

Multiple Representations and Algorithms for Sequence Learning

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Humans and primates can learn a large variety of skills and patterns of movement. How is the information about their spatio-temporal patterns encoded in our brain? Recent animal experiments and human brain imaging studies suggest that the global networks linking specific parts of the cerebellum, the basal ganglia, and the cerebral cortex are involved in learning and execution of sequential movement. Execution of sequential movement initially requires attention but becomes automatic after repeated practice. We postulate that this process is supported by the use of different coordinate systems as well as different algorithms.

In a visuo-motor task, a sequence can be defined either as a series of moving targets in the visual space or as a series of body movement (Figure 1B). We propose that visual representation of sequence is used in the circuit linking the anterior basal ganglia and the prefrontal cortex (the visual network) while body-based representation is used in the circuit linking the posterior basal ganglia and the motor cortex (the motor network). Sequence representation using the visual coordinate is advantageous for quick learning whereas sequence representation in the motor coordinate is advantageous for real-time control.

We built a neural network model of visuo-motor sequence learning which included two recurrent networks, one using visual coordinate and the other using motor coordinate (Figure 2). Learning is based on the "temporal difference" reinforcement learning paradigm, which has recently been proposed as a functional model of the midbrain dopaminergic system (Schultz et al., 1997). The model was used to simulate the sequence learning exper-

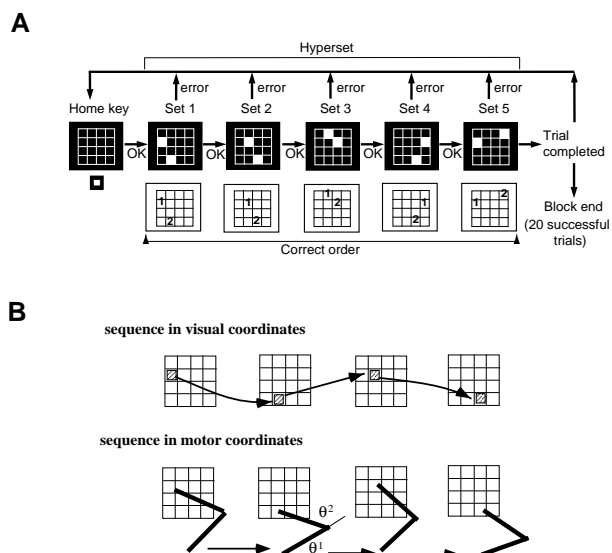


Figure 1: **A.** The 2x5 task for monkeys (Hikosaka et al., 1995). A subject presses five sets two LED buttons in a pre-determined order, which has to be found by trial and error. Liquid reward is given after completion of each *set* of two key presses. The amount of reward is increased as the progress through a five-set sequence, called a *hyperset*. When the subject makes an error, the trial is terminated and restarted. A hyperset is used repeatedly until the number of successfully completed trials reaches to a criterion (10 or 20). Each training day, several hypersets are used for training; some of them are repeatedly used everyday and others are newly generated and used only once. **B.** Two possible ways of representing a movement sequence. Upper panel: to encode the sequence of the visuospatial locations of the buttons to be pressed (visual sequence). Lower panel: to encode the sequence of target postures, for example, by arm joint angles (motor sequence: lower panel).

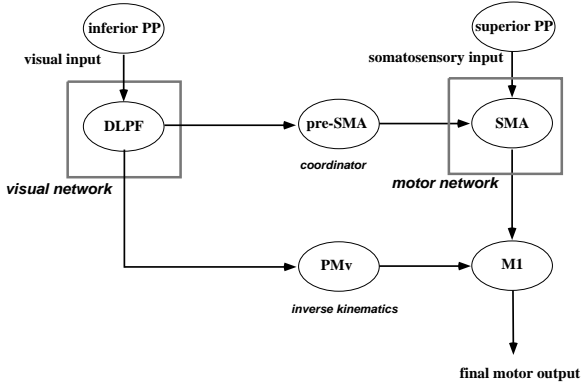


Figure 2: The network model of sequence learning using visual and motor representations (Nakahara et al., 1997). The visual network corresponds to the anterior basal ganglia and its target cortical area, the dorsolateral prefrontal cortex (DLPF). The motor network corresponds to the posterior basal ganglia and its target cortical area, including the supplementary motor area (SMA). The pre-SMA, which links the visual and motor networks, works as a coordinator between the two networks by modulating the the motor network output based on the visual network output. The ventral premotor are (PMv) transforms the visual network output, which is in visual coordinate (target spatial position), into motor coordinate (desired joint angles). The outputs of the visual and motor networks converge at the primary motor cortex (M1). A sequence is learned simultaneously by the visual and motor networks based on a reinforcement learning algorithm known as “temporal difference (TD)” learning.

iments in monkeys, called the “2x5 task”. It was found in monkeys that the blockade of the anterior basal ganglia disrupted acquisition of new sequences whereas the blockade of the posterior basal ganglia disrupted execution of well learned sequences (Miyachi et al., 1997). The network model replicated this experimental result with the blockade of the visual and motor networks (Nakahara, 1997; Nakahara et al., 1997).

We further performed a human behavioral experiment to investigate the hypothesis that a subject initially uses visual representation and gradually depends more on motor representation of sequence. Subjects pressed a series of keys on a keypad in response to the visual stimuli on the screen. Transfer of response time performance was tested in two altered conditions: VISUAL condition in which the same key was pressed using dif-

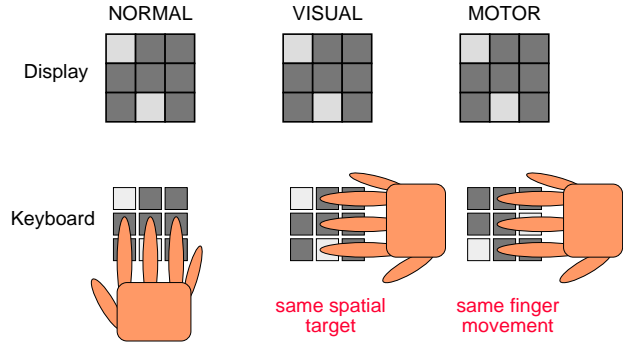


Figure 3: The experiment for assessing the representations of movement sequence (Bapi et al., 1998, 1999). A subject is trained in the 2x10 task, which is similar to the 2x5 task described in Figure 1, in the NORMAL display-keypad setting. The performance of the subject was tested in two altered settings. In VISUAL setting, the orientation of the hand is rotated 90 degrees, requiring different finger movement for pressing the same key sequence. In MOTOR setting, the keypad is also rotated 90 degrees, resulting in the same finger movement as in NORMAL to reach spatially relocated keys.

ferent finger movement and MOTOR condition in which the keys were relocated but the same finger movement was used to press the keys. The response time was initially similar for both conditions, but after about one hour of practice, significantly better transfer was seen in MOTOR condition (Bapi and Doya, 1998, 1999).

In addition to the use of multiple representations, the differential involvement of brain areas in early and late stages of sequence learning may also be due to the use of different action selection algorithms. Experimental and theoretical evidence suggests that the the cerebellum, the basal ganglia, and the cerebral cortex are specialized, respectively, in supervised, reinforcement, and unsupervised learning paradigms (Doya, 1999). The theory of reinforcement learning and dynamic programming and provides several candidate architectures for utilizing those learning modules. The simplest architecture involves a stochastic action selection network and a state evaluation of the current state (Figure 4A). The evaluation network learns to predict future reward based on the current state. The temporal difference in the predicted reward is used as the reinforcing signal for the action selection network. In a

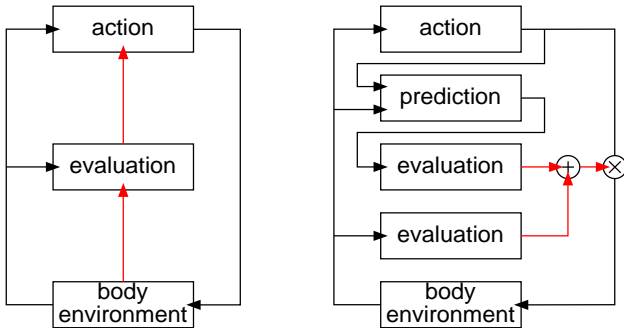


Figure 4: Possible implementation of different sequence learning algorithms in the circuit linking the cerebellum, the basal ganglia, and the cerebral cortex. **A.** A reactive, stochastic action selection network is trained with the help of a predictive reward signal from the evaluation network. The evaluation network trains itself by comparing its prediction with the actual delivery of reward. Such a mechanism can be implemented, for example, by the network linking the supplementary motor area (SMA) and the posterior basal ganglia. **B.** A candidate of action is fed, together with the current state of the body and the environment, to the internal model of the body and the environment to predict the next state. The evaluation of the predicted state is compared with that of the current state. The candidate action is put to execution if it is expected to improve the state. Such a mechanism can be implemented by the network linking the prefrontal and rostral premotor cortices, the ventral lateral cerebellum, and the anterior basal ganglia.

more elaborate architecture (Figure 4B), an internal model of the environmental dynamics is used for the prediction of the next state if a candidate of action is taken. The evaluations for the predicted and the current states are compared and the action is executed if it is expected to improve the evaluation. Results of brain imaging and neuron recording suggest that the first algorithm that uses reactive, stochastic action selection is used in the network linking the SMA and the basal ganglia. The second algorithm can be implemented in the network linking the prefrontal and rostral premotor areas, the ventrolateral cerebellum, and the basal ganglia.

In summary, humans and primates can utilize multiple representations and algorithms for learning and control of sequential movement. Multiple parallel loops linking the cerebellum, the basal ganglia, and the cerebral cortex would enable both quick acquisition and robust, automatic execution. Similar mech-

anisms may be used for cognitive tasks that involve sequential processing.

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