Probabilistic Information Processing in Humans and Recurrent Neural Networks

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Abstract

In nature, sensory inputs are often highly structured, and statistical regularities of these signals can be extracted to form expectation about future sensorimotor associations, thereby facilitating optimal behavior. To date, the circuit mechanisms that underlie these probabilistic computations are not well understood. Through a human electrophysiolgical experiment and a recurrent neural network (RNN) model, the present study investigates how the brain extracts, processes, and utilizes probabilistic structures of sensory signals to guide behavior. To achieve this goal, we first constructed and trained a biophysically constrained RNN model to perform a probabilistic decision making task similar to task paradigms designed for humans. Specifically, the training environment was probabilistic such that one stimulus was more probable than the others. We show that both humans and the RNN model successfully extract information about stimulus probability and integrate this knowledge into their decisions and task strategy in a new environment. Specifically, performance of both humans and the RNN model varied with the degree to which the stimulus probability of the new environment matched the formed expectation. In both humans and RNNs, this expectation effect was more prominent when the strength of sensory evidence was low. These findings suggest that both humans and our RNN model placed more emphasis on prior expectation (top-down signals) when the available sensory information (bottom-up signals) was limited. Finally, by dissecting the trained RNN model, we demonstrate how competitive inhibition and recurrent excitation form the basis for neural circuitry optimized to perform probabilistic information processing.

1 Introduction

The brain contains billions of neurons, each connecting with up to 10,000 other neurons. Together, these neurons continually produce electrical signals to represent and relay information about the sensory environments. Notably, this task is made more challenging by the fact that sensory inputs are highly dynamic and often ambiguous, especially as animals traverse novel environments. In addition, naturalistic sensory environments are inherently probabilistic and certain stimuli are subsequently encountered more frequently than others. To optimize sensory processing, the brain needs to extract the statistics of the sensory environments to form expectation against which incoming signals are compared [1]. This expectation captures the inherent probabilistic structures of the sensory environments and can be used to fine-tune and adapt behavioral responses as the animals encounter novel environments. For example, knowledge of statistical regularities in the environment can lead to faster recognition of objects when they are encountered in an expected context (e.g., a bird in a backyard) than when they are encountered in an unlikely context (e.g., a bird in a washing machine; [2, 3]). While certain aspects of probabilistic information processing have been investigated through

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human psychophysics, neuroimaging, and lesion studies, the circuit mechanisms that underlie this complex cognitive function is not well understood.

Recent work in patients with bilateral damage to the hippocampus demonstrates that an ability to learn stimulus probability and use this knowledge to perform cognitive tasks circumvents the main hippocampal pathway which mediates various other kinds of learning [4]. In addition, human electrophysiological and pyschophysical studies have shown that learned expectation based on stimulus probability improved behavior by primarily modulating post-perceptual processes including the selection and execution of motor responses rather than directly sharpening sensory signals in the primary visual areas [5, 6]. To investigate the circuitry that underlies probabilistic information processing, the present study examines how humans and recurrent neural network (RNN) model process and utilize information about stimulus probability in a perceptual decision making task. We show that both humans and the RNN model extract and use probabilistic information of the sensory stimuli to improve their performance in an environment where the stimulus probability closely aligns with the learned expectation. In addition, we show that the enhanced processing of the highly probable (expected) stimulus can be attributed to a combination of decreased inhibition and increased recurrent excitation within a neuronal subgroup selective for the expected stimulus. This unique circuit mechanism gives rise to a sub-population of neurons with enhanced neural activity which has been previously observed in experimental studies.

2 Human behavioral data

Expectation based on stimulus regularities exert a powerful influence on human perception and decision making. To examine how humans process and use probabilistic information to guide behavior, we tested human participants on a perceptual decision making task where the stimulus probability and the amount of sensory strength were manipulated. On each trial, participants monitored a display of flickering randomly-oriented red and blue bars and reported a brief target display which was either red or blue bars coherently oriented at 0° (horizontal) or 90° (vertical; Figure 1a). Electroencephalography (EEG) was concurrently measured as the participants performed this task. Stimulus probability was manipulated on a block-to-block basis such that within each block of trials, one target feature (e.g., horizontal orientation) was more prevalent (70%) than the other feature (i.e., vertical orientation; 30%). In addition, experimental blocks where the target features (e.g., orientation) was counterbalanced (50% each) were also interleaved throughout the experiment and were used as a neutral testing context to evaluate if stimulus probability was learned on the previous (training) block. Finally, sensory strength was manipulated through the frequency at which the red and blue bars were being rendered. In this study, we considered two strength values: low flicker frequency at 33 Hz and high frequency at 50 Hz.

Together, this behavioral paradigm incorporates three comparison conditions by varying the stimulus probability on a block-to-block basis: (1) 'expected' condition where two adjacent blocks shared the likely target stimulus (e.g., coherently horizontal bars presented as targets more often in two adjacent blocks), (2) 'unexpected' condition where two adjacent blocks did not share the likely target stimulus (e.g., coherently horizontal bars presented as targets more likely in one block and coherently vertical bars as targets more likely in the next block), and (3) 'neutral' condition where the coherently horizontal and coherently vertical bars were presented as targets equally likely in each block. Finally, the manipulation of the flicker frequency allowed us to investigate the probabilistic information processing under different levels of sensory strength.

3 RNN model

Recurrent neural network (RNN) models have recently been used to investigate various components of neural computations such as perceptual inference and working memory [7, 8]. Because RNN models allow an experimenter to manipulate many aspects of the sensory environment and learning processes–including the network architecture, the task, and the stimulus set–these models offer a complementary approach to in-vivo methods. To date, RNN models have been primarily trained in an environment where a stimulus space is counterbalanced and unbiased to ensure that each stimulus is equally represented and accounted for by the neural dynamics of the trained models. However, naturalistic sensory environments are inherently probabilistic and certain stimuli are subsequently encountered more frequently than others.

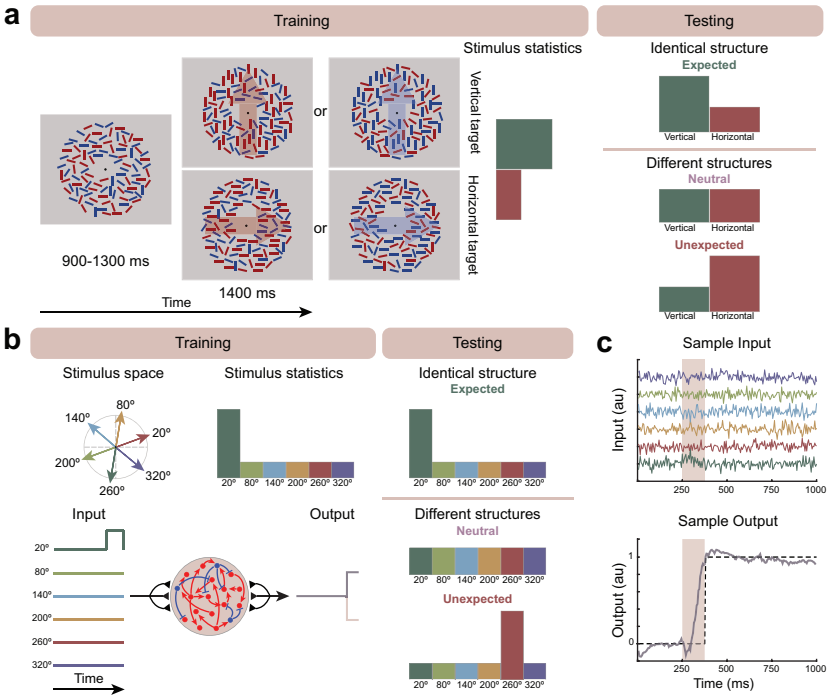

Figure 1: Task paradigms for humans and RNN model. **a.** Probabilistic decision making task. Human participants reported an orientation (horizontal or vertical) of coherently oriented red or blue bars. In this task paradigm, vertically oriented bars (green bar in the histogram) were more likely to be the targets as compared to horizontally oriented bars (red bar in the histogram) during training. After training, the participants were tested on three different 'environments' (right panel). **b.** Probabilistic decision making task used to train and test the RNN model. **c.** Network input and output from a sample RNN model on a trial where the presented stimulus was highly probable (i.e., Stimulus 1).

In order to model more realistic and biased sensory environments, we developed a simple training paradigm that resembled the one used in human studies (Figure 1b). In this paradigm, one input stimulus (out of 6 possible stimuli) was over-represented and presented to our RNN model more often than the rest of the stimuli during training. More specifically, the 'expected' stimulus was present in 80% of the training trials, while the other five 'unexpected' stimuli were equally represented (4% each). On each trial, one out of 6 possible stimuli was presented for 125 ms. The stimulus signals were modeled as white-noise signals (drawn from the standard normal distribution) with a constant offset value added during the stimulus window (Figure 1c, top panel). The offset value was varied to model the sensory strength and coherence (i.e., flicker frequency in the human data). The offset value of 0.6 and 0.7 were used to simulate the low and high flicker frequency, respectively. In total, we trained 30 RNNs of 200 units (80% excitatory and 20% inhibitory units) to perform this task.

Using this paradigm, we trained a continuous rate RNN model to produce an output signal approaching +1 when the expected stimulus was shown and 0 when an unexpected stimulus was given (Figure 1c). The RNN model employed in this study was similar to the one used in [9], and we used a gradient-descent method to train the model.

4 Results

In the human dataset, stimulus probability influenced behavioral performance such that accuracy was higher in the expected context than in the neutral and unexpected context in both low and high flicker frequency conditions (Figure 2a). Accuracy was also higher on trials where stimuli were rendered at a high flicker frequency (strong sensory strength) compared to the trials with a low flicker frequency. In addition, improvement in accuracy from the unexpected to expected context was more prominent in the low flicker frequency condition, suggesting that participants relied on their formed expectation more when the available sensory information was limited. This finding illustrates an interplay of

top-down (e.g., expectation) and bottom-up (e.g., sensory strength) signals and is in line with several theoretical and empirical work [10–13].

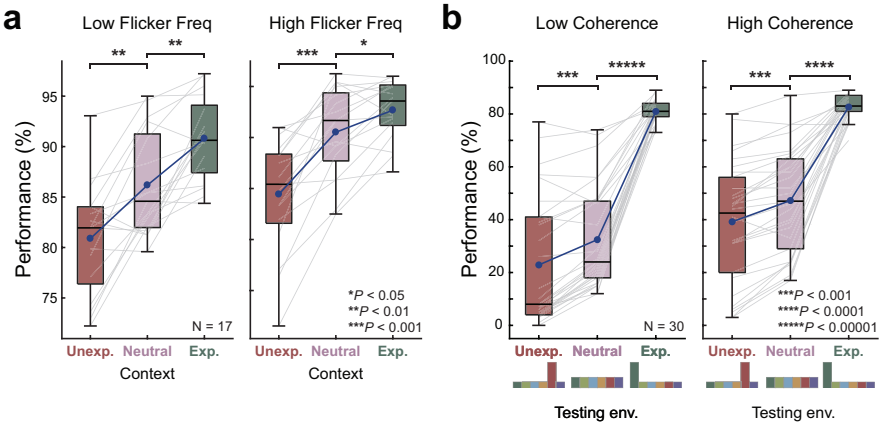

Figure 2: Performance on the probabilistic decision making task across contexts and testing environments as a function of the strength of sensory evidence. **a.** In humans, accuracy was higher in the expected context than in the neutral and unexpected context in both low and high flicker frequency conditions. Accuracy was also higher on trials where stimuli were presented at a high compared to a low flickering frequency. **b.** The RNN models exhibited similar performance trends as the human participants where performance was highest when the stimulus probability of the testing environment matched the learned expectation for both levels of sensory strength.

We observed similar task performance trends in our RNN model. When the stimulus probability was identical during the testing phase (i.e., Stimulus 1 was over-represented), our RNN model performed the task with high accuracy (Figure 2b) in both coherence conditions. When the stimulus environment was dramatically changed (i.e., one of the unexpected stimuli was over-represented), the model task performance significantly decreased (Figure 2b). The model performance for the 'neutral' environment, where all 6 stimuli were equally represented, was significantly higher than the performance from the 'unexpected' testing environment but lower than the one from the 'expected' condition. Overall, our RNN model findings are closely aligned with the results from the human behavioral data.

Although the exact circuit mechanisms underlying probabilistic information processing are not known, a recent experimental study revealed that probabilistic learning led to a group of neurons in the mouse primary visual cortex responding more robustly to expected or likely stimuli [14]. In order to investigate if such subgroup of neurons also exists in our RNN model, we first classified all the neurons in each trained RNN model based on their firing patterns in response to the six stimuli. For example, if a neuron fired more often when Stimulus 1 was presented, the neuron was assigned to the 'Stimulus 1' cluster. Using this method, we identified 6 subgroups of neurons in each RNN. For each subgroup, we then characterized its connectivity patterns to the rest of the subgroups. The resulting connectivity patterns revealed that the subgroup corresponding to the expected stimulus (i.e., Stimulus 1) had significantly stronger within-group excitation than across-group excitation for both coherence levels (Figure 3). In addition, the subgroup also exhibited significantly weaker within-group inhibition than across-group inhibition (Figure 3). Interestingly, the low coherence condition accentuated these differences in excitation and inhibition (Figure 3 d–f). Therefore, training our RNN model using a biased set of stimuli led to emergence of a subgroup of neurons that were more likely to stimulate themselves and inhibit other neurons resulting in enhanced neural responses at baseline.

5 Conclusions and future directions

In the present study, we employed a biophysically constrained RNN model to investigate the circuit mechanisms that underlie probabilistic information processing. By devising an RNN paradigm that resembles the perceptual tasks used to study probabilistic learning in humans, we validated and compared model performance to that of humans. Specifically, the model and humans both displayed

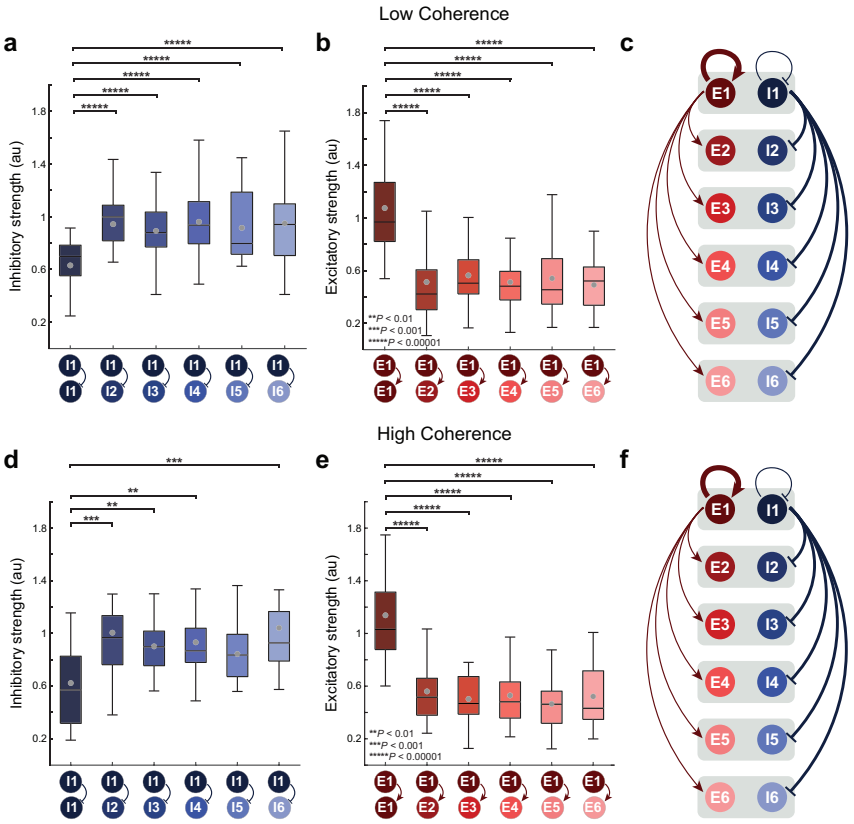

Figure 3: Network connectivity of the RNN models trained on an environment where stimulus 1 was highly probable (i.e., expected). Strength of pairwise inhibitory (left panel) and excitatory signals (middle panel) between neuron subgroups selective for each of the 6 stimuli were plotted. I_i and E_i represent the inhibitory and excitatory subgroup selective for stimulus i, respectively. **a.** In the low coherence condition, the neuron subgroup selective for the expected stimulus displayed a weaker within-group inhibition than across-group inhibition. **b.** The subgroup selective for the expected stimulus also exhibited a stronger within-group excitation than across-group excitation. **c.** A summary diagram of the pairwise inhibitory and excitatory strength in the low coherence condition. **d-f.** In the high coherence condition, the RNN models exhibited similar network connectivity patterns as observed in the low coherence condition. Boxplot central lines, median; gray circles, mean; bottom and top edges, lower and upper quartiles; whiskers, 1.5*interquartile range; outliers not plotted. $^{**}P < 0.01$, $^{***}P < 0.001$, $^{*****}P < 0.00001$ by Kruskal-Wallis, Dunn's multiple comparisons post hoc.

similar performance trends such that task accuracy increased with the degree of similarity between the stimulus probability of the testing and training environment or context. In addition, this expectation effect on behavior was accompanied by a combination of decreased within-group inhibition and increased within-group excitation of the neuronal subgroup selective for the expected stimulus.

Future works include comparing the RNN model connectivity results with animal electrophysiological data such as EEG and local field potentials (LFP). In particular, the behavioral improvement in the expected context reported in our human study was accompanied by changes in the pattern of parietal alpha and frontal theta oscillatory signals, previously used to index task effort and cognitive control. Specifically, parietal alpha power showed a sustained decrease in the unexpected context condition. This is consistent with the notion that violations of expectation require greater and prolonged task engagement [15]. Further, we observed an increase in frontal theta power when the target appeared in the unexpected context. This pattern is consistent with the hypothesis that unexpected contexts require greater executive control during later stages of decision-making including preparation and execution of motor responses [16]. Further analyses of the RNN network structures could shed light on the circuitry that gives rise to these oscillatory differences as a basis for probabilistic information processing in the human cortex.

Broader Impact

By analyzing both human and model data, the present study proposes an experimentally testable neural circuit mechanism important for decision making. Elucidating circuit mechanisms required for decision making will help better understand how such mechanisms are disrupted in neuropsychiatric disorders such as Alzheimer's disease and schizophrenia. We believe that the present study poses no negative ethical or societal issues.

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