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Adapting to target error without visual feedback

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ABSTRACT

What information is necessary for the motor system to adapt its behaviour? Visual hand-to-target error provides salient information about reach performance, but can learning proceed without this information? We investigated adaptation to an unperceived target perturbation under visual open-loop conditions. Participants looked and reached, without any vision of their hand, to a target that jumped rightward at saccade onset (Perturbation condition) or remained stationary throughout the trial (Stationary condition). The target jump in the Perturbation condition was tied to the saccade, such that participants were unaware that it had occurred. Each type of exposure was followed by a posttest, in which participants reached to a target that disappeared at saccade onset. In the posttest, participants reached farther following exposure to the perturbation than they did following exposure to the stationary target, indicating that participants had learned from systematic exposure to the jump. These findings imply that online error induces motor learning, even when participants receive no visual information about their performance.

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1. Introduction

One of the ways that we refine our movements is by comparing the endpoint of a movement to a desired endpoint. When we reach for and miss a target, for instance, a visual error signal can update commands for future reaches (Magescas & Prablanc, 2006). But what if there is no visual information about the success or failure of a reach? Can the motor system use an internal estimate of limb position to adaptively modify subsequent reaches? The present study addressed this question.

We already know that visual feedback is not required for *real-time* motor responses to target error. If a target jumps during a reach, the unseen hand will automatically deviate toward it, even when the participant is unaware of the jump (Goodale, Pelisson, & Prablanc, 1986; Prablanc & Martin, 1992). The online correction that occurs under these conditions may be driven by a proprioceptively-derived estimate of limb position or it may be driven by a forward-model-derived estimate of limb position, wherein a copy of the motor command is used to predict the limb's future position. Arguments for the involvement of forward models in these online corrections are based on the rapidity with which appropriate corrections can occur and on the observation that a deafferented patient was able to perform such corrections (Bard et al., 1999; Desmurget & Grafton, 2000).

However, it is not clear if the online error signal described above operates only in real-time, to drive the online correction, or whether it also acts as a training signal, modifying subsequent motor performance. Recent work from our group showed that unseen online target jumps produced motor adaptation, even though the online corrections eliminated terminal error (Cameron, Franks, Inglis, & Chua, 2011). In that study, we exposed participants to repeated rightward target jumps during reaches with an unseen hand, and we observed adaptation to the perturbation (cf. Magescas, Urquizar, & Prablanc, 2009). However, while vision of the hand was not available during the reach in the study of Cameron et al. (2011), vision was reintroduced at the end of each reach. So, although online correction of the reach eliminated terminal error between the hand and the target, there was visual confirmation that the target had been acquired. The present study tested for adaptation when neither online nor terminal visual feedback was available. That is, we tested whether people developed reach aftereffects after aiming to a target that imperceptibly jumped during their movement, in the absence of any real-time or terminal visual feedback.

Such stimulus conditions are reminiscent of those used to induce saccadic adaptation, where the gain of saccades is adaptively altered by systematically changing the location of the saccade target while the eyes are moving (e.g., Deubel, Wolf, & Hauske, 1986; McLaughlin, 1967; Wallman & Fuchs, 1998). When the initial saccade is complete, a different distance is present between the foveated location and the location of the target than was anticipated at the start of the saccade. After repeated exposure to such error, primary saccades gradually become larger or smaller, depending on the direction of the perturbation. A key difference between motion of the eyes and the hand, however, is that the former are capable of very little, if any, online control, whereas

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the latter is capable of online corrections that can eliminate some or all of the initial error in the movement. Indeed, Magescas and Prablanc's (2006) original study demonstrating adaptation of the hand to target perturbations had a protocol designed precisely to prevent any online corrections to the reach; the target was presented at its perturbed location only after completion of the reach, mimicking the error signal that is present during saccadic adaptation. Magescas and Prablanc (2006) demonstrated robust adaptation of reaching movements under such conditions, showing that terminal visual error – in the absence of any visual perturbation of the effector – was sufficient to drive adaptation. In the present study we considered a contrasting set of conditions, where online correction was possible and no visual error signal was available, to investigate whether the error signal that drives real-time reach corrections might also produce adaptive changes in the motor system.

We emphasize that the present study was designed to test the role of an online error signal in the training of subsequent movements. It did not allow us to determine whether the nature of the error signal was proprioceptive and/or efference copy-based, and we made no assumptions about which of these signals was potentially driving adaptation.

2. Materials and methods

2.1. Participants

Eight participants from the university community (4 male, 4 female; ages 20–22) completed the study. All participants were self-described right-handed, had normal or corrected-to-normal vision, and were naïve to the aims of the study. All participants provided informed consent prior to the experiment, and the study was conducted in accordance with the guidelines of the university's research ethics board.

2.2. Apparatus

Stimuli were projected onto a half-silvered mirror mounted midway between a horizontal reaching surface and an inverted LED array, such that targets (LEDs) appeared to be in the same plane as the reaching hand. Participants rested their head in a chin-rest, such that their eyes were 50 cm from the reaching surface. Vision of the hand was occluded when a white light below the mirror was extinguished. The apparatus was located in a dark room. Electrooculography (EOG) was used to monitor horizontal saccades. Disposable Ag–AgCl surface electrodes were placed at the outer canthi of the eyes with a reference electrode on the forehead. EOG signals were amplified (5–10 K) and band-pass filtered (0.1–30 Hz) with an AC preamplifier (Grass Instruments P511). The experimenter manually set a voltage threshold for each participant such that the trigger would occur within approximately the first half of the saccade. The first peak in the EOG signal was interpreted as completion of the primary saccade. The experimenter used an onscreen display of the EOG signal to visually estimate the magnitude of the participant's saccades and then set the voltage threshold accordingly. Precise calculation of saccade magnitude was done offline.

Hand movements were recorded with Optotrak (Northern Digital), sampling at 500 Hz. An infrared emitting diode was mounted on the tip of a hand-held stylus. The stylus was also equipped with a pressure sensitive tip that was used to record movement onset and end.

The experiment was run with a dedicated computer running DOS, with a digital I/O card with high-resolution timers (10 kHz). For control of the target jump within a trial, the analog EOG signal was fed through an independent hardware analog circuit that, when the EOG signal exceeded a set threshold, set a transistor–transistor logic trigger. This trigger (square wave) signal was used to trigger the LED onset/offset for the target jump. The delay between this trigger being set and the LED being triggered was less than 1 ms.

2.3. Task

Participants began each trial with the stylus placed at the home position and their eyes on the fixation point, 18.5 cm above the home position. After a variable foreperiod a target would appear 21 cm to the right of fixation (Center location), coincident with the offset of fixation. On look-and-reach trials (indicated by a red fixation point), the participant's task was to look and reach to the target in a single, smooth, and accurate motion. If movement time was faster than 300 ms or slower than 600 ms, participants were asked to slow down or speed up on the next trial, accordingly. On look-only trials (indicated by a green fixation point), the participant's task was to only look at the target, keeping their hand at the home position. Look-only trials were interleaved with reaching trials in the Practice and Exposure phases of the experiment, described next.

2.4. Conditions and phases

Each participant completed two conditions on the same day, an experimental condition (Perturbation) and a control condition (Stationary), the order of which was counterbalanced across participants. Each condition consisted of 4 phases: Practice (12 look-and-reach trials, 12 look-only trials), Exposure (35 look-and-reach, 35 look-only), Posttest 1 (20 look-and-reach), and Posttest 2 (10 look-and-reach), in that order. In the Practice phase, participants received full vision of their hand and the target throughout each trial. In all other phases, vision of the hand was available at the start of the trial, but then extinguished for the entirety of the reach (lights off at saccade start). One second after completion of the reach, the target was extinguished (if it was present) and a tone was sounded, indicating to participants that they could return their hand to the home position. Then, 750 ms after the participant began to return to the home position, vision of the hand was re-introduced to allow precise placement of the stylus at the home position.

The only difference between the Perturbation and Stationary conditions occurred in the Exposure phase. In the Perturbation condition, the target jumped during the Exposure phase: 4.7 cm right (from Center to Right location) on look-and-reach trials and 4.7 cm left (from Center to Left location) on look-only trials. We included look-only trials in order to inhibit the accumulation of any saccadic adaptation on look-and-reach trials (Cameron et al., 2011; Magescas et al., 2009). If such adaptation occurred, it might transfer to the reaching limb (Bekkering, Abrams, & Pratt, 1995). The target jump, which consisted of extinguishing an LED at one location and immediately illuminating an LED at another location, was triggered during the saccade to eliminate any awareness of the jump (Bridgeman, Hendry, & Stark, 1975). In the Stationary condition, the target did not jump during the Exposure phase. Instead, it initially appeared at the Right location and remained at that location throughout the reach (look-and-reach trials) or initially appeared at the Left location and remained at that location throughout the eye-movement (look-only trials).

On Posttest 1 trials the target appeared at the Center location, then disappeared at saccade start and did not reappear. This first posttest, in which no target was present during the reach, was designed to detect any changes in movement planning that resulted from exposure to the perturbation. If adaptation was to accumulate, it should manifest in Posttest 1 as positive endpoint bias in the Perturbation condition relative to the Stationary condition. This contrasts with Posttest 2 trials, in which the target appeared at the Center location and remained lit until 1 s after movement completion. This second posttest, in which a stationary target was visible during the reach, was designed to wash out any accumulated adaptation. Here, we would expect online correction to the stationary target and an unlearning of any adaptation that may have occurred during exposure.

Our protocol was designed for a comparison between the Perturbation and Stationary conditions in the posttest phases, rather than a

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