to understand the temporal relationship between neural firing activity and behavior.

What we found was that most neurons displayed more than one consistent tuning cluster from dbscan results (n = 171/236 for AV time-lagged tuning; n = 202/236 for LV time-lagged tuning). In addition, among neurons who displayed more than one tuning cluster, the range and the time-lag of the peak of the central peak cluster was calculated for each neuron that met the criteria (Figure 5). AV: n = 63/171, mean time-lag of the central peak = -0.48s, std = 1.62s; median = +0.3s, IQR = -1.57 – +0.62). Based on the results from dbscan, preferred latencies for angular speed are slightly skewed retrospectively, reflecting the past behavior of the animal. The temporal window of integration is longer than Alexander at el. (2022) found in the study (dbscan: mean = 5s).

With the limitations of dbscan, we did not find significant results for linear speed and its relationship with neural firing activities.

Self-motion decoding is accurate for extended temporal window in a well-structured environment

Building upon what we found previously, the evidence for the path integration was established by decoding the neural spiking activity and making a prediction on the animal's speed. We used a neural decoding toolbox (Meyers, 2013; http://www.readout.info/), which takes the spike train of a neuron and uses an algorithm to predict the animals' speed. The output is the accuracy of the prediction.

In order to test the decoder accuracy when the spike train is shifted relative to the linear and angular speeds, we shifted the spike train of each neuron 15s into the past and 15s into the future and decoded self-motion. If the decoding accuracy increased when we shifted the spike train backwards, this implicated that the neural firing rate was more correlated with past behavior. If the decoding accuracy increased when we shifted the spike train forwards, the neural firing rate was more correlated with the future behavior (Alexander et al., 2022).

First, we tested the validity of the decoding toolbox on the linear speed decoding accuracy as well as the distribution of preferred latency regarding the linear speed. The reason we tested this is that due to the computer capacity and capability, the computer was not able to handle the heavy workload of using the decoding toolbox to predict the rat's angular speed. Therefore, we used half of the recording data to test the preferred latency on angular speeds. By testing the validity, the decoding toolbox can predict the rat's linear and angular speeds (Figure XX, Rho = 0.273 with even higher correlation value near the time-lag 0). This is significant based on the bootstrapping results.

The results show that neurons over the course of a few seconds are responding to linear and angular speed in a reliable way. The integration window was assessed by calculating the half-width of the central peak of all neurons (n = 236 cells, LV: mean = 4.08s, std = 1.37s, AV: mean = 4.44s, std = 1.44s).

The decoding accuracy curve from our study shows an expanded integration window and more peaks (Figure 9). The integration window is longer than the pursuit condition from Alexander et al. (2022). This indicates that in a complex environment, the integration window is longer when the rat performs a complex task. Additionally, there are more peaks in the decoding accuracy curve when rats perform a Triple-T task (Figure 9). In order to make sense of these results, we need to acknowledge that the tuning can be as complicated as it can be, as long as it can be predictable.

In addition, the preferred latency of linear speed tuned neurons showed tight distribution compared to angular speed tuned neurons (Figure 8). These parietal neurons displayed a larger range of the preferred latency than the data from Alexander et al. (2022).

Discussion

In reality, rats and humans often move through space along a line or pathway in a well structured environment. We developed a task that puts the rat in this context. In our experiment, we used a triple-T maze with embedded complex pathways and we had a working memory task for the rats. We demonstrated (1) the action tuning of PPC neurons to linear and/or angular speeds, (2) a path integration across time, and (3) a longer temporal integrative window in the parietal cortex.

Through long history of studying the parietal cortex, neurons in the PPC displayed action-correlated tuning and route-specific firing activity (Chen et al., 1994; Whitlock et al., 2012; Wilber et al., 2014; Wilber et al., 2017; Nitz, 2006, Nitz, 2012). Consistent with some studies from the past, some populations of the PPC neurons were tuned to linear and/or angular speeds in the Triple-T task (Whitlock et al., 2012; Alexander et al., 2022). When we looked at the firing activity of PPC neurons to angular speeds, we found that many individual PPC neurons surprisingly encoded angular velocity for turning left and right when the rat performed the triple-T task. By looking at the population tuning curves of linear speeds, we found that each neuron is tuned to one specific linear speed, which is consistent with the finding from previous study (Whitlock et al., 2012; Alexander et al., 2022). This tuning to two different turning behaviors adds to our understanding of the role PPC plays in motor planning by suggesting that more generalized forms of egocentric motion are being encoded upstream of the more specific types of egocentric coding seen in supplemental motor cortex (Olson & Johnson et al. (2021), and motor cortex (Pruszynski et al., 2007).

In addition, the significance of path integration is it could potentially help us understand how a system that is very sensitive to angular and linear speeds can end up with route-specific activity. Some neurons in the parietal cortex are not only sensitive to left/right turns but the position of that left/right turn. This means that serious of actions may be important. In other words, positions in a route can change the action tuning of the PPC neurons because the parietal cortex is able to map locations in a route (Nitz, 2006; Alexander et al., 2022).

In the parietal cortex, we also found that those neurons can integrate the past, present, and future of self-motion, which has been proposed from the past (Alexander et al., 2022). We followed the same method Alexander et al., (2022) used in their paper and found evidence that supports self-motion integration. The distribution of the preferred latencies for linear speed is narrower compared to the angular speed. Both displayed bias to retrospective tuning, which supports the finding of Alexander et al., (2022) and contrasts to some previous findings of primarily anticipatory responses in the parietal cortex (Moor et al., 2017; Whitlock et al., 2012). Additionally, based on the distribution of preferred latencies which define the integration window, it is broader than the previous reports (Alexander et al., 2022). The integration window of each PPC neuron is also assessed. From the previous study, the extended integration window of self-motion was observed during pursuit conditions because the linear and angular speeds were maintained for longer temporal duration (Alexander et al., 2022). Evidence for longer self-motion integration in even more complex tasks (triple-T task) supports the idea that the tuning of PPC neurons could potentially adapt to new tasks or more complex environments when the spatial working memory task is heavier.

Conclusion

In conclusion, there is a path integration in the parietal cortex across time in a well-structured space. The structured environment appears to support the parietal cortex encodes of actions across a long period of time. It also aids the ability of the PPC to integrate information across a longer time window. Parietal cortex is capable of integrating trajectories across fairly long time periods (many seconds) in a way that contributes to the performance of this complex triple-T task.

Limitations of the study

There are some limitations in this study. First, there is no direct comparison between triple-T task and free foraging, which then could not provide any in-depth evidence or support on adaptation of self-motion tuning in the parietal cortex. Future study could consider recording the firing activity of the same parietal neuron when the rat was performed on both structured maze and open platform. In addition, with the limited capacity of my computer, we have to cut the recording into first and second half in order to use the neural decoding toolbox.

Although we have not done this in the current study, a future direction could address how the integration window can change for neurons in the parietal cortex. Another possibility for the future would be to investigate what kinds of network connectivity is required for some neurons that reflect the past, present and future of self-motion.

Methods

The following data is from Olson & Johnson et al. (2021). The methods for generating and analyzing tuning curves are based on Olson & Johnson et al. (2021) and Alexander et al. (2022).

Subjects

The subjects for this study include 5 rats. The data was previously recorded with implanted microdrives targeting the PPC dorsal and dorsal-CA1 region of each rat's brain. The rats had dietary restrictions to maintain 85 - 95% of their normal weight for motivation purposes.

Apparatus

Triple-T maze

The triple-T maze is a custom built platform by graduate students in Professor Nitz's lab, which is made of black plastics with a thin sheet layer on top acting as tracks. The overall dimension of the environment (recording room) is 4m x 6m. The maze is 20cm off the ground. The outer bounds of the maze is 2cm so the rat can see the room which contains distal visual cues.

Working memory task

The task is to navigate through internal tracks of the maze to the food rewarded points. In this experiment, there are four rewarded sites located at another long edge of the maze. The reward is manually delivered by the experimenter in every block. The rat is trained to start at the middle of the long edge of the maze. At the center of each "T", the animal is able to freely make a choice of turning right or left. Therefore, with different options of turning right or left, the difference between each path are the action sequence as well as the location and shape of the path itself. The spatial working memory task is relatively simple. By beginning at the starting points, the rat is required to navigate through the internal paths to the reward site without turning back in the middle. The rat would receive rewards when re-visiting a rewarded site only after collecting all other rewards.

After collecting the reward, the animal can freely choose to turn right or left in order to return back to the starting point.

Surgery

Each rat has 4-12 tetrodes implanted inside them, made with 17μm polyimide-insulated nickel-chromium. Those tetrodes are twisted and stored in a custom built microdrive placed on each rat's skull. The surgery was performed when the rat was under isoflurane anesthesia.

Neural and Behavioral Recordings

After surgery recovery, the rat was trained again for one week on the maze with the same tasks as before the surgery and recording. The data used for analyses are all from well-trained rats.

Neural recording

Each microdrive is connected to an amplifier through electrical interface boards. Signals are amplified (50x) and filtered through a high pass filter (>150 Hz). The signal is then processed by the Plexon SortClient software, filtered at 0.45 - 9k Hz, and amplified 1-15x in addition to the 50x amplified signal. The Plexton OfflineSorter software is then used to discriminate single neurons from waveforms. After identifying single neurons from groups of cells and removing artifacts, the data will then be processed by MATLAB for further analysis.

Behavioral recording

LED lights (red and blue) were attached to the center of the animal's head on the microdrive. During the recording, the lighting of the environment is dim. The camera, which is hung up on the ceiling 2.6m above the floor, can then capture the animal's position as well as the relative orientation of its head to its trunk. The light was captured at 60 Hz. The angular linear velocity and the animal’s head direction are calculated based on the angle between the two lights. The angle is 0° when the animal is facing the “room north” direction.

Histology

After completing all recordings, the rats were perfused under deep anesthesia. Brains were dissected and sliced into thin layers. Nissl stains were applied to the brain slide in order to reveal the accurate location of each electrode.

Analyses

Behavior assessment

Each recording session was around 45 minutes. The data of the animal's behavior was captured by camera and sent to the computer as a digital video tracking profile. All the labeling for the recording sessions as well as discrimination of different routes were done on MATLAB. The data was then processed by several pre-programmed MATLAB functions: the behavior scoring helps identify and label the beginning and the end of each route; the ratemapper generates the neural spike train as well as the animal's angular, linear velocity and head direction. In this study, all data is from Olson & Johnson et al. (2021).

Construction of self-motion tuning curves

The self-motion tuning curve was constructed for every recorded neuron according to Olson & Johnson et al. (2021) and Alexander et al. (2022). For each recording session, the linear velocity is discretized into 29 bins ranging from 0 to 50 cm/s. The angular velocity is discretized into 32 bins ranging from -30 to 30 degree/sec. The data used here is cropped so only the portion of the recording when the animal is physically on the route will be analyzed. Next, we computed 1000 tuning curves of linear and angular velocities. The minimum occupation time at each bin was identified. We then randomly sub-sampled all possible neuron spiking activities at each binned speed to match the minimum occupation time minus 1 second (so there will be variability when sampling the data). All tuning curves are calculated as the mean of 1000 sub-sampled tuning curves. The null tuning curve for each neuron was then calculated by the following method: the spike train was randomly shifted 100 times relative to the fixed behavior (linear and angular velocity). Tuning curves were calculated for each of the 100, then the mean of those values were obtained for the null tuning curve.

Then we bootstrapped the tuning curves for each neuron by comparing the null tuning curve with the original tuning curve in order to assess if the neuron firing activity is significant. A neuron tuning curve is significant only if the value of each bin on the tuning curve outside the range of the threshold range (mean +/- 3 standard deviations of the 100 null tuning curves for one neuron)

Construction of shifted self-motion tuning curves

In order to understand the firing activity of PPC neurons, we also generated shifted self-motion tuning curves of linear and angular velocities for each neuron. Instead of only computed tuning curves at the present time (at 0 lag), we shifted the spike train from -15s to 15s in 100ms increments relative to a fixed behavior in order to assess the temporal relationships between neural spiking activity and its behavior. When we shifted the spike train backward relative to the behavior, it reflected the animals past behavior (history-dependent) because the spiking activity occurred after the behavior. When we shifted the spike train forward relative to behavior, it reflected the animals future behavior (anticipatory) because the spiking activity occurred before the behavior.

Identifying the central peak of each shifted self-motion tuning curve

In each shifted self-motion tuning curve graph, the peak and valley bin was identified as greater or lesser than 99th percentile of the distribution of the reliability score. All percentile tasks were done by comparing the real tuning curve with the randomized (null) tuning curve described above. The central peak was defined as a group of bins marked as 1 and the central valley was marked as -1. Then the data was processed by ‘dbscan’ (MATLAB function) to identify each central peak or valley.

Decoding of self-motion

Decoding of self-motion for each neuron was conducted using smCorrDecoder, an implementation of the NDT (Neural Decoding Toolbox) maximum correlation coefficient classifier by Alexander et al. (2022) from the Neural Decoding Toolbox (Meyers, 2013; http://www.readout.info/). The temporal resolution of spike train and behavior were matched (60Hz) for all given neurons (n = 236). The spike train of each neuron was smoothed using a Gaussian filter with a 200 ms standard deviation. Then the spike train was separated into 50% training and 50% testing blocks. The training block of the spike train and corresponding behavior vector was used by the smCorrDecoder to train the classifier. The classifier learned the mean population vector of the training block as a template. The testing block was then tested by the classifier. When the classifier was tested, the correlation coefficient value was assessed between the testing block and templates of each class (speed). The largest correlation coefficient value returned as an output along with the predicted behavior.

Decoding of self-motion with the shifted spike train

To understand the temporal relationship between behavior and neural firing activity, we also conducted analyses on decoding of self-motion with the shifted spike train for each neuron according to Alexander et al. (2022). Instead of shifting the spike train from -2 s to +2 s in 100ms increments (Alexander et al. (2022)), the spike train was shifted from -15 s to +15 s in 100ms increments (301 bins in total) relative to the fixed behavior (linear and angular velocity).

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Figures

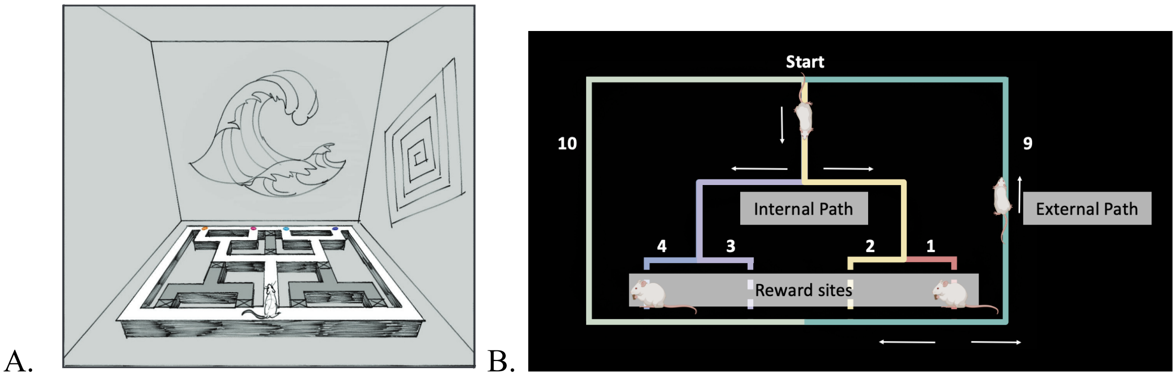

Figure 1. A (Olson & Johnson et al. (2021). B. An illustration of the triple-T maze and the spatial working memory task.

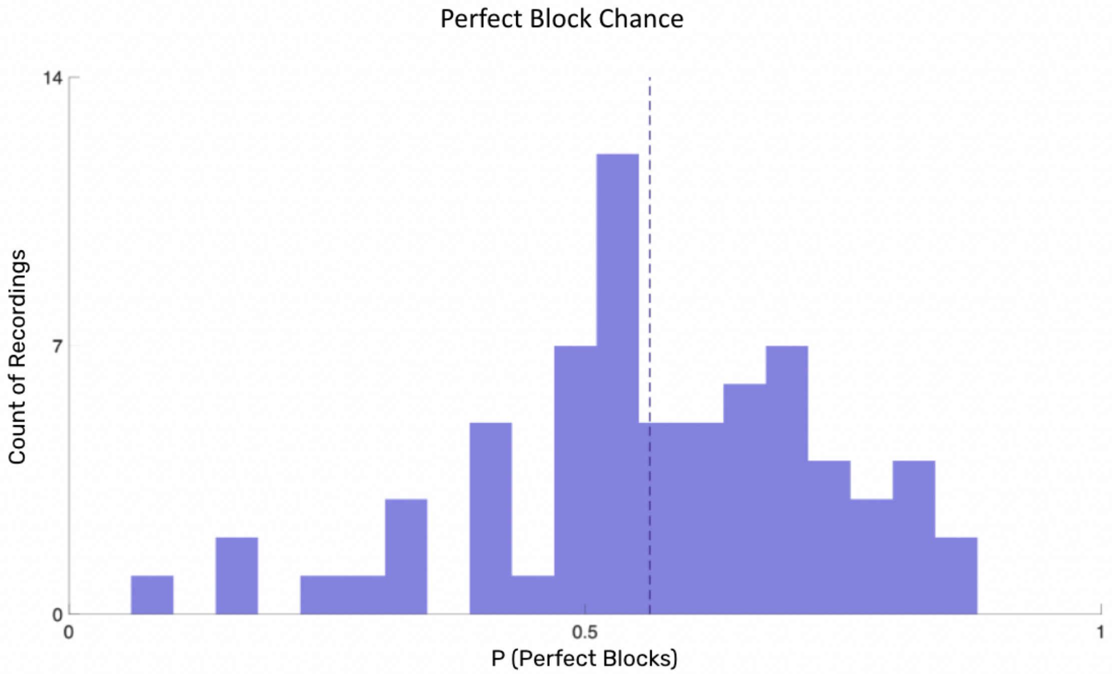

Figure 2. Distribution of the perfect block chance.

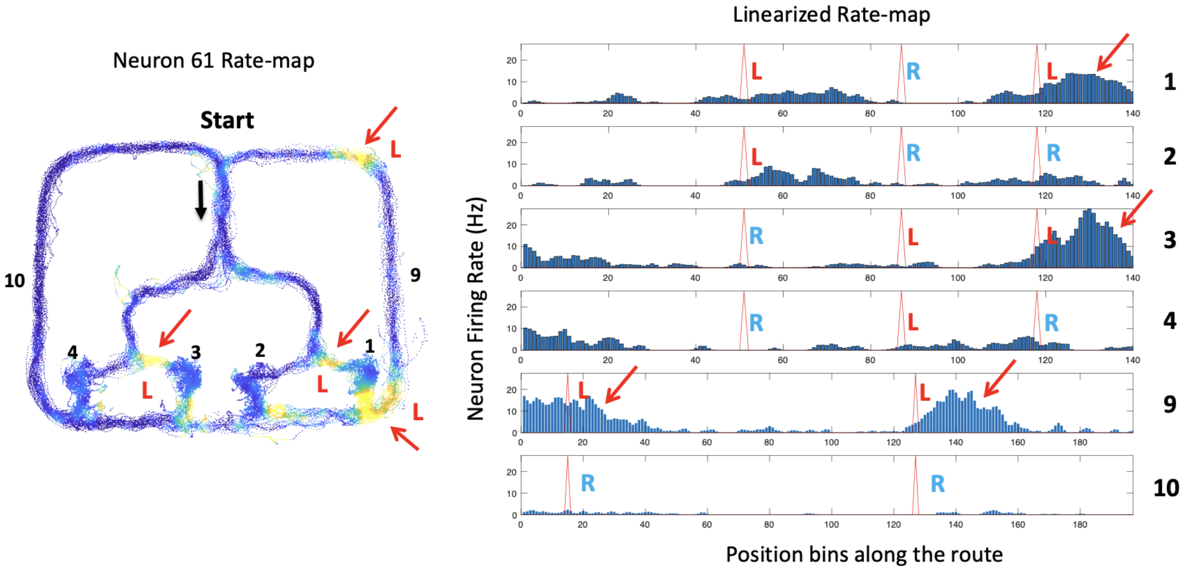

Figure 3. The rate-map and the linearized rate-map for neuron 61. (Left: Rate map; Right: Linearized rate map)

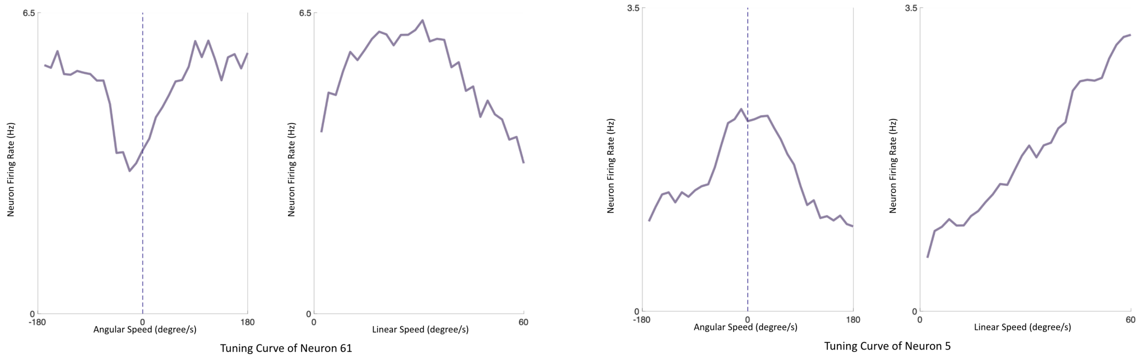

Figure 4. Neuronal tuning curves of the parietal cortex. Left: Neuron 61; Right: Neuron 5.

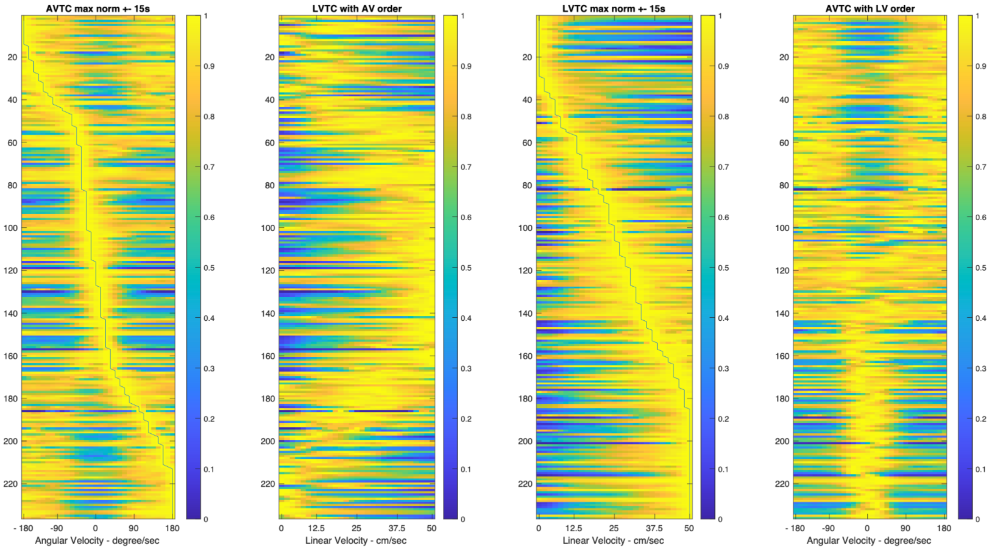

Figure 4. Distribution of the self-motion tuning curve. A: max normalized AV turning curve (ordered by the degree the neuron is tuned from left (-180) to right (180)) degree/sec. B: the same neuron order as A but it is a population LV tuning curve. C: max normalized LV turning curve (ordered by the degree the neuron is tuned from low (0) to high (50)). D: the same neuron order as C but it is a population AV tuning curve.

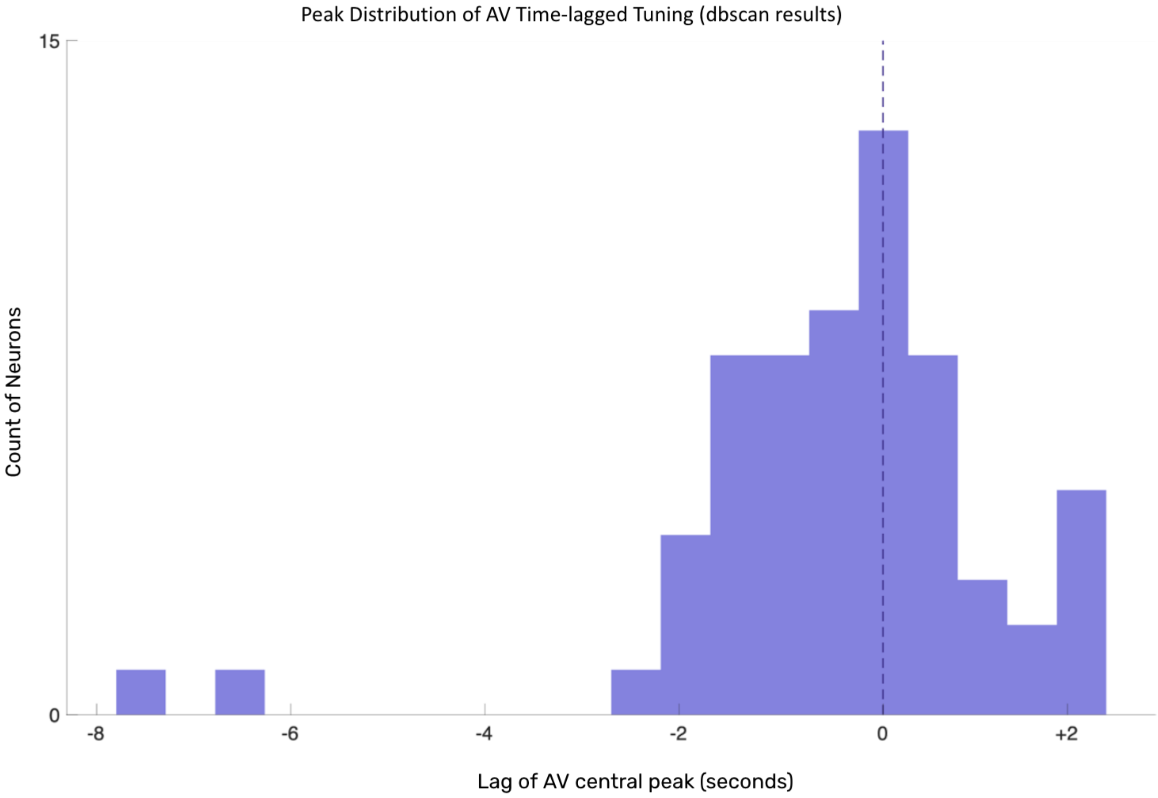

Figure 5. Distribution of time-lag of AV central peaks.

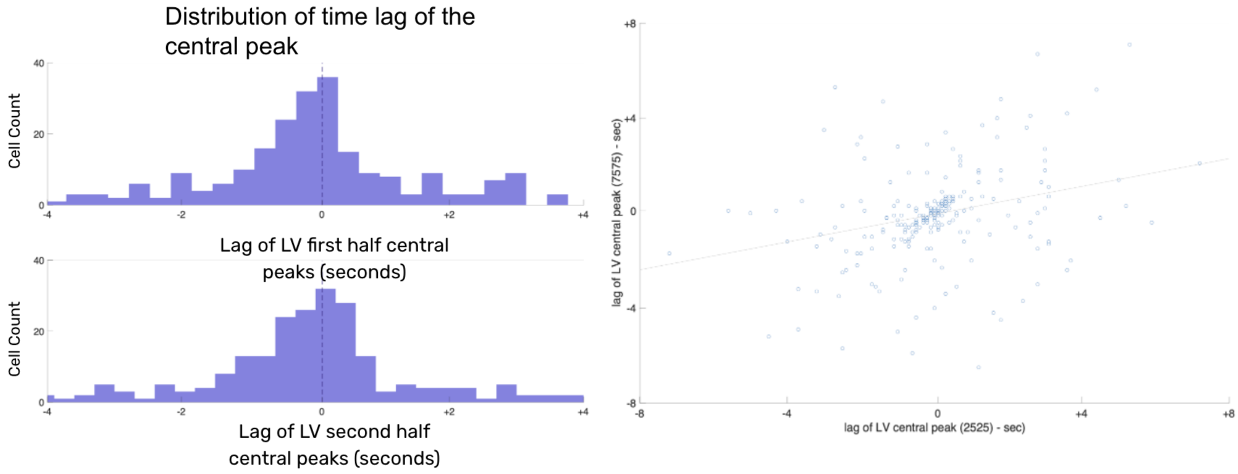

Figure 6. Distribution of time-lag of central peak. Up left: the time lag of LV central peak from first-half of the data. Down left: the time lag of LV central peak from the second-half of the data. Right: correlation of the LV central peaks between the first and second half of the data.

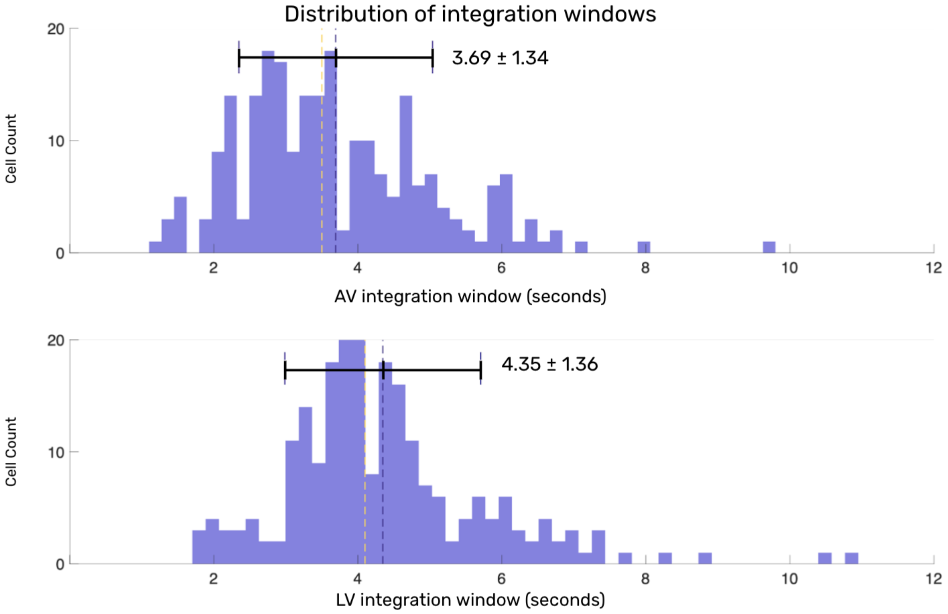

Figure 7. Distribution of the integration window. Up: Distribution of AV integration window. Down: Distribution of LV integration window.

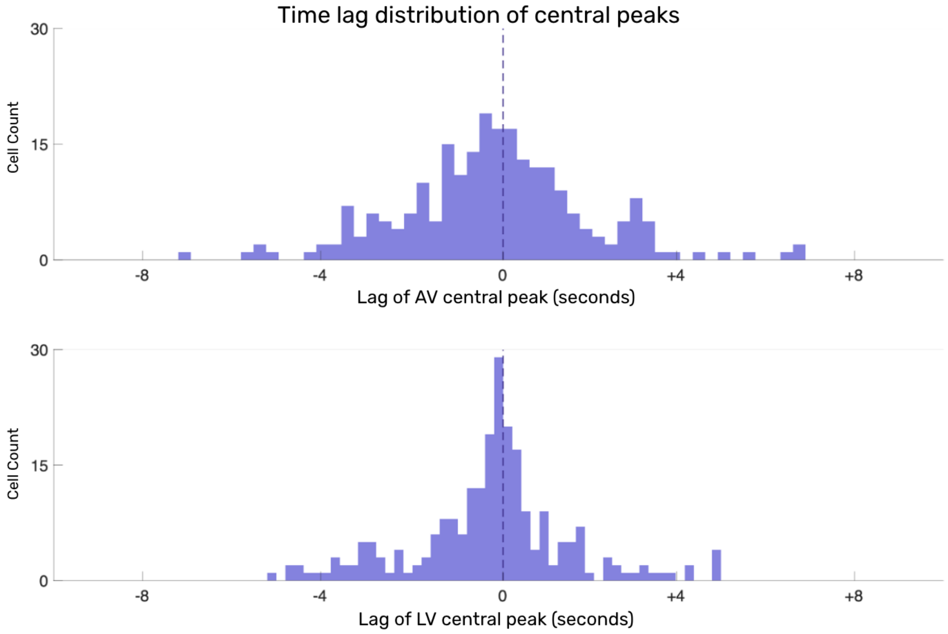

Figure 8. Distribution of central peaks. Up: distribution time-lag of AV central peaks. Down: distribution of time-lag of LV central peaks.

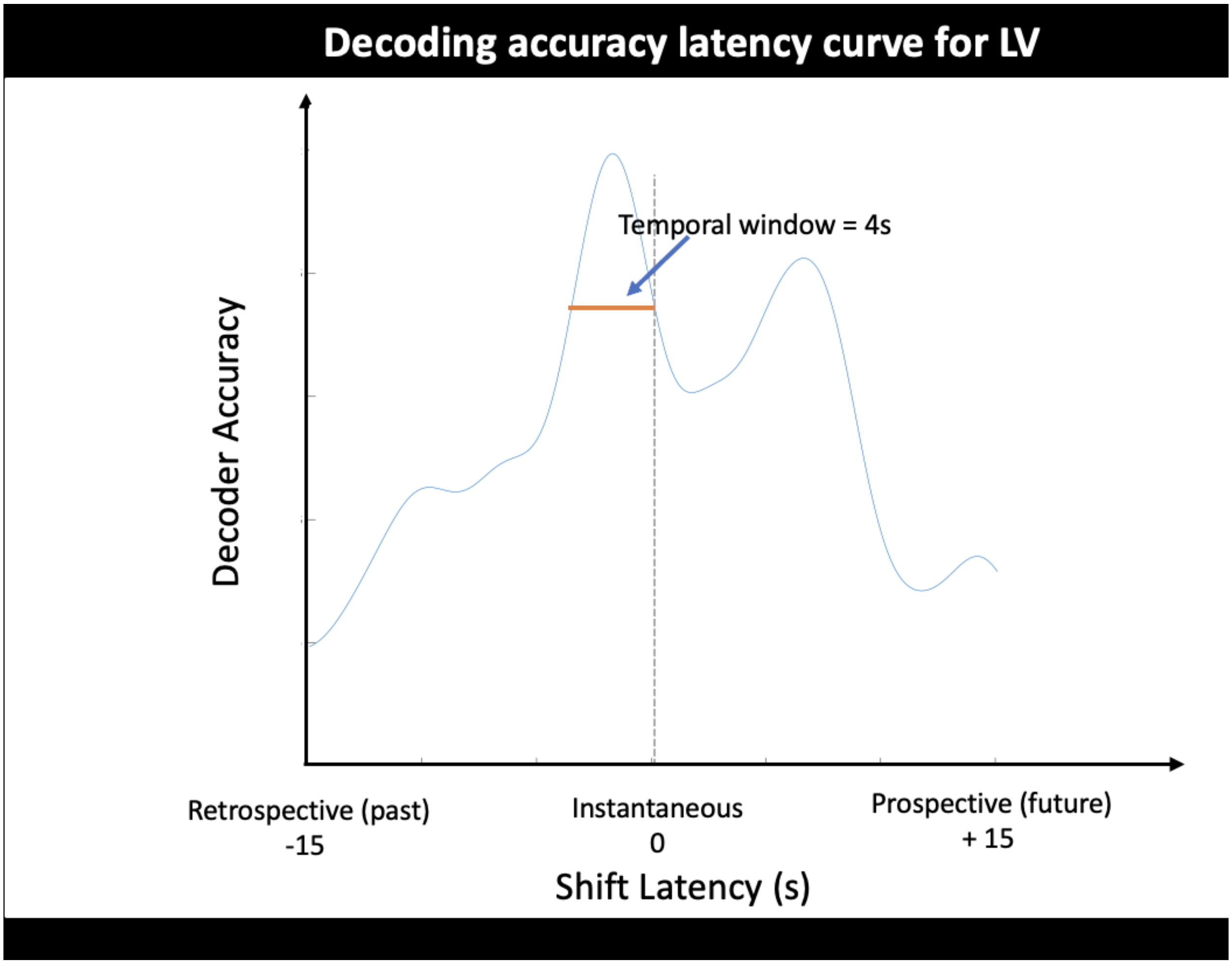

Figure 9. Decoding accuracy latency curve for LV (neuron 61).