



Research report

Relation between reaction time and reach errors during visuomotor adaptation

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ABSTRACT

Adaptation of reaching movements to visuomotor transformations is generally thought to involve implicit or procedural learning. However, there is evidence that explicit or cognitive processes can also play a role (Redding and Wallace, 2006 [31]). For example, the early phase of adaptation to a visuomotor rotation appears to involve spatial working memory processes linked to mental rotation (Anguera et al., 2010 [11]). Since it is known that cognitive processes like mental rotation lead to larger reaction times (Georgopoulos and Massey, 1987 [12]), here we explored the relation between reaction time (RT) and reach error reduction. Two groups of subjects adapted their reaching movements to a 60° visuomotor rotation either without RT constraints or with RT limited to 350 ms. In the unconstrained group, we found that adaption rate varied widely across subjects and was strongly correlated with RT. Subjects who decreased hand direction error (DE) rapidly exhibited prolonged RTs whereas little RT cost was seen in subjects who decreased DE gradually. RTs were also correlated with after-effects seen when the visuomotor rotation was removed. Subjects with the longest RTs exhibited the smallest after-effects. In the RT constrained group, all subjects exhibited gradual DE adaptation and large after-effects, similar to the fast responders in the free group. These results suggest that adaptation to a visuomotor rotation can involve processes that produce faster error reductions without increasing after-effects, but at an expense of larger reaction times. Possible candidates are processes related to spatial working memory, and more specifically, to mental rotation.

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1. Introduction

An important aspect of motor learning involves mastering novel transformations between motor commands and sensory outcomes. Such learning has been investigated by examining how people adapt their reaching and throwing movements to altered visual feedback produced by displacing or inverting prisms (e.g., [1–3]) or using visuomotor rotations where the viewed position of the hand (or cursor representing the hand) is rotated about a start position (e.g., [4–7]).

Previous work has shown that adaptation of arm movements to visuomotor perturbations can be affected by secondary tasks [8]. However, the deleterious effects of such tasks is most significant during the early stages of motor adaptation, leading to the suggestion that cognitive resources could be needed mostly at the beginning of the training [9]. It has been suggested that working

memory processes might contribute to visuomotor learning [10] and this suggestion is supported by recent evidence showing that performance on a spatial working memory test correlated with the rate of early visuomotor learning [11].

One way to test if a spatial working memory component related to mental rotation participates in visuomotor learning would be to measure reaction times. Georgopoulos and colleagues [12,13] found that when subjects are required to generate straight line reaches to a location that is rotated away from the visual target, reaction time (RT) increased with rotation angle. They also found that across subjects, RT on the reaching task was positively correlated with RT on a mental rotation task, suggesting a role of a mental rotation process in the reaching task. The aim of the current study was to test if there is any correlation between RT and reach error reduction in a visuomotor adaptation task that could suggest the participation of cognitive processes linked to spatial working memory or mental rotation.

We examined adaptation of reaching movements to a visuomotor rotation of 60°. We hypothesized that if a cognitive strategy was implemented to more rapidly reduce reach direction errors, then adaptation rate would be directly proportional to RT. Because cognitive strategies to reduce errors do not necessarily result in after-effects [1,14–16], we also predicted that subjects who exhib-

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ited the largest RTs at the end of adaptation would exhibit the smallest after-effects following removal of the visuomotor rotation. Finally, we also predicted that if we restricted RT, any working memory or mental rotation process would be compromised, resulting in gradual visuomotor adaptation with large after-effects.

2. Methods

2.1. Subjects

Twenty-seven subjects were recruited from the Queen's University undergraduate and graduate student community after the experimental protocol received approval by the Queen's University General Research Ethics Board. These subjects provided informed consent and received course credits or monetary compensation for their participation.

2.2. Apparatus

Subjects grasped the handle of a lightweight manipulandum (Phantom Haptic Interface 3.0, Sensable Devices, MA) mounted on an air sled that slid across a horizontal glass surface. The manipulandum measured the position of the handle at 1000 Hz with a spatial resolution of 0.1 cm. A virtual reality display system was used to present the start position, the target, and the position of the hand; all represented as circles 2 cm in diameter, in the horizontal plane of the hand. This system consisted of a CRT projector (Electrohome 9500 Ultra with a refresh rate of 150 Hz) that projected onto a screen positioned above a semi-silvered mirror located midway between the screen and the plane of hand motion. Subjects could not see their actual hand or arm.

2.3. Tasks and groups

Three groups of 9 subjects were tested. Two groups adapted to a visuomotor rotation of 60°. Subjects in the unconstrained RT group were told to reach to the target as soon as it was presented but we did not set any time limit for their RT. In the constrained RT group we set a time limit of 350 ms to start the reaching movement following target presentation. If RT exceeded this time limit, the visual display was blanked and a new trial was started. This time limit was chosen for two reasons. First, pilot work showed that subjects could consistently initiate their movements within 350 ms and that doing so resulted in gradual adaptation. Second, the results from the unconstrained group showed that at the end of the practice phase, and at the end of the de-adaptation phase, most subjects exhibited RTs slightly less than 350 ms. A third group performed in a 60° mental rotation task. This mental rotation group was included to estimate the mental rotation RT under our experimental conditions.

2.4. Procedure

Subjects began each trial by aligning the hand cursor to a central start position, located about 10 cm below the shoulder in the mid-sagittal plane. Targets were presented in one of the 8 locations directed radially from the start position. The targets were evenly spaced 45° apart and located 15 cm from the start position. Targets were presented in blocks containing all 8 targets and target order was randomized within each block.

In the visuomotor rotation experiments, subjects began with 3 blocks (24 trials) of normal reaching and then completed 40 blocks (320 trials) with the visuomotor transformation (a 60° counterclockwise rotation of the hand cursor) imposed. They then completed 20 blocks of normal reaching, allowing us to assess after-effects. Subjects were asked to move the cursor controlled by the hand as soon as the target appeared. They were asked to make a continuous out and back movement and not to make on-line movement corrections during the trial. Subjects could see the hand cursor during the movement along with the start position and target.

Subjects in the mental rotation group began with 3 blocks (24 trials) of normal reaching and then completed 20 blocks (160 trials) of the mental rotation task in which they were asked to move the cursor to a location rotated 60° clockwise from the target about the start position. Similar to the unconstrained visuomotor rotation group, they were asked to move as soon as the target appeared and to make a continuous out and back movement equal in amplitude to the distance to the target (i.e., 15 cm). The start position and target were displayed throughout the trial. During the movement, the hand cursor was removed from view. After the movement, a circle (2 cm in diameter) was displayed at the rotated goal (i.e., the location they were instructed to reach towards). This feedback proved effective in that subjects were very successful at reaching in the appropriate direction and with the appropriate amplitude (see Section 3).

2.5. Data analysis

Hand position data were smoothed using a fourth-order low-pass Butterworth filter with a cut-off frequency of 14 Hz. Movement onset was defined as the time at which hand speed (i.e., the magnitude of the resultant velocity of the hand) exceeded 10 cm/s and RT was defined as the time period between presentation of the target

and the onset of hand movement. The initial direction of the hand was defined as the vector from the start position to the location of the hand 150 ms after movement onset and thus before substantial corrections to the hand trajectory, based on visual feedback, would be observed. Hand direction error (DE) was defined as the angular difference between the initial direction of the hand movement and the required direction of hand movement (i.e., 30, 60 or 180° clockwise from the visual target). For each block of 8 trials, we computed the median DE and RT and all data analyses are based on trial blocks. We used median values as an extra safeguard against outlying or erroneous data points. For statistical tests, an alpha level of 0.05 was considered to be significant.

To quantify adaptation, we fit exponentials of the form $y = ae^{bx} + c$ to the DE adaptation data of each subject. To quantify RT, we first normalized each subject's RTs to their baseline RT. Specifically, for each block we computed ΔRT by subtracting the RT on the final de-adaptation block (block 60) from the RT on that block. Because we expected the use of a strategy to be most likely during early learning [27], we computed, for each subject, the mean ΔRT over blocks 2–11. We excluded the first block because we did not expect increases in RT over the first few reaches.

3. Results

3.1. Adaptation to the 60° visuomotor rotation without RT constraint

Fig. 1A and B show mean hand direction error (DE) and reaction time (RT), averaged across subjects, as a function of trial block in the 60° visuomotor rotation group without RT constraint. Each plot shows data for the 3 practice blocks, the 40 visuomotor rotation blocks (adaptation phase), and the subsequent normal reaching blocks (de-adaptation phase). As expected, the initial DE during the adaptation phase was initially slightly less than the imposed rotation angle, gradually decreased over the first 20 blocks, and leveled out during the last 20 blocks. The DE at the end of the adaptation phase remained elevated. Specifically, the DE in the last adaptation block (block 40) was significantly greater than zero ($t_8 = 3.42$; $p < 0.01$). On average, RT increased from the first to the second block of the adaptation phase, decreased over the next 20 blocks or so, and then leveled out. During the de-adaptation phase, the average DE gradually decreased towards zero and the average RT gradually decreased towards the baseline level seen at the end of the initial practice blocks. Importantly, the average RT remained elevated even at the end of the adaptation phase. A paired t -test revealed that RT in the last adaptation block (block 40) was significantly greater ($t_8 = 2.81$; $p = 0.02$) than the RT in the last de-adaptation block (block 60).

The substantial increase in average RT observed during the adaptation phase suggests that at least some subjects may have been using a cognitive strategy to help reduce DE. If so, then we might expect subjects with larger RTs to reduce DE more rapidly. In addition, we would expect subjects with larger RTs to exhibit smaller after-effects. To assess these predictions, we plotted the DE and RT functions for each of the 9 subjects who experienced the 60° visuomotor rotation (Fig. 1C–H). To illustrate the correspondence between DE and RT, we show these subjects' data in three panels. Subjects shown in Fig. 1C and D rapidly decreased DE and exhibited the longest RTs, especially over the first 20 trial blocks. Moreover, DE was decreased close to 0°. In contrast, subjects shown in Fig. 1G and H gradually decreased DE and exhibited the shortest RTs. Indeed, with the exception of a few blocks at the start of the adaptation phase, their RTs were similar to those observed during the normal reaches at the end of the de-adaptation phase. In addition, a substantial steady-state DE was observed at the end of the adaptation phase. Subjects shown in Fig. 1E and F were intermediate between the two other groups in terms of adaptation rate, RT, and steady-state DE. Fig. 1I shows the adaptation exponentials as well as exponentials fit to the DE de-adaptation data. Fig. 1J shows the mean ΔRT over blocks 2–11 and block 40. Note that it is over the initial phase of adaptation that the greatest differences in DE are seen across subjects.

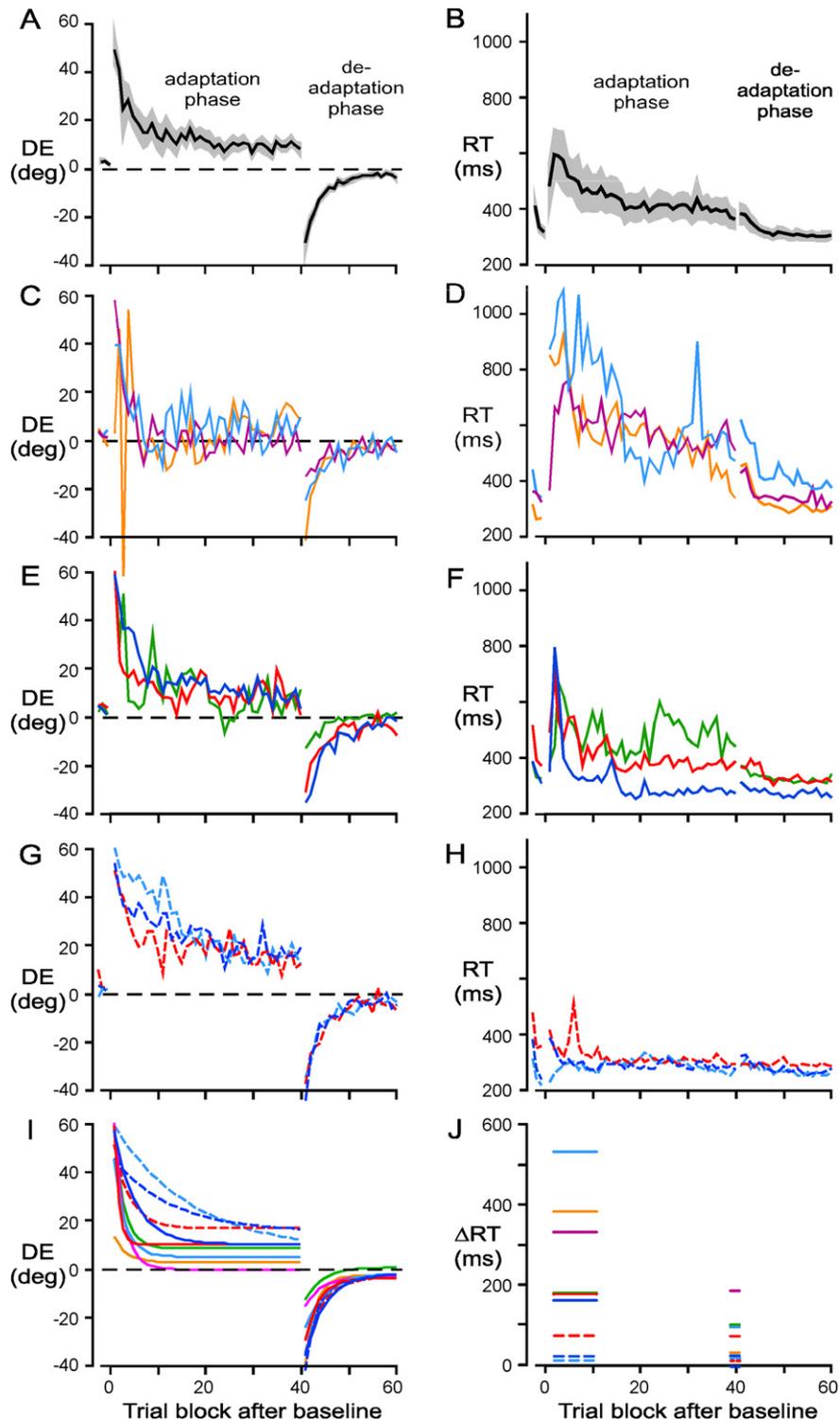


Fig. 1. Direction error (DE) and reaction time (RT) adaptation data for the 60° visuomotor rotation. (A and B) DE and RT as a function of trial block including 3 practice blocks of normal reaching, 40 adaptation blocks with the visuomotor rotation, and 20 de-adaptation blocks with normal reaching. The curves represent means averaged across subjects and the height of the shaded areas represents ± 1 standard error. (C–H) DE and RT data for individual subjects identified by line type and color. The three rows show subjects who adapted rapidly (C and D), at an intermediate rate (E and F), and gradually (G, H). I: exponentials fit to the DE adaptation and de-adaptation data for each subject. (J) Mean ΔRT (increment in RT from baseline) over trial blocks 2–11 and block 40. (I and J) Line types and colors are the same in C and H. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

To assess the relation between adaptation rate and RT, we regressed the DE half-life against the mean ΔRT over blocks 2–11 (see black dots in Fig. 2A) and found a significant negative correlation ($p=0.05$). We also found a reliable negative correlation ($p=0.03$) between the DE asymptote and the mean ΔRT over blocks 2–11 (black dots in Fig. 2B). These results confirm that an increase

in RT during early adaptation was associated with a more rapid and more complete reduction in DE. It should be noted, however, that there was not a correlation between the last baseline trial RT and the mean RT over trial blocks 2–11 of the adaptation phase ($r^2=0.17$; $p=0.27$), suggesting that the RT during the adaptation phase cannot be predicted by the baseline RT. To assess the rela-

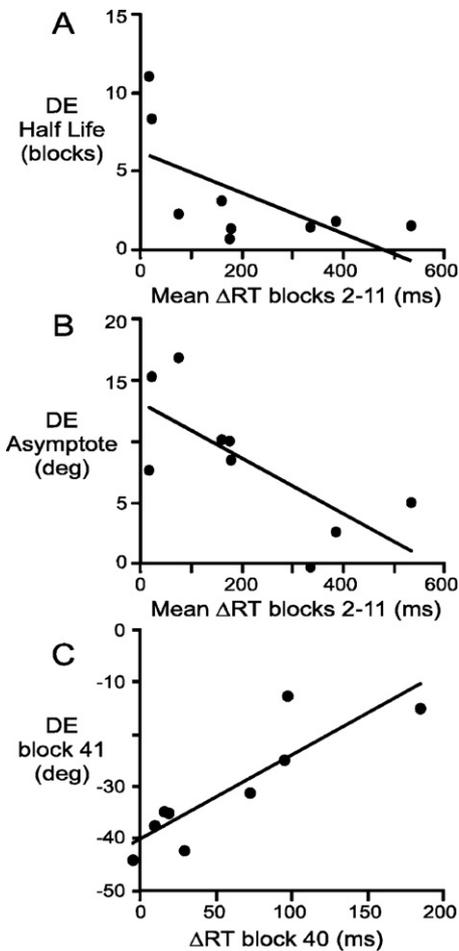


Fig. 2. Relation between reaction time (RT) and direction error (DE) during adaptation and de-adaptation to 60° visuomotor rotation without RT constraint. (A and B) Half-lives (A) and asymptotes (B) of exponentials fit to the DE adaptation data plotted against the mean Δ RT (increment in RT from baseline) over trial blocks 2–11. Each point represents a single subject and the lines were obtained using least squares regression. (C) DE on the first block of the de-adaptation phase against RT on the last block of the adaptation phase.

tion between RT and after-effects, we regressed the DE on the first block of the de-adaptation phase (block 41) against the Δ RT on the last block of the adaptation phase (block 40; see black dots in Fig. 2C). A significant correlation was observed ($p < 0.01$).

The above analysis provides a global assessment of the relation between DE and RT. However, we were also interested in the relation between DE and RT at different points during adaptation. For this analysis we computed, for each subject, the average DE and Δ RT for each successive set of 5 blocks during the adaptation phase (making 8 sets). Fig. 3 shows Δ RT as a function of DE for each set. Reliable correlations ($p < 0.05$) between Δ RT and DE were observed in all 8 sets. Thus, throughout adaptation to the 60° visuomotor rotation, decreased DE was associated with increased RT.

Inspection of Fig. 1C, E and G suggests that subjects who decreased DE rapidly also exhibited greater block-to-block variance in DE, even at the end of the adaptation phase where the average DE had leveled out. To assess this quantitatively, we regressed the SD of DE over the last 5 blocks of the adaptation phase against DE half-life. A significant negative correlation was observed ($p = 0.04$) suggesting that DE at the end of adaptation was more variable in subjects who adapted quickest.

The above results are consistent with the idea that, when faced with the large initial errors associated with a 60° visuomotor rotation, some subjects adopt a strategy to more rapidly reduce DE.

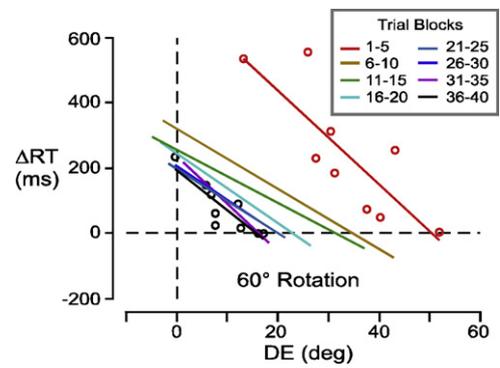


Fig. 3. Relation between reaction time (RT) and direction error (DE) for each of the 8 successive sets of 5 trial blocks during adaptation to the 60° visuomotor rotations. For each set and subject, we computed the mean Δ RT and DE averaged across the 5 blocks per set. The red and black dots show these mean values for sets 1 and 5. The color-coded lines represent linear regression lines fit to the mean values of each set. For clarity, data points were included only for the two extreme sets (sets 1–5 and 36–40). Reliable correlations ($p < 0.05$) between Δ RT and DE were observed in all 8 sets. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

However, the putative use of this strategy comes at a cost in terms of RT. If the strategy adopted by the subjects resembles mental rotation that would explain the more rapid decrease in DE as well as the increase in RT. The results are also consistent with the view that explicit or strategic adaptation occurs in parallel with implicit or automatic learning and that the relative contribution of these two mechanisms varies across subjects.

The intertrial interval (ITI), which we did not specifically control in our experiments, is another variable that could affect the rate of adaptation [17,18]. To assess this possibility, we examined the relation between average ISI during the adaptation phase, determined for each subject, and adaptation rate. A linear regression between DE half-life and ITI was not significant ($r^2 = 0.25$; $p = 0.17$), suggesting that individual differences in ITI do not account for individual differences in adaptation rate.

3.2. Adaptation to the 60° visuomotor rotation with RT constraint

Fig. 4A and B shows mean hand direction error (DE) and reaction time (RT), averaged across subjects, as a function of trial block in the 60° visuomotor rotation group with RT time constraint. Each plot shows data for the 5 practice blocks, the 40 visuomotor rotation blocks (adaptation phase), and the subsequent normal reaching blocks (de-adaptation phase). For comparison, curves from a single subject from the group without RT constraint who exhibited a short RT are included. The DE gradually decreased over the entire 40 blocks, and still remained elevated at the end of the adaptation phase. Specifically, the DE in the last adaptation block (block 40) was significantly greater than zero ($t_8 = 6.18$; $p < 0.001$). On average, RT increased slightly from the practice blocks to the first block of the adaptation phase, showing only a small reduction over the 40 blocks. RT in the last adaptation block was shorter than in the first adaptation block ($t_8 = 4.31$; $p < 0.003$). During the de-adaptation phase, the average DE gradually decreased towards zero and the average RT kept gradually decreasing towards the baseline level seen at the end of the initial practice blocks.

3.3. Mental rotation reaching task

Previous studies have shown that when subjects are required to reach to locations that are rotated from visible targets, RT increases with the rotation angle [12]. This finding suggests that subjects use a mental rotation strategy in order to perform this task. Specifically,

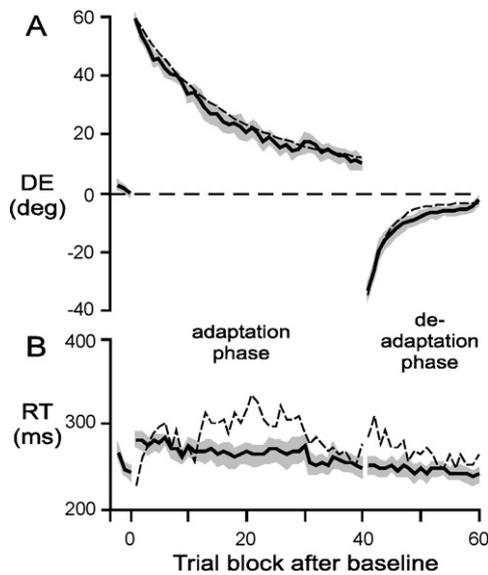


Fig. 4. Direction error (DE) and reaction time (RT) adaptation data for the 60° visuomotor rotation group with a RT constraint of less than 350 ms. (A and B) DE and RT as a function of trial block including 3 practice blocks of normal reaching, 40 adaptation blocks with the visuomotor rotation, and 20 de-adaptation blocks with normal reaching. The curves represent means averaged across subjects and the height of the shaded areas represents ± 1 standard error. The dashed line represents DE and RT data for a subject, from the group without RT constraint, who exhibited a short RT (from Fig. 1G and H). Note the similar behaviour of this subject with the average from the RT constrained group.

it has been suggested that subjects mentally rotate the visible target about the hand start position in order to generate an internal reach target [12,13,19–21]. Because we are suggesting that subjects often use a mental rotation strategy when adapting to a visuomotor rotation, and that RT reflects the magnitude of this rotation, we felt it was important to determine the mental rotation RT within our experimental set-up. Fig. 5A and B shows mean DE and mean RT as a function of trial block for the group of subjects who performed the 60° mental rotation task. The plot shows data for the 3 practice blocks and the 20 mental rotation blocks. A large increase in RT was observed when the mental rotation task was introduced. RT then decreased over the first few mental rotation blocks but then leveled out and remained elevated for the remainder of the mental rotation task. The DE was close to zero throughout.

The mean RTs observed in the 60° mental rotation tasks is clearly much longer than the mean RTs seen in the 60° visuomotor rotation tasks (Figs. 1B and 4B). This is not unexpected for two reasons. First, not all subjects appeared to employ a strategy when adapting to the visuomotor rotation. Second, most subjects who appeared to use a strategy did not rotate movement direction by the full 60° rotation and instead only partially compensated for the visuomotor rotation via this putative strategy. Nevertheless, it is worth noting that subjects who showed the most rapid decrease in DE when adapting to the 60° rotation (Fig. 1C) exhibited initial RTs (Fig. 1D) that are similar to those seen at the start of the mental rotation task (i.e., around 900 ms). This finding could suggest that these subjects employed large mental rotation angles at the start of adaptation.

4. Discussion

Our results show that given a large visuomotor rotation, subjects exhibit a range of RTs that correlate positively with reach error reduction rates and negatively with after-effects. When RT is constrained to a maximum of 350 ms, subjects show a slow error reduction rate and a large after-effect, similar to the fast responders in the unconstrained RT group. Finally, the mental rotation group

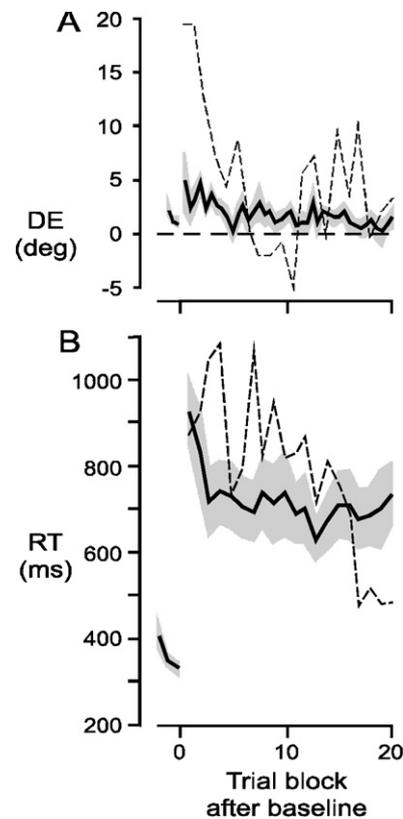


Fig. 5. Direction error (DE) and reaction time (RT) adaptation functions for the 60° mental rotation reaching task group. (A and B) DE (A) and RT (B) as a function of trial block including 3 practice blocks of normal reaching and 20 blocks with the visuomotor reversal. The curves represent means averaged across subjects and the height of the shaded areas represents ± 1 standard error. The dashed lines represent DE (A) and RT (B) data for a subject from the group without RT constraint, who exhibited a long RT (from Fig. 1C–D).

showed RTs similar to the average RT shown initially by subjects who decreased reach error the quickest in the unconstrained RT group.

4.1. Reaction time in visuomotor learning

Although measures of RT have been widely used in studies of motor sequence learning (e.g., [22,23]) and motor planning and trajectory specification [24,25], RT measures have seldom been considered in the context of visuomotor, or force field, adaptation. The aim of the current study was to examine possible changes in RT when reaching under, and adapting to, visuomotor perturbations. We first examined the relation between RT and adaptation parameters when learning a 60° visuomotor rotation. We found that RT during early learning was positively correlated with both the rate and extent of decreases in reach direction errors. Subjects who exhibited large increases in RTs during the early phase of learning decreased direction errors rapidly and nearly completely, whereas subjects who showed little or no RT cost decreased direction errors gradually and exhibited substantial direction errors at the end of adaptation. This gradual adaptation seen in some subjects could be due to different factors, including short ITIs that could result in having too little time to process the results of the movement [17,18], or a lack of attention to the motor errors [8]. However, the lack of correlation between DE half-life and ITI seems to suggest that the gradual adaptation shown by these subjects was not the result of short ITIs.

One explanation for these results is that some subjects employ a cognitive strategy that could be related to spatial working memory

[10,26]. Specifically, previous reports have suggested a possible role of mental rotation in visuomotor learning [11,27]. Based on previous studies in which subjects are explicitly instructed to reach to a location rotated away from a visible target [12,13], we would expect RT to increase with the angle between the internal and visible target. Assuming that subjects rotate the internal target appropriately so as to reduce direction error, we would also expect a positive relation between increases in RT and decreases in reach direction error. The idea that a cognitive mental rotation strategy can be exploited to more rapidly adapt to a visuomotor rotation is consistent with the recent results of Anguera et al. [11]. These authors showed that, across subjects, performance on a mental rotation task is correlated with the rate of early, but not late, adaptation to a visuomotor rotation.

4.2. Visuomotor learning and mental strategy

Although the use of a mental rotation strategy would be expected to result in a correlation between RT and adaptation rate, the fact that we observed a correlation does not necessarily imply the use of such a strategy. That is, the link between RT and adaptation rate may arise for other reasons. For example, it is possible that subjects who exhibited prolonged RTs processed errors from the previous movement more thoroughly, prior to initiating the current movement, and therefore reduced direction errors more quickly. However, that would not explain why the performance of these subjects appears to be more unstable once their reach errors leveled out (see Fig. 1C–H). Note that our results cannot be explained simply in terms of a speed-accuracy trade-off. This trade-off is typically concerned with the relation between movement speed and movement variability, rather than RT and biases in movement direction.

4.3. Implicit and explicit processes in visuomotor learning

The idea that implicit and explicit processes contribute to the adaptation is not new. Previous reports have shown, for example, that simply by making subjects aware of the visual displacement by providing them with explicit information about the prisms leads to reduced levels of adaptation [28,29]. In a study by Mazzoni and Krakauer [30] subjects were asked to move a cursor to targets under a 45° visuomotor rotation. The subjects were told about the rotation and given an explicit strategy to correct for it. Specifically, they were told to aim to another target located 45° away from the cursor target. Although subjects could initially implement this strategy with success, performance deteriorated because they could not stop implicitly adapting to the visuomotor rotation, presumably based on the error between the aim target and the cursor, and thus overcompensated for the rotation. However, the same experiment suggests that there was a continuing interaction between the implicit adaptation and the cognitive component because the level of implicit adaptation was less than that seen in a control group who were not given the explicit strategy. This led to the authors to suggest that when the explicit strategy failed, subjects searched for alternative strategies [30] such that both processes continued to interact.

Our results are consistent with the idea that explicit and implicit processes occur in parallel and suggest that the relative contribution of these two processes to reducing direction error can vary considerably across subjects. Our results also suggest that the relative contribution of these two putative processes can vary during the course of adaptation. We found that, on average, RT decreased during adaptation to the 60° visuomotor rotation without a RT constraint. Although not all subjects showed an increase in RT when first encountering the visuomotor rotation, for those who did, RT tended to decrease during the adaptation phase. Our results cannot

confirm if the RT decrease is the result of a shift from relying on explicit processes (e.g., a mental rotation strategy) to relying on implicit adaptation. This possibility would agree with the results of Anguera and colleagues [11] showing that performance on a mental rotation task is correlated with early, but not late, adaptation to a visuomotor rotation.

4.4. After-effects, visuomotor learning and cognitive strategies

In the constrained RT experiment, all subjects exhibited large after-effects consistent with the idea that adaptation (and subsequent de-adaptation) primarily involved procedural processes. In the unconstrained RT experiment, after-effects were also observed in all subjects, suggesting that implicit learning occurred by the end of adaptation [31]. However, some subjects showed smaller after-effects than others. Reduced after-effects could arise either because (1) the subject used a cognitive strategy throughout the adaptation phase, resulting in a less procedural learning, and then stopped using this strategy at the start of the de-adaptation phase or (2) because the subject used a cognitive strategy during early adaptation and then again during early de-adaptation. In any event, our finding that RT drops back to baseline levels by the end of the adaptation phase indicates that subjects stop using any cognitive strategy by the end of this phase.

4.5. Visuomotor adaptation and mental rotation

If subjects are using a mental rotation-like process, then a reduction in the mental rotation angle may account for the decrease in RT that was observed. We found that subjects who decreased DE most rapidly when adapting to the 60° visuomotor rotation also exhibited greater DE variance at the end of adaptation. This greater variance may arise because these subjects were using a mental rotation strategy and would be trying to update the magnitude of mental rotation to compensate for implicit adaptation. In other words, the use of a mental rotation strategy may lead to performance that is less stable than that seen when adaptation is achieved via implicit learning alone, just as described for subjects using a cognitive strategy and implicit learning to compensate for a rotation [30]. In contrast, the constrained RT group showed more stable performance that was characterized by slow learning and low variance. This suggests that if RTs are kept short, discouraging the use of time-consuming processes like mental rotation, responses will show the slow error reduction and persistent after-effects typical of implicit procedural learning [2].

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