Gaze locations affect explicit process but not implicit process during visuomotor adaptation

Miya K. Rand and Sebastian Rentsch
Leibniz Research Centre for Working Environment and Human Factors (IfADo), Dortmund, Germany

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Rand MK, Rentsch S. Gaze locations affect explicit process but not implicit process during visuomotor adaptation. J Neurophysiol 113: 88–99, 2015. First published September 24, 2014; doi:10.1152/jn.00044.2014.—The role of vision in implicit and explicit processes involved in adaptation to novel visuomotor transformations is not well-understood. We manipulated subjects’ gaze locations through instructions during a visuomotor rotation task that established a conflict between implicit and explicit processes. Subjects were informed of a rotated visual feedback (45° counterclockwise from the desired target) and instructed to counteract it by using an explicit aiming strategy to the neighboring target (45° clockwise from the target). Simultaneously, they were instructed to gaze at either the desired target (target-gaze group), the neighboring target (hand-target-gaze group), or anywhere (free-gaze group) during aiming. After initial elimination of behavioral errors caused by strategic aiming, the subjects gradually overcompensated the rotation in the early practice, thereby increasing behavioral errors (i.e., a drift). This was caused by an implicit adaptation overriding the explicit strategy. Notably, prescribed gaze locations did not affect this implicit adaptation. In the late practice, the target-gaze and free-gaze groups reduced the drift, whereas the hand-target-gaze group did not. Furthermore, the free-gaze group changed gaze locations for strategic aiming through practice from the neighboring target to the desired target. The onset of this change was correlated with the onset of the drift reduction. These results suggest that gaze locations critically affect explicit adjustments of aiming directions to reduce the drift by taking into account the implicit adaptation that is occurring in parallel. Taken together, spatial eye-hand coordination that ties the gaze and the reach target influences the explicit process but not the implicit process.

sensorimotor learning; implicit adaptation; explicit strategy; vision; reaching

Adaptation to novel visuomotor rotations occurs regardless of whether individuals have explicit knowledge of a perturbed visuomotor mapping (Kagerer et al. 1997; Klassen et al. 2005; Peled and Karniel 2012). Such explicit knowledge is nearly absent during adaptation to a visuomotor rotation when the rotational angle of visual feedback is small (e.g., 30°; Heuer and Hegele 2008; Peled and Karniel 2012; Rentsch and Rand 2014) but is often present when the angle is large (e.g., 60, 75°; Heuer and Hegele 2008; Werner and Bock 2007). With explicit knowledge, strategic adjustments of reaching directions can be made to compensate for the rotation, thereby increasing the magnitude of the overall behavioral adaptation (Heuer and Hegele 2008; Werner and Bock 2007). In addition to the size of rotational angles, the type of visual feedback of hand movements [e.g., online (concurrent) vs. endpoint (terminal)] also affects the involvement of implicit and explicit processes in adaptation to visuomotor rotations. Online visual feedback seems to be important for implicit adaptation (Hinder et al. 2008, 2010; Peled and Karniel 2012; Shabbott and Sainburg 2010), although implicit adaptation can also occur when using endpoint feedback (Taylor and Ivry 2011; Taylor et al. 2014). Furthermore, endpoint feedback is shown to enhance the process of strategic adjustments of reaching direction more compared with online feedback (Taylor et al. 2014). Thus the involvement of implicit and explicit processes in visuomotor adaptation changes depending on various factors.

To examine the different contributions of an explicit strategy and an implicit adaptation to learning of a visuomotor rotation, Mazzoni and Krakauer (2006) developed a paradigm that presented an additional hand target (where the hand had to reach for counteracting the rotated visual feedback) and instructed subjects to make explicit aiming movements toward it. This procedure initially eliminated behavioral errors but soon afterward resulted in overcompensation for the visuomotor rotation, which then required a long practice to be corrected (Mazzoni and Krakauer 2006; Taylor and Ivry 2011). Such overcompensation due to explicit aiming is called a drift (Taylor and Ivry 2011) and reveals a nontrivial relationship between an implicit adaptation and an explicit strategy in visuomotor learning. The drift is manifested as aiming movements gradually drift away from the hand target in the direction that further counteracts the rotation. It is explained by the theory that the explicit strategy, which is based on behavioral error between the target and visual feedback of the movement, is overridden by implicit motor adaptation, which is based on aiming error between a predicted aiming direction and visual feedback (Mazzoni and Krakauer 2006; Shadmehr et al. 2010; Taylor and Ivry 2011). Thus the drift reflects parallel implicit and explicit processes involved in learning of novel visuomotor transformations.

Notably, the magnitude of drift is increased when the hand target is visible but decreased when it is invisible (Taylor and Ivry 2011). Thus visual information of the hand target for explicit aiming and the related gaze locations should play an important role for the drift. However, the role of eye movements for implicit and explicit processes in visuomotor learning is poorly understood. We therefore examined what effects different gaze locations (looking at target, hand target, or anywhere) during strategic aiming have on the drift phenomenon. Different gaze locations alter spatial eye-hand coordination for strategic aiming, namely, the aiming target is in a central vision under the hand-target gazing but in a peripheral vision under the target gazing. This manipulation changes the underlying neural processes (Bédard et al. 2013; Prado et al. 2005; Vesia and Crawford 2012) as well as the quality of visual
estimate of behavioral and aiming errors for explicit and implicit processes. The results will show that gaze locations do not affect the emergence of the drift (implicit process) but that they do affect the subsequent drift elimination (explicit process).

MATERIALS AND METHODS

Subjects

Thirty-six young adults (mean ± SD: 23.1 ± 3.0 yr; 19 men and 17 women) participated in the study. All subjects were right-handed and had normal visual acuity. They had no history of neurological or movement impairments and gave written, informed consent before participation. The study was conducted in accordance with the Declaration of Helsinki and with general approval by the ethics committee of the Leibniz Research Centre for Working Environment and Human Factors. Subjects were randomly assigned to one of three groups (target-gaze, hand-target-gaze, or free-gaze).

Apparatus

Subjects were seated at a table on which a 22-in. LCD monitor (Dell P2210) was placed in average 66.5 ± 3.3 (SD) cm from their eyes. A digitizer tablet (Wacom Intuos4 XL) was placed on the table between the subjects and the monitor. The starting position centered on the monitor was aligned with the subjects’ median plane. They held a stylus with their right hand in a manner similar to holding a pen for handwriting and made horizontal aiming movements to a target. They were instructed to slide the stylus tip on the digitizer surface during movements and not to stop on the target but move through it. Movements of the stylus on the tablet and those of a cursor displayed on the monitor had a one-to-one ratio with respect to distance. An opaque board placed above the subjects’ arm blocked their view of the hand movements. The x- and y-positions of the tip of the stylus were recorded at 200 Hz with a spatial resolution of 0.005 mm.

Horizontal eye movements were recorded by using iView X RED500 (SensoMotoric Instruments), which was positioned below the monitor. This noninvasive system, which is based on using infrared light to visualize the pupil and corneal reflections, sampled the movement of each eye at 500 Hz and recorded average gaze positions of both eyes. To increase the stability and precision of eye recording, the subjects rested their chin on a chin rest. Spatial resolution and accuracy of the system were 0.03 and 0.4°, respectively. The eye tracker was calibrated for each subject before data recording using nine saccadic targets across the monitor. To synchronize the digitizer and the eye tracker, the onset of data acquisition was marked by 10.220.32.246 on September 29, 2016 http://jn.physiology.org/ Downloaded from by 10.220.32.246 on September 29, 2016

procedures

The general task procedures were relatively similar to those described in Taylor and Ivry (2011). The start position (SP; closed black circle, 0.5 cm in diameter) was located in the center of the monitor. Around the SP, eight targets (open blue circles, 0.5 cm in diameter each) were evenly distributed and formed an invisible ring with a radius of 10 cm. The targets were not at cardinal directions but started at 22.5° and increased in 45° steps. Although the eight target locations were displayed on the monitor, only four of them (at 22.5, 112.5, 202.5, and 292.5°) were used as the targets for the visuomotor rotation task.

At the beginning of each trial, the subjects were guided to the invisible SP by one or two out of four arrows pointing to the left, right, up, and down presented in the periphery of the monitor. The SP and the cursor became visible when the stylus was within a radius of 1.5 cm from the SP to assist the subjects in reaching the SP accurately. When the cursor had reached the SP and had been held in that position for 1 s, the eight targets (open blue circles) appeared on the monitor. After a random delay of 1–2 s, the color of one of the eight targets was changed to black, which served as a go signal and the target for reaching. In response, the subjects made a ballistic aiming movement toward the target and moved through it. Subjects were instructed to move as quickly as possible to reach the target, whereas a rapid start of movements was not stressed. A cursor (closed red circle, 0.5 cm in diameter) provided visual feedback of the hand movements. There was no feedback during the movement, but once the hand crossed the invisible ring, a stationary red feedback cursor was displayed for 1,000 ms at that spot. The distance between the feedback cursor and the black target indicated a behavioral error (i.e., target error) to the subjects. After the display of the feedback cursor, the subjects were visually guided back to the starting position for the next trial.

Experimental Conditions

The experiment consisted of a fixed order of the following conditions: baseline-I, pretest, strategy-only, baseline-II, rotation-only, practice (i.e., rotation + strategy), posttest, maintenance, and test of explicit knowledge (Fig. 1F). Visual feedback was not provided in the pretest and posttest. The visual feedback was rotated by 45° to the counterclockwise (CCW) direction in the rotation-only, practice, and maintenance conditions. A total of 382 experimental trials were recorded.

In the baseline-I condition [Fig. 1A; 48 trials (4 target locations × 12 trials)], the subjects were trained to make rapid aiming movements from the SP to the target. If the duration of movement until crossing the invisible ring was >300 ms, a beep sound was delivered to notify the subjects that their movement was too slow. They were also trained to make precise directions of their movements toward the targets. The subjects were instructed that the goal of their task was to reduce the distance between the red feedback cursor and the black target so that the cursor was aligned with the target.

After the baseline-I condition, the pretest [Fig. 1B; 12 trials (4 target locations × 3 trials)] was performed under the same procedure except that no visual feedback was provided at the end of each trial. Next, in the strategy-only condition [Fig. 1C; 20 trials (4 target locations × 5 trials)], subjects learned to use a 45° clockwise (CW) strategy. When one of the open blue targets turned black to indicate the target location, the subjects were instructed to make aiming movements to the neighboring target located in a 45° CW direction. The task goal in this condition was to align the feedback cursor with the neighboring target. After the strategy-only condition, the baseline-II condition [20 trials (4 target locations × 5 trials)] was carried out to stabilize the baseline performance. The procedure was the same as the baseline-I condition.

Following the baseline-II condition, 2 trials were performed as the rotation-only condition (Fig. 1D). The visual feedback was rotated for 45° to the CCW direction from the actual hand position without informing the subjects. Consequently, the target error increased dramatically without warning. After completing these 2 trials, the subjects were informed of the introduction of visual feedback rotation and that a compensation strategy to counteract the rotation completely for getting the cursor into the target would be to move the hand to the neighboring target in 45° CW direction from the black target. The subjects were instructed to use this strategy thereafter [Fig. 1E]. The subjects performed the next 240 trials with this procedure [i.e., practice condition (4 target locations × 60 trials)].

Next, in the posttest [20 trials (4 target locations × 5 trials)], the subjects were informed that the rotated visual feedback had been
removed so that they did not need to use the compensation strategy and move the hand directly to the target. They were also informed that no feedback cursor would appear on the monitor. In effect, this procedure was the same as the pretest. Afterward, the maintenance condition [12 trials (4 target locations × 3 trials)] followed. For this condition, the visual feedback was again turned on, and the rotation of visual feedback was reintroduced. The subjects performed the same task as that of the practice condition.

Following the maintenance condition, a test of explicit knowledge was carried out [8 trials (4 target locations × 2 trials)], A similar explicit test was used in previous studies (Heuer et al. 2013). A line was presented on the monitor with its 1 end in the SP. It rotated slowly around the SP. The subjects instructed the examiner to stop and finely adjust the orientation of the line to match the direction of the hand movement they judged to be correct for the target presented. For this judgment, the subjects were informed that the rotation of the visual feedback was still in effect.

In addition to the above procedures of visuomotor learning, other instructions regarding gaze location were given to subjects in the strategy-only, practice, and maintenance conditions. For this purpose, the subjects were divided into three experimental groups. In the target-gaze group (n = 12, 5 women, 7 men, ages 19–29 yr), subjects were instructed to look at the black target (Fig. 1E, hand target) during the strategic aiming movements. In the hand-target-gaze group (n = 12, 6 women, 6 men, ages 18–27 yr), subjects were instructed to look at the black target (Fig. 1A, hand target) during the strategic aiming movements. In the free-gaze group (n = 12, 6 women, 6 men, ages 20–28 yr), subjects were free to look anywhere. No specific gaze instruction was given to the subjects of all groups in the other conditions so that they looked naturally anywhere during hand movements.

The viewing distance of the eyes to the monitor was 67.6 ± 5.5 (mean ± SD), 65.9 ± 1.4, and 66.2 ± 1.2 cm in average across subjects in the free-gaze, hand-target-gaze, and target-gaze groups, respectively. The group difference was not significant [F 2, 33 = 0.90, P > 0.05]. The average distance across all subjects was 66.5, resulting in ~8.60° of a visual angle from the SP to the targets and 6.52° between the target and the hand target.

Data Analysis

For the analysis of hand movement, x- and y-position data were resampled at 500 Hz and subsequently low-pass filtered at 10 Hz by using fourth-order Butterworth filter. Velocity was calculated as the first derivative of position data by using two-point central-difference algorithm. Movement onset was determined using a threshold criterion of 5 mm/s. When the velocity profile was above this threshold for 200 ms, the last data sample before crossing the threshold was determined as the movement onset. Movement offset was determined as the time when the hand moved through the invisible ring (10-cm radius centered on the SP). These landmarks were first automatically detected using computer software. Subsequently, the results of this automatic procedure were inspected and corrected manually as needed.

Target error (Fig. 2A) was calculated in each trial as the angle between the direction of the vector originating from the SP to the target error (Fig. 2B, C) was calculated in each trial as the angle between the direction of the vector originating from the SP to

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and SP. Mid area refers to the area between T area and HT area. Target and visual feedback is thought to drive adjustment of explicit aiming contrast, target error (i.e., behavioral error regarding the task goal) between the direction of the movement. Aiming error between the predicted direction of the planned movement (Aim). C refers to a visual feedback cursor (Fig. 2A). In plot B, 3 black dots indicate the target (T), the hand target (HT), and SP. Mid area refers to the area between T area and HT area. Target (i.e., SP-target vector) and the direction of hand movement (which was determined by the line connecting the SP and the movement offset). Exclusively for rotation-only and the practice conditions where the feedback cursor was rotated to the 45° CCW direction, target error was adjusted by adding 45°. Thus, when hand movements overcompensated the rotated visual feedback during practice, the sign of the target error became positive. The target error was used to assess the quality of planned movement direction because aiming movements were ballistic and no visual feedback was provided during movements.

For calculating aftereffect, all posttest trials were divided into 5 blocks with 4 trials (1 trial for each target), and mean target error was calculated for each block in each subject. Subsequently, aftereffect was calculated by subtracting the mean target error across all trials of the pretest condition from the mean target error of posttests in each block. For the explicit test, the judged angle was measured in each trial as the direction of the line at which the judgment was made and the direction of the SP-target vector. The mean angle across all trials was calculated for each subject.

For analysis of the movement accuracy, all trials of the strategy-only and the baseline-II and practice conditions were divided into 5 blocks with 4 trials (1 trial for each target), and those of the practice conditions were divided into 60 blocks of 4 trials each. Mean target error across 4 trials was calculated for each block. Furthermore, the largest target error among all trial blocks of the practice condition was used as a maximum drift measure.

Gaze locations during the practice condition were analyzed in each trial at 6 different timings relative to hand movements (200, 150, and 100 ms before the movement onset, the movement onset, 100 ms after the movement onset, and the movement offset). We defined 4 gaze areas for this analysis: the target (T) area, the hand-target (HT) area, Mid area, and the SP area (Fig. 2B). The SP area was a circular area around SP (2 cm in radius). The T, Mid, and HT areas are a part of another, larger circle centered on the SP (12 cm in radius) but excluding the SP area. The T area ranged between ±11.25° with the central direction defined by the SP and the target. The HT area ranged between ±11.25° with the central direction defined by the SP and the hand target. The Mid area was the area between the T and HT areas and ranged 22.5°. We identified to which area gazes went at each of the above 6 timings in each trial. Subsequently, the number of the incidents was counted, and the incidence was calculated as the percentage of trials per block for the practice condition. Furthermore, we examined the relation between the decline of gaze incidence at the HT area and the reduction of target error after the maximum drift (i.e., reduction of drift) in the free-gaze group. The following two analyses were performed in the practice condition. For the first analysis, the trial block immediately after the maximum drift was identified as the onset of the reduction of drift in each subject. Next, a block of trials, where gaze incidence at the HT area was reduced for the first time for the amount ≥50% compared with the gaze incidence recorded in the first five blocks of trials, was identified as the onset of gaze-incidence decline in each subject. Each individual’s block numbers from the two parameters were correlated to see whether the onsets of drift reduction and the gaze-incidence decline for the HT area were related to each other. For this analysis, we have also tried 25%, or 75% as the above threshold aside from 50%. However, 50% produced the strongest correlation, and this result was reported. For the second analysis, the slope of the gaze incidence against the block of trials was calculated in each participant by using a linear regression. The slope of mean target error against the block of trials was also calculated in the same way. For those slope calculations, only the blocks of trials including and after the maximum drift were used. Each individual’s slope values from the two parameters were correlated to see whether the rates of the drift reduction and the gaze-incidence decline for the HT area were related.

In addition to the above analysis of gaze locations based on the four gaze areas (Fig. 2B), we measured gaze directions at 100 ms after the onset of hand movement. Gaze direction was defined as an angle between the direction of the SP-target vector and the direction of eye movement (which was determined by the line connecting the SP and the gaze location at 100 ms after the onset of hand movement). For this measurement, the direction of the SP-target vector was defined as 0°, and the CCW direction had a positive sign. We performed this measurement for the last 20 trials of the practice condition, but trials where gazes fell in the SP area (Fig. 2B; 16.8, 0.9, and 1.3% for the free-gaze, hand-target-gaze, and target-gaze groups, respectively) were excluded.

The data were screened for outliers among trials. For hand movements, trials where the subjects did not move or did not reach to the vertical ring were initially removed (69 trials). Subsequently, mean and SD of target error across all remaining trials (except those in the explicit test) across all subjects were calculated. For this calculation, target error values of the strategy-only condition and rotation-only condition were adjusted as target error minus 45° and target error plus 45°. Based on all excluded trials of the free-gaze group, the mean target error across subjects was 1.2 ± 2.7° (SE), which was similar to the comparable measurement (2.2 ± 1.3°) based on the remaining trials of the same group. This suggests that hand performance was unaffected by whether aiming movements involved a saccade or no saccade (i.e., only moving hand during central fixation).
analyzed using a 3 ANOVA with group as a between-subject factor (free-gaze, hand-target-gaze, and target-gaze) and trial block as a within-subject factor (1–5) for the baseline-II condition, the strategy-only condition, the early (i.e., 1st 5 trial blocks) and late (i.e., last 5 trial blocks) phases of the practice condition, and aftereffects. Group differences in the maximum drift and judged angles of the explicit test were examined by using a 1-way ANOVA. Whether the aftereffects were different from 0 was tested by using a 1-sample t-test. Learning-related changes of gaze incidences were compared in each gaze area between the early and late practice phases by using a 2 × 5 ANOVA with phase (early and late) and trial block (1–5) as within-subject factors. This ANOVA was performed on the arcsine-transformed incidence values to address the nonnormality of proportions (Winer 1971). The probability level for statistical significance was \( P < 0.05 \).

RESULTS

Results of hand movements will be reported first followed by those of gaze locations.

Hand Movements

Baseline, strategy-only, and rotation-only conditions. Mean target error across subjects in the baseline-II condition did not differ among the 3 groups [3 (group) × 5 (trial block) ANOVA, \( F_{(2.33)} = 0.79, P > 0.05 \); Fig. 3]. However, mean target error across all groups gradually but significantly increased from the 1st trial block [−6.4 ± 0.7° (SE)] to the last trial block [−3.5 ± 0.6°, trial block effect; \( F_{(4,132)} = 4.80, P < 0.01 \), post hoc, \( P < 0.05 \)]. There was no group-by-trial-block interaction (\( P > 0.05 \)). Overall, the movement direction was shifted ~5° in the CCW direction when aiming at each target. Such a shift is consistent with a previous study (Ghilardi et al. 1995). The overall mean target error across all subjects and all groups for the strategy-only condition was 44.6 ± 0.5° (Fig. 3). A 3 × 5 ANOVA revealed no significant main effect (\( P > 0.05 \)). Mean target error in the rotation-only condition was −52.9 ± 1.3, −50.9 ± 1.3, and −47.5 ± 1.2° for the free-, hand-target-, and target-gaze groups, respectively (Fig. 3). The group difference was significant [1-way ANOVA, \( F_{(2.33)} = 4.44, P < 0.05 \)]. A post hoc test revealed a significant difference between the free and the target-gaze groups (\( P < 0.05 \)).

Practice condition. Leaning curves of the target error are shown in Fig. 3. Target errors were generally positive for all groups, showing a drift phenomenon that reflects an overcompensation of the rotated visual feedback. Target error increased gradually during the early practice phase for all groups. A 3 (group) × 5 (trial block) ANOVA showed a significant trial block effect [\( F_{(4,132)} = 5.63, P < 0.001 \)]. Post hoc tests revealed that target errors of the 4th trial blocks were significantly greater than those of the 1st or 2nd trial blocks (\( P < 0.05 \) for both comparisons). There was no other main effect (\( P > 0.05 \)). Over the course of practice, the drift in the free-gaze group (Fig. 3) increased until the 6th trial block and thence gradually decreased until the end of practice. A relat-
tively similar pattern was found in the target-gaze group (Fig. 3), although the increase of the drift lasted longer until the 16th trial block. In contrast, the drift of the hand-target-gaze group increased initially until the 13th block and was plateaued -2/3 into the practice condition (Fig. 3). Thereafter, it gradually increased during the late practice period until a drop in the latest trial block. In the late practice phase, there was a significant group effect [3 (group) × 5 (trial block) ANOVA, \( F_{(2,33)} = 5.84, P < 0.01 \). A post hoc analysis revealed that the hand-target-gaze group had a significantly greater drift than the other 2 groups (\( P < 0.05 \)), which did not differ from each other (\( P > 0.05 \)). There was no group effect or group-by-trial block interaction (\( P > 0.05 \)).

Furthermore, to determine whether the magnitude of drift was different among the 3 groups, the maximum drift across all trial blocks was calculated in each subject. Mean maximum drift across subjects was 14.7 ± 1.3 (SE), 16.8 ± 1.7, and 16.2 ± 2.2° for the free-, hand-target-, and target-gaze groups, respectively. The group difference was not significant [1-way ANOVA, \( F_{(2,33)} = 0.33, P > 0.05 \)].

**Aftereffects and explicit judgments.** All 3 groups produced small aftereffects throughout the posttest (Fig. 3). Mean aftereffects across all trial blocks and all subjects were 3.2 ± 1.1 (SE), 4.9 ± 0.8, and 3.5 ± 1.1° for the free-, hand-target- and target-gaze groups, respectively. A 3 (group) × 5 (trial block) ANOVA revealed no main effect (\( P > 0.05 \)). To examine whether the aftereffects were >0, individual mean aftereffects across all trial blocks were subjected to 1-sample \( t \)-test in each group. The aftereffects in all groups were significantly greater than 0 [free-gaze: \( t_{(11)} = 2.45, P < 0.05 \); hand-target-gaze: \( t_{(11)} = 4.96, P < 0.001 \); target-gaze: \( t_{(11)} = 2.69, P < 0.05 \)], indicating that implicit knowledge of the visuomotor rotation was present.

The mean magnitudes of direction in explicit judgments across subjects were 31.1 ± 1.9 (SE), 33.5 ± 2.0, and 36.1 ± 1.8° for the free, hand-target and target-gaze groups, respectively. This indicates that all 3 groups had clear, explicit knowledge of the rotation of visual feedback. There was no significant group effect [1-way ANOVA, \( F_{(2,32)} = 1.68, P > 0.05 \)].

**Gaze Locations**

Gaze locations of all trials in the practice condition were analyzed at 6 different timings: -200, -150, -100, 0, and 100 ms relative to the onset of hand movement and the offset of hand movement. Consistent gaze patterns relative to hand movements were not established by 150 ms before the onset of hand movement. Figure 4 shows the incidences of gazes landed in four different areas [T, Mid, HT, and SP; Fig. 2B] at 200 ms before the onset of hand movement. The data are based on all trials in the practice condition. In the free-gaze group, gazes were distributed over the four areas (Fig. 4A). The subjects gazed at the T and HT areas for -33% of trials each. The hand-target-gaze group showed a similar pattern as the free-gaze group, although the most frequent gaze area was clearly the HT area ( -47%; Fig. 4B). The gaze pattern of the target-gaze group (Fig. 4C) was different from those of the other groups. The subjects gazed at the T area for most of trials ( -80%), whereas the gaze incidences in the other target areas were rather low. Thus their gazes settled at the instructed location at an earlier timing compared with those of the hand-target-gaze group.

Consistent gaze patterns were established by 100 ms before the hand-movement onset in all three groups and maintained at least until the hand-movement offset. The most consistent gaze patterns during this period were observed at 100 ms after the hand-movement onset, and, hence, we will next report the gaze patterns observed at that timing. To examine whether gaze patterns changed throughout practice, the incidences of gaze locations were analyzed for each trial block (4 trials) of the practice condition (Fig. 5). Following the instruction about gaze locations, the hand-target-gaze group showed consistently high incidences of looking at the hand-target area throughout practice (Fig. 5).
The incidences did not significantly differ between the early and late practice phases \((2 \text{ (phase)} \times 5 \text{ (trial block)} \text{ANOVA}, P > 0.05)\). The target-gaze group looked at the T area at high percentages of trials throughout the practice condition (Fig. 5A), showing that they also followed the gaze instruction. At the early practice trials, however, this group had low incidences \((\sim 20\%)\) of looking at the HT area (Fig. 5B) instead of the T area, probably due to the explicit strategy of moving the hand to the HT target. This incidence was reduced as the practice progressed, and the incidence of gazing at the T area was increased instead (Fig. 5A and B). These observations were confirmed by a significant reduction of the incidences for the HT area \(F_{(1,11)} = 6.16, P < 0.05\) and a significant increase of the incidences for the T area \(F_{(1,11)} = 8.62, P < 0.05\) from the early to the late practice phase. There was no trial block effect or phase-by-trial block interaction in any of the above comparisons \((P > 0.05)\).

The free-gaze group initially looked at the HT area in most trials \((\sim 95\%)\) but gradually reduced this incidence as the practice progressed (Fig. 5B). In the late practice phase, only \(\sim 53\%\) of trials showed this pattern, and the reduction from the early to the late practice phase was significant \((2 \text{ (phase)} \times 5 \text{ (trial block)} \text{ANOVA}, F_{(1,11)} = 26.78, P < 0.001)\). Accompanying this reduction, the incidences of gazing at other areas had slightly increased at the end of practice. The difference between the early and late phases was significant for the Mid area \([F(5C; F_{(1,11)} = 12.46, P < 0.01]\), and such a trend was also found in the T area \([F(5A; F_{(1,11)} = 4.44, P = 0.059]\) and in the SP area \([F(5D; F_{(1,11)} = 4.49, P = 0.058]\). Thus the subjects gradually changed gaze locations for the hand movements from the hand target to various other locations. No trial block effect or phase-by-trial block interaction was found in any of the above comparisons \((P > 0.05)\).

Since each of the T, Mid, and HT areas had a relatively large range \((22.5^\circ)\) of gaze directions in the above analysis, some

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Fig. 5. Time course of the changes of gaze locations during the practice condition. Gaze locations were analyzed at 100 ms after the onset of hand movements. Average incidences of gazes are plotted for 4 different areas of workspace (see Fig. 2B for details): the T area (A), the HT area (B), the Mid area (C), and the SP area (D). The incidences are averaged across 4 trials per trial block. The error bars represent the SE. Following the gaze instructions, the target-gaze group (open squares) mostly looks at the T area, whereas hand-target-gaze group (triangles) mostly looks at the HT area. The free-gaze group (closed squares) looks at the HT area in most trials in the early practice but reduces such incidence in the late practice while increasing the gaze incidences for other areas. *\(P < 0.05\); (*)0.05 < \(P < 0.1\) between the early and late practice phases.
fine changes of gaze directions due to practice might have gone undetected. To obtain a more fine-grained view, gaze directions of all trials from the late practice phase across all subjects were measured. The trials where gazes fell in the SP area were not included in this analysis. Histograms of gaze directions for all three groups are presented in Fig. 6. The target-gaze group and the hand-target-gaze groups produced single-peak distribution profiles of gaze direction with mean values of $-3.5^\circ$ and $-42.3^\circ$, respectively (Fig. 6). Thus the mean gaze direction of each group reflected the instructed gaze direction. The free-gaze group, however, produced a two-peak distribution profile, with the peak directions being similar to those of the hand-target-gaze and the target-gaze groups (Fig. 6). The mean value of gaze direction across all trials across all subjects was $-31.6^\circ$. The two-peak profile indicates that the subjects either changed gaze directions toward the target in the late practice phase or maintained toward the hand target. These observations were consistent with the above results (Fig. 5) based on the analysis using the four gaze areas.

Finally, we analyzed the relation between the decline of gaze incidence at the HT area (Fig. 5B) and the reduction of target error after the maximum drift (i.e., reduction of drift; Fig. 3) in the free-gaze group. The trial block including the onset of gaze-incidence decline and the block including the onset of target-error reduction were identified in each subject. These parameters are plotted against each other for all subjects in Fig. 7. As seen in the figure, when the reduction of target error, and thus the reduction of drift, came sooner, the decline of gaze incidence at the HT area occurred earlier during the practice. Each individual’s trial blocks of these two measurements were significantly correlated ($r = 0.680$, $P < 0.05$, slope = 0.485).

Note that there were two subjects whose gaze incidence decline did not reach the threshold (Fig. 7), and their values were excluded from the above correlation calculation. However, their drift reduction occurred relatively late during practice, thereby showing a pattern similar to that of other subjects. Next, the relation between the rates of decline for gaze incidence at the HT area and target error was assessed. For this purpose, the slopes of these two parameters against trial blocks were calculated separately by using a linear regression in each subject. When each individual’s slopes of these two parameters were correlated with each other in all subjects, the correlation was not significant ($r = 0.106$, $P > 0.05$).
DISCUSSION

The present study examined the role of gaze locations on concurrent processes of an explicit strategy and implicit adaptation during a visuomotor rotation paradigm. Subjects applied strategic aiming movements to the hand target to counteract the rotation while gazing at different prescribed locations (target-gaze, hand-target-gaze, and free-gaze). The results showed 1) that the magnitude of maximum drift did not vary with the gaze locations, 2) that the drift was reduced in the late practice phase for the free-gaze and target-gaze groups but not for the hand-target-gaze group, and 3) that the free-gaze group reduced the frequency of gazing at the hand target as the practice progressed.

Effects of Gaze Locations on Implicit Adaptation

Consistent with previous studies (Mazzoni and Krakauer 2006; Taylor and Ivry 2011), making strategic aiming movements to the hand target resulted in a drift, revealing an explicit strategy overridden by an implicit adaptation. The implicit adaptation is in theory driven by aiming errors between predicted aiming direction toward the hand target and visual feedback of the movement (Fig. 2A; Mazzoni and Krakauer 2006; Taylor and Ivry 2011). Hence, one may predict that the magnitude of maximum drift would be greater for the hand-target-gaze and free-gaze groups compared with the target-gaze group because the former two groups gaze at the hand target either through an instruction or a natural gaze pattern for aiming. This allows a person to make more precise visual assessment of the hand target, which leads to more precise assessment of aiming errors for the implicit adaptation. Indeed, in the previous study (Taylor and Ivry 2011), the most salient hand target resulted in the largest magnitude of drift.

Contrary to such a prediction, there was no effect of prescribed gaze locations on the magnitude of maximum drift in this study. The likely reason is that the hand target was constantly visible for all groups regardless of gaze locations. Thus, even though the quality of visual assessment of the hand target might have been different because of the use of central or peripheral vision, constant visibility of that target in the workspace was enough to register the aiming error. Consequently, the implicit process worked to reduce this error by adjusting reaching direction, resulting in the implicit adaptation. This in turn suggests that the implicit process can be operated through neural structures involved in reach control to a target both in peripheral and central vision (Clavagnier et al. 2007; Prado et al. 2005; Vesia and Crawford 2012).

Even though the reduction of the drift in the late practice phase depended on the prescribed gaze locations, observed aftereffects of the visuomotor learning did not. Thus implicit knowledge of the visuomotor rotation was acquired and maintained throughout the practice regardless of whether the drift was reduced in the end. This effect is consistent with previous studies (Mazzoni and Krakauer 2006; Taylor and Ivry 2011). These results mean that to achieve the task goal, the drift reduction is accomplished through explicit adjustments of aiming directions by taking into account behavioral errors caused by the implicit adaptation. Therefore, implicit adaptation and explicit adjustments to novel visuomotor transformations have independent functions (Sülzenbrück and Heuer 2009). Implicit adaptation to a visuomotor rotation is possibly mediated by interactions among the posterior parietal cortex and motor cortex and cerebellum (Tanaka et al. 2009) and between the caudal superior parietal lobule and the dorsal premotor cortex (Granek et al. 2013), whereas explicit adjustments are possibly mediated by interaction among inferotemporal cortex or the inferior parietal lobule and the prefrontal and promotor cortices (Granek et al. 2013; Pisella et al. 2006).

Effects of Gaze Locations on Explicit Strategy

Another informative finding of this study is that the target-gaze group reduced the drift in the late practice phase, whereas the hand-target-gaze group did not. The possible reason for this difference is that explicitly gazing at the target in a central vision allows a precise assessment of target error (i.e., behavioral error) between the target and visual feedback of the movement (Fig. 2A). This error is thought to drive explicit adjustments of aiming directions to achieve the task goal (Mazzoni and Krakauer 2006; Taylor and Ivry 2011). Hence, gazing at the target helps to reduce the drift. Conversely, explicitly gazing at the hand target allows a precise assessment of aiming error for the implicit adaptation, thereby being conducive to the drift increase but unconducive to its reduction.2 Our results from the free-gaze group also support these postulates. Namely, the subjects mostly gazed at the hand target in the early practice phase, but they reduced such an incidence and increased incidences of gazing at other areas that are more related to the target (Fig. 5). Furthermore, the onset of drift reduction during the practice was correlated with the onset of a declined gaze-incidence for the hand-target area (Fig. 7).

However, one should not overlook the fact that gazes of the free-gaze group in the late practice phase still went to the hand-target area for about half of the trials (Fig. 5). This gaze location was similar to that of the hand-target-gaze group. Thus, although gazing at the hand target is unconducive to the drift reduction, gaze locations were not completely changed to the target area that is more conducive to the drift reduction. This reflects the robustness of natural eye-hand coordination that couples gaze location and the goal of aiming actions (Neggers and Bekkering 2000; Prablanc et al. 1979b; Rand and Stelmach 2010). Interestingly, despite similar gaze locations used between the hand-target-gaze and the free-gaze groups, only the free-gaze group reduced the drift (Fig. 3). Hence, gazing at the hand target itself is not a prerequisite for the failure of drift reduction. Furthermore, the free-gaze group could reduce the drift to the same level as the target-gaze group in the late practice, although the respective gaze patterns were different. This also means that gazing at the target itself is not a prerequisite for the drift reduction.

What made the three gaze groups different in terms of reducing the drift? The most likely factor is the combination of the foveated location and dual-intentional control of spatially coupled eye and hand movements. Regarding hand-target-gaze group, both an explicit (intentional) gaze and an explicit aiming were directed to the same location (i.e., hand target). Such dual-intentional control should enhance visuomotor

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2 Even though explicitly gazing at the hand target was detrimental to the drift reduction, the hand-target-gaze group considerably reduced the drift in the very last practice block compared with the prior blocks, which had large drifts (Fig. 3). Thus, when the size of drift becomes large enough, it may still trigger subjects’ response to adjust the aiming direction to reduce the drift (Taylor and Ivry 2011).
transformation processes related to reaching to a foveated location (Andersen and Cui 2009; Clavagnier et al. 2007; Medendorp 2011; Prado et al. 2005; Vesia and Crawford 2012). Consequently, information of the foveated hand target, which is conducive to the aiming error assessment for implicit adaptation, was likely processed with strong ties to aiming actions. As a result, the drift remained.

Regarding the target-gaze group, conversely, dual-intentional control with the eyes and hand was also involved, but intentional gazing was directed to a different location (target) from that of intentional aiming (hand target). Such spatial decoupling between eye and hand motions is known to weaken eye-hand coordination and its associated visuomotor processes (Adam et al. 2012; Neggers and Bekkering 2000; van Donkelaar 1997). Consequently, information of the target in central vision, which is conducive to the target error assessment for the explicit adjustments of aiming directions, was likely processed with less interference from control of aiming actions, thereby allowing processing of the target error information. Therefore, despite the dual-intentional control, this group was able to reduce the drift.

Contrary to the above two groups, the free-gaze group engaged in only a single intentional control with the hand, and, hence, there was no robust spatial coupling between the eyes and hand. Therefore, even though gazes in half of the trials during the late practice phase still went to the hand target area, this group was still able to process the target error information to adjust explicit aiming directions, thereby reducing the drift.

Aside from the aforementioned role of eye-hand coordination based on dual-intentional control, we cannot exclude a possibility that an attention shift may have played a role in the drift reduction. If the free-gaze group shifts covert attention to the target and feedback to process target error, the drift can be reduced despite gazing somewhere else. Such covert attention while keeping the gaze elsewhere has played a role in other types of visuomotor learning (Grigorova et al. 2006; Grigorova and Bock 2006). Furthermore, the reason for the failed drift reduction in the hand-target-gaze group can also be explained as that the dual-intentional control depleted attentional resources needed to apply a covert attention to the target and feedback to process target error. Indeed, several dual-task studies on visuomotor learning showed that dual-tasking impedes the learning capability (Eversheim and Bock 2001; Grigorova et al. 2006; Ingram et al. 2000; Redding et al. 1985). A future study will be necessary to determine which of these factors plays a role.

From the perspective of dual-task designs and their influence on implicit and explicit processes, a dual-task design should affect explicit process but not implicit process (Frensch 1998; Redding et al. 1992). In agreement with this notion, the dual-intentional control (target-gaze and hand-target-gaze groups) or the single-intentional control (free-gaze group) did not affect the magnitudes of maximum drift and aftereffects that are related to implicit adaptation. Conversely, the dual-control designs affected the drift reduction in the late practice phase that is related to explicit strategy. These results again point to independent explicit and implicit processes subserving visuomotor learning. The present study further revealed the distinction between the two processes. The explicit process under dual-control designs is differently affected depending on whether the reaching target is seen in central or peripheral vision, whereas the implicit process is unaffected by it.

Factors that Affect Gaze Behaviors During Visuomotor Adaptation

Gazing at the target during reaching is a typical eye-hand coordination pattern for goal-directed actions. Processing of retinal and extraretinal information due to gazing at the target improves control of movements both for the ballistic and feedback control phases (Abrams et al. 1990; Prablanc et al. 1979a). This gaze pattern helps to update the planning of ongoing reaching (Gaveau et al. 2008; Goodale et al. 1986; Prablanc et al. 1986), predict the arrival of upcoming reaching to the target (Bowman et al. 2009; Johansson et al. 2001), and verify the reaching termination (Rand 2014; Rand and Stelmach 2010). Since the current study employed endpoint visual feedback and no terminal-accuracy demand of the hand movement, gazes were controlled mainly to plan the reaching direction, and the gaze was fixated to one location before and during the movement. Throughout practice, the free-gaze group reduced the gaze incidence for the hand target down to ~50% of trials. However, if online feedback and a terminal accuracy demand were employed, that incidence would have decreased much more, and the gaze incidence of the target would have dramatically increased to bring the cursor precisely onto the target. Such change would have occurred not only during reaching in each trial, but also over the course of practice. To support this postulate, the typical gaze fixation pattern to the target was gradually emerging during the course of visuomotor learning when online feedback and a terminal accuracy demand were employed (Rentsch and Rand 2014; Sailer et al. 2005).

Additionally, the magnitude of aftereffects found in the current study was smaller than those found in previous studies (Mazzoni and Krakauer 2006; Taylor and Ivry 2011). Although the exact reason for the discrepancy is unknown, it was previously shown that endpoint visual feedback often leads to smaller aftereffects than online visual feedback (Hinder et al. 2008, 2010; Shabbott and Sainburg 2010; Taylor et al. 2014). Thus, had the present study employed online visual feedback, the aftereffects would likely have been amplified.

Regarding the effects of target visibility, Taylor and Ivry (2011) previously showed that the drift was minimized when all targets were invisible. This was probably because aiming error for implicit adaptation was not precisely estimated due to the lack of visual targets and memory-guided planning of reaching movements. Thus, if all targets had been invisible in the present study, the need for explicit adjustments of reaching direction to reduce the drift also would have been minimized. Consequently, the free-gaze group would have maintained gazing at the hand-target area throughout practice.

In addition, another factor related to target visibility may be the distance between the target and the hand target for the visual processing of both targets to plan the strategic aiming under the current task. A previous study showed that when this distance was much greater than that of the current study due to a larger rotation angle, the strategic aiming to compensate for the imposed rotation was abandoned during the early practice phase (Hegele and Heuer 2010).
Different visuomotor processes underlying reaching movements between natural and tool-use settings were highlighted recently (Granek et al. 2012, 2013; Pisella et al. 2009). In the current study, gazes were made on a vertical monitor, reaches on a horizontal digitizer. Vision and proprioception of hand movements also referred to different objects (cursor and hand, respectively). Thus subjects had to deal with the kinematic transformation of the tool to make visually guided reaching (Heuer et al. 2013). In a natural setting, in contrast, subjects have a direct view of the hand, and vision and proprioception refer to the same object (i.e., hand). Previously, reaching movements in tool use were shown to be deteriorated compared with natural ones (Granek et al. 2012, 2013). Sequential reaches in tool use (Rand 2014) also had longer movement time and gaze-shift latency from one target to another compared with natural ones (Rand and Stelmach 2010, 2011). However, despite these temporal differences, the typical eye-hand coordination that couples gaze location and the goal of aiming actions was observed in both settings. Thus, had the current study used a natural setting, the results would have been similar in terms of effects of prescribed gaze locations on the drift and adaptive gaze patterns of the free-gaze group.

Possible Neurophysiological Substrates for Learning of Visuomotor Rotation

Previous literature has reported a number of brain areas involved in learning of a visuomotor rotation such as the primary motor cortex (Eisenberg et al. 2011; Paz and Vaadia 2004; Paz et al. 2005), the ventral (Krakauer et al. 2004) and dorsal (Anguera et al. 2007) premotor cortex, the supplementary motor area (SMA; Paz et al. 2005) and pre-SMA (Krakauer et al. 2004), the posterior parietal cortex (Anguera et al. 2007; Diedrichsen et al. 2005; Inoue et al. 1997; Krakauer et al. 2004), and the cerebellum (Imamizu et al. 2000; Krakauer et al. 2004; Rabe et al. 2009; Tseng et al. 2007). The emergence of the drift due to an implicit adaptation is presumably driven by aiming error between the predicted aiming direction and feedback of the movement. A recent computational model study has suggested that interaction among the posterior parietal cortex, motor cortex, and cerebellum is important for this process (Tanaka et al. 2009). Furthermore, critical involvement of the caudal superior parietal lobule in such an implicit process has been also demonstrated, especially when reaching is made in tool use (Granek et al. 2012, 2013; Pisella et al. 2009) and under a 90° visuomotor rotation where a gradual recalibration between vision and proprioception is mainly required (Granek et al. 2013).

In the current study, after subjects became aware of the emergence of the drift, explicit adjustments of strategic aiming directions were made to reduce the drift to achieve the task goal. Accompanying such adjustments, gaze directions were also adjusted to dissociate spatially the gaze location and the reaching target. Such an explicit process may be mediated by the prefrontal association cortices, pre-SMA, and cingulate areas together with the basal ganglia because these areas were known to be involved in volitional control of movements and/or switching from automatic to controlled goal-directed actions (Haggard 2008; Hallett 2007; Hikosaka and Isoda 2008; Isoda and Hikosaka 2011). Interestingly, the above studies by Granek and colleagues have also shown that the caudal superior parietal lobule is not critical for applying an explicit strategy under a 180° visuomotor rotation, thereby supporting a postulate that the involvement of more ventral pathways (from the inferotemporal cortex or the inferior parietal lobule to the prefrontal cortex and then to premotor cortex) may be used for the planning of explicit reaching adjustments (Granek et al. 2013; Pisella et al. 2006).

In summary, the results of this study support two conclusions: 1) that prescribed gaze locations do not interfere with an implicit process of adjusting reaching directions during adaptation to a visuomotor rotation; but 2) that the gaze locations are critical for explicit adjustments of reaching direction to accomplish the task goal by overcoming the implicit adaptation occurring in parallel. These differential gaze-location effects strengthen the notion that implicit and explicit processes, which use different error signals to control reaching directions, are mediated by distinct neural mechanisms.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS

M.K.R. conception and design of research; S.R. performed experiments; M.K.R. analyzed data; M.K.R. and S.R. interpreted results of experiments; M.K.R. prepared figures; M.K.R. drafted manuscript; M.K.R. edited and revised manuscript; M.K.R. and S.R. approved final version of manuscript.

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Gaze Locations Affect Explicit but Not Implicit Process