



2013 Special Issue

Transfer of memory trace of cerebellum-dependent motor learning in human prism adaptation: A model study

Soichi Nagao^{a,*}, Takeru Honda^{a,b}, Tadashi Yamazaki^c

^a Laboratory for Motor Learning Control, RIKEN Brain Science Institute, Hirosawa 2-1, Wako, Saitama 351-0198, Japan

^b Japan Society for the Promotion of Science, Chiyoda 1-8, Tokyo, 102-8472, Japan

^c Graduate School of Informatics and Engineering, The University of Electro-Communications, Chofugaoka 1-5-1, Chofu, Tokyo 182-8585, Japan

ARTICLE INFO

Keywords:

Cerebellum
Nondeclarative memory
Memory transfer
Voluntary movement control
Motor learning
Prism adaptation

ABSTRACT

Accumulating experimental evidence suggests that the memory trace of ocular reflex adaptation is initially encoded in the cerebellar cortex, and later transferred to the cerebellar nuclei for consolidation through repetitions of training. However, the memory transfer is not well characterized in the learning of voluntary movement. Here, we implement our model of memory transfer to interpret the data of prism adaptation (Martin, Keating, Goodkin, Bastian, & Thach, 1996a, 1996b), assuming that the cerebellar nuclear memory formed by memory transfer is used for normal throwing. When the subject was trained to throw darts wearing prisms in 30–40 trials, the short-term memory for recalibrating the throwing direction by gaze would be formed in the cerebellar cortex, which was extinguished by throwing with normal vision in a similar number of trials. After weeks of repetitions of short-term prism adaptation, the long-term memory would be formed in the cerebellar nuclei through memory transfer, which enabled one to throw darts to the center wearing prisms without any training. These two long-term memories, one for throwing with normal vision and the other for throwing wearing prisms, are assumed to be utilized automatically under volitional control. Moreover, when the prisms were changed to new prisms, a new memory for adapting to the new prisms would be formed in the cerebellar cortex, just to counterbalance the nuclear memory of long-term adaptation to the original prisms in a similar number of trials. These results suggest that memory transfer may occur in the learning of voluntary movements.

© 2013 Elsevier Ltd. All rights reserved.

1. Introduction

The gain adaptation of the vestibulo-ocular reflex (VOR) and optokinetic response (OKR), as well as the delayed eyelid conditioning, provides an experimental paradigm of cerebellum-dependent motor learning (e.g. Ito, 1984, 2001, 2011). Although both VOR and OKR are driven by the relatively simple neural network composed of the cerebellar flocculus and vestibular nuclei (Fig. 1), the site of the memory trace of adaptation was an issue of debate for over twenty years (Melvill-Jones, 2000). Now, the multiple distribution of the memory trace of adaptation, which was originally proposed conceptually (Galiana, 1986; Quinn, Didier, Baker, & Peterson, 1998; Raymond & Lisberger, 1996), has been supported by studies of the adaptation of mouse OKR (Okamoto, Endo, Shirao, & Nagao, 2011a; Shutoh, Ohki, Kitazawa, Itohara, & Nagao, 2006), and cat (Kassardjian et al., 2005) and monkey (Anzai, Kitazawa, & Nagao, 2010; Nagao & Kitazawa, 2003) VOR. These experimental

studies consistently suggest that the memory trace of adaptation is initially encoded in the cerebellar cortex, and later is transferred outside the cerebellar cortex after repetitions of training. The most likely site for the storage of long-term adaptation of VOR/OKR is now assumed to be within the cerebellar (vestibular) nuclei (VN, Fig. 1). Recent computational studies have also supported such a training-history-dependent memory transfer in delayed eyelid conditioning (Ohyama, Nores, Medina, Riusech, & Mauk, 2006) and adaptation of ocular reflexes (Masuda & Amari, 2008; Yamazaki & Nagao, submitted for publication). However, whether memory transfer may occur in the learning of voluntary movements has not been clarified.

Several experimental paradigms have been developed to study the learning of human voluntary movement. Thomas Thach and his colleagues have developed a paradigm of throwing darts while viewing the target through prisms (Martin et al., 1996a, 1996b), also see Thach, Goodkin, and Keating (1992). In their study, when a subject threw darts wearing left-shifting prisms, initially the subject threw darts leftward, but soon recalibrated the throwing direction by gaze and threw darts to the center of the target. This short-term prism adaptation is considered to be dependent on

* Corresponding author. Tel.: +81 48 467 9794; fax: +81 48 467 9793.

E-mail addresses: nagaos@brain.riken.jp, nagao-so@umin.ac.jp (S. Nagao), takeru@brain.riken.jp (T. Honda), nn12@neuralgorithm.org (T. Yamazaki).

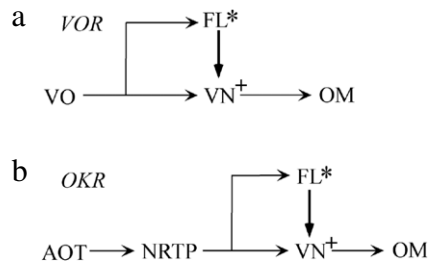


Fig. 1. Neural circuits of horizontal vestibulo-ocular reflex (VOR, a) and optokinetic response (OKR, b) eye movement, and the sites of memory trace of adaptation. *, + respectively show the sites for the memories of short- and long-term gain adaptation. AOT, accessory optic tract; FL, cerebellar flocculus; NRTP, nucleus reticularis tegmenti pontis; OM, motor neurons of extraocular muscles; VN, vestibular nucleus; VO, vestibular organ.

cerebellar learning, because it is impaired in patients with cerebellar disease, most profoundly in the patient with lesions restricted to the inferior olive (Martin et al., 1996a). Monkey lesion (Baizer, Kralj-Hans, & Glickstein, 1999) and pharmacological inactivation (Norris, Hathaway, Taylor, & Thach, 2011) studies have also suggested that the cerebellum plays an essential role in prism adaptation. Interestingly, when a subject was trained to throw darts wearing the prisms repetitively for 3 months, a long-term prism adaptation occurred and the subject became able to throw darts to the center in the first trial even when wearing prisms (Martin et al., 1996b). We implemented our model (Yamazaki & Nagao, submitted for publication), in which the memories of short- and long-term adaptations are respectively formed in the cerebellar cortex and CN, to the data of Martin et al. (1996a, 1996b). We assume that the memory formed in CN through the memory transfer is robust and keeps much longer than the memory formed in the cerebellar cortex by short-term adaptation, so that we consider that the memory formed in CN is used for normal throwing. We interpreted some of the behavioral observations as being due to the cooperation of memories formed in the cerebellar cortex and CN. Results of our model study suggest that memory transfer may occur in the learning of voluntary movements which is controlled by cerebro-cerebellar networks.

2. Results

2.1. Behavioral characteristics of short- and long-term prism adaptation

Fig. 2(a) shows the time course of short-term prism adaptation in the study by Martin et al. (1996a). In their experiment, the subject threw darts wearing 50 cm-left-shifting prisms (L-prisms). Initially, the subject threw darts 50 cm leftward from the center of the target. After 30–40 trials of dart throwing wearing L-prisms, the subject learned to throw darts to the center. After the completion of adaptation to L-prisms, the subject took off the L-prisms and threw darts. The dart shifted 50 cm rightward in the first trial, suggesting that the subject learned to throw 50 cm right from the gaze direction when wearing the L-prisms (III in Fig. 2(a)). By repetition of throwing with normal vision, the subject relearned to throw darts to the center. It is notable that the time courses of learning and relearning were similar.

Fig. 2(b) and (c) show the behavioral characteristics of long-term prism adaptation (Martin et al., 1996b). When the protocols of short-term prism adaptation (Fig. 2(a)) were repeated 4 times/week for 6 weeks, the subject was able to throw the dart to the center wearing the L-prisms even in the first trial (VII in Fig. 2(b)), i.e., the subject learned to throw darts rightward from the gaze direction when wearing the L-prisms. This is long-term prism adaptation, because the memory persisted more than 2 years (Martin et al., 1996b). After such a long-term adaptation to L-prisms, the prisms were changed to new 50 cm-right-shifting prisms (R-prisms). In the first trial, the dart shifted 100 cm rightward from the center of the target (B in Fig. 2(c)). After 30–40 trials of throwing darts wearing R-prisms, the subject learned to throw darts to the center of the target (C in Fig. 2(c)). Then, the subject took off the R-prisms and threw the dart only once. The dart shifted 50 cm leftward from the center (D in Fig. 2(c)), suggesting that learning to throw 50 cm rightward from the gaze direction occurred by short-term adaptation to R-prisms. Again, the subject wore the original L-prisms and threw the dart (E in Fig. 2(c)). The dart also shifted 50 cm leftward from the center in the first trial. After 30–40 trials of dart throwing wearing L-prisms, the subject learned to throw

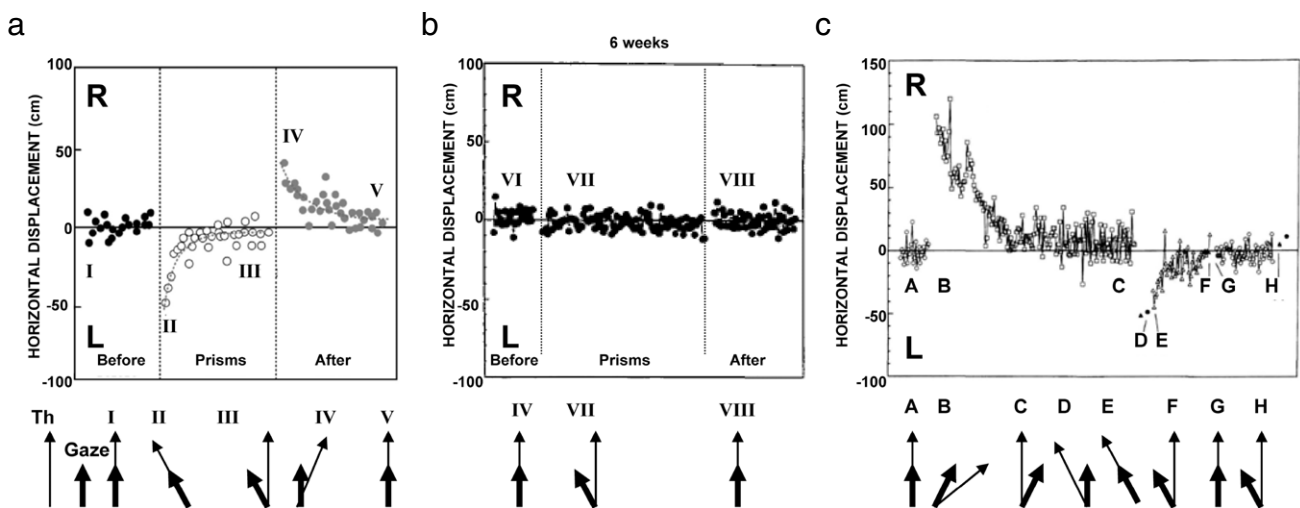


Fig. 2. Characteristics of dart throwing in short-term prism adaptation (a), and long-term prism adaptation (b and c) in Martin et al. (1996a, 1996b). (a): Dart throwing before (before), during (Prisms), and after (After) wearing 50 cm-left-shifting prisms (L-prisms) for one healthy subject. Dotted curves show best-fitted curves for the difference from the center of the target in 40 trials. (b): Similar to a, but for the subject who had been trained to throw darts wearing L-prisms for 6 weeks (4 sessions/week). Note that the subject threw darts to the center of the target in the initial trial, irrespectively of wearing or not wearing prisms. (c): After 6 weeks of adaptation to L-prisms (A), the prisms were switched to new 50 cm-right-shifting prisms (R-prisms, B). Immediately, the subject learned to throw darts to the center (C). Then, the subject threw the dart without any prisms once (D). Again, the subject wore the original L-prisms and threw darts (E). Immediately, the subject relearned to throw straight (F). Finally, the subject threw darts not wearing (G) or wearing (H) the original L-prisms. Thick and thin arrows in the bottom (I–VIII and A–H) respectively show the directions of gaze (Gaze) and dart-throwing (Th) during sessions of prism adaptation.

Download English Version:

<https://daneshyari.com/en/article/6863372>

Download Persian Version:

<https://daneshyari.com/article/6863372>

[Daneshyari.com](https://daneshyari.com)