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Alteration of a motor learning rule under mirror-reversal transformation does not depend on the amplitude of visual error

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ABSTRACT

Human's sophisticated motor learning system paradoxically interferes with motor performance when visual information is mirror-reversed (MR), because normal movement error correction further aggravates the error. This error-increasing mechanism makes performing even a simple reaching task difficult, but is overcome by alterations in the error correction rule during the trials. To isolate factors that trigger learners to change the error correction rule, we manipulated the gain of visual angular errors when participants made arm-reaching movements with mirror-reversed visual feedback, and compared the rule alteration timing between groups with normal or reduced gain. Trial-by-trial changes in the visual angular error was tracked to explain the timing of the change in the error correction rule. Under both gain conditions, visual angular errors increased under the MR transformation, and suddenly decreased after 3–5 trials with increase. The increase became degressive at different amplitude between the two groups, nearly proportional to the visual gain. The findings suggest that the alteration of the error-correction rule is not dependent on the amplitude of visual angular errors, and possibly determined by the number of trials over which the errors increased or statistical property of the environment. The current results encourage future intensive studies focusing on the exact rule-change mechanism.

1. Introduction

Humans have an ability to adapt their movements to changes in the internal/external environment. For example, using arm-reaching tasks, many studies have shown experimentally that people can adapt to a novel dynamical environment such as a viscous force field (Shadmehr and Mussa-Ivaldi, 1994; Thoroughman and Shadmehr, 2000), and to a novel visuomotor environment such as visuomotor rotation (Krakauer et al., 2000; Mazzoni and Krakauer, 2006) and lateral displacements (Harris, 1965; Hatada et al., 2006). Such ability is underpinned by sophisticated trial-by-trial error correction mechanisms during the adaptation process. For example, the mechanisms correct movement errors implicitly (Mazzoni and Krakauer, 2006) and respond to errors even when they fall within natural movement variability (van Beers, 2009).

However, this normally effective system turns out to be harmful to motor control during leftward-rightward mirror-reversal (MR) of visual feedback. Under the MR condition, the normal error correction rule (i.e., inter-trial learning rule) may further aggravate even very small error to be amplified across trials (Lillicrap et al., 2013), and make the motor control system unstable. For example, in the normal error correction rule, we may correct movements in the leftward direction when we observe a visual angular error (i.e., an angular deviation between visual feedback and the target) in the rightward direction. However, under the MR condition, such leftward error correction results in an increase of errors in the leftward direction (Fig. 1). Nevertheless, some studies report that humans can successfully adapt to this visual environment after a substantial amount of exposure (Kohler, 1964; Day and Lyon, 2000; Sekiyama et al., 2000; Gritsenko and Kalaska, 2010).

The mechanism of learning the MR transformation is quite different from that of other types of visuomotor transformation. As mentioned, under the MR transformation condition we are never able to adapt to the environment without alterations of the error correction rule itself (Lillicrap et al., 2013), otherwise the error

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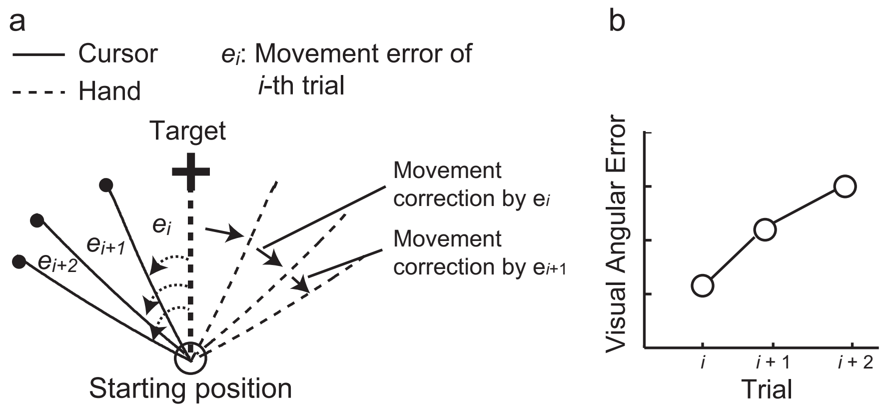

Fig. 1. Schematic example of error increase. (a) Using a normal error-based correction rule, the error in trial i will be corrected in the opposite direction in trial $i+1$. However, this amplifies the error under the MR transformation condition. The effect recurs between trials $i+1$ and $i+2$, illustrating increase of errors. Black lines indicate cursor trajectories and dotted lines indicate hand trajectories. (b) A schematic plot of the cursor error increase described in (a).

would be accumulated trial by trial. That people can adapt to the MR transformation (Sekiyama et al., 2000) strongly suggests that they acquire an alteration in the error correction rule. Such rule alterations can never occur in previously mentioned types of visuomotor transformation, such as visuomotor rotation (Krakauer et al., 2000; Mazzoni and Krakauer, 2006) and lateral displacements (Harris, 1965; Hatada et al., 2006). Therefore, in order to understand the flexibility of our motor control system, MR transformation is one of the most appropriate paradigms for investigating how the brain fulfills a need for drastic modifications to the system when required by the environment.

The underlying mechanism of MR adaptation has been investigated in several studies, focusing for example, on aspects of adaptation of "sensitivity derivatives", which are variables that describe the relationship between changes in motor commands and task errors (Abdelghani et al., 2008; Abdelghani and Tweed, 2010; Lillicrap et al., 2013). However, the problem (Fig. 1) of how the trial-by-trial error correction rule is altered during MR adaptation has not been fully investigated.

To reveal the unknown mechanism of adaptation to the MR transformation, we need to investigate by what cue(s) the error correction rules (i.e., sensitivity derivatives) are reversed during trials. It is naively assumed that the amplitude of error-predicting signals arising during goal-directed movements may be a determinant, because these are critical signals for determining the state of a motor learning system (Taylor and Ivry, 2011). However, considering the ability of our brain to adapt behaviors to the environment based on statistical estimations (Körding and Wolpert, 2004), there are also other possible cues that inform participants of abnormality of the movement, such as how many trials the errors has been increased. Therefore, in the current study we asked participants to perform a simple arm-reaching task to a single target seen directly in front of the participant on a virtual reality display under the MR transformation over two days (800 trials in total). To clarify whether the amplitude of visual angular errors was a determinant of the alteration of the error-correction rules, we manipulated the amplitude of visual angular errors by reducing the gain of the lateral displacement of a cursor during the experiments.

2. Materials and methods

2.1. Ethics statement

This study was conducted according to the Declaration of Helsinki. The experimental procedures were approved by the ethical committees of the Faculty of Science and Technology, Keio University. Written informed consent was obtained from all participants prior to the experiments.

2.2. Participants

Fifteen neurologically normal individuals (eight women and seven men, aged 20–26 years) participated in the experiments. All except for one participant were right-handed (Laterality Quotient = 71.7 ± 13.2; data values expressed as means ± SE), as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971). The participants were randomly assigned to each of two groups: the normal-gain group and the reduced-gain group (i.e., seven participants in the normal-gain group and eight participants in the reduced-gain group, each participant being included in only one experiment).

2.3. Apparatus

The experiment was performed using the KINARM exoskeleton robotic device (BKIN Technologies Ltd., Kingston, Ontario) (Scott, 1999). Participants sat in a chair with each arm supported in the horizontal plane by the robotic exoskeleton, which monitored shoulder and elbow motion. They could move their arms in the horizontal plane and viewed a virtual reality display (47 in., LG 47LD452C, LG, Korea) showing a 6-mm diameter white circular cursor indicating a fingertip position through a half mirror (72 cm × 35 cm) (Fig. 2a). A shutter under the display prevented participants from directly seeing their arms. The participants controlled the cursor by performing reaching movements with their right hand from a starting position marked by a 12-mm diameter circle toward a target marked by a cross 16 mm long and composed of lines 1.5 mm wide, both of which also appeared on the display. The starting position was located midway between the points where the fingertips of each arm were located when the shoulder angles were 30° and the elbow angles were 90° (full elbow extension was 0°). The target was 10 cm away from the starting position. The position and velocity of the arms were A/D-converted initially at 1.129 kHz and then re-sampled and recorded at 1 kHz for offline analysis.

The delay of visual feedback (i.e., the temporal delay from the measurement of the hand position to the presentation of the cursor) in the current experimental system was ~50 ms, though the delay differs depending on the location in the display due to the refresh rate of the display (60 Hz). We believe that this constant delay did not affect the performance of the current task.