

A Computational Model to Account for Dynamics of Spatial Updating of Remembered Visual Targets across Slow and Rapid Eye Movements

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After an intervening eye movement, or saccade, humans and animals are able to localize previously perceived visual targets. In other words, when their eyes fall in the final post-saccadic position, the remembered visual information is updated relative to the new gaze position. This process is known as trans-saccadic spatial updating. Although efforts have been made to discover the mechanism underlying spatial updating in humans and animals, there are still many unanswered questions about the neuronal mechanism of this phenomenon. We developed a nonlinear state space model (SSM) for updating target-related spatial information in gaze-centered coordinates with the following dynamical equations:

$$s_{k+1} = f(s_k, u_k, w) + v_k \quad (1)$$

$$y_k = h(s_k, u_k, w) + n_k \quad (2)$$

where s_k is a vector representing the hidden states, u_k denotes the control input, y_k is called noisy observation in the concept of state space model, v_k and n_k are respectively state transition noise and observation noise, f and h represent the model structure and are implemented through a multi-layer RBF neural network, finally w shows the weight vector of the neural network. The structure of the model is demonstrated in Figure 1. We considered three types of input in our proposed model: 1) an efference copy signal, inspired by motor burst signal in SC, 2)

an eye position signal, found in many LIP, VIP, MT and MST neurons and 3) 2D visual topographic maps of visual stimuli, located in SC. To model the internal neuronal behaviour of the system, we developed a radial basis function (RBF) neural network which can be trained with sequences of input-outputs using a version of the Kalman filter known as Extended Kalman filter. This neural network represents the state space from which we can obtain a topographic map of the remembered target in the hidden layer. Finally, the output of our proposed model is the decoded location of the remembered target. In order to find the hidden states in our model, we employed Kalman filtering approach.

To explore the internal mechanism underlying updating process, we trained this model on a double step saccade-pursuit or pursuit-saccade task. After training, the receptive fields of state-space units replicated both predictive remapping during saccades (Duhamel et al. *Science* 1992) and continuous eye-centered updating during smooth pursuit (Dash et al. *Current Biology*, 2015). In addition, during trans-saccadic remapping, receptive fields also expanded (Figure 2). To our knowledge, this predicted expansion has not yet been reported in the published literature.

