Research report

Modulation of prism adaptation by a shift of background in the monkey

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HIGHLIGHTS

- In monkeys, prism adaptation can be canceled or enhanced by a shift of the background during each reaching movement.
- The shift of the background alone increased the motor error in the direction of the shift.
- A small but salient figure could not serve as a background.
- The monkey and the human share the same neural mechanisms for representing a target relative to the background.

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ABSTRACT

Recent human behavioral studies have shown that the position of a visual target is instantly represented relative to the background (e.g., a large square) and used for evaluating the error in reaching the target. In the present study, we examined whether the same allocentric mechanism is shared by the monkey. We trained two monkeys to perform a fast and accurate reaching movement toward a visual target with a square in the background. Then, a visual shift (20 mm or 4.1°) was introduced by wedge prisms to examine the process of decreasing the error during an exposure period (30 trials) and the size of the error upon removal of the prisms (aftereffect). The square was shifted during each movement, either in the direction of the visual displacement or in the opposite direction, by an amount equal to the size of the visual shift. The ipsilateral shift of the background increased the asymptote during the exposure period and decreased the aftereffect, i.e., prism adaptation was attenuated by the ipsilateral shift. By contrast, a contralateral shift enhanced adaptation. We further tested whether the shift of the square alone could cause an increase in the motor error. Although the target did not move, the shift of the square increased the motor error in the direction of the shift. These results were generally consistent with the results reported in human subjects, suggesting that the monkey and the human share the same neural mechanisms for representing a target relative to the background.

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1. Introduction

Our brains are able to encode a target position not only relative to body-centered coordinates but also relative to landmarks in the background, when we are forced to complete a delayed reaching task after the target has disappeared [1–5]. In these studies, the

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errors in reaching was reported to decrease when landmarks were available as compared to when they were not available. However, the decrease became apparent only when the delay was as long as, or longer than 2 s, and was not significant when participants were allowed to make a reach to the target as soon as it disappeared. This raised a question as to whether such an allocentric representation of a target is essential in our daily life, in which we are allowed to make an immediate reach to the target without waiting for its disappearance or waiting further for 2 s.

We addressed this question recently, and showed that the target position is automatically encoded relative to a background square without any effort, and that the allocentric representation makes a significant contribution to the evaluation of the error in each immediate reach [6]. Others also showed recently that a visual stimulus is instantly and automatically encoded relative to a background square while participants performed visual perception task [7,8]. These studies clearly show that the brain represents a target position instantly and automatically relative to a square in the background.

In our recent functional imaging study with human participants, we further showed that the background coordinates that work automatically without endeavor are likely to be represented in the right precuneus [9]. However, noninvasive studies with human participants are not sufficient to explore the neural codes underlying the allocentric coding and decoding processes. It is therefore important to test whether the same experimental paradigm for the human participants yield the same results in the monkey. In the present study, we used two monkeys to examine whether the target position is automatically encoded and decoded relative to the background square, by using the similar experimental procedures that we used in our previous study [6]. In Experiment 1, we used prism adaptation and examined if adaptation could be canceled or enhanced by shifting a square in the background in midflight of each reaching movement (Fig. 1a and b). In Experiment 2, we did not use prisms but just shifted the target and/or the background in midflight of a reach (Fig. 1c). In both experiments, a shift of the background induced an effect that was predicted from the existence of the background coordinate.

2. Materials and methods

2.1. Animals

Two male adult monkeys (*Macaca fuscata*, monkey A, 7.8 kg; monkey O, 7.0 kg) were used. Both monkeys participated in Experiment 1, and one monkey (monkey A) participated in Experiment 2. The procedures were in accordance with the Guidelines for Proper Conduct of Animal Experiments established by the Science Council of Japan and were approved by the Ethics Review Committee for Animal Experimentation of Juntendo University School of Medicine and Graduate School of Frontier Biosciences, Osaka University.

2.2. Surgery

Before training, surgery was performed under aseptic conditions to fix a head-restraining device to the skull. The monkeys were first administered ketamine (10 mg/kg body weight) intramuscularly and then received an intravenous injection of pentobarbital sodium (20 mg/kg body weight). After partially exposing the skull, polycarbonate screws (3 mm in diameter and 5 mm in length) were used to firmly attach the head-restraining device to the skull. The screws and head-restraining device were fixed with dental acrylic resin. Before the surgery, the monkeys were administered an analgesic (Butorphanol Tartrate 0.2 mg, i.v.). The monkeys received systemic antibiotics (cefazolin 50 mg/kg, i.m.) for 1 week after surgery. The monkeys were also given water and chow ad libitum for at least 1 week after surgery. After the monkeys had completely recovered from surgery, training was initiated.

2.3. General task procedures

The monkey was seated on a primate chair with its head fixed to a stable frame and with its right forelimb gently restrained to an armrest to expedite the use of the left arm. The monkey was trained to make rapid reaching movements with its left arm toward a visual target that appeared on a screen located 280 mm from its eyes (Fig. 1a). The monkey viewed the screen through a refractor in front of the right eye that restricted the field of view to 8.9° in radius. The refractor was equipped with a pair of motor-driven wedge prisms inside that were designed to achieve a desired displacement of 0–24D (0–14°) in any direction in response to a command from a PC.

A trial began when the monkey entered its index finger into a slit that was positioned 260 mm below the eyes. A target (5 mm diameter yellow circle superimposed on a cross, 15 × 15 mm) and a red square then appeared after a random delay (800–1200 ms). The target was presented at a random location in a square target zone (40 × 40 mm) in the center of the visual field, while the square was always presented in the center until reaching was initiated. The monkey had to release the button within 400 ms of the appearance of the target and touch the screen within 400 ms of releasing the button. The monkey's view of its hand and the target were blocked at the release of the button by a liquid-crystal shutter in front of the refractor. The shutter opened again when the screen was touched, allowing the monkey to see the target, the square, and the final position of its hand for 300 ms. The touch position was detected with a touch sensor (ERTS1701, EIT, Tokyo) that covered the surface of the screen. The monkey had to maintain the final hand position for 1000 ms until a reward was given. To encourage accurate reaching, the size of the reward was inversely proportional to the magnitude of the error [10].

2.4. Design of the experiments

Each run of the experiments consisted of three periods: (1) pretest (15 trials), (2) exposure (30 trials), and (3) post-test (30 trials).

2.4.1. Experiment 1

Two monkeys participated. During the exposure period, the visual field was displaced by 20 mm (4.1°) to the left or right. The direction of the visual displacement was kept constant through each exposure period. No visual displacement occurred during the pre- and post-test periods. During the entire exposure period, the square was not shifted (no shift condition, Fig. 1b left), shifted in the direction of visual displacement by the same amount (ipsilateral shift condition, Fig. 1b middle), or shifted in the opposite direction (contralateral shift condition, Fig. 1b right). Because the cross never moves, prism adaptation should not be altered at all if the brain can ignore the background, or the brain just relies on the error between the hand and the target itself (target error, Tgt error). By contrast, if the target position is automatically encoded and decoded relative to the background (dotted circle in Fig. 1b), the brain would rely on the error between the hand and the target position encoded in the background coordinate (background error, Bkg error) rather than the Tgt error. In the no-shift condition, the two errors are identical (Fig. 1b, left). Thus the ordinary prism adaptation should be observed. In the ipsilateral shift condition, the Tgt error remains the same whereas the Bkg error is annulled because the hand lands on the initial position of the target relative to the background. Then, the prism adaptation should be canceled if the brain relies on the