

1 Introduction

1.1 Introduction of Feedforward Recurrent Hypothesis

Cortical circuits embody remarkably reliable neural representations of sensory stimuli that are critical for perception and action. Cortical circuits were thought to emerge from a developmental sequence that includes two distinct phases: an early period before the onset of experience during which endogenous mechanisms are thought to formulate the initial and a subsequent period during which these early networks are refined under the influence of experience[?, ?, ?, ?], and a subsequent period during which these early networks are refined under the influence of experience [?, ?, ?, ?, ?].

The fundamental structure of cortical network representations is thought to arise early in development before the onset of sensory experience. However, how these endogenously generated networks respond to the onset of sensory experience, and the extent to which they reorganize with experience remains unclear [?].

In earlier work from the lab of M. Kaschube and D. Fitzpatrick [?], they focused on the problem of "nature-nurture transform". They tried to clarify the understanding of the capacity of the endogenous cortical network to reliably represent stimulus orientation at the onset of visual experience and the degree to which visual experience alters endogenous network structure to achieve mature stimulus representations.

To explore these early developmental dynamics, they applied data from the visual cortex of the newborn ferrets obtained through chronic *in vivo* calcium imaging [?]. Visually evoked activity in the visual cortex of postnatal ferrets before and following the onset of visual experience was employed. The visual cortex of higher mammals has served as a powerful model for exploring the contributions of these different phases to the development of mature cortical networks. Before the onset of visual experience, activity-independent mechanisms combine with activity-dependent mechanisms driven by patterns of endogenous activity derived from the retina and the lateral geniculate nucleus (LGN) [?, ?, ?] (Figure 1.1) to generate a robust modular network structure in visual cortex that is evident in patterns of spontaneous activity [?, ?]. This endogenously generated functional network is thought to form the initial framework for the emergent cortical representation of stimulus orientation since visual stimulation at or before eye-opening drives weakly orientation-selective responses at the cellular and modular scale [?, ?, ?, ?, ?] and spontaneous activity before eye-opening is predictive of the representations of stimulus orientations at eye opening [?].

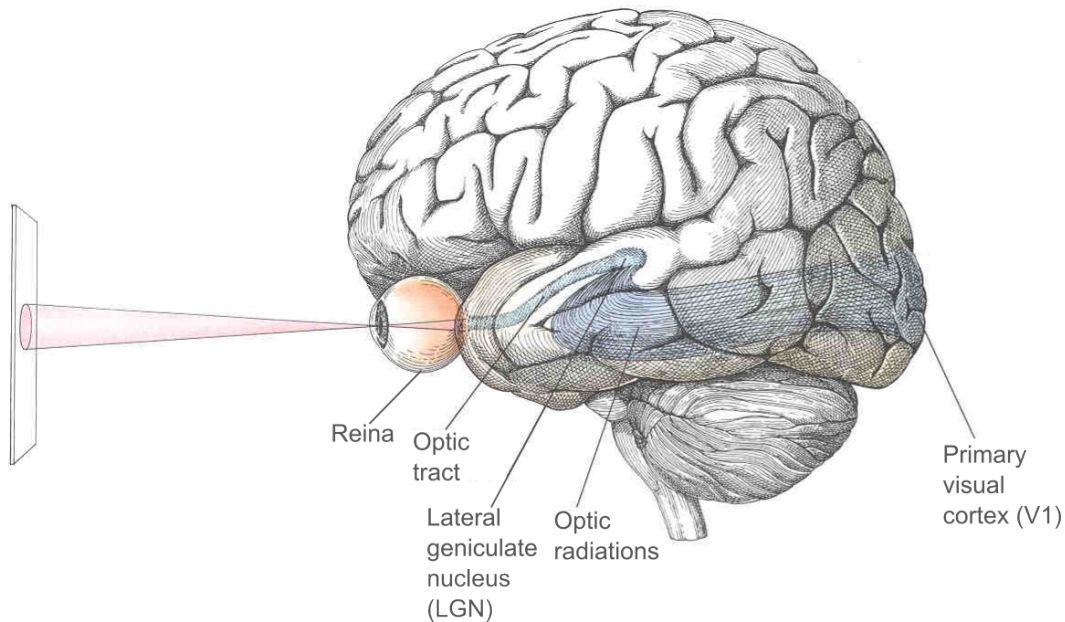


Figure 1.1 Central visual pathway in primates. The major pathway that visual information goes through from the eye to the primary visual cortex is shown. Signals are produced by receptors in the retina and are then transferred to a major relay station, the lateral geniculate nucleus (LGN) via the optic tract. Signals then travel through optic radiations to selected areas of the primary visual cortex (V1). From then on, signals are sent to higher areas of the cortex. [?, ?, ?]

The ferret is a species with a well-defined modular network of orientation-selective responses. Newborn ferrets open their eyes around thirty days after they are born. More than two days before eye-opening, the visual cortex was assumed to be visually naive. At least four days after eye-opening, the cortical network can gather information environment to become experienced (Figure 1.2). The data was collected at different time points from visually naive and experienced visual cortex [?, Figure 1a]. In visually naive animals, their network responses are strong but highly variable, while in visually experienced animals, the diversity of responses was reduced and responses became more reliable.

To explore the underlying mechanism that builds reliable network responses, authors in the work from the lab of M. Kaschube and D. Fitzpatrick [?] developed the "feedforward recurrent alignment hypothesis". The hypothesis proposed that the initial evoked activity pattern reflects novel visual input that is only poorly aligned with the endogenous networks and that highly reliable visual representations emerge from a realignment of feedforward and recurrent networks that is optimal for amplifying these novel patterns of visually driven activity.

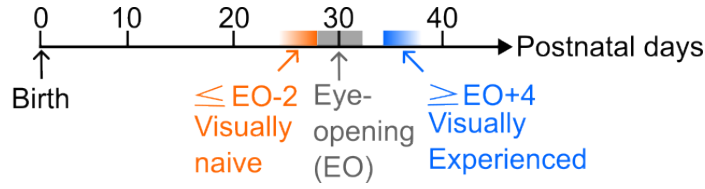


Figure 1.2 Timeline for ferret visual cortex development. Ferrets open their eyes around thirty days after birth. The visual cortex that is more than two days (inclusive of two days) before the eye-opening (EO) is considered to be visually naive. After four and more than four days from eye-opening, the visual cortex should already get enough training information from the environment and is therefore considered to be visually experienced [?].

1.2 Theoretical Exploration and Extensions

Ample computational work suggests that recurrent connections can give rise to amplification within subnetworks of coactive network units [?, ?, ?, ?, ?, ?]. Input that aligns more with such a subnetwork is expected to elicit a more robust response. Therefore, the "feedforward recurrent alignment hypothesis" was developed based on a conceptual computational network model of the early cortex and its response to visually evoked input using a minimal linear recurrent network [?]. Each unit represents the pooled activity in a local group of neurons. Connections between units describe the net interactions between local pools. For simplicity, it was assumed that the net interactions are symmetric, resulting symmetric interaction matrix for the recurrent network. They found out that the differences in the degree of feedforward recurrent alignment could reproduce the characteristics of network behavior from experimental observations that distinguish naive and experienced visual cortex-evoked responses (Method section ?? and Results section ??).

To explore the potential of the feedforward recurrent alignment hypothesis, we develop some theoretical explorations and extensions in this work on the existing feedforward recurrent alignment model. The explorations cover the perspectives of different recurrent network structures, experimental usability, and plasticity.

The first part of the exploration is to adapt the feedforward recurrent alignment modeling on asymmetric net interactions. The previous model considered for simplicity symmetric net interaction, which however loses the biological generality of cortical network structure. Asymmetric networks represent a more general cortical network structure but can raise more complicated dynamics and result in patterns in complex planes. To solve this problem, we try out different modifications to adapt the prior feedforward recurrent alignment modeling. At the same time, the modified model should still reflect the experimental observations from data gathered in the earlier work from the lab of M. Kaschube and D. Fitzpatrick [?]. The detailed method for this part is introduced in section ?? and the corresponding results in section ??.

The second part focuses on another recurrent network structure suggested by [?, ?, ?]. The authors mentioned that large-scale neural recordings have established that the transformation of sensory stimuli into motor outputs relies on low-dimensional dynamics at the population level, while individual neurons exhibit complex selectivity. Prior experiments in behaving animals have found that trajectories of neural activity are typically restricted to low-dimensional manifolds in that space [?, ?, ?, ?, ?, ?, ?, ?]. Besides, they introduced the class of models, low-rank recurrent networks, directly embodies the idea of low-dimensional collective dynamics, opens the door to relating connectivity and dynamics, and provides a framework that unifies a number of specific RNN classes [?]. Low-rank RNNs rely on connectivity matrices that are restricted to be low-rank, which directly generate low-dimensional dynamics. Therefore, we are also interested in the adaptation of feedforward recurrent alignment on the promising low-rank recurrent network. Methods for the construction of low-rank recurrent networks are introduced in section ?? and its corresponding results in section ??.

The third part is related to the perspective of experimental usability of feedforward recurrent alignment. Since the whole cortical network structure is difficult to access during laboratory experiments, the degree of alignment between feedforward inputs and recurrent network structure is out of accessibility. Therefore, it could be helpful if the feedforward recurrent alignment model could be reformulated only demanding experimental measurable information. The work by [?] pointed out that the reliability of evoked dynamics in recurrent networks is dependent on the stimulus used. [?] then further gave the prediction that stimulus inputs that aligned with the structure of endogenous subnetworks would be recurrently amplified, leading to more reliable evoked responses and constraining the potential outputs of the network. Based on an experimental method introduced by the lab of H.Mulholland [?], white-noise evoked activity can be used to generate spontaneous-like activity patterns. Thus, inspired by the series of works, we explore the possibility of modifying the feedforward recurrent alignment with white-noise evoked activity. Since the original recurrent network structure is assumed to be unknown, we call it the black box recurrent network model. The method for this part is described in section ?? and the results in section ??.

Finally, the last part regards the feedforward recurrent alignment hypothesis from the perspective of network learning and plasticity. Connection strengths can be modified by learning from experience, and the degree of learning from each experience is a parameter that can be modified. The simplest kind of learning is Hebbian learning (Hebb, 1949), where the weight between a sending and a receiving node increases if the two nodes are active at the same time. In other words "Nodes that fire together, wire together." This enables learning the correlational structure of the environment [?]. Thus, including the learning rule in the feedforward recurrent network could also be a potential perspective to explore the mechanism for the

experience-driven change of response reliability. The methods for the exploration of feedforward recurrent alignment considering simple Hebbian rule are introduced in section ?? and the results for it in section ??.

The Figure 1.3 illustrates the summarized perspectives of this work from paragraphs above.

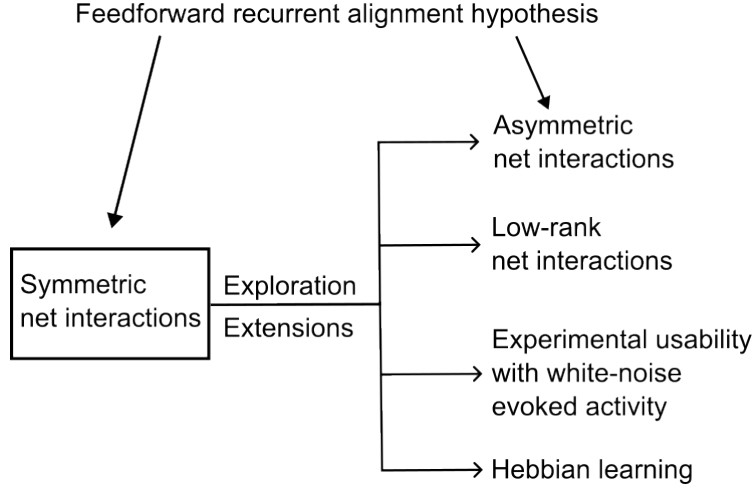


Figure 1.3 Included extensions and explorations in the work. Based on the prior work from the lab of M. Kaschube and D. Fitzpatrick [?], the feedforward recurrent alignment hypothesis was developed with a conceptual network model. For simplicity, the symmetric net interactions were considered. In this work, theoretical explorations and further extensions of the prior network model are carried out in multiple perspectives. It includes adapting the model to more biologically realistic net interaction structures, for example, asymmetric and low-rank. Moreover, due to the difficult accessibility of whole net interaction during experiments, white-noise evoked activity is chosen to modify the modeling. Last but not least, Hebbian learning as the basic learning rule is taken into account to explore the dynamic of feedforward recurrent alignment.