Mathematical Model of Memory Consolidation Using Alternate Sampling between Neocortex and Hippocampus

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Abstract—It has long been controversial how different stages of sleep are involved in the process of memory consolidation. Experimental observations [1] lead to a possibility that during slow-wave sleep the pathway from hippocampus to neocortex is dominant, while during rapid eye movement sleep the opposite directional pathway becomes dominant. In this paper, we propose a mathematical model of memory consolidation based on the hypothesis. In this model, two parameterized probability distributions, corresponding to neocortex and hippocampus, alternately update their parameters using samples generated by themselves. We show that this learning scheme is efficient to avoid local optima traps, which implies a new interpretation of the functional meaning of sleep.

1. Introduction

Memory consolidation is a phenomenon in which temporally-stored labile memories are slowly organized, stabilized, and integrated with pre-existing knowledge in a brain. According to a widely-accepted explanation called the 'standard model' [2, 3], memories are firstly formed intermediated by hippocampus that has high plasticity. Then, the stored memories are replayed many times, which causes moderate updates of connections in neocortex. Finally, the memories are well established in neocortex so that they are no longer dependent on hippocampus. There are also some criticisms against the standard model, though [4].

Focusing on when memories are replayed and consolidated, sleep has been paid much attention [5, 6, 7, 8]. In fact, many experimental results support the idea that memory replay occurs during particular stages of sleep: slowwave sleep (SWS) and rapid eye movement (REM) sleep. In addition, both the two stages are related to dreaming.

However, the accumulated evidences also contain many conflicts, and it has long been controversial how different stages of sleep are involved in the process of memory consolidation [5, 9, 10, 11]. Some scientists suspect that REM sleep is not related to memory consolidation at all, because no obvious memory deficits can be observed after long-term inhibition of REM sleep [12, 13].

Among many hypotheses, Hasselmo [1] proposed a hypothesis in which during active waking the pathway from neocortex to hippocampus is dominant, while during quiet waking and SWS the opposite directional pathway becomes dominant. His hypothesis is mainly based on the change of acetylcholine levels in a brain, and REM sleep may be naturally categorized as the former class. In fact, Hasselmo did not do so in complicated circumstances. However, we think it is not wrong to assume that during REM sleep the pathway from neocortex to hippocampus is dominant because of the high acetylcholine level.

In this view point, SWS and REM sleep would have symmetrical roles. In SWS memories stored in hippocampus would be replayed, and they would be used for learning of neocortex. On the other hand, in REM sleep memories would be recalled in neocortex, and they would be used to update hippocampus.

In this paper, we propose a mathematical model of memory consolidation based on this hypothesis. We consider it in the framework of parameter estimation of probability distributions, and regard the roles of SWS and REM sleep as alternate sampling and learning between two probability distributions. The advantages of this learning scheme are discussed. They imply a new possible interpretation of functional meaning of sleep.

2. Alternate Sampling Method

Generative model based approach is often used to understand the function of a brain, especially in the field of visual perception [14]. We regard neocortex and hippocampus as two generative models. Let $\mathcal{M}_1 = P(x, y_1 | \theta_1)$ and $\mathcal{M}_2 = P(x, y_2 | \theta_2)$ denote generative models representing neocortex and hippocampus, respectively. Here *x*, *y_k*, and θ_k denote observable variables, latent variables, and parameter vectors, respectively. In the real brain, θ_k corresponds to synaptic weights. Here the hyper parameters of the generative models, which correspond to the number of neurons

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or the network structure, are omitted.

Given a set of data $D = \{x^1, ..., x^m\}$, we want to estimate the parameter vectors θ_k . This calculation corresponds to maximizing the posterior distributions below:

$$P(\theta_k \mid D) = \frac{P(D \mid \theta_k) P(\theta_k)}{P(D)} \quad (k = 1, 2).$$
(1)

The log-likelihoods $\ln P(D \mid \theta_k)$ (k = 1, 2) are described as follows if the samples are independent:

$$\ln P(D \mid \theta_k) = \ln \prod_{j=1}^m P(x^j \mid \theta_k),$$

$$= \sum_{j=1}^m \ln \sum_{y_k \in \mathcal{Y}} P(x^j, y_k \mid \theta_k),$$

$$= \sum_{j=1}^m \ln \sum_{y_k \in \mathcal{Y}} P(x^j \mid y_k, \theta_k) P(y_k \mid \theta_k), (2)$$

where the latent variables y_k are marginalized over.

Now we consider cases where the posteriors are so complicated that the optimal solutions cannot be analytically obtained, and we have to update θ_k step by step. These include both deterministic methods such as the expectationmaximization (EM) algorithm and stochastic methods such as the Markov chain Monte Carlo (MCMC) method. In addition, in some cases we use batch learning in which all *m* samples are used in each step, while in other cases incremental learning may be used in which only one sample is dealt with per step.

Based on the above-mentioned hypothesis, we derive a learning scheme for the parameter estimation problem. In this scheme, the three phases below are repeated in sequence:

- 1. Update \mathcal{M}_1 and \mathcal{M}_2 by using D (Wake phase),
- 2. Update M_1 by using new samples D_2^l generated by M_2 (SWS phase), and
- 3. Update M_2 by using new samples D_1^l generated by M_1 (REM phase),

where l denotes the iteration index.

The three phases correspond to waking, SWS, and REM sleep, respectively. In the wake phase, both models are updated by using the original data set *D* as usual. For simplicity, no interactions between the two models are considered, and we neglect the difference between active and quiet waking. In the SWS phase, new samples $D_2^l = \{x_2^{(l-1)m'_2+1}, \ldots, x_2^{lm'_2}\}$ of size m'_2 are generated by \mathcal{M}_2 . These represent memories recalled in hippocampus during SWS. Then, \mathcal{M}_1 is updated to maximize $P(\theta_1 \mid D_2^l)$ rather than $P(\theta_1 \mid D)$. Similarly, the REM phase is performed oppositely. The newly generated samples D_1^l of size m'_1 now represent memories recalled in neocortex during REM sleep.

In reality, we repeat several sleep cycles every night. For simplicity, however, we just go back to the wake phase when the REM phase finished in each cycle.

3. Application to a mixture of normal distributions

To investigate how the alternate sampling method works, we apply it to a mixture of normal distributions:

$$P(x \mid \theta) = \sum_{i=1}^{n} a_i N(x \mid \mu_i, \Sigma_i), \qquad (3)$$

where a_1, \ldots, a_n are the mixture weightings that satisfy $\sum_{i=1}^{n} a_i = 1$, and $N(x \mid \mu_i, \Sigma_i)$ is a two-dimensional normal distribution:

$$N(x \mid \mu_i, \Sigma_i) = \frac{1}{2\pi |\Sigma_i|^{1/2}} \exp\left(-\frac{1}{2}(x - \mu_i)^{\mathrm{T}} \Sigma_i^{-1}(x - \mu_i)\right), \quad (4)$$

where $|\cdot|$ denotes determinant.

It is useful to introduce a latent variable *y*. Then, Eq. 3 can also be viewed as a marginalization over it:

$$P(x \mid \theta) = \sum_{i=1}^{n} P(y = i \mid \theta) P(x \mid y = i, \theta).$$
(5)

The parameter vector θ consists of a_i , μ_i , and Σ_i (i = 1, ..., n). To estimate the parameter vector θ , the EM algorithm was used. In practice, a normal distribution tends to be infinitely sharp when it covers only one sample. To avoid this, an ad hoc approach was taken instead of introducing prior distributions of Σ_i ; all eigenvalues of the covariance matrices under a threshold *d* were reset to *d*.

In the following simulations, the two models have the same degree of freedom, and only the initial values of the parameters are different between them. The original data set D (m = 500) is shown in Fig. 1. The length of the three phases in the alternate sampling method are 50, 25, and 25 steps per cycle. Other parameters are set as follows: n = 5, $m'_1 = m'_2 = 500$, and d = 0.005.

4. Result

At first, the standard EM algorithm and the alternate sampling were compared. Figure 2 shows the learning

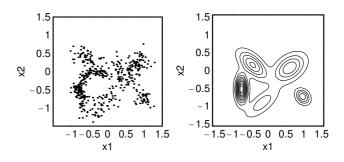


Figure 1: Training data set (m = 500) and the best configuration (n = 5, $-\ln P(D \mid \theta) = 501.33$). There exist many other locally optimal configurations.

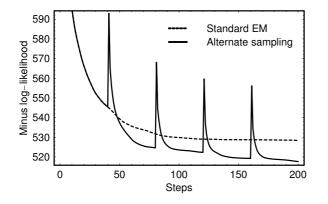


Figure 2: Averaged learning curves. Four jumps of the alternate sampling correspond to the applications of the SWS and REM phases, and only the behavior of the wake phases is plotted.

curves averaged over 100 trials. Since no significant differences between the two models of the alternate sampling were seen, the results of the two models were merged together. In the SWS and REM phases (not shown in Fig. 2), the values of the minus log-likelihoods increased, and later in the wake phases the two models tended to find better solutions. Therefore, it was shown that the alternate sampling method is efficient to avoid local optima traps.

The distribution of the configurations at the end of each trial is shown in the Fig. 3. The dot near the bottom left edge represents the state where both the two models obtained the best configuration. Compared with the expected distribution calculated by using the results of the standard EM, many configuration pairs fell in the apparent three lines: a diagonal line and the two parallel to the axes.

It may be possible to interpret these as absorbing regions. When one of the two models obtains the best configuration, the samples it generates would be similar to the original data. Therefore, the effect of the SWS or REM phase would be weakened. Similarly, if the two models happened to get close at an undesirable state, the influence may also decrease. Eventually, the stability of a configuration pair would be determined by the balance between the strength of the effect and the stability of the local optima.

Next, to investigate the effect of sampling fluctuations, we considered a simplified learning scheme in which one model updates its parameters using samples generated by itself during the sleep phases. Figure 4 shows the results. As the number of samples increases, the performance of the self-sampling scheme got to be comparable to the standard EM, while the alternate sampling still had significant improvements. Therefore, while the effect of sampling fluctuations does exist with a small number of samples, the difference of the two models is also important.

The effect of the number of cycles was also investigated. As expected, the advantage against the standard EM was

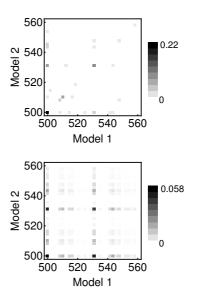


Figure 3: (Top) the distribution of the configurations at the end of each trial of the alternate sampling, and (bottom) the expected distribution calculated by using the results of the standard EM.

lost with both too few cycles and too many cycles, and the best performance was obtained around 4 or 5 cycles.

Finally, the Gibbs sampling was simulated instead of the EM algorithm. Figure 5 shows the result of the Gibbs sampling. The number of cycles was changed to 20. After a long run, both two cases reached to a similar distribution. However, the alternate sampling approached it a little more rapidly. The distance between the two averaged curves was largest around 100 steps.

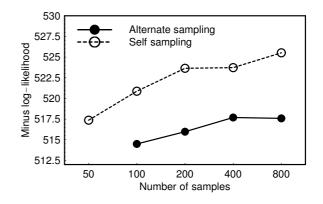


Figure 4: Comparison between the alternate sampling and the self-sampling.

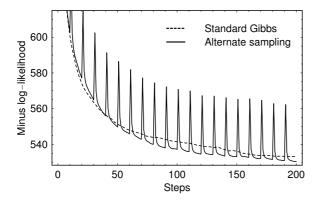


Figure 5: Averaged learning curves of the Gibbs sampling.

5. Conclusion

To understand how different stages of sleep are involved in the process of memory consolidation, we have proposed a mathematical model in which two parameterized probability distributions, corresponding to neocortex and hippocampus, alternately update their parameters using samples generated by themselves. We have found that this learning scheme is efficient to avoid local optima traps, which implies a new interpretation of the functional meaning of sleep.

In this paper, we dealt with cases where the hyper parameters of the two models are the same. When we use different models or different step sizes for updating parameters, the two models would come up with shortcomings each other keeping their own advantages. This aspect is consistent with the general explanation how neocortex and hippocampus contribute to learning [15]. The study on such heterogeneous cases is an important future problem.

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