Neural signatures of coping with multiple tasks in mouse visual cortex
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Abstract

Flexibly adapting to different task requirements is a key challenge of the visual system. In particular, depending on a potentially unobserved context the same stimuli might require different behavior. While task-related activity has been identified as early as the primary visual cortical (V1) activity in mice, it remained unknown if and how the visual cortex primarily dealing with feed-forward input contributes to efficient arbitration between tasks. Mice were trained to perform a multimodal task-switching paradigm where animals were required to make decisions either based on the identity of visual or that of auditory stimuli. Neural activity was recorded from all layers of V1 on 128 channels with extracellular electrodes. Our analysis has identified task-related variables in population responses. Importantly, while task-related variables could be identified mostly during stimulus presentation, the variable that could identify the specific task being performed could be reliably decoded from intertrial intervals, indicating a representation which is aware of the across trial contingency of task context. These results provide insights into how continual learning, the major challenge concerning the acquisition of multiple tasks relying on the same neural circuitry, can be achieved in biological agents.

Results

Isolated units were extracellularly recorded with 2x64 electrode shanks from all layers of V1 of 14 mice performing a multimodal (visual and auditory) perceptual discrimination task. Animals were rewarded for licking upon perceiving a go signal and avoided delay of the next trial for withholding licking at the no-go signal. The modality of the go/no-go pair was not constant in a recording session but the animals were required to switch the relevant modality. Cuing epochs, featuring trials where stimuli with a single modality were present, were followed by dual-modality epochs in which both modalities were present but animals were required to make decisions based on the modality presented in the preceding epoch while ignoring the other (Fig. 1). This setting permits the study of task-related signals since the same pair of stimuli could appear in different task contexts.

Representation of behavioral choice. First, following earlier indications (Reynolds & Heeger, 2009) that stimuli relevant to a particular task are represented with higher precision, we trained a linear decoder for decoding the orientation of the visual stimulus on two subsets of trials: first, when the animal was required to make its decision based on this stimulus modality; second when it was required to ignore it. Decoding visual information was more efficient at most, albeit not all animals when attended to, compared to when ignored (Fig. 2). Similarly, we repeated the analysis with a focus on the representation of the auditory stimulus. Interestingly, the...
analysis for the auditory modality yielded similar results, with a more pronounced improvement when attended. These results confirm that attended task-relevant stimulus can be more efficiently readout from the neuron population.

Next, our goal was to elaborate on population phenomena leading to a more efficient readout of information when a particular modality is relevant. We investigated population responses with a linear unsupervised method, tensor component analysis (Williams et al., 2018, TCA), which indicated that variability is induced in population responses by a number of easily interpretable features related to task execution (data not shown). To explicitly test the contribution of different task-related variables, we constructed decoders for these variables, including visual stimulus identity, auditory stimulus identity, the choice the animal made (Fig. 3A,B,D). While most reliable decoding can be achieved for the visual stimulus identity, both auditory stimulus identity and choice identity could be obtained with different time courses. Importantly, since animals were required to be able to perform multiple tasks, the task identity (referred later as context) is also a relevant factor, and we constructed a specific decoder for this variable (Fig. 3C). Importantly, high decoding performance of task identity indicates that context contributes to population activity by driving it to separate subspaces when context changes.

Using the insight obtained from the decoding analysis, we wanted to investigate the source of performance improvement when the decoded variable is relevant for decision. In particular, we wanted to test if the more reliable representation of stimulus identity is a result of increased separability of stimuli along the axis where changes in stimulus identity introduce variance, or changes in other task-related variables. We used the decision boundaries determined by the linear decoders of (Fig. 3) to establish the directions in the population activity space along which population responses can be classified. We used the normal vectors of the decision boundary hyperplanes as basis vectors spanning particular subspaces, and projected instantaneous firing rate vectors of the population onto these subspaces. In particular, to investigate performance improvement in visual decoding, we used the decision normal vectors of visual and choice decoders as a basis to construct a two-dimensional subspace, on which the projection of individual trials are represented as individual points (Fig. 4). The bases obtained from the multimodal blocks are not orthogonal, meaning that these variables are correlated, but are consistently linearly highly independent (blue and yellow lines). Trial-by-trial analysis of the planar subspace under the ignore visual condition (purple and red symbols) reveals that in this task condition the decision normal alone would be closer to orthogonal to the choice condition. However, upon performing the attend to visual task a shift is introduced in the population response vectors along the choice direction (blue and turquoise symbols). This systematic shift introduces larger separation which accounts for decoding performance improvement when the visual stimulus is relevant for decisions. Importantly, the separation is more pronounced if we take into account the performance of the animal: in incorrect trials separation is less pronounced thus decreasing the separation of the responses according to stimulus identity. In summary, these results indicate that the attention-related im-

Figure 1: Task switching between contexts. Top: Stimuli and role of stimulus modalities in dual-modality tasks. Bottom: Block layout of an experimental session.

Figure 2: Stimuli decoding difference between attended to and ignored blocks, for visual and audio respectively; integrals of accuracy timecourse 95% confidence interval. Panel A: Visual accuracy, Panel B: Audio accuracy, Panel C: Context accuracy, Panel D: Choice accuracy. s.e.m. for 11 mice, boxplots: mean, 25%, 75%, 95% confidence interval, whiskers: minimum, maximum.

Figure 3: Time course of linear decoding of task variables in multimodal trials for a well-trained mouse. Decoder performance was measured at different time windows along the trial (10 ms resolution sliding 50 ms wide windows of instantaneous firing rate). Grey: stimulus present. Panels correspond to visual and audio stimulus identity, context and choice for panels A-D, respectively.
provement can be traced back to the introduction of a choice variable that operates in a subspace linearly independent form the subspace where the stimulus identity introduces variability.

**Representation of context.** Earlier accounts of learning identified a task-specific signal in a period preceding the appearance of the target stimulus, which has been speculated to be linked to reward expectation (Jaramillo & Zador, 2011; Poort et al., 2015). Our task design permits a more detailed investigation of prestimulus task-related activity. More specifically, we address the question if prestimulus task-related activity conveys information solely about the expected reward or about the actual task context as well. Linear decoding analysis of the activity during stimulus presentation (ON-stimulus activity) reveals that stimulus and task variables can be identified from ON-stimulus activity (Fig. 5A, left). Critically, our analysis on the identification of task context based on the V1 population activity shows a relatively stable representation of spontaneous activity not only during stimulus presentation, but task identity can be identified with equally high reliability beyond stimulus presentation (Fig. 3C). Indeed, while other variables cannot be identified in the population activity preceding stimulus presentation, the contextual variable identifying the task can (Fig. 5A, center). Decodability of task context both from the prestimulus and ON-stimulus activities does not ensure that the prestimulus and ON-stimulus activities would be decoded along the same activity subspace. We therefore designed an analysis which tests if the prestimulus activity distribution represents the context variable identically to that in the ON-stimulus activity distribution. We used a decoder trained on a short period during the prestimulus activities of the multimodal tasks (the same period as the one shown on Fig. 5B) but tested on activity distributions obtained from a different time window in the prestimulus period and on a time window during ON-stimulus activity. This across-time test revealed equally efficient task context decoding both during the prestimulus period and during ON-stimulus period (Fig. 5A, right). Thus, in the period preceding the stimulus not simply reward expectation but also a signal specific to the task is present. Furthermore, this task-specific signal is invariant across on-stimulus and off-stimulus periods.

Task learning is a delicate problem and studies of classical conditioning indicate that animals are able to build parsimonious models of environmental variables during learning (Courville, Daw, & Touretzky, 2006). It is unclear if the task variable we identified in the prestimulus activity reflects such a parsimonious representation of the task. In particular a parsimonious representation would indicate that the task is identical if the set of stimuli used for making decisions are not changing irrespective if other distractor stimuli are present (in our case these are the non-attended stimuli). We tested if the context variable that we identified in the V1 population activity in multimodal trials is invariant to the presence or absence of the unattended stimuli. We used the decoder trained on the prestimulus activity of multimodal trials to assess context in single-modality trials (Fig. 5B). Decoding context from the first block of the experiment revealed that the behaviorally relevant modality reliably predicted population activity along the dimension defined by the context variable both in the prestimulus (Fig. 5B) and in the ON-stimulus periods (Fig. 5B). Interestingly, this block being at the very beginning of the session the animal had no exposure to multimodal stimuli. Still, the context variable reliably identified the whole task and data indicates that animals recognize the task almost immediately after the start of the block. A similar analysis of the single-modality block separating the two multimodal blocks reveals that the population activity gradually drifts from one context to the other context (Fig. 5B), with considerable variability in speed of adaptation across animals. These results indicate that task context variable reflects a parsimonious representation of the task.

The robust presence of the task context variable in both prestimulus and on-stimulus activities indicates that the activity of the neuron population reflects the characteristics of the specific task. In particular, even if bottom-up signals have overlapping representations in different tasks, the context variable distinguishes the two representations. We wanted to test if the representation of the context variable is related to other measures that reflect task acquisition. We used the task-specificity of the prestimulus activity as a measure for the efficiency of task representation. The prestimulus task-specificity of the activity across the whole population of recorded animals is well reflected in the task specificity in ON-stimulus periods (Fig. 5C). Interestingly, the decodability of choice from ON-stimulus activity was also highly predictable based on the
Conclusions

Using a multimodal decision making task we have demonstrated that signatures of a sophisticated representation can be found which can be an underpinning of arbitrating between multiple tasks using the same sensory cortical circuitry. Key to our study is that identical stimuli are used in multiple contexts, which made it possible to identify a task-specific variable for context and a choice variable that was invariant across tasks. Our results provide insights into how continual learning can be achieved without catastrophic forgetting.

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References


