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RESEARCH NOTE

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Anticipatory adjustments in the unloading task: Is an efference copy necessary for learning?

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Abstract In the unloading task, a weight is held in the palm of one hand. When an external agent removes the weight, an upward perturbation of the loaded hand is observed. However, when a person removes the weight by lifting it with their own hand, the perturbation is attenuated due to an anticipatory adjustment of the flexor muscles in the load-bearing arm. An experiment was conducted to examine conditions under which this anticipatory response could be learned. Using a virtual reality system with force-feedback robotic arms, normal subjects performed the unloading task under one of four learning conditions: (a) the participant initiated the unloading by pressing a button, (b) the unloading was cued by a brief visual stimulus, (c) the unloading was performed by a virtual "hand" that moved smoothly towards the object, and (d) the unloading followed three rhythmic force-pulses applied to the finger of the participant. After extended practice (192 trials) we found a significant reduction of the upward perturbation only in the button pressing condition. Control conditions indicated that the acquired response was due to an anticipatory feedforward response rather than due to a change in tonic state such as an increase in arm stiffness. These results indicate that a voluntary action is necessary to acquire an anticipatory adjustment in the unloading task.

Keywords Anticipatory adjustments · Movement control · Bimanual skill learning · Internal models

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Introduction

Anticipation is a fundamental characteristic of the human motor system. Changes in the environment or in posture constantly alter the forces that affect our limbs. We are able to prevent the resulting limb instabilities by adjusting muscular activation, even before proprioceptive or kinesthetic information is available. For example, to prevent slippage, grip-forces are adjusted when changes in the weight of an object can be anticipated (Johansson and Westling 1984, 1988; Blakemore et al. 1998). In the "unloading task," where one hand unloads a weight held by the other hand, the loaded muscles show an anticipatory decrease in activity (Massion 1984; Lum et al. 1992). Generating such anticipatory adjustments (AAs) requires a controller that predicts the expected perturbation based on an efference copy of the voluntary action (Miall and Wolpert 1996; Wolpert and Kawato 1998). This prediction can then be used to generate the appropriate adjustment to counteract the perturbation.

One of the fundamental issues of anticipatory motor behavior is whether these adjustments only occur when the perturbation is self-produced or whether these adjustments can be performed when the perturbation is made predictable by sensory information. This issue is theoretically important as it pertains to the question of how to characterize the controllers governing anticipatory motor behaviors. According to an "encapsulated process" view, the AAs are an integral part of the voluntary action that leads to the perturbation (e.g., Aruin and Latash 1995). Thus, the anticipatory response can only occur in conjunction with the eliciting action. In contrast, a "parallel process" view conceptualizes the controller of the anticipatory adjustment as being accessible to other inputs. Under this view, the controller can also learn to react to perturbations that are predictable on the basis of incoming sensory information.

Anticipatory adjustments of grip and load forces are only present when the perturbation is self-elicited (e.g., Struppler et al. 1993; Aruin and Latash 1995). Anticipatory changes in muscular activity are not observed when the perturbation is signaled by an auditory tone (Dufossae et al. 1985; Witney et al. 1999) or when the force changes are generated externally in a predictable, sinusoidal manner (Blakemore et al. 1998). In contrast, when catching a falling object, a sizable anticipatory response to the expected impact is observed even if the release of the object is not self-produced (Lacquaniti and Maioli 1989a, 1989b; Shiratori and Latash 2001). These adjustments are triggered solely by the visual information provided from the falling object.

The failure to find AAs in grip and load forces prior to predictable external perturbation (Dufossae et al. 1985; Struppler et al. 1993; Witney et al. 1999) may be due to two factors. First, the sensory signals may not have provided sufficient information concerning the timing of the forthcoming perturbation. In the aforementioned studies, discrete auditory signals indicated the time of the disturbance. A similar discrete signal was insufficient to elicit an AA prior to catching, whereas observing the whole trajectory of the ball from release to impact was sufficient (Lacquaniti and Maioli 1989a). Providing predictive information in a continuous manner might elicit AAs in the unloading task. Second, some amount of exposure to the predictable external perturbation may be crucial for acquiring an appropriate AA. Paulignan et al. (1989) studied anticipatory changes when the unloading of a weight was self-initiated by a button press performed by the other hand. After several hundred trials of practice, participants were able to acquire an anticipatory response. Thus, substantial training with a predictable external perturbation may also lead to the acquisition of an AA.

To evaluate different methods for signaling a forthcoming force perturbation in the unloading task under extended practice we used a visual-haptic virtual-reality environment (see Fig. 1a, “Materials and methods”). There were four training protocols, all involving situations in which the load was removed by an external force. In the *vision-discrete* condition, the color of the object changed 300 ms before the start of unloading. In the *vision-continuous* condition participants saw a virtual robotic arm approaching (over a 600-ms window; speed increasing monotonically) and upon contact unloading the object. This condition was designed to mimic the continuous visual information available when catching an object. In the *volitional-action* condition, unloading was triggered when the participant pressed a button with their other hand. Finally, in the *haptic* condition, participants also pressed a button, but here this response initiated a series of three rhythmic force pulses delivered to the finger at a rate of 600 ms. Unloading occurred simultaneously with termination of the last pulse. This condition was designed to provide similar proprioceptive and haptic feedback as the button-action condition, but without a volitional action that triggers the unloading directly.

We also included two baseline tasks. In natural self-unloading, the participants used their other hand to lift the object. In the external-unloading condition, no cues were provided to indicate the onset of the unloading.

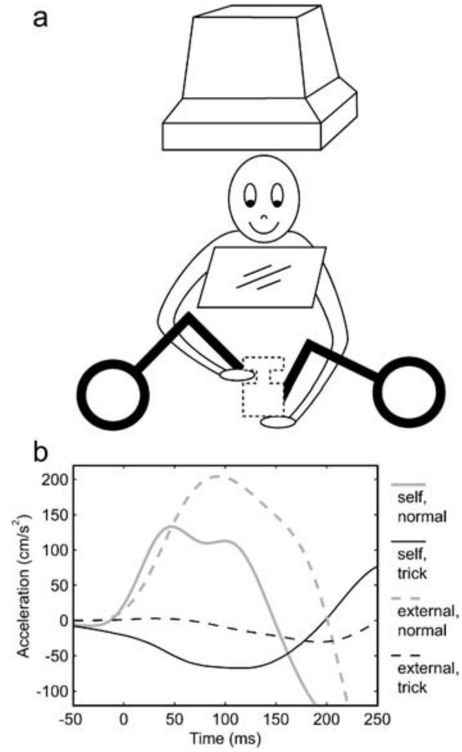

Fig. 1 **a** Experimental apparatus. A virtual object was presented on a monitor, which participants viewed via a mirror. The index fingers of each hand were connected to a programmable robot arm (SensAble Technologies), which simulated the forces generated in the interaction with the virtual object (*dashed outline*). **b** Acceleration functions for self-unloading and external-unloading trials, averaged over pre- and post-training phase and the four different conditions. Traces are aligned to the onset of unloading (0 ms). Standard trials (*gray*) lead to an upward perturbation, whereas trick trials (*black*) lead to a downward perturbation indicating a feedforward postural adjustment

Perturbations following unloading can be attenuated in one of two ways. The participant may either generate an anticipatory response consisting of the relaxation of the load-bearing muscles or the stiffness of the load-bearing arm can be increased (Biryukova et al. 1999). To distinguish between these two responses, we included “trick” trials. For these, the same cues were provided as on regular trials and the visual image of the object was displaced when force was applied to it. However, the weight on the loaded hand did not change. If participants relaxed the load-bearing muscles in an anticipatory fashion, their arm would be deflected downward on trick trials given the absence of the expected weight displacement. On the other hand, if the arm was stiffened, no perturbation should be observed on trick trials.

Materials and methods

Participants

Thirty-two students (17 male, 15 female, mean age = 22.7 years, 2 left-handed) from the University of California, Berkeley, were recruited and financially compensated for their time. All participants were naive to the purpose of this study. Approval for the project was granted by the local Committee for the Protection of Human Subjects.

Apparatus and stimuli

Participants viewed a virtual 3D environment displayed on a 24” computer monitor reflected by a mirror through stereoscopic shutter glasses (80–120 Hz). Within a 20×20×22-cm workspace, participants saw a virtual object. This object was a 5-cm cube with a T-shaped handle connected to the top surface (2 cm wide at the neck, 4 cm wide at the handle). In addition, the workspace included two 0.8-cm spheres, corresponding to the positions of the two index fingers and, in the volitional action and the haptic condition, a 4×1.5-cm button, appearing on the floor of the workspace, 6 cm from the object.

Each index finger was linked to a robotic arm (PHANToM 1.5 System, SensAble Technologies). These robots were used to simulate interactive forces. For the cube, these forces were created by assuming an object weight of 330 g. For the button, the forces were created to simulate a spring constant of 0.5 N/mm over a 7-mm travel distance for full depression. Measurements of each finger’s position and force were sampled at 200 Hz.

Procedure

To initiate each trial, the participant placed one hand under the base of the object, lifted it about 3 cm off the floor, and maintained this position for 1.5 s. In the self-unloading condition, the handle turned red and the participant was instructed to lift the object with the other hand. In all other conditions, the object was displaced upward by the computer. This displacement occurred in a stereotypical manner[1] based on pilot work to define the shape and speed of natural unloading.

Participants were assigned to one of four training conditions. Before and after training, participants completed six blocks: self unloading, external unloading, and a block in their specific training condition. Each of these was performed once with the left and once with the right hand supporting the object. Each block consisted of 24 trials, 16 standard trials and 8 randomly interspersed trick trials. The block sequence was counterbalanced across participants. Training was limited to either the left or the right hand and consisted of eight blocks of 24 trials. No trick trials were included during training.

Data analysis

Position and force traces of each trial were aligned to the start of unloading, defined by the moment when force was applied to the object either by the other hand or by the computer. Traces were averaged for each block[2], with separate averages created for normal and trick trials during the pre- and post-training phases. The largest perturbation of the postural hand relative to a 200-ms baseline window prior to unloading was determined. Peak acceleration before maximal perturbation was also calculated (Lum et al. 1992). The time between the start of the unloading action and the moment at which the lifting force reached 85% of the object’s weight was used as a measure of unloading rate.

[1] The unloading by the computer was achieved by applying a virtual force to the object that increased smoothly and reduced the force on the loaded hand by 85% within the first 176 ms. The force increased in a negatively accelerated fashion according to the formula:

$$F(t) = \left\{1 - e^{-5.4 \cdot t}\cos(7.6 \cdot t)\right\} 330\,g \cdot 9.81\frac{m}{s^2}.$$

[2] We also estimated the size and time of maximal acceleration based on individual trials. While this method yielded higher estimates of acceleration, the overall pattern of results was similar to that presented in the main text.

Results

The self and external unloading trials provide a baseline measure of performance. To approximate the mean rate of self-unloading trials to the rate of the external unloading trials (176 ms), we selected a subset of the self-unloading trials in which the speed was faster than 250 ms (69% of all trials). For non-trick trials, peak acceleration was greater in the external unloading condition (207 cm/s^2) than in the self-unloading condition (137 cm/s^2), $F_{(1,28)}$=48.62, P<0.001 (Fig. 1b). On trick trials, the downward acceleration was higher for self unloading (–90 cm/s^2) than for external unloading (–49 cm/s^2), $F_{(1,28)}$=25.40, P<0.001, and also occurred substantially earlier (150 ms vs 201 ms postunloading), $F_{(1,28)}$=57.44, P<0.001. None of these measures differed between groups (all Fs<1), nor did they vary significantly between pre- and post-test (all Fs<2.2). These results indicate that that we were successful in replicating the basic features of the unloading task in our virtual environment.

We next analyzed changes in performance over the training blocks (Fig. 2). A two-factor ANOVA verified a significant mean difference between conditions, $F_{(3,28)}$=10.0, an effect of block, $F_{(7,196)}$=25.50, and a Condition × Block interaction, $F_{(21,196)}$=6.17 (all Ps<0.001). A linear regression for each condition revealed statistically significant learning for the volitional-action condition, $F_{(1,62)}$=23.64, P<0.001, and less, but still significant, learning for the vision-continuous condition, $F_{(1,62)}$=17.09, P<0.001. No reduction in peak acceleration was observed in the vision-discrete, $F_{(1,62)}$=2.05, P=0.156, and in the haptic condition, $F_{(1,62)}$=0.64, P=0.42.

Learning was assessed by comparing pre- and post-test performance in a Condition × Phase × Hand (trained vs untrained) ANOVA. On non-trick trials, the difference in maximum acceleration between pre- and post-test interacted with condition, $F_{(3,28)}$=9.57, P<0.001. This interaction reflected the fact that a significant reduction in maximum acceleration was only observed in the volitional-action condition (see Fig. 3). Moreover, this

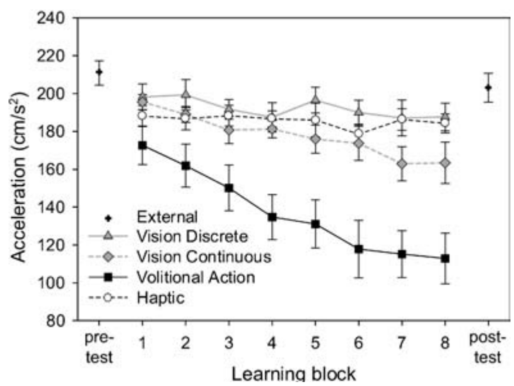

Fig. 2 Average peak acceleration for the four conditions in the learning phase. The values of external unloading in pre- and post-test for the trained hand are shown as baseline. *Error bars* indicate between-subject standard error

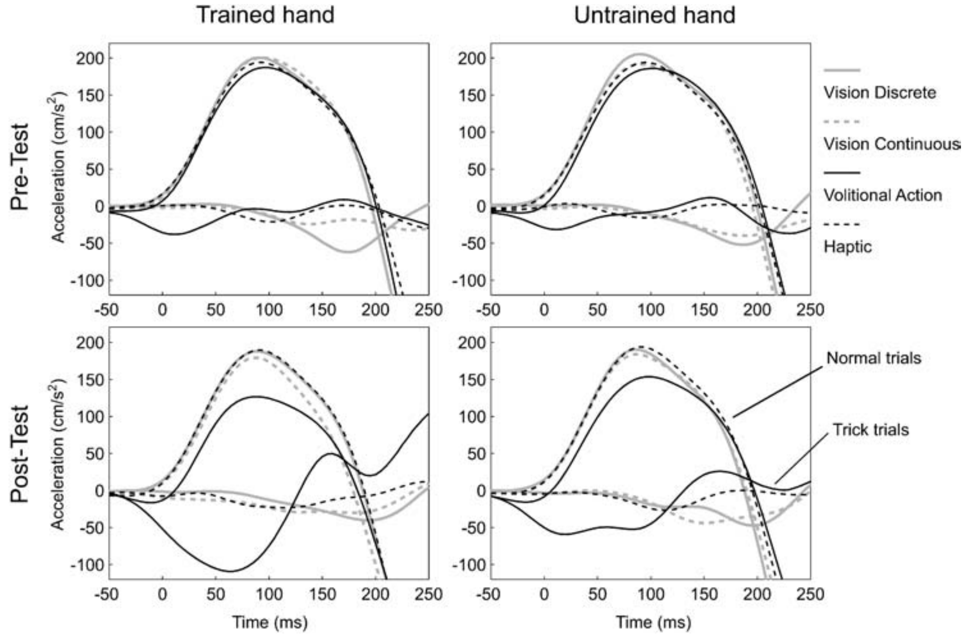

Fig. 3 Acceleration functions for the four learning conditions in pre- and post-training and for the trained or untrained hand. Only the volitional-action (*black solid*) condition showed a substantial reduction of upward acceleration in standard trials and a trick response indicating a feedforward anticipatory adjustment

reduction was more pronounced in the trained hand than in the untrained hand, $F_{(1,28)}$=13.40, P=0.001, indicating that much of the learning was effector-specific.

The trick trials provide further evidence that a true AA was only acquired in the volitional-action condition. Following training, the size of the downward acceleration was greater for this condition than in the external unloading condition, $t_{(7)}$=3.51, P<0.001. No other condition showed a change in the trick response (all $t_{(7)}$<0.5). Moreover, maximal downward acceleration occurred 100 ms earlier in the volitional-action condition than in the other three conditions, $F_{(3,28)}$=3.34, P=0.033.

Discussion

We investigated the prerequisites for acquiring an anticipatory adjustment in the unloading task. A feedforward AA was only learned when the unloading was directly triggered by a volitional button press. We also found a significant reduction in maximum acceleration during training in the continuous-vision condition. However, the lack of a change from pre- to post-test for standard and trick trials in this condition suggests that this learning was not of an AA but rather of a correctly timed increased stiffness of the postural arm.

These results indicate that the development of an AA is dependent on its association with a volitional action, even when the relationship between the action and its consequence is fairly abstract (Aruin and Latash 1995; but see Dufossae et al. 1985).

The failure to find an AA in the absence of a volitional action is consistent with a number of other studies (Dufossae et al. 1985; Struppler et al. 1993; Aruin and Latash 1995; Blakemore et al. 1998; Witney et al. 1999). The current results extend this by showing that an AA is still not learned even with highly predictive sensory information and extended practice. In contrast to the results from unloading and force grip tasks, it does appear that an AA can be elicited solely on the basis of visual information during ball catching (Lacquaniti and Maioli 1989a, 1989b; Shiratori and Latash 2001). Ball catching may be qualitatively different in nature to unloading (Dufossae et al. 1985) or grasping (Blakemore et al. 1998; Witney et al. 1999). Moreover, as pointed out by Aruin and Latash (1995), small movements of the catching hand towards the ball could help trigger the AA in ball catching, blurring the distinction between a voluntary action and the anticipatory adjustment.

Further evidence that anticipatory adjustments associated with ball catching and unloading are qualitatively different comes from probes of intermanual transfer. If the AA is an integral part of the triggering action, one would expect learning to be specific to the executing hand. In contrast, nearly complete intermanual transfer might be demonstrated if the behavior is governed by a more abstract representation (Gordon et al. 1994; Shadmehr and Mussa-Ivaldi 1994; Hemminger et al. 2001). For ball catching, Morton et al. (2001) reported an intermanual transfer rate of 68%. In the current study, the intermanual transfer score in the volitional-action condition was only 36%[3] (see also Ioffe et al. 1996). The substantial transfer during ball catching suggests that the AA associated with this task relies, at least to a higher degree than in the unloading task, on external task

[3] For the non-trick trials, transfer was calculated as:

$$\frac{Acc_{Untrained,post} - Acc_{Trained,L1}}{Acc_{Trained,post} - Acc_{Trained,L1}} \cdot 100$$

Acc is the peak acceleration in the first learning block (L1) and the post-test (post). For trick trials, this measure could not be calculated, as they were not included in the learning phase.

parameters (ball height, impact time) rather than on internal sensorimotor parameters (dynamics of hand-ball interactions).

The current results are consistent with the view that during unloading the process generating the anticipatory adjustment is linked to the action required for the arbitrary button press. It remains unclear why the same process could not be similarly linked to predictive sensory events. Impairments in the acquisition of such adjustments would prove useful in identifying the neural structures involved in the development of internal models for sensorimotor control.

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