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Neural implementation of categorization in a motion discrimination task[☆]

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ABSTRACT

Human being can categorize one object into different classes depending on the reference used, a cognitive capacity, i.e., context-dependent categorization, which is fundamental in our daily life. In the present study, we explore one possible neural mechanism underlying a motion discrimination task, in which the neural system needs to judge whether a motion direction embedded in a random dot kinematogram is clockwise or anticlockwise with respect to a reference direction that varies over time. We construct a spiking-neuron network model to implement this task. The model consists of three parts: (1) a working memory circuit, which holds the information of the reference direction; (2) two information extraction circuits, referred to as clockwise-preferred circuit and anticlockwise-preferred circuit, respectively, which extract either the clockwise or anticlockwise information about the test direction; and (3) a decision-making circuit, which reads out the category decision. At the core of the network is the assumption of an asymmetric offset and rotational invariance of the connectivity profile. Our model successfully implements the context-dependent categorization of motion direction where the reference varies over time. And it reproduces the experimental results that with higher similarity between the reference and test direction or lower coherence level of the random dot kinematogram, the performance gets worse (lower accuracy and longer reaction time).

1. Introduction

The ability to categorize the same object or stimulus into different classes according to variable criteria is a remarkable brain function, which is very important in our daily life because we are always making decisions based on varying environment. Besides our human being, monkeys have the same ability. Experiments have shown that monkeys can learn to classify motion speed of a random dot kinematogram (RDK) into slow or fast according to variable criteria [1], or successfully categorize a motion direction as clockwise or anticlockwise [2], or differentiate a vibration frequency as higher or lower [3,4], or classify a morphological image as cat or dog [5], or categorize a stimulus as strongest or others [6], or even group the stimuli as same (match) or different (nonmatch) [7,8]. Neural activities related to categorical behaviors have been found in the temporal [9–11], the parietal [7,12,13], and the frontal cortex [5,10,14–17]. And the hallmarks of these neural activities include ramping-up responses to one category while ramping-down responses to the others, and larger differences in response to stimuli from different categories while smaller differences in response to stimuli from the same category. In spite of extensive experimental studies, the neural mechanism underlying the context-dependent categorization needs further investigation.

In general, a categorization task consists of three stages: (1) acquiring a criterion from internal memory or from an external stimulus and keeping it in working memory; (2) encoding the test stimulus and comparing it with the criterion; and (3) deciding which category the test stimulus belongs to according to the criterion. The slow recurrent excitation balanced by fast feedback inhibition has been thought as the neural mechanism underlying the third stage – decision making [18–21]. However, the first two stages are quite complicate due to different encoding mechanisms of stimuli applied in different tasks (tactile stimulus in [3,4] and visual stimulus in [1,2,7]). For the discrimination task about tactile vibration stimulus, Miller and Wang proposed a model with inhibitory control provided by an integral feedback signal in prefrontal cortex for discriminating the frequencies of sequential vibration frequency [22]. Machens et al. used mutual inhibition

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[☆] This document is a collaborative effort.

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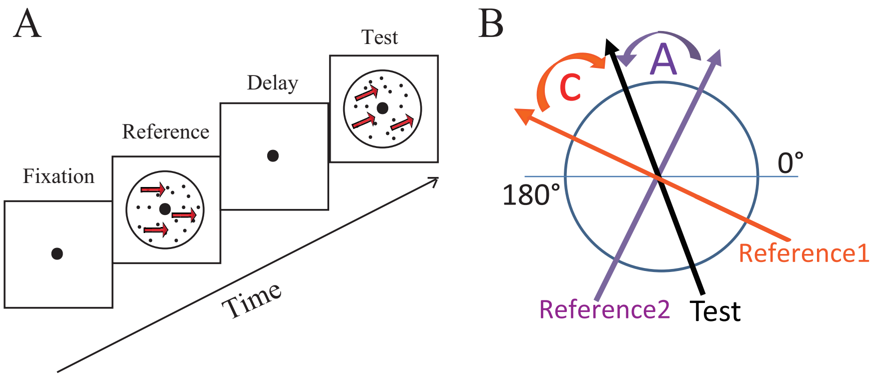

Fig. 1. *The schematics of a motion direction categorization task.* (A) The schematics of the task. Two successive displays of random moving dots, representing the reference motion direction and test motion direction respectively, are shown on a screen sequentially, separated by a brief delay. Whether the test is clockwise or anticlockwise with respect to the reference is required to report. (B) The flexibility of the categorization. The test direction (black) is clockwise with respect to *Reference*1, while anticlockwise with respect to *Reference*2.

between nonlinear units to implement frequency discrimination [23]. A highly organized line attractor model, a randomly connected network with chaotic activity, and several models have been compared with the electrophysiological data recorded during a delayed vibrotactile discrimination task [24]. For the tasks involving motion direction, Engel and Wang advanced a neural circuit model composed of three parts (working memory + comparison + decision making) to explore the mechanism underlying the same-or-different classification [25]. Reciprocal inhibition of feedforward lateral inhibition has been suggested as the mechanism underlying flexible categorization of strongest versus others [26]. A simple model, consisting of a clockwise preferred and an anticlockwise preferred neuron pool, has been proposed to explain the experimental observations in a fine reference-unchanged direction discrimination task [2]. Therefore, we often need to develop specific neural models to investigate the neural mechanisms underlying different categorization tasks.

In this paper, we study context-dependent categorization through a motion discrimination task (see Fig. 1). The task originates from an extensively used task in visual perceptual learning with minor revisions [27]. In the field of perceptual learning, subjects are often trained to discriminate a test orientation (or motion direction) clockwise or anticlockwise with respect to a reference orientation (or motion direction), with the reference changeable after training procedure to investigate the learning transfer. In our task, a display of RDK containing a coherent motion direction was first presented for a brief period, which was used as the reference to judge whether the following coherent motion direction, embedded in the second RDK, was clockwise or anticlockwise (see Section 2.5 for details). Since the coherent motion direction in the first display changes trial by trial, the neural system needs to flexibly categorize the motion direction in the second display, i.e., the report may be different given one fixed test direction but different references. Electrophysiological studies have revealed that: (1) neurons in the middle temporal cortex (MT) encode the motion direction [28–31]; (2) neurons in the supplementary eye field (SEF) memorize the direction during the delay period [32,33]; and (3) neurons in lateral intraparietal area (LIP) give rise to the categorical response [34–38]. These experimental observations provide information about the encoding of motion direction and the final report stage, but we still do not know how the neural system compare the stimulus with a variable memorized reference to form the final categorization.

Considering the importance of flexible categorization in our daily life and the extensive applications of the flexible clockwise/anticlockwise discrimination task in perceptual learning research, we proposed one possible neural mechanism to implement this task and tested it through a spiking-neuron network. The network consists of a working memory circuit (WMC) to hold the reference direction, two information extraction circuits (i.e., clockwise preferred circuit, CPC, and anticlockwise preferred circuit, APC) to encode the difference between reference and test, and a decision circuit to report the categorization result. At the core of the network is the assumption of an asymmetric shift and rotational invariance of the connectivity profile. The former ensures that CPC (or APC) has stronger response when the test direction is clockwise (or anticlockwise) with respect to the reference direction, and the latter guarantees the feasibility of the network under variable references. The simulations demonstrate that our network can perform the task and correctly reproduces observations that the performance gets worse (lower accuracy and longer reaction time) with higher similarity between the reference and test direction or lower coherence level of the RDK. Further, the simulation results show that model performance varies with the asymmetric connection offset.

2. Material and methods

2.1. Network architecture

The spiking-neuron network model is shown in Fig. 2. WMC is composed of 2048 pyramidal cells and 512 interneurons. The structure of WMC is adapted from Compte et al. [39] with minor revisions. Pyramidal cells are arranged on a circle according to their preferred motion directions θ. The connections between pyramidal cells are all-to-all connections but with different strengths, i.e., pyramidal cell j projects to i with strength: $W(\theta_i - \theta_j) = J^- + (J^+ - J^-)\exp\left[-(\theta_i - \theta_j)^2/2\sigma_{con}^2\right]$ $(\forall\, i \in [1, 2048], j \in [1, 2048])$. J^- is the cross-directional connection strength, J^+ is the iso-directional connection strength, and σ_{con} is the width of the connection profile. Note that only J^+ and σ_{con} are set to be adjustable parameters (here $J^+ = 4.02$ and $\sigma_{con} = 30°$), as J^- is determined by normalization condition $\frac{1}{360}\int_0^{360} W\left(\theta_i - \theta_j\right)d\theta_j = 1$. The connections from pyramid cells to interneurons and from interneurons to pyramid cells are uniform, and there is no connection between interneurons. The coherent motion direction in the first RDK elicits localized persistent activities in WMC, which mimics neural activities in SEF [32,33]. The number of neurons and the profiles of recurrent connections between neurons in CPC (and APC) are the same as those in WMC. A test coherent motion in the second RDK will elicit localized activities in CPC and APC, mimicking neural activities in MT [29,30].

Considering that intensive synapses from SEF to MT have been

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