

Journal Club

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Motion Processing and Categorical Decisions in Medial Superior Temporal and Lateral Intraparietal Areas

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Review of Zhou et al.

Neurons in different brain regions code information for various types of decisions. Decision-making tasks based on the direction of moving dots have been used extensively to research how different brain regions process information during perceptual decisions. For example, neurons in the middle temporal (MT) and the lateral intraparietal (LIP) areas have been shown to encode motion direction and categorical information in perceptual decisions, respectively (Freedman and Assad, 2006). MT was thought to represent momentary evidence, and LIP was thought to integrate outputs from MT (Gold and Shadlen, 2007). However, LIP does not merely integrate information but also shows a choice-dependent ramping signal, which is independent of motion information in MT (Yates et al., 2017). Medial superior temporal (MST) area is reciprocally connected to both MT and LIP (Lewis and Van Essen, 2000) and has also been implicated in coding information about motion directions rather than categorical decisions (Williams et al., 2003; Zaidel et al., 2017). Understanding how MST codes information during perceptual decisions could provide us with a better understanding of information processing in

MT, MST, and LIP because the three areas are interconnected and code information at various stages of perceptual decisions.

In their recent article published in *The Journal of Neuroscience*, Zhou et al. (2022) investigated the roles of MST and LIP during perceptual decisions. Two monkeys performed a delayed match-to-category task in which they were trained to report whether the test stimuli belong to the same or different category by releasing or holding a touch bar. Moving-dots stimuli consisted of two possible categories (C1, C2) and 10 possible directions (15°, 35°, 55°, 75°, 135°, 195°, 215°, 235°, 255°, 315°) separated by a learned category boundary oriented at 45° (Zhou et al., 2022, their Fig. 1a,b). The authors' use of category and direction enabled them to differentiate whether single-neuronal activity represents (low-level) motion directions or (high-level) categorical decisions. Their analysis revealed that LIP was more category-selective than MST during the early sample period, but MST was more selective than LIP during the late sample and the delay periods (Zhou et al., 2022, their Fig. 2g). Surprisingly, a support vector machine (SVM) analysis showed that MST performance in the early sample period was substantially below chance level (Zhou et al., 2022, their Fig. 2i). The reason the accuracy was below chance was not addressed by the authors, but one could speculate that the lower accuracy from MST might have occurred because MST neurons are more tuned to motion directions than categories during the early

sample period. Because the motion directions were not evenly distributed (C1: 55°, 75°, 135°, 195°, 215°; and C2: 35°, 15°, 315°, 255°, 235°), category decoding might fall below chance level when MST neurons exhibit similar responses to motion directions that belong to different categories yet are closer to the category boundary oriented at 45°.

The authors assessed the temporal stability of category selectivity by expanding their SVM decoding analyses across different time epochs (Zhou et al., 2022, their Fig. 3). While it was difficult to draw quantitative conclusions from this analysis, LIP had a peak in category decoding when an SVM classifier was trained in the sample epoch and tested in the test epoch and another peak when the classifier was trained in the test epoch and tested in the sample epoch. MST, however, lacked these two peaks. This might be because MST activity in the early sample epoch is noisy and does not provide robust information for SVM classifiers to decode accurate category information. Among neurons that were direction-selective but not category-selective, those from MST produced significantly higher accuracy of motion direction decoding than those from LIP in the SVM analyses (Zhou et al., 2022, their Fig. 4f). Trial-to-trial categorical decisions were correlated with neuronal signals from both MST and LIP (Zhou et al., 2022, their Figs. 5 and 6), consistent with the authors' hypothesis that both areas code categorical decisions. However, taken as a whole, the findings do

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not completely rule out the alternative hypothesis that MST and LIP code low-level motion direction and high-level categorical decisions, respectively. The SVM analysis in the early sample period indicated that the MST neurons might be more tuned to motion directions than categorical decisions (Zhou et al., 2022, their Fig. 2i), and the SVM analysis across different time epochs showed that the MST neurons might not provide robust information for categorical decisions (Zhou et al., 2022, their Fig. 3a).

Zhou et al. (2022) also analyzed local field potentials (LFPs) from the two areas during categorical decision-making. Beta band LFP power (12–30 Hz) from both areas showed task-specific modulations in the late sample and the delay periods, but there was no task-specific modulation in gamma band (70–150 Hz) (Zhou et al., 2022, their Fig. 7). The authors evaluated beta band LFP activity by quantifying category-selective power across frequencies and argued that the category-selective power in beta band is significantly higher in correct trials than in error trials. However, the effect was not limited to the beta band. In one animal (Monkey M), the category-selective power was also higher in correct than in error trials below 12 Hz (Zhou et al., 2022, their Fig. 8). This animal was trained and tested on a more difficult version of the task than the animal that showed effects only above 12 Hz. Therefore, more difficult tasks might result in modulations in LFP activity in across a broader range of frequencies. LFP activity from Monkey M but not Monkey Q also exhibited suggestive modulations in gamma band, although the authors did not provide a quantitative evaluation (Zhou et al., 2022, their Fig. 7a, b). Future studies examining whether and how task difficulty affects the frequency range of category selectivity in LFP power might be useful for testing whether more difficult tasks result in broader frequency modulations.

The relative roles of MST and LIP are an important question for information processing in perceptual decision-making. Zhou et al. (2022) report that neuronal signals in both MST and LIP were correlated with categorical decisions. However, as suggested above, latency and decoding analyses from the two areas at the

population level show that MST might be coding low-level motion direction rather than high-level decisions. This might be because MST neurons process a mixture of motion direction and categorical decisions and therefore have high-dimensional mixed selectivity of task variables (Rigotti et al., 2013). One could hypothesize that both MST and LIP have selectivity to both motion directions and categorical decisions, and that activity in MST and LIP might be better explained by motion directions and categorical decisions, respectively. Alternatively, the mixed selectivity analysis might reveal that MST is indeed better explained by categorical decisions. Using dimensionality reduction methods to study how much variance can be explained by either the task or latent variables might help us better understand the relative roles of MST and LIP (Cunningham and Yu, 2014).

Studying communication between MST and LIP should give us insight into how the two areas process different task-relevant information during categorical decisions. This might be done by collecting neuronal data simultaneously from both areas and quantifying communication between the two areas. For instance, Yates et al. (2017) used task variables and neuronal activity from two or more areas to model spike production, and they quantified coupling filters in their generalized linear model as a measure of how much information is transmitted from one area to another area. Zhou et al. (2022) recorded neuronal responses from either MST or LIP, but not from both at the same time. Future studies using simultaneous recordings could be used, along with the method from Yates et al. (2017), to clarify which task variables are coded in which areas and the direction of communication between MST and LIP. Quantifying inter-areal communication using both spikes and LFP data from the two areas would also be useful. Causality-based analyses of spike-LFP or LFP-LFP relationships (Schneider et al., 2021) might provide stronger evidence for or against the possibility that the two areas code task-relevant information in categorical decisions in different frequencies. If MST and LIP subserve motion direction and categorical decisions, respectively, one could hypothesize that information

would primarily flow from MST to LIP during the sample period so that LIP receives information about motion direction from MST. If both MST and LIP subserve categorical decisions, the inter-areal communication between the two areas might be reciprocal.

In conclusion, Zhou et al. (2022) showed that MST and LIP process motion direction and categorical decisions. Yet, whether and how the two areas process different “mixtures” of the two task variables and how communication between the two areas supports categorical decisions still remain unclear. Future studies will be necessary for us to fully understand the roles of MST and LIP in categorical decision-making.

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