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Feedback delay attenuates implicit but facilitates explicit adjustments to a visuomotor rotation

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A B S T R A C T

We examined the effects of delaying terminal visual feedback on the relative contribution of explicit and implicit components of adaptation to a visuomotor rotation. Participants practiced a 30° rotation while receiving terminal visual feedback with either a short (0 ms), medium (200 ms), or long (1500 ms) delay. Explicit and implicit adjustments were dissociated by a series of posttests. While overall adaptation did not differ significantly between groups, aftereffects progressively decreased with increasing feedback delay. Moreover, explicit knowledge of the rotation increased in both the medium and high delay groups relative to the short delay group, but did not differ between the former two. This finding of feedback delay differentially affecting implicit adjustments as indexed by aftereffects and conscious strategic corrections based on explicit knowledge of the transformation substantiates the importance of distinguishing implicit and explicit components of adaptation even with rotations of smaller size and emphasizes the need to consider time delays in the interpretation of adaptation experiments and potentially in the design of training environments.

1. Introduction

Adapting to novel transformations between bodily movements and their visually perceived consequences is an intricate part of learning to master modern tools such as a computer mouse or two-sided levers involved in laparoscopy. Adaptation to such visuomotor transformations embraces different components, and a fundamental distinction can be drawn between implicit and explicit adjustments (Hegele & Heuer, 2010; Taylor & Ivry, 2011). Previous studies of adaptation to novel visuomotor transformations suggest that delays in the presentation of visual feedback modulate implicit visuomotor adaptation, but the effect on explicit visuomotor adaptation is unclear (Brudner, Kethidi, Graeupner, Ivry, & Taylor, 2016; Held, Efstathiou, & Greene, 1966; Hinder, Riek, Tresilian, de Rugy, & Carson, 2010; Hinder, Tresilian, Riek, & Carson, 2008; Honda, Hirashima, & Nozaki, 2012b; Kitazawa, Kohno, & Uka, 1995; Peled & Karniel, 2012; Schween, Taube, Gollhofer, & Leukel, 2014; Shabbott & Sainburg, 2010). In the present study, we show that feedback timing modulates the relative contribution of implicit and explicit adjustments in visuomotor adaptation.

Explicit adjustments refer to the conscious alteration of otherwise spontaneously executed movements by cognitive strategies, e.g. pointing to a location different from the visual target (Heuer & Hegele, 2008; Taylor & Ivry, 2011). These strategies rely on explicit knowledge about the transformation (Hegele & Heuer, 2013; Mazzoni & Krakauer, 2006), can be applied relatively flexibly (Taylor & Ivry, 2011) and have been shown to be affected by aging (e.g. Buch, Young, & Contreras-Vidal, 2003; Heuer & Hegele, 2008; McNay & Willingham, 1998). Alternatively, the motor system can adjust to novel transformations implicitly, i.e. outside of conscious awareness. Implicit adjustments have frequently been described in terms of developing an internal model that mimics the input-output-characteristics of the transformation (Heuer, 1983; Wolpert & Kawato, 1998), but also comprise additional processes such as reinforcement learning and use-dependent plasticity (Huang, Haith, Mazzoni, & Krakauer, 2011; Izawa & Shadmehr, 2011; Therrien, Wolpert, & Bastian, 2016).

An established paradigm for the experimental study of the processes underlying sensorimotor learning is adaptation to a visuomotor rotation, i.e. a rotation of the direction of a moving cursor representing hand motion. Such a rotation of cursor feedback typically results in a strong performance decrement initially that is then gradually reduced as adaptation proceeds. When the transformation is switched off after practice, participants typically display an error in the direction opposite to the rotation. This error is

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referred to as (negative) aftereffect and has been conceived to reflect implicit processes of adaptation. Explicit components of adaptation to these rotations have often been inferred indirectly, but can also be assessed more directly (Heuer & Hegele, 2008; Taylor, Krakauer, & Ivry, 2014).

An important factor modulating visuomotor adaptation is timing of visual feedback regarding the outcome of reaching. Several studies have compared the continuous availability of visual feedback during movement execution (concurrent feedback) to the availability of visual feedback only near the end of, or after movement execution (terminal feedback; Hinder et al., 2008, 2010; Schween et al., 2014; Shabbott & Sainburg, 2010; Taylor et al., 2014). In spite of considerable methodological differences, those studies consistently found that implicit adaptation, as indexed by aftereffects, was smaller after practice with terminal feedback (but see Bernier, Chua, & Franks, 2005). Explicit adjustments have been found to increase with terminal as compared to continuous feedback, and it has been speculated that they compensate the reduction in implicit adjustments (Hinder et al., 2008, 2010; Shabbott & Sainburg, 2010; Taylor et al., 2014).

A crucial methodological difference between these studies however pertains to the exact time point at which terminal feedback was given. In studies that did not find any significant implicit adjustments, terminal feedback was not delivered immediately but with varying delays[1] (Hinder et al., 2008, 2010; Schween et al., 2014; Shabbott & Sainburg, 2010). Conversely, studies that report attenuated but significant aftereffects delivered terminal feedback immediately upon passage of a target amplitude (Taylor et al., 2014). This indicates that, in addition to the mere availability of error information, the timing of feedback may be a crucial determinant of the effect on implicit adjustments. This hypothesis gains support from a recent study by Brudner et al. (2016) who examined the impact of a 5-s-delay on visuomotor adaptation while monitoring participants' aiming strategies during practice. They found a significant attenuation of aftereffects with delayed feedback. Interestingly, in spite of comparable overall adaptation in the no-delay and the 5-s-delay groups, they did not find any effect of feedback delay on explicit aiming strategies. This finding seems at odds with the interplay of implicit and explicit learning suggested previously based on the comparison of concurrent and terminal feedback. However, the absence of a delay effect on explicit learning could be a result of the reporting paradigm itself, as being asked to report an aiming strategy on every trial may increase subjects' inclination to develop such strategies. The absence of group differences in strategy use could therefore be a result of ceiling effects in strategy use rather than indicating the absence of a delay-effect on strategy generation.

Therefore, the purpose of the current experiment was to determine the impact of feedback time delay on explicit and implicit visuomotor adaptation. In order to avoid drawing subjects' attention to the generation of aiming strategies, we assessed participants' explicit knowledge of the rotation by means of a (nonmotor) posttest where subjects judged the required direction of arm movements given a target direction (Hegele & Heuer, 2010, 2013; Heuer & Hegele, 2008, 2015). Based on previous results from prism adaptation (Kitazawa & Yin, 2002; Kitazawa et al., 1995), and the investigation of terminal feedback, we hypothesized that aftereffects would decrease across three delays. Furthermore, in line with previous reasoning that explicit learning compensates reduced implicit learning (Hinder et al., 2008, 2010; Shabbott & Sainburg, 2010; Taylor et al., 2014), we expected explicit learning to increase across these delays.

2. Materials and methods

2.1. Participants and experimental groups

Participants were assigned to a short, medium or long-delay terminal feedback group. The short-delay group (15 women, 5 men, mean age: 22.1 years (SD 2.6), range: 19–28 years) received terminal feedback after movement termination as soon as was allowed by the internal delay of our system (see Section 2.4). The medium delay group (18 women, 3 men, mean age: 21.5 years (SD 2.2), range: 19–27 years) received terminal feedback with an additional delay of 200 ms, the long-delay group (16 women, 5 men, mean age: 23.9 years (SD 4.6), range: 19–37 years) with an additional delay of 1500 ms. Data from one additional participant from the short and one from the long delay group were excluded as they could not finish testing due to scheduling constraints. Assignment to the short and long delay group was performed by block randomization balanced for sex. The medium delay group was added a posteriori and therefore not randomized. We chose this a posteriori addition to get a more complete picture of the effect of delay on adaptation. After observing the effect on explicit learning with the "large" 1500 ms delay, we were particularly interested if the smaller 200 ms delay would already affect explicit learning as studies have found delays in this range to affect sensory processing despite being hardly noticeable (Blakemore, Frith, & Wolpert, 1999). All participants were students of Giessen University and received course credit for their participation. Six participants (1 short, 4 medium, 1 high delay) were not right-handed according to the handedness-test from the (unrevised) German version of the lateral preference inventory (Büsch, Hagemann, & Bender, 2009, p. 18–19), but all subjects performed tests with their right hand. Written, informed consent was obtained from all participants before testing.

2.2. Apparatus

The experimental setup is illustrated in Fig. 1. Participants sat at a glass-covered table, facing a 22-in., 120 Hz LCD-Screen (Samsung 2233RZ) approximately at head height 1 m in front of them, and had a plastic sled (50 × 30 mm base, 6 mm height) strapped to their right index finger that minimized both, friction and haptic feedback when moving on the glass surface. The sled carried a vertically oriented sensor (Model M800) of a trakSTAR system (Ascension Technology, Burlington, VT, USA) directly above the fingertip, that was tracked at 120 Hz. A black occluder 20 cm above the table prevented vision of the hand. Data collection and stimulus presentation were controlled by custom scripts in Matlab (2010b, RRID: SCR_001622) using the Psychophysics toolbox (RRID:SCR_002881).

2.3. Experiment overview

Participants moved towards visual targets from a common central start location by sliding the sled over the glass surface and received visual feedback about their movement by an on-screen cursor. The experiment comprised a baseline phase, a practice phase where subjects encountered a $-30°$ visuomotor rotation (where the minus sign means counterclockwise), and a posttest phase (Fig. 2, see Section 2.5), containing 160 trials in total. Trials were arranged in blocks of ten with each block containing an equal

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[1] Specifically, Hinder et al. (2008) report that they presented terminal feedback at a fixed interval of 4 s after trial start. Considering a random delay of 1–2 s at the beginning of the trial, a reaction time (RT) of about 0.3–0.6 s and a movement time (MT) of about 1 s, we estimate a feedback delay of 0.4–1.7 s from movement termination. Hinder et al., 2010 used a fixed interval of 5 s and random delay 1–2 s and observed RTs of 0.5–0.9 s and MTs of 0.5–0.7 s, leaving feedback delays of 1.4–3 s. Shabbott and Sainburg (2010) do not report delays, but note that "The [terminal feedback] group was instructed to reach their final position and to remain there until [terminal feedback] was displayed" (p. 78), implying that there were noticeable delays. The setup of Schween et al. (2014) also presented feedback at a fixed point in time and therefore allowed noticeable delays depending on movement time.