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Motor awareness and dissociable levels of action representation

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Abstract

The present study evaluated the performance of a tracking task during which no, a small (subliminal: 20°) or a large (conscious: 60°) rotational perturbation was implemented. The instantaneous as well as carry-over effects of the perturbations were assessed. The subjective reports revealed that the subjects did not discriminate between the 0° and 20° perturbation conditions, despite increased trajectory error and directional trajectory changes in the latter than former condition, which suggests augmented error processing and task monitoring. Conversely, the 60° perturbation condition was characterized by subjective awareness in association with objective performance changes. Furthermore, a carry-over effect for the 60° but not for the 20° perturbation was observed when the distortion was removed midway into the trajectory. Together, the data underline distinct functioning of motor control and motor awareness with implications across time scales.

Keywords: tracking, perturbation, carry-over effects

Introduction

Achieving a successful motor goal usually requires performance monitoring on the basis of external and/or internal feedback. This process allows establishing whether the produced and intended responses are consistent with one another. In case of a discrepancy, an error signal is generated that facilitates realignment of the output. In routine situations, monitoring and associated error processing occur in an automatic (implicit) manner. However, these functions become explicit (conscious) in conditions that introduce incongruence between sensory modalities or between intentions and sensorimotor consequences [4,11,23].

Unawareness of performance details or of the process by which sensory information fine-tunes output may result in large deviations from baseline performance. For example, Fourneret and Jeannerod [5] observed that subjects adjusted their reaching profiles in response to spatial deviations of the trajectory, despite being unaware of making the deviant movements. Along a similar line, Knoblich and Kircher [14] noticed that subjects compensated for changes in visuomotor coupling during a tracking task well before becoming aware of the discrepancy. Together, these examples illustrate that participants have inadequate conscious monitoring of motor execution details. This divergent relationship between motor control and motor awareness has been associated with the premise that it is the predicted rather than the actual sensation that is used for error detection [23]. The distinction further underlines processes of motor control that are distinct from those that generate conscious judgment. In other words, motor awareness does not depend on those signals that arise during movement regulation [12].

In order to detail the dissociation between motor control and motor awareness, the present experiment assessed error processing and performance monitoring of a visuomotor tracking task during which no, a small (subliminal) or large (conscious) rotational perturbation was implemented during the trajectory. Awareness of the distortion was measured by means of subjective reports that reflected the participants' opinion of the level of perturbation they believed had been imposed on the trajectory. Besides evaluation of the instantaneous adaptation to the perturbation, this work also examined the carry-over effect once the distortion was removed midway into the trial. The latter would permit to assess whether a motor performance relies on the context set by the task history.

Methods

Participants

Ten right-handed participants (age: 28.4±2.6 years) as determined by the Edinburgh handedness inventory [17] gave informed consent to take part in the study, which was approved by the local ethics committee.

Task and procedure

Participants were asked to perform a visuomotor tracking task with their right hand using an ink- and wireless pen on a Wacom digitizing tablet. The trajectories were acquired in x- and y-coordinates using E-Prime 1.2 (Psychology Software Tools Inc., Pittsburgh, USA). The drawing task was displayed on an LCD monitor, placed vertically in front of the participants. The display on the monitor was the only source of visual input.

In the tracking task, the participants followed a moving trackball, from a start to a target position, on the monitor with a cursor that was controlled by the pen. Each trial started with a fixation cross at either the centre of the screen or at the final location of the previous trial. After 2000 ms, the fixation cross was replaced by the trackball that moved for 3000 ms with a speed of 2.91° visual angle/s towards the target position (Fig. 1). After 3000 ms, the trackball disappeared and a fixation cross appeared again until the participant had positioned the cursor on the target location for at least 500 ms, followed by an intertrial interval of 769±395 ms.

Insert Fig. 1 about here

To introduce sensorimotor incongruence, a rotational perturbation was implemented that established a directional bias around the tracking hand. The perturbation of 20° or 60° (clockwise or counter-clockwise) occurred during the entire trajectory (entire perturbation condition), the first 1500 ms of the trajectory (start perturbation condition) or not at all (control condition). The perturbation was implemented by tracking the position of the pen on the tablet at 80 Hz such that the movement direction was altered each sampling point by 20° or 60° before the cursor position was updated. During the no perturbation (control) condition and the unperturbed part of the start perturbation condition, there was 0° distortion. Conditions were randomized across blocks, each including 10 trials (or trajectories) and repeated 8 times. For the first trial of a block, the angle of the start to target position was randomized. On every other trial, the target position was the same as the start position of the preceding trial. The 3rd, 5th, 7th and 9th trial included angles that were each 72° rotated (clockwise or counter-clockwise) compared to the preceding odd trial. For example, if the first trial included a trajectory of 20°, the 3rd, 5th, 7th and 9th would be 92°, 164°, 236° and 308° or 308°, 236°, 164° and 92°, whereas each even trial would be a copy of the preceding trial, but presented in a backward manner. Short breaks were included throughout the experiment. Upon completion of a block of trials that consisted of the same performance condition, participants expressed their subjective opinion of the level of perturbation they believed had been imposed on the trajectory. Results are presented as mean ± SD per condition.

Analysis and Measurements

The blocked trials of the same performance condition were used for analysis, excluding the first trial. Various measurements were included to study error processing and performance monitoring due to instantaneous and carry-over effects of the perturbation:

Subjective report. Following each block, participants provided the degree of experienced perturbation by drawing an angle in a quarter of a circle using the digitizing tablet and pen.

Trajectory error score. The trajectory error was defined as the RMSE and represented the smallest distance of each collected time point to the linear trajectory that connected the start and target position.

Directional changes (number and duration). The number of directional changes was obtained from the positional data of the trajectory by detecting whenever direction changed between two consecutive time points. A threshold of 0.5º was used. These data were then matched with the error data in order to determine whether the new direction resulted in reduced error (closer to the linear trajectory) or increased error (further away from the linear trajectory). The directional changes that associated with no change in error score were not included in the analysis. Percentage scores of the correct and incorrect responses with respect to the total number of directional changes were also determined in addition to the duration of the directional changes. As the rotational perturbations cause the subjects to move away from the straight path towards the target position, the directional changes measure the adjustments to accomplish the tracing task successfully. As the number of correct and incorrect directional changes did not differ significantly for clockwise and counterclockwise rotations in the 20° and 60° perturbation conditions (separate t-tests, $p>.05$ for all), the data were collapsed for analysis of the performance measurements. The duration of the directional changes was determined as the time lapse during which a participant continued to draw in a particular direction (correct or incorrect) before changing course.

Initiation error (peak and time). The error peak was obtained by detecting the highest score at which the trajectory error first decreased following movement initiation. The peak time referred to the moment at which the error started to decrease. These measurements were accordingly only calculated in the entire perturbation conditions.

Results

Instantaneous effect of the perturbation

To establish the instantaneous effect of the rotational perturbation, the analysis contrasted the 0°, 20° and 60° entire perturbation conditions by means of one-way ANOVA's. Post-hoc comparisons were conducted where necessary.

Subjective reports. The reports showed an effect of Perturbation, $F(2,18)=31.02$, $p<.01$. Post-hoc analysis showed that the 0° and 20° perturbations did not differ from one another ($p>.05$) whereas both differed from the 60° perturbation ($p<.01$). The mean scores were 8.3±3.6°, 11.5±4.7° and 51.2±7.1° for the 0°, 20° and 60° entire perturbation conditions, respectively. Correlations of the subjective scores showed that the 0° and 20° conditions correlated with one another (r=.90, p<.05) whereas the 0° and 20° conditions did not correlate with the 60° condition (r=-.08, and r=-.12, p>.05 for both).

RMSE. The trajectory error score revealed an effect of Perturbation, F(2,18)=54.10, p<.01. Post-hoc analysis indicated that the 0° and 20° perturbations differed from one another (p<.05) and from the 60° condition (p<.01 for both). The mean error scores were 1.82±0.34, 3.52±0.74 and 16.86±3.82 pixels for the 0°, 20° and 60° entire perturbation conditions, respectively. Correlations of the error scores demonstrated that the 0° and 20° conditions correlated with one another (r=.91, p<.05) whereas the 0° and 20° conditions did not correlate with the 60° condition (r=.44, and r=.60, p>.05 for both). The subjective scores did not correlate with the RMSE scores across trials per performance block (p>.05), nor with those of the last trial of each performance block (p>.05). The mean error scores for the last trial were 1.90±0.55 3.69±1.00 and 17.05±4.63 pixels for the 0°, 20° and 60° entire perturbation conditions, respectively.

Directional changes, number. The *correct* directional changes indicated an effect of Perturbation, F(2,18)=8.77, p<.01. Post-hoc analysis showed that the 0° and 20° conditions differed from one another (p<.05) and from the 60° condition (p<.01 for both). The mean scores were 13.61±3.20 (46%), 15.05±3.42 (48%) and 16.97±3.72 (50%) for the 0°, 20° and 60° entire perturbation conditions, respectively. The *incorrect* directional changes revealed an effect of Perturbation, F(2,18)=21.72, p<.01. Post-hoc analysis showed that the 0° and 20° perturbations did not differ from one another (p>.05) whereas both differed from the 60° perturbation (p<.01 for both). The mean scores were 7.08±1.21 (24%), 8.32±1.40 (26%) and 11.18±2.23 (33%) for the 0°, 20° and 60° entire perturbation conditions, respectively. Fig. 2A illustrates profiles of the *incorrect* directional changes in the 0°, 20° and 60° entire perturbation conditions.

Directional changes, duration. The *correct* directional changes showed no effect of Perturbation (p>.05). The mean durations were 158±11, 161±15 and 160±14 ms for the 0°, 20° and 60° entire perturbation conditions, respectively. The *incorrect* directional changes highlighted an effect of Perturbation, $F(2,18)=4.60$, $p<.05$. Post-hoc analysis denoted that the 0° and 20° perturbations did not differ from one another ($p>.05$) whereas both differed from the 60° condition ($p<.05$ for both). The mean durations were 168±18, 169±15 and 158±10 ms for the 0°, 20° and 60° entire perturbation conditions, respectively.

Initiation error, peak. The peak error score revealed an effect of Perturbation, $F(2,18)=126.10$, $p<.01$. Post-hoc analysis specified that the 0° and 20° perturbations did not differ from one another ($p>.05$) whereas both differed from the 60° condition ($p<.01$ for both). The mean error scores were 2.54±0.61, 4.80±0.71 and 27.92±5.39 pixels for the 0°, 20° and 60° entire perturbation conditions, respectively.

Initiation error, time. The peak time indicated an effect of Perturbation, $F(2,18)=3.99$, $p<.05$. Post-hoc analysis specified that the 0° and 20° conditions did not differ from one another ($p>.05$) whereas both differed from the 60° condition ($p<.05$ for both). The mean scores were 729±132, 786±150 and 889±179 ms for the 0°, 20° and 60° entire perturbation conditions, respectively.

Insert Fig. 2 about here

Carry-over effect of the perturbation

To establish the within-trial carry-over effect of the perturbation, the unperturbed parts of the 0°, 20° and 60° start perturbation conditions were compared by means of one-way ANOVA's. Post-hoc comparisons were conducted where necessary.

Subjective reports. The reports revealed an effect of Start perturbation, $F(2,18)=18.98$, $p<.01$. Post-hoc analysis showed that the 0° and 20° perturbations did not differ from one another ($p>.05$) whereas both differed from the 60° perturbation ($p<.01$ for both). The mean scores were 8.4±3.1°, 10.6±4.3° and 43.7±6.5° for the 0°, 20° and 60° start perturbation conditions, respectively.

RMSE. The error scores revealed an effect of Start perturbation, $F(2,18)=20.89$, $p<.01$. Post-hoc analysis showed that the unperturbed part following the 0° and 20° perturbations did not differ from one another ($p>.05$) whereas both differed from the 60°

perturbation ($p<.01$ for both). The mean error scores were 1.89±0.47, 2.55±0.78 and 7.93±2.86 pixels for the 0°, 20° and 60° start perturbation conditions, respectively. Correlations of the error scores between the perturbation (first 1500 ms) and post-perturbation (second 1500 ms) parts were .82 ($p<.05$), 74 ($p<.05$) and .38 ($p>.05$) for the 0°, 20° and 60° start perturbation conditions, respectively. To examine the progress of the error scores in the post-perturbation part in relation to the 0° condition, we observed that significant error reduction ended 105 ms and 300 ms after withdrawl of the 20° and 60° perturbation, respectively. This indicates that error stabilized early on in the post-perturbation part, and suggests a carry-over from the previously experienced perturbation.

Directional changes, number. The *correct* directional changes showed an effect of Start perturbation, $F(2,18)=11.80$, $p<.01$. Post-hoc analysis showed that the unperturbed part following the 0° and 20° perturbations did not differ from one another ($p>.05$) whereas both differed from the 60° perturbation ($p<.01$ for both). The mean scores were 6.75±1.10 (46%), 7.27±1.32 (47%) and 8.81±1.83 (51%) for the 0°, 20° and 60° start perturbation conditions, respectively. Correlations of the directional changes between the perturbation (first 1500 ms) and post-perturbation (second 1500 ms) parts were .92 ($p<.05$), .90 ($p<.05$) and .56 ($p>.05$) for the 0°, 20° and 60° start perturbation conditions, respectively. The *incorrect* directional changes showed no effect of Start perturbation, $p>.05$. Fig. 2B shows profiles of the *incorrect* directional changes in the 0°, 20° and 60° start perturbation conditions, and shows that midway removal of the perturbation resulted in a short-lasting adaptation of reduced directional changes. In particular, the number of directional changes was significantly reduced for 66±8 ms following the 20° perturbation ($p<.05$) and for 200±19 ms following the 60° perturbation ($p<.05$) as compared to the 0° perturbation.

Directional changes, duration. The *correct* directional changes showed an effect of Start perturbation, $F(2,18)=4.52$, $p<.05$. Post-hoc analysis showed that the unperturbed part following the 0° and 20° perturbations did not differ from one another ($p>.05$) whereas both differed from the 60° perturbation ($p<.01$ for both). The mean duration scores were 162±16, 160±20, and 182±24 ms for the 0°, 20° and 60° start perturbation conditions, respectively. The *incorrect* directional changes showed no effect of start perturbation ($p>.05$).

Discussion

Awareness reflects a state of conscious experience that is normally accessible for verbal subjective report. In the context of motor control, previous studies have shown that sensations associated with actual movement are largely unavailable to awareness [3,5,6,14,15,22]. For example, Fourneret and Jeannerod [5] observed that subjects produced deviant movements in order to generate a straight line on a computer screen, despite verbal accounts of poor awareness of the modified behaviour. This observation was supported by Knoblich and Kircher [14] who instructed subjects to draw circles which they saw reproduced by a moving dot. When velocity variations occurred between the actual movement and its visual consequences, subjects compensated for the changes in visuomotor coupling before they were aware of the discrepancy. These examples underline segregated processes of motor control and motor awareness. In order to detail this segregation, the present study evaluated the performance of a tracking task during which no, a small (subliminal: 20°) or a large (conscious: 60°) rotational perturbation was implemented. Various measurements were used to evaluate error processing and performance monitoring in relation to instantaneous as well as carry-over effects of the perturbations.

Subjective reports and instantaneous effect of the 20° and 60° perturbation

There is not a conventional means of measuring motor awareness. However, an agreed notion is that participants are able to report the kinematic details of the produced movements [13]. Therefore, in the present study, subjects were asked to reproduce the trajectory of the movement they had just made. In this respect, the reports revealed that there was no subjective discrimination between the 0° and 20° perturbation, which is in line with previous work that has shown that people have flawed trajectory knowledge of an earlier produced action [5,9]. Despite a similar subjective impression, an increased error and a higher number of directional changes were observed in the 20° than 0° perturbation condition. This finding suggests augmented error processing and performance adjustments, albeit below a level of motor awareness. That subjects are often unaware of the sensations that elicit corrective responses has become evident from the double-step paradigm. In this situation, a target changes its location during the saccade that precedes the reaching movement towards that target. Although subjects may remain unaware of the displacement, they correctly point at the target location [10,18]. When awareness of the target shift happens, it occurs after initiation of the movement correction, which underlines that the circuits that trigger conscious processing are distinct from those that execute the visuomotor responses [2].

The 20° perturbation contrasted with the 60° perturbation for which distinct subjective as well as objective performance changes were noticed in terms of error and directional changes. This distinction between both types of perturbations, supported by the correlation analyses of the error scores, suggests implicit (20°) vs. explicit (60°) processing, which has been associated with lower-order sensorimotor vs. higher-order frontal regulation, respectively [1,16,21]. In other words, when the error is small, movement-related signals may be processed automatically. Only when there is a large discrepancy between the actual and intended pattern does it become available to awareness, allowing inhibition of invalid implicit processing and elaboration of strategic processing [20]. Accordingly, awareness also impacts on sensorimotor integration and adaptation. In particular, unperceived discordance causes proprioception to remain unattended because of visual dominance, whereas detected conflict triggers processing with realignment from both modalities [1]. It is likely that this remapping prohibited efficient online corrections as evidenced from the directional trajectory changes that remained fairly similar, in number and duration, independent of the degree of rotational perturbation. However, the data do underline a distinctive threshold for unconscious vs. conscious adjustments when sensory perturbations arise during motor responses.

Carry-over effect of the 20° and 60° perturbation

An alternative method to quantify error compensation is to examine changes in the same trial. In particular, a within-trial analysis allows investigating carry-over effects that would point to limitations on processing capabilities. In this respect, the present design permitted to compare the unperturbed trajectories following the removal of a perturbation of

0°, 20° or 60°. The results showed that there was no difference between the unperturbed parts when the imposed distortion had been 0° or 20°. This observation suggests no carry-over effects when the previously experienced perturbation associated with error processing and performance monitoring below a threshold of motor awareness. Conversely, a 60° distortion influenced subsequent unperturbed movement production, reflecting an extrapolation of error after the perturbation had been removed. The reliance on contextual settings in this particular situation shows the impact of preceding processing demands, and extends observations that task history operates as an internal constraint for motor performance [19]. Hence, the current data in combination with the correlation analyses illustrate that actions rely on previous context, albeit in relation with intricate processing that associates with motor awareness. Accordingly, preceding processing biases current processing, with may accordingly impact on efficiency. Together, these observations further confirm regulatory mechanisms that distinguish signals of motor control and motor awareness [9].

Conclusion. The data have illustrated that error processing and performance monitoring occurs in the absence of awareness, suggesting that automatic adaptation steers goal achievement. Conversely, significant motor errors link with awareness for preserving motor performance. Furthermore, the results revealed that actions rely on previous task history, but only when the preceding processing demands associate with motor awareness. Together, the data underline distinct functioning of motor control and motor awareness with implications across time scales.

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Figure caption

Fig. 1. Schematic representation of the tracking task. Participants were required to track a ballpoint (grey dot) to a target position with a cursor (black dot). In the performance conditions, the movement direction was rotated by 0°, 20° or 60° from the actual direction (a), which potentially affected the participants' tracking behaviour (b, as indicated by the dotted line). The trajectory error (RMSE) is illustrated by the grey striped area. The start perturbation condition (not shown) implicated 0°, 20° or 60° perturbation during the first 1500 ms of each trial.

Fig. 2. (A) Profiles of the incorrect directional changes in the 0°, 20° and 60° entire perturbation conditions. (B) Profiles of the incorrect directional changes in the 0°, 20° and 60° start perturbation conditions. Midway removal of the perturbation resulted in a transient adaptation. Individual data.

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Fig. 1

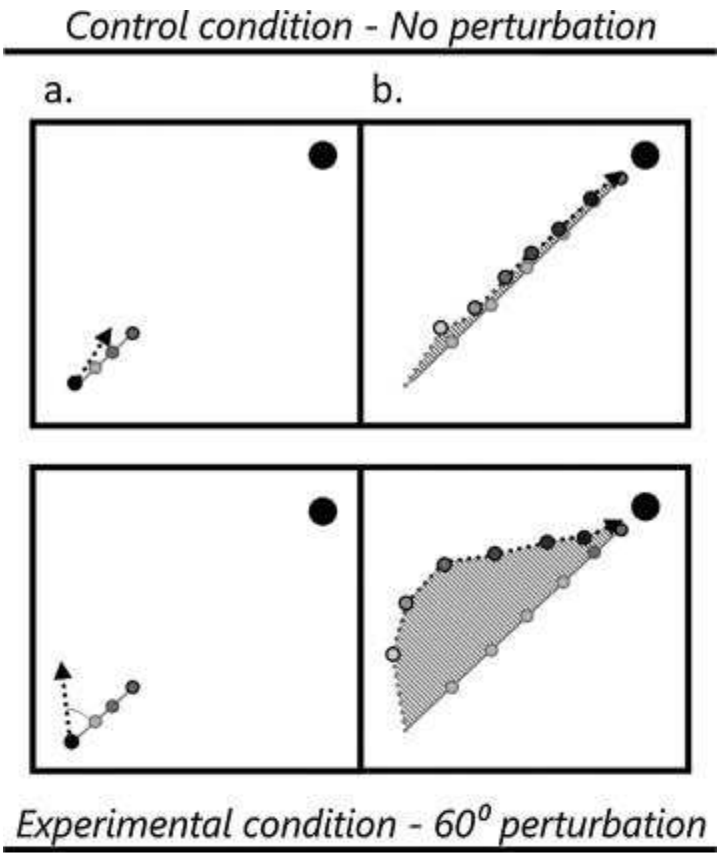
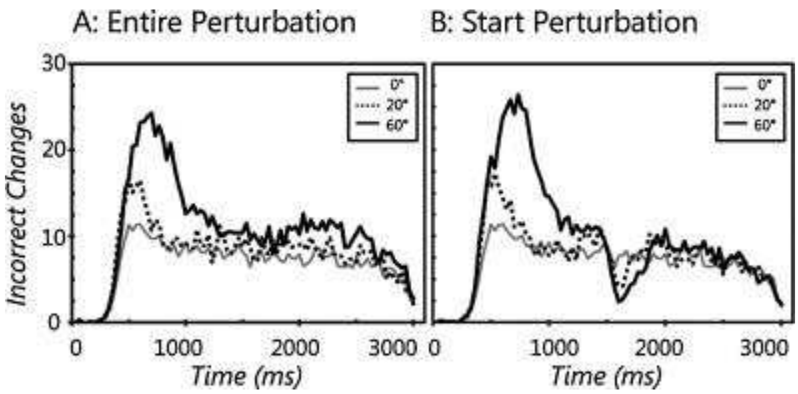

Control condition - No perturbation
a.
b.
Experimental condition - 60° perturbation

Fig. 2


A: Entire Perturbation
B: Start Perturbation
Incorrect Changes
Time (ms)
Time (ms)
0°
20°
60°
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20°
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