Internal Models and Transfer of Learning in Pursuit Tracking Task

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Abstract

Visuomotor manual tracking is a well-established method for studying the neural processes and computations underlying skilled action. Human subjects quickly and efficiently learn to track a target moving at constant velocity. Here, we measure tracking performance in two separate groups of participants while either the target or the manual cursor was suppressed for a brief period during each tracking trial. Subjects learned to maintain accurate tracking through periods of target or cursor suppression. During the suppressed period, feedback-error-driven mechanisms cannot be used, and tracking performance therefore relies on prediction alone. We used this manipulation to show that motor learning involves acquiring predictive models of the target motion and also of one's own hand movement. We also used a transfer of learning design to investigate whether acquiring models of target motion and of one's own hand motion involved linked or independent neural modules. We found clear positive transfer from learning to predict one's own manual action to learning target motions, and no evidence for transfer in the reverse direction. This asymmetric pattern suggests specific predictive neural mechanisms for learning to control one's own action, as opposed to general prediction of external events. We suggest that learning internal representations of one's own motor systems may play an important role in learning about the perceptual world.

Introduction

Motor learning is a fundamental feature of all motor performance. Pursuit tracking is well-established experimental paradigm for studying motor learning (Poulton, 1974). In pursuit tracking, the subject moves a manual lever to ensure that a visual cursor tracks a moving visual target on a screen. Early studies of tracking distinguished two components of the tracking motor response. First, subjects may make rapid movements to reposition their cursor on the target, typically catching up with the target, and then falling behind again. Such movements are intermittent, often with a frequency of around 1-2 Hz (Miall et al., 1993; Netick & Klapp, 1994). Tracking becomes more intermittent when the target moves unpredictably. Therefore, this component of the tracking response is assumed to involve visual feedback-error-driven correction. The subject sees a visual discrepancy between target position and cursor position, and moves the cursor to reduce this error to zero, only for the error to increase again.

Several lines of evidence suggest, however, that tracking is not purely feedback-driven, but also involves prediction. For example, motor output during tracking can be smooth rather than intermittent, and can sometimes lead the target rather than lag behind it. Moreover, tracking performance is typically better when the target moves in a predictable fashion (e.g., at constant velocity), than when it moves less predictably (Poulton, 1974). Finally, subjects can track accurately even when absence of either the target or the cursor signal makes error-detection impossible (Beppu et al., 1987).

The predictive element of tracking is often attributed to learning of internal models. Several studies have suggested the existence of internal models in addition to sensory feedback mechanisms. For example, functional imaging studies have separated specific neural activity related to acquisition of internal models from other neural activity associated with error correction (Imamizu et al., 2000). However, it is unclear precisely what is represented by such models, and how many separate models are involved. In computational terms, successful tracking requires a representation of current target position and of current hand/cursor position. Models which estimate the current output of a system given its inputs are termed 'forward models'. Thus, tracking performance could potentially involve two separate internal forward models. One model would estimate or predict the current position of the target based on its previous kinematic history. Another would estimate or predict the current position of the hand-cursor, based on the current motor command and any available proprioceptive feedback. We will call these putative models the target forward model and motor forward model respectively.

Learning is a key feature of all internal models. In manual tracking, the goal is to make the output of the motor forward model equal to the output of the target forward model. Clearly, internal models are useful for tracking only if their predictions are correct. According to one computational theory, visual feedback error provides an important learning signal which can be used to update the internal models (Kawato & Gomi, 1992).

Relatively few studies have investigated whether skilled tracking involves the learning and use of two dissociable models for target and for motor output, respectively. Evidence for predictive mechanisms in tracking is consistent with either a target forward model, or a motor forward model, or both. Recent computational studies have demonstrated efficiency and robustness of modular architectures for model learning. For example, multiple motor models may be learned, with one model corresponding to each task performed or object used (Wolpert & Kawato, 1998; Wolpert et al., 1998). However, in those architectures, the brain is assumed to learn multiple instances of the same general type of model. In pursuit tracking, however, the putative target model and motor model would use qualitatively different types of information. They perform dissociable information-processing functions, rather than being parallel instances of a single function. For example, the motor model refers to effects of the subject's voluntary motor commands on hand position, while the target model refers only to visual objects in external space.

One promising method for investigating the possible dissociation of target and motor models in tracking involves comparing the effects of target suppression and cursor suppression (Beppu et al., 1987). In target suppression, subjects track a predictably moving target. The target disappears at some point during the track, while the cursor remains visible. In cursor suppression, the cursor disappears but the target remains visible. Subjects continue to track for some interval, and the target or cursor display is then restored. No visual error signal is present during target-suppressed and cursor-suppressed tracking. Target and cursor are not simultaneously visible, so their discrepancy cannot be computed.

Thus, tracking performance during suppression reflects only the contributions of internal models, but the involvement of these models depends on what is suppressed. When the target is suppressed, the only representation of the tracking target comes from a putative target model which predicts the current target position from its previous motion. Therefore, poor tracking during target suppression can be attributed to an incorrect target model. Conversely, when the cursor is suppressed, the only representation of the current cursor position comes from the putative motor model. This model predicts the current cursor position from current motor commands and proprioceptive information. Therefore, poor tracking during cursor suppression can be attributed to an incorrect motor model.

If the target reappears after a period of target suppression, or if the cursor reappears after a period of cursor suppression, a visual feedback error signal is again available. This error signal can be used to update the target model in the case of target suppression, or the motor model in the case of cursor suppression. Learning and updating of these models would lead to improved tracking performance during the suppression period of subsequent trials.

We have used the target and cursor suppression approach to investigate the internal models used during tracking, and their updating during motor learning. We have focused on identifying differences in tracking behavior between target and cursor suppression conditions. If target-suppressed and cursor-suppressed conditions show differences in either short-term performance, or in longer-term learning, then this would provide strong evidence for the existence of separate and dissociable internal models for these two components of skilled action. We therefore measured tracking error during both target and cursor suppression, and described the learning curve in each condition. We assumed that suppression tracking involves a number of dissociable processes. First, when the target or cursor disappears and suppressed tracking begins, the subject must rely on internal model-based tracking. Second, when the target or cursor reappears, a second, visual feedback process will detect any error, and issue a feedback-driven motor correction. We wanted to distinguish between these two processes, and obtain separate psychophysiological measures of learning-related changes in each of them. Finally, we investigated whether tracking involves learning just one internal model, or involves separate target and motor models using a learning transfer approach. We reasoned that asymmetric transfer of between target suppression and cursor suppression conditions would imply separable learning processes under these conditions, and thus distinct internal models in each case.

Methods

Apparatus

The experimental apparatus consisted of a joystick and computer display for tracking measurement system (Kobori & Haggard, 2003). The apparatus is shown in Figure 1.

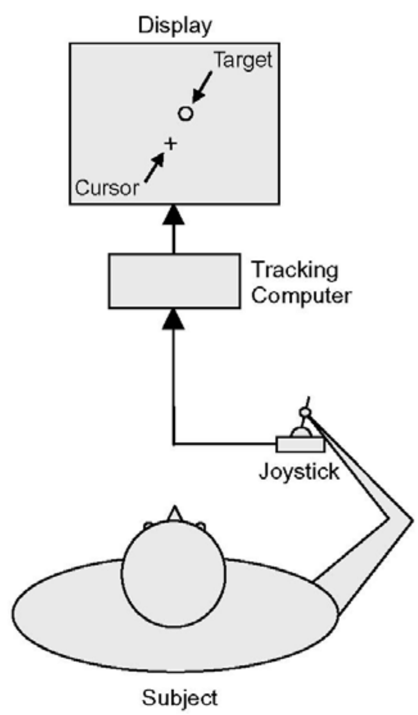

Figure 1: Experimental apparatus.

Tracking

Subjects observed a circular target (diameter 13 mm) moving at constant tangential velocity along a clockwise circular trajectory (diameter 148 mm) on a computer screen. The target cycle was 5 sec. The viewing distance was 66 cm. Each trial lasted 20 sec. Subjects held a modified joystick in their right hand, and moved it so that a visual cross hair cursor (width 13 mm) tracked the target as closely as possible. 1 degree of joystick movement produced a cursor movement of 0.39 degrees of visual angle. Target and cursor positions were digitized and stored on the computer at 30 Hz. Unsigned tracking error was calculated in subsequent analysis.

Tracking trials were of 2 types, normal and suppressed tracking. In normal trials, the movements of the joystick produced congruent movements of the subject's cursor on the screen. In suppressed tracking, we blanked out either the target or the cursor during the trial. The disappearance occurred at an unpredictable time between 5 and 7 sec. Then, the target or cursor reappeared at a random time between 11 and 13 sec.

Tracking error data from suppressed trials were aligned either to the time of disappearance, or reappearance of target/cursor as appropriate. An epoch from 4 sec before until 4 sec after was selected for display. Tracking error traces were then made for each subject in each block of the experiment. Analyses of normal trials used the average time of disappearance and reappearance across all suppressed trials (6 sec and 12 sec from trial onset) as the fictitious "event" for defining analysis epochs.

Experimental design

All experimental blocks consisted of 5 trials. Before the experiment, we explained the tracking task to the subject, and familiarized them with the equipment and apparatus. Then the experiment began with a pretest block of normal tracking trials.

Next, subjects performed 6 learning blocks of target or cursor suppressed trials each. Then, subjects performed a posttest block of normal trials similar to the pretest block. The experiment ended with 2 transfer blocks of the other kind of suppressed trials which was not performed in the learning phase.

Subjects took a break of a few minutes halfway through the experiment, between blocks 3 and 4 of the learning phase. The subjects were instructed to continue tracking as accurately as possible when target or cursor disappeared. The procedures were approved by the local ethical committee.

20 subjects were recruited from among the students of Ryukoku University. Subjects' ages ranged between 19 and 24 years. 10 subjects were male, and 10 were female. None had any known neurological abnormality, and all were naive to the purposes of the experiment.

We divided the subjects into 2 groups. Each group included 5 males and 5 females. The target suppression group performed target-suppressed trials in the learning blocks and cursor-suppressed trials in transfer blocks. The cursor suppression group performed cursor-suppressed trials in learning blocks and target-suppressed trials in transfer blocks.

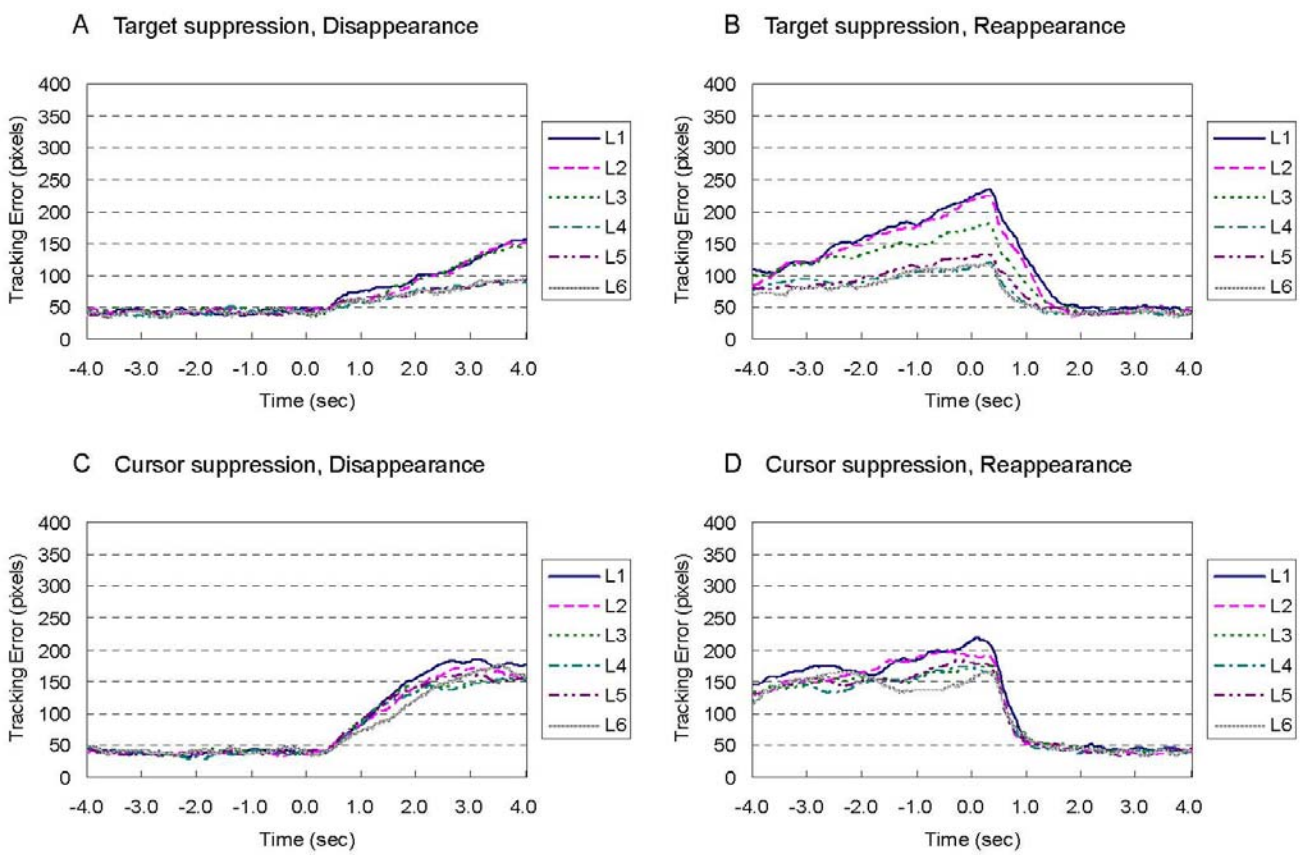

Figure 2: Grand average tracking error waveforms arranged by learning block.

Results

Tracking data

The grand average traces of unsigned tracking error for each learning block are shown in Figure 2. Data from suppressed trials are aligned either to the time of disappearance, or the time of reappearance as appropriate. The upper row shows the performance of the target suppression group at the point of target disappearance (panel A), and reappearance (panel B). The data for the cursor suppression group is shown in the lower row (C, D). L1 refers to learning block 1.

Figure 2 shows that tracking error is low prior to disappearance in both groups, and was comparable to pretest and posttest normal tracking trials (not shown). Second, tracking error increases gradually and monotonically after disappearance, and continues until just after the reappearance of the target or cursor. The initial increase in tracking error is more abrupt for the cursor suppression group than for the target suppression group. Error then decreases quickly and returns to the level before disappearance. Third, and most importantly for our purpose, the error during the suppression period varies across the learning blocks. In the target suppression group, tracking error is clearly higher for blocks 1-3 than blocks 4-6. The cursor suppression group also shows differences between blocks, but these are somewhat smaller than in the target suppression group.

The improvement across blocks in tracking during the suppression period arises from learning an internal model of either the target movement (target suppression group) or the subject's own movement (cursor suppression group). We therefore calculated mean tracking error on each trial during an epoch from the time of disappearance to 2 sec after reappearance. We compared the tracking error in the first and last learning blocks, using a mixed ANOVA with factors of group (between-subjects) and block (within-subjects). This showed a significant effect of block [$F(1,18) = 11.514$, $p = .003$] with lower tracking error in block 6 than in block 1, as predicted. There was no significant effect of group [$F(1,18) = 3.701$, $p = .070$] and no interaction [$F(1,18) = 1.859$, $p = .190$]. We also compared the tracking error in the first and last learning blocks in each group separately. The results showed significant effects of learning in target suppression group [$t(18) = 2.722$, $p = .0007$] and also in cursor suppression group [$t(18) = 1.923$, $p = .0035$]. Thus, subjects learned to track during the suppression period.

Transfer of Learning

We investigated transfer of internal-model learning by comparing tracking performance on the two transfer blocks with tracking performance on the first two learning blocks (Adams, 1987). A hypothesis of no transfer between one suppression condition and the other would predict that tracking error during the suppression period on the transfer task would be no better than at the very start of learning: subjects would need to learn the new suppression condition de novo. Conversely, if learning during one suppression condition transferred to the other condition, then performance on the transfer blocks should be better than the initial learning blocks. If no transfer between the two suppression conditions were observed, we would conclude that learning an internal model of the target and learning an internal model of the manual action were quite different processes, which involved separate internal models. However, if perfect transfer were found, we would conclude that a single, common learning process underlay both suppression conditions.

However, transfer between two tasks may also be asymmetric, and the direction of asymmetry gives important information about the underlying cognitive operations that are learned. In this experiment, for the group who learned target suppression, positive transfer to the subsequent cursor suppression test would suggest that learning an internal model of the target is sufficient for learning about the actions to track it. For the group who learned cursor suppression, positive transfer to the subsequent target suppression test would imply that learning an internal model of one's own action is sufficient for learning trajectories of external visual objects.

We therefore subjected the tracking error data to a mixed ANOVA model with factors of learning group (target suppression, cursor suppression) and learning phase (learning, transfer). The results showed a non-significant effect of group [$F(1,18) = 4.188$, $p = .056$], with those initially learning cursor suppression showing slightly better performance overall. There was a significant effect of learning phase [$F(1,18) = .401$, $p = .021$], due to an overall positive transfer effect. That is, performance in the transfer blocks was significantly better than initial learning. Most importantly, there was a significant interaction [$F(1,18) = 11.341$, $p = .003$]. Follow-up simple effects testing was used to investigate the source of this interaction. The results are shown in Figure 3. The group who initially learned with target suppression, showed a non-significant negative transfer to subsequent testing with cursor suppression [$t(18) = .001$, n.s.]. In contrast, the group who initially learned with cursor suppression showed significant positive transfer to subsequent testing with target suppression [$t(18) = 2.460$, $p = .024$].

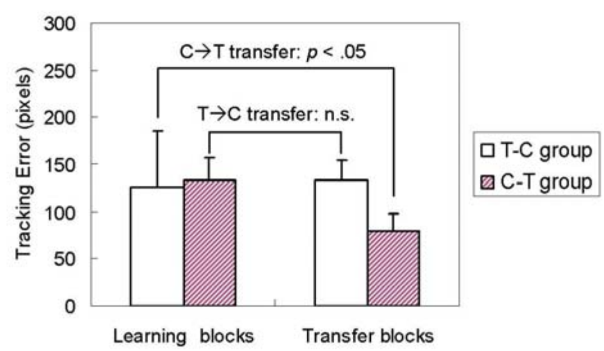

Figure 3: Transfer of learning.

Discussion

Predictive models in visuomotor learning

This paper has used a conventional pursuit tracking task with suppression of the tracking target or of the subject's own movement cursor as a method to investigate two kinds of predictive learning involved in visuomotor control. Suppressing either the target or the cursor removes the possibility of visual feedback-driven error corrections, and requires the subject to continue tracking based on purely predictive representations. In target suppression, the subject must predict the current position of the target, yet the cursor continues to give visual information about hand position. In cursor suppression, the subject must estimate or predict the current position of the cursor corresponding to their own hand position, although they continue to see the visual target. We found clear evidence for learning in both situations, based on a reduction in tracking error during the suppression period. Since feedback-error-driven correction cannot occur during either target or cursor suppression, improvements in suppressed tracking during the course of the experiment suggest that subjects must learn internal representations of the target movement, and also of their own movement. Many studies of tracking behavior agree that the motor learning underlying tracking performance is predictive in nature (Craik, 1947). Improvements in tracking performance may therefore occur because prediction improves with practice: subjects learn to predict. For example, the intermittent corrections associated with sampling methods of tracking control decreased over 5 days of learning (Miall & Jackson, 2006).

Learning about cursors or about targets

However, few tracking studies explicitly distinguished between prediction of the target trajectory, and prediction of one's own motor output. Beppu et al. (1987) reported tracking performance during periods of cursor suppression and target suppression in healthy volunteers, and cerebellar patients. They found that suppressing either signal prevented intermittent visual feedback-driven corrections, but they did not distinguish between target and cursor suppression. Haggard et al. (1995) distinguished between two error-correction processes in pursuit tracking, based on visual feedback-driven corrections and internal model estimates of current target and hand positions respectively. They found that both cursor suppression and target suppression had slight effects on normal subjects' tracking, but dramatically reduced intermittent feedback-driven corrections in cerebellar patients. More interestingly, cursor suppression, but not target suppression, produced a strongly cumulating pattern of error in the patients, where tracking movements became effectively open-loop. They interpreted this result in terms of an internal forward model of current hand position, which contributed to tracking performance both during normal and suppressed tracking. Cerebellar damage, however, impaired output of this model, making effective control of movement impossible.

Studies of model learning

Many recent studies have compared brain activity before and after tracking learning, and interpreted the observed differences as the result of learning an internal model. Many of these studies have focused on learning novel sensorimotor transformations (Imamizu et al., 1998, 2000). For example, Imamizu et al. (2000)'s subjects learned to move a computer mouse in a condition involving rotated visual feedback. After controlling for changes in brain activity related to tracking error, a further learning-related process was identified in the cerebellum. As this area was more active in rotated than in direct tracking, it was interpreted as an internal forward model of the sensorimotor transformation between the subject's movement and the on-screen cursor movement. However, their design cannot separate the operation of the internal model from the visual feedback from the cursor, in the same way that cursor-suppressed tracking does.

Study of target prediction

Grafton et al. (2001) studied the process of learning to predict target motions. Subjects tracked a target which alternated between a random and a predictable sequence. An implicit learning paradigm showed that subjects learned the predictable target sequences, with corresponding reduction in tracking error. Data from a similar PET experiment showed that this target learning was associated with increased activity in contralateral sensorimotor cortex, and decreased activity in ipsilateral cerebellum. However, these changes could reflect either changes in error signals or changes associated with learning a model of the target motion.

Transfer of learning

The suppression technique allows learning about the target to be clearly separated from learning about one's own movement. An important question is whether we learn two separate internal models; one for the target motion and a second for their own manual movement, or whether there is a single visuomotor learning process which generalizes across these two components. We used a classical transfer of learning design to investigate this issue. Our results showed a clear positive transfer from learning about one's own manual movement to learning about target motion, but not in the other direction. This finding has two important implications. First, learning internal models for motor control involves a distinct process from general prediction of external events. Second, our results suggest a hierarchical organization of visuomotor control. When subjects track in the cursor suppression condition, they learn an internal motor model. Acquisition of this motor model also implies learning about purely perceptual events in the external world, since those subjects then perform well on target-suppressed trials which require them to have an internal model of the target motion. Conversely, when subjects track in the target suppression condition, they learn an internal model which supports perceptual prediction of the target motion. However, acquisition of the target model does not assist in learning about one's own motor control, because those subjects subsequently perform badly on cursor-suppressed trials which require an internal motor model. From the point of view of underlying internal models, motor learning includes, or at least generalizes to, external perceptual learning. In contrast, external perceptual learning is quite distinct from motor learning. Our result implies an internal-external gradient of learning. Psychological theories have shifted from emphasis on passive perception to emphasis on interactive perception over recent decades (Goodale & Milner, 1992; Wexler & van Boxtel, 2005). We suggest that learning internal representations of our own action systems may play an important role in learning about our perceptual world.

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