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RESEARCH ARTICLE

Planning and online control of goal directed movements when the eyes are 'relocated'

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Abstract We investigated the effects of different viewpoints on remapping visuo-motor space, and whether remapping happens differently during the planning and the online control phase of goal-directed movements. Participants tapped targets on a monitor that was placed horizontally flat and flush with the table in front of them. They viewed the layout of the scene, including the monitor, and their hand, through video goggles attached to a camera. The camera could be moved along a semi-circle with the monitor as the circle's center. On each trial, the camera was randomly positioned at one of seven locations on the semi-circle (-90 to +90° in 30° steps), always at eye height. The time needed to tap the target was quickest when the camera was approximately facing the participant and progressively increased when the camera was located more to the sides (Experiment 1). There was no effect of camera location on performance when participants only saw the static layout of the scene and were not allowed to see the scene or their hand during the movement (Experiment 2). By comparison, the dependency of performance on camera location increased when participants did not have information about the layout of the scene at the start of the trial, and could only perform remapping when their hand was visible during the movement (Experiment 3). These results indicate that visuo-motor remapping happens differently during the planning phase when only static information about the layout is available, and during the control phase when dynamic information about the moving hand is also available.

Keywords Visuo-motor · Reference frames · Pointing · Remapping · Planning · Control

Introduction

To effectively interact with the environment, the visuo-motor system has to accurately map visual information to appropriate motor commands (Soechting and Flanders 1989; Flanders et al. 1992; Kalaska and Crammond 1992). The spatial location of objects in the visual field critically depends on the location of the eyes whereas these objects have a fixed position in the environment. For example, an object in front of an observer projects to the center of the visual field when that observer fixates the object. By comparison, the object will project to the right part of the visual field when the observer fixates to the left of the object. In both cases, however, the observer must make the same forward movement to reach the object. Therefore, to localize targets and make correct movements towards them, visuo-motor remapping is necessary.

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Previous studies have shown that humans and monkeys make appropriate goal-directed movements to the location of a flashed target, even when the eye position changed between the flash and the movement (Sparks and Mays 1983; Blouin et al. 1998; Medendorp et al. 2002). These findings suggest that visuo-motor remapping can be accomplished on the basis of efferent signals, proprioception, or vestibular information. Some investigators have suggested that the location of the object may be updated each time the eyes had moved (Henriques et al. 1998). Others have suggested that objects are initially coded relative to a more stable reference frame (Sparks and Mays 1983; Andersen et al. 1985).

Several studies have also shown that visuo-motor remapping can be accomplished on the basis of visual information alone. For example, visuo-motor remapping has been studied using prisms that shift a target's location in the visual field. In this case, proprioceptive and efferent information about the eyes relative to the hand are not informative, at least not during the first goal-directed movement. However, if both the target and the hand are visible, people can immediately make successful movements by using visual cues about the difference between the hand and target location (Redding and Wallace 1996). There are other tasks in which the visual information about the effector in relation to the visual environment seems to be the most important for guiding actions, rather than non-visual information about the position of the eyes and the hand. These tasks include moving a cursor on a vertical display by using the mouse, teleoperation (when the person who controls a robotic device from a distance gets visual feedback from a camera that records the device), and immersive video games. In the present study we used a visuo-motor remapping task in which proprioceptive, efferent, and vestibular signals about the eyes' spatial location are not informative for making goal-directed movements. Rather, to make successful movements in this task, participants needed to rely on visual information about the scene.

For goal-directed movements, planning is often distinguished from online control. Whereas a goal-directed movement cannot start before it has been planned, online control plays an important role in reducing errors after the movement has started, even for quick movements (Prablanc and Martin 1992; Brenner and Smeets 1997; Brouwer et al. 2003; Bédard and Proteau 2004). Furthermore, it has been proposed that planning and control utilize different visual representations, and that these components of goal-directed movements are subserved by separate anatomical parts of the brain (Glover 2004). Whether planning and control are based on different representations is still under debate. It is an obvious fact that different visual information is available during these two phases. For planning a goal-directed movement, observers can use the visual layout of the scene with the target to plan the movement. If the hand is also visible in the scene, the static information completely specifies how to move the hand to the target. For online control of movements, observers can additionally use the visual information about the hand's movement, such as its direction of motion. Saunders and Knill (2004) showed that indeed, visual information about both the hand's direction of motion and its position are used for online control throughout the whole movement.

Here, we investigated whether visuo-motor remapping occurs differently during the planning phase, when only static information is available, as opposed to the control phase, when dynamic information is available as well. Participants in our experiments tapped targets on a horizontally oriented surface while viewing the scene from the viewpoint of a camera that was elevated at approximately eye height and could be positioned at several locations along a semi-circle with the workspace as the circle's center. The experimenter moved the camera from trial to trial so that there was no proprioceptive, efferent, or vestibular information about the location of this 'artificial eye,' and so that participants could not adapt to specific camera locations. To successfully perform the task, participants had to map the visual information about the layout of the scene from the viewpoint of the camera to appropriate motor actions on each trial anew. In three experiments, we measured how performance on this visuo-motor remapping task depended on camera and target location. In Experiment 1, participants were provided with visual information to both plan and control their movements toward the targets. Thus, they could perform visuo-motor remapping during both phases of the movement. This experiment served as a baseline condition. In Experiments 2 and 3, participants were provided with information to perform remapping only during planning or only during online control, respectively. Our results suggest that visuo-motor remapping happens differently during the planning phase when only static information is available, and during the online control phase when dynamic information is also available.

Experiment 1

Methods

Participants

Eight right-handed participants from the Tübingen community volunteered to take part in Experiment 1 for payment, after being informed about what they would be required to do. The present study is part of ongoing research that has been approved by the local ethics committee.

Apparatus

The experimental setup is depicted in Fig. 1. Participants were seated in front of an ELO 19 flat-panel LCD touch screen monitor. The resolution of the monitor was 1,024×768 pixels. The monitor had a positional standard deviation of less than 2.03 mm. It required less than 113 g of force to register a contact.

The monitor was laid horizontally flat and flush with the top of a table. Its lower edge was aligned with the edge of the table. Participants sat approximately 30 cm from the lower edge of the monitor. They could comfortably reach the top of the screen (the part of the monitor that was furthest away from where they sat). The experiment was run on a PC laptop using the Psychophysics Toolbox for Windows (Brainard 1997; Pelli 1997).

A grayscale CCD camera was rigged to a girder. The girder was constrained to move in a 180° arc in front of the participant. The camera was always elevated 45° from the table on this girder, which was approximately at eye height. It was fixed at 57 cm from the center of the monitor, and was focused on that location. The field of view of the camera encompassed the starting position of the hand and part of the body (see Fig. 1c). Participants wore SONY LDI-100B head mounted display goggles that received input from the camera. A cardboard mask was fixed to the front of the goggles to ensure that participants could not see their surroundings except through the display screens of the goggles.

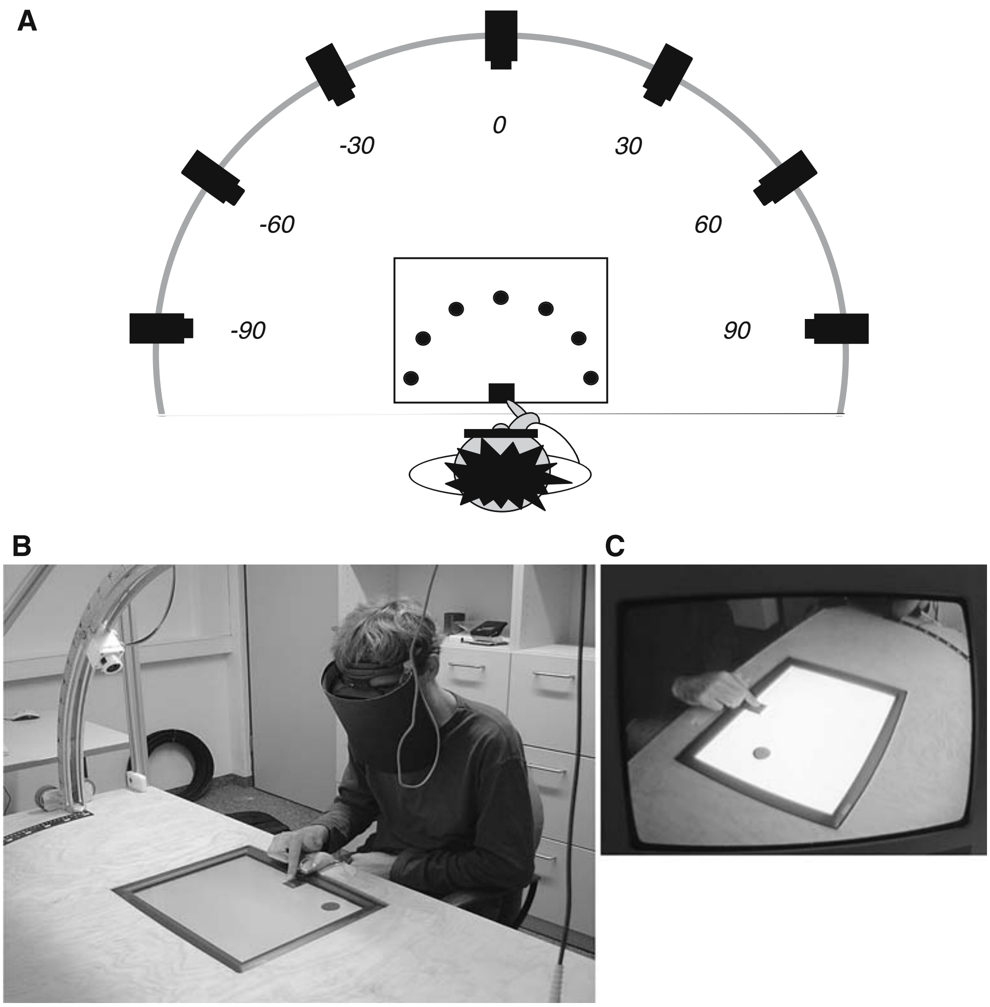

Fig. 1 A schematic top view of the setup indicating the different possible camera and target locations (a), a picture of the experimental setup (b), and a picture of a monitor that displays the camera's view when it was at a 60° location, indicating what was in the participant's field of view (c)

The participants' task was to tap targets presented on the screen using their index finger. The target was a circular black disk with a radius of 3.6 cm. It was presented on a gray background. The experiment was conducted in a lit room.

Design

There were two within-subjects factors: the location of the camera and the location of the target on the screen. On each trial, the camera was randomly positioned by the experimenter at one of seven possible locations from -90 to +90° in 30° steps. At 0°, the camera was directly opposite the participant; at -90°, it was to the left of the participant; and at +90°, it was to the right (Fig. 1a). Note that when the camera faced the participant (0°), movements to the right resulted in movements to the left in the visual field, and not to the right as would be the case when facing a mirror. Similar to the camera location, the target could be randomly positioned at one of seven possible locations from -90 to +90° in 30° steps on the screen (Fig. 1a). The target was always 12.6 cm from the starting position of the hand.

There were 49 possible trial conditions (seven camera locations × seven target locations). Each participant was run in two blocks of 98 trials (two repetitions of each condition) for a total of 196 trials. Within each block, the trials were presented in random order. There was a short break between the two blocks. All participants responded with their right hand.

Procedure

We designated the center of the base of the monitor as the Finger-Start Position. In addition, we presented a black square (3.6×3.6 cm) on the screen immediately above the starting position to serve as the Stimulus-Onset Square (Fig. 1a).

At the beginning of each trial, participants started with their right index finger on the Finger-Start Position, with their eyes closed. When instructed by the experimenter, they opened their eyes and touched the Stimulus-Onset Square to display the target at one of the seven possible locations. They then touched the center of the target as quickly and as accurately as possible. Only after they arrived within 7.2 cm from the center of the target, the trial ended. After the end of the trial, participants returned their finger to the Finger-Start Position and closed their eyes. The experimenter then moved the camera and informed the participant when the next trial started.

Analysis

Tapping time Our main dependent variable was tapping time, which was defined as the time interval between the onset of the stimulus (i.e., when the participant touched the Stimulus-Onset Square) and the offset of the target (i.e., when the target was tapped). We evaluated the effects of camera and target locations on tapping time by using repeated measures analyzes of variance (ANOVA) with these variables as within-subjects factors. We adopted 0.05 as the level of significance for all experiments.

Tapping errors We determined three kinds of tapping error measures. First, the constant error described how far participants were away from the target's center in the horizontal direction (with a negative value for touching the screen to the left of the target's center, and a positive value for touching to the right) and in the vertical direction (with a negative value for touching the screen below the target's center, and a positive value for touching above). Second, the horizontal and vertical variable errors were the standard deviations of the horizontal and vertical constant errors, computed separately for each participant and condition. Finally, the absolute error was defined as the distance between the location of the touch to the center of the target.

In this and subsequent experiments the errors did not depend on the experimental manipulations as clearly as the tapping time did. However, in order to interpret tapping time directly, we needed to know whether it was confounded by a speed-accuracy trade-off (Fitts and Peterson 1964), i.e., whether in some condition participants reached the target quickly but also made large errors. For each experiment, we performed regressions of tapping time onto the absolute tapping error, using the mean values for each camera location in one regression, and using the mean values for each target location in another regression. This informed us about the relation between tapping time and the general accuracy (how close participants ended up to the target's center). As participants could be very precisely hitting the same location but with a bias from the target's center (a large absolute error), we were also interested in the relation between tapping time and variable error. Thus, the same regressions were done for tapping time and horizontal variable error as well as for tapping time and vertical variable error. Of the ten regressions on absolute error (two regressions for each of the three main experiments, and two for each of the two used hands in Experiment 1a), seven showed a significant positive relation between the variables or a positive trend. There were no significant negative relations. Of the 20 regressions on horizontal and vertical variable error (four regressions for each of the three main experiments, and four for each of the two used hands in Experiment 1a), 15 showed a significant positive relation between the variables or a positive trend. There was one significant negative relation. From this we can conclude that on the whole, tapping time was not confounded with a speed-accuracy trade-off and could be interpreted directly. Any relation between tapping time and error would rather go into the direction of small errors being associated with fast movements and large errors with slow movements, i.e., good or bad performance in both the temporal and spatial domain. We therefore focus on tapping time in the present study, but we show the error data for each experiment in plots.

Results

To control for outliers, we discarded eight of 1,568 trials because of extraordinary long tapping times (>5,000 ms).

Figure 2 shows the tapped locations relative to the target locations separately for each camera location (a, expressed as horizontal and vertical error) and for each target location (b, expressed as location on the touch screen monitor). Figure 3 shows tapping time as a function of camera location (a) and target location (b). In Fig. 4, we plotted the absolute error (a, b) and variable error (c, d) as a function of camera location (a, c) and target location (b, d).

As indicated by the large error bars in Fig. 3, there was a large difference in the overall mean tapping time across participants, varying between 1,080 ms for the quickest participant and 2,227 ms for the slowest participant. However, the participants' tapping time depended in a consistent way on both the camera and target location. The repeated measures ANOVA indicated significant effects of camera and target location on tapping time ($F_{(6, 42)}$=9.55, P<0.01 and $F_{(6, 42)}$=5.73, P<0.01, respectively). There was no interaction between these two factors ($F_{(36, 252)}$=1.15, P=0.27).

The data points in Fig. 3a suggest that tapping time gradually decreased as the camera location approached

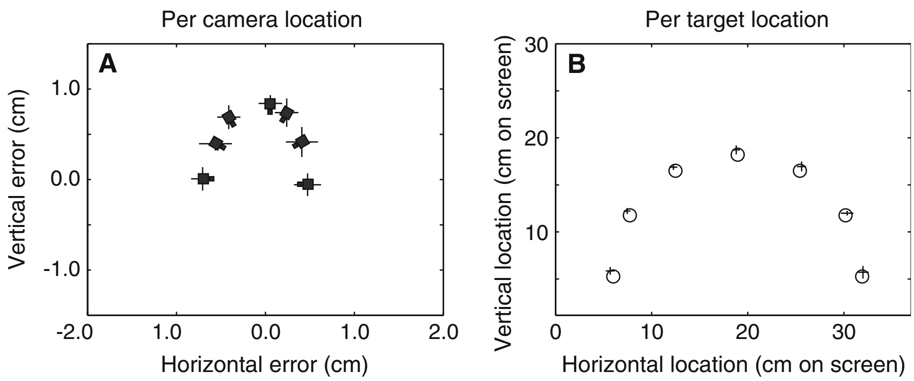

Fig. 2 Tapping locations relative to target locations in Experiment 1. The *symbols* in (**a**) are schematic top views of the camera, representing for each corresponding camera location the mean tapping error in horizontal and vertical direction relative to the center of the target. *Error bars* represent standard errors of the mean. The *circles* in (**b**) are the target locations on the screen in screen co-ordinates. Each cross consists of *error bars* representing the standard deviations of tapping location in the horizontal and vertical direction for each target location; the crossing of the *error bars* represents the mean tapping location. Note that here we depicted standard deviations rather than standard errors to make the data more easily visible (depicting the standard error of the mean would have decreased the size of the *error bars* by a factor of 2.8)

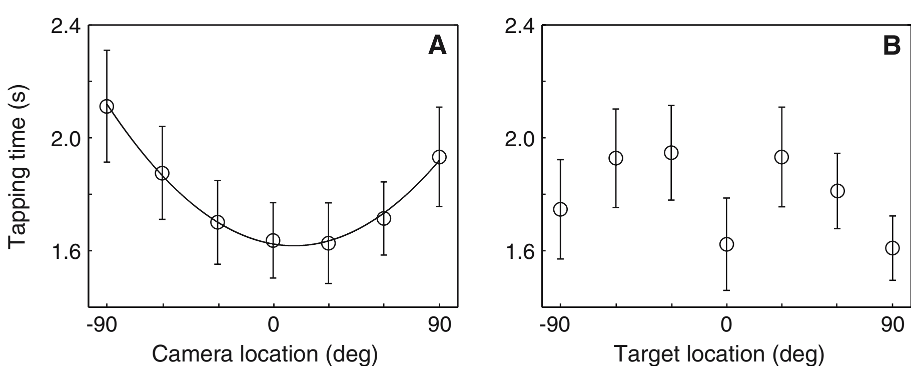

Fig. 3 Tapping time as a function of camera location (**a**) and target location (**b**) in Experiment 1. *Error bars* represent standard errors of the mean. The quadratic function that is shown in 1a is fitted to the average data of all participants; for analyzing purposes quadratic functions were fit for each participant separately

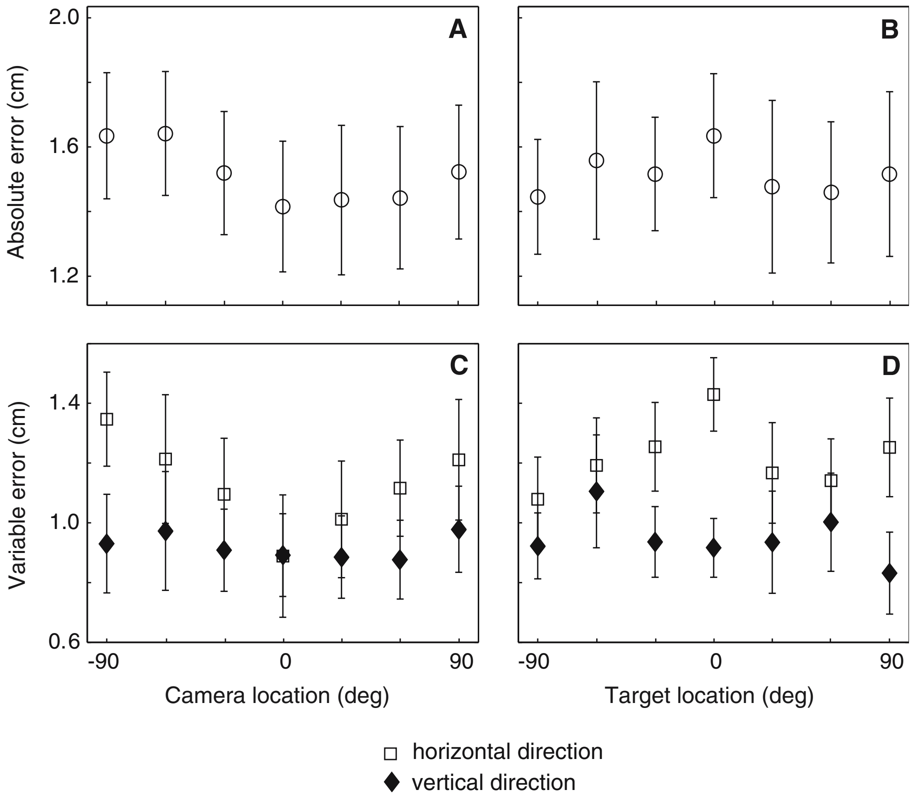

Fig. 4 Absolute error (**a**, **b**) and variable error (**c**, **d**) for each camera location (**a**, **c**) and each target location (**b**, **d**) in Experiment 1. The variable errors in the horizontal and vertical direction are depicted separately by *empty squares* and *filled diamonds*, respectively. *Error bars* represent standard errors of the mean

0°, a pattern we describe as a U-effect. Indeed, a trend analysis showed a significant quadratic trend ($F_{(1, 7)}$=35.98, P<0.01). Linear, cubic, and higher order trends were not significant. To quantify the effect, we fitted a quadratic curve ($y=ax^2+bx+c$) through the mean tapping time as a function of camera location for each participant. The constant, *a*, indicates the magnitude or strength of the U-effect and its direction (i.e., whether positive or negative). We also determined the location of the extreme (in this case always the minimum rather than the maximum) of the function for each participant. A one sample *t*-test indicated that *a* (M=0.049, SEM=0.009) was significantly larger than zero (t_7=5.16, P<0.01). The minima of the U-curves tended to be shifted on average 17.34° (SEM=7.51°) to the right of 0°. A one sample *t*-test indicated that this shift was marginally significantly different from zero (t_7=2.31, P=0.054).

As indicated by the ANOVA, tapping time also depended on target location. Figure 3a shows that participants were quickest when the target was straight ahead (0°) or to either sides (±90°), and slowest when the target was on the oblique axes. We call this pattern the M-effect. A post-hoc contrast with weights of -4 for the targets in the direction of the cardinal axes (target locations -90, 0, and +90°) and weights of three for the targets in the oblique directions (-60, -30, +30, and +60°) indicated that the data indeed followed this pattern ($F_{(1, 7)}$=7.35, P=0.03).

Experiment 1a

In Experiment 1, our (right-handed) participants always used their right hand to tap the targets. As there was a tendency for the optimal camera location (resulting in the quickest tapping times) to be shifted to the right of the center, the optimal camera location might depend on either the handedness or the used hand. To distinguish between these two possibilities, we repeated Experiment 1 with four right-handed and four left-handed participants. They were run in four blocks of 49 trials (one repetition of each condition). They alternated the hand they used to touch the target on each block. Half of the right-handed participants and half of the left-handed participants started the series of blocks with their right hand (RLRL), and the other half started with their left hand (LRLR). We analyzed the data in the same way as in Experiment 1.

Results

We discarded eight of the total of 1,568 trials according to the same criterion used in Experiment 1.

Figure 5 shows the tapped locations relative to the target for each camera location (a) and each target location (b). Figure 6 shows tapping time as a function of camera location (a) and target location (b), separately for each hand used. The absolute and variable

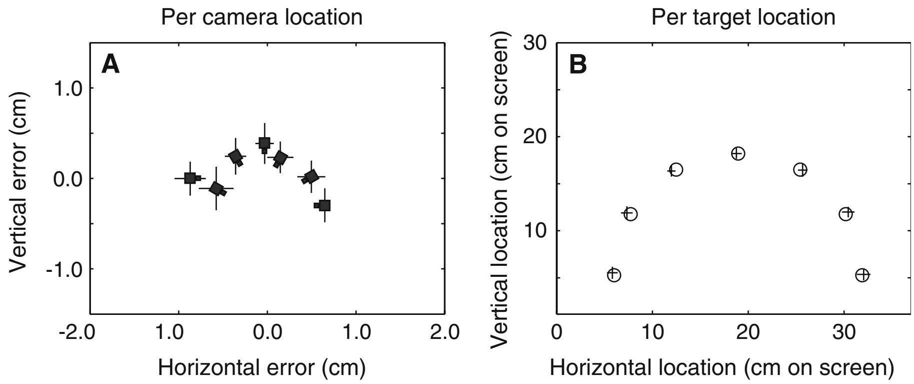

Fig. 5 Tapping locations relative to target locations in Experiment 1a. Further, conventions as in Fig. 2

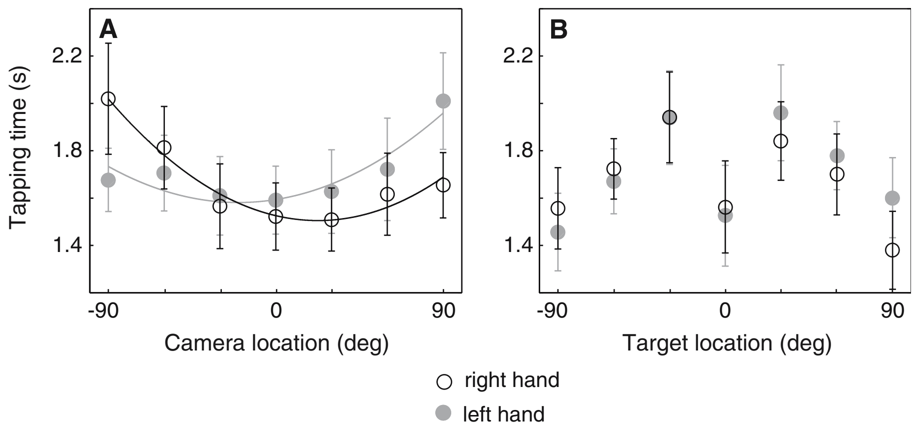

Fig. 6 Tapping time as a function of camera location (**a**) and target location (**b**) in Experiment 1a. The *black curve* and *empty symbols* represent the data of the right hand; the *gray curve* and *filled symbols* represent the data of the left hand. *Error bars* represent standard errors of the mean

errors are shown in Fig. 7 (right hand used) and Fig. 8 (left hand used).

Again, we found that tapping times were longest when the camera was positioned at large azimuths and shortest when it was close to the 0° location. The location of the minimum tapping time was not to the right of the 0° location for the right-handed participants (M = −4.64°, SEM=26.36°) and not to the left for the left-handed participants (M=3.43°, SEM=13.29°). Rather, the hand used to perform the task induced the bias of the optimal camera location that we found before.

Repeated measures ANOVAs with camera location and target location as within-subjects factors were conducted separately on tapping times for each hand used. For both analyzes, there were significant effects of camera location and target location (right hand: $F_{(6, 42)}$=12.00, P<0.01 and $F_{(6, 42)}$=12.16, P<0.01, respectively, left hand: $F_{(6, 42)}$=7.30, P<0.01 and $F_{(6, 42)}$=8.59, P<0.01, respectively). For the right hand, there was no interaction between camera and target location ($F_{(36, 252)}$=1.00, P=0.48), for the left hand, there was an interaction between these two factors ($F_{(36, 252)}$=1.55, P=0.03). There were significant quadratic trends in tapping time as a function of camera location for both hands (right hand: $F_{(1, 7)}$=30.80, P<0.01, left hand: $F_{(1, 7)}$=31.56, P<0.01). The minima of the U-curves shifted to the right when the right hand was used (M=25.07°, SEM=7.02°, t_7=3.57, P<0.01) and they tended to shift to the left when the left hand was used (M = -25.22°, SEM=11.20°, t_7 = -2.25, P=0.06). A paired sample t-test indicated that the shifts were different for the left and right hands (t_7=4.46, P<0.01). As in Experiment 1, a (right hand: M=0.048, SEM=0.010; left hand: M=0.043, SEM=0.010) was different from zero (right hand: t_7=4.67, P<0.01, left hand: t_7=4.24, P<0.01).

Figure 6b shows replications of the M-effect found in Experiment 1. Post-hoc contrasts with weights of -4 for the targets in the direction of the cardinal axes and weights of three for the targets in the oblique directions indicated that tapping time was longer for the latter, both for the right and the left hand (respectively $F_{(1, 7)}$=8.82, P=0.02 and $F_{(1, 7)}$=10.69, P=0.01).

Summarized results experiments 1 and 1a

We found that viewpoint systematically affected performance in a visuo-motor remapping task. Tapping time decreased with the angle that the camera was rotated away from the location of the eyes (the U-effect). However, the optimal camera location, yielding the

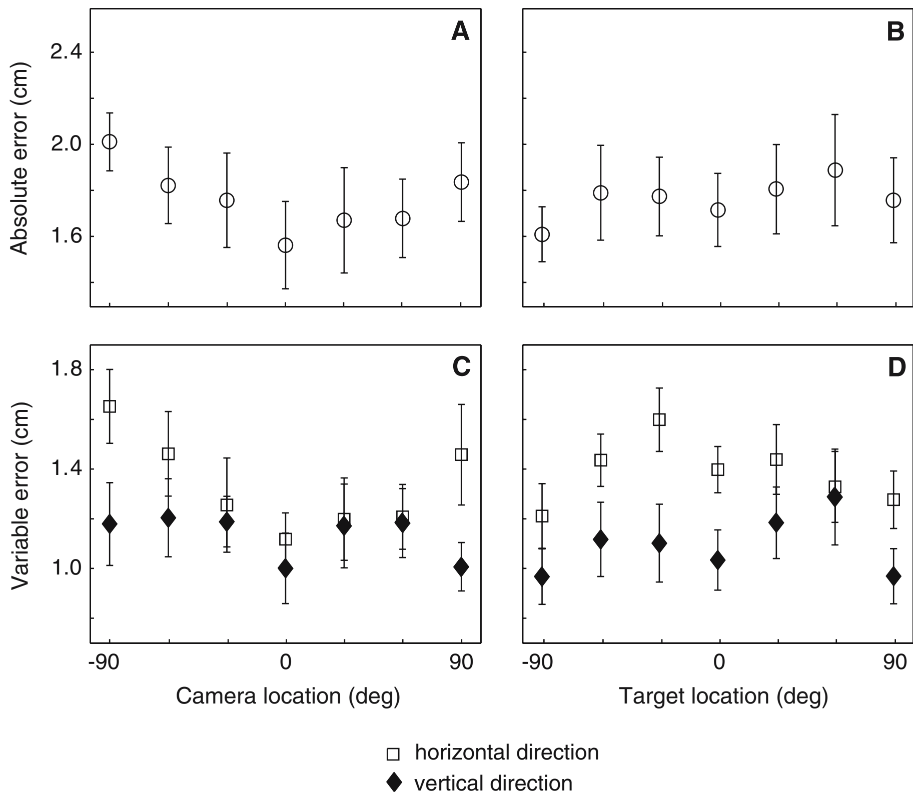

Fig. 7 Absolute error (**a**, **b**) and variable error (**c**, **d**) for each camera location (**a**, **c**) and each target location (**b**, **d**) in Experiment 1a, when the right hand was used. *Error bars* represent standard errors of the mean

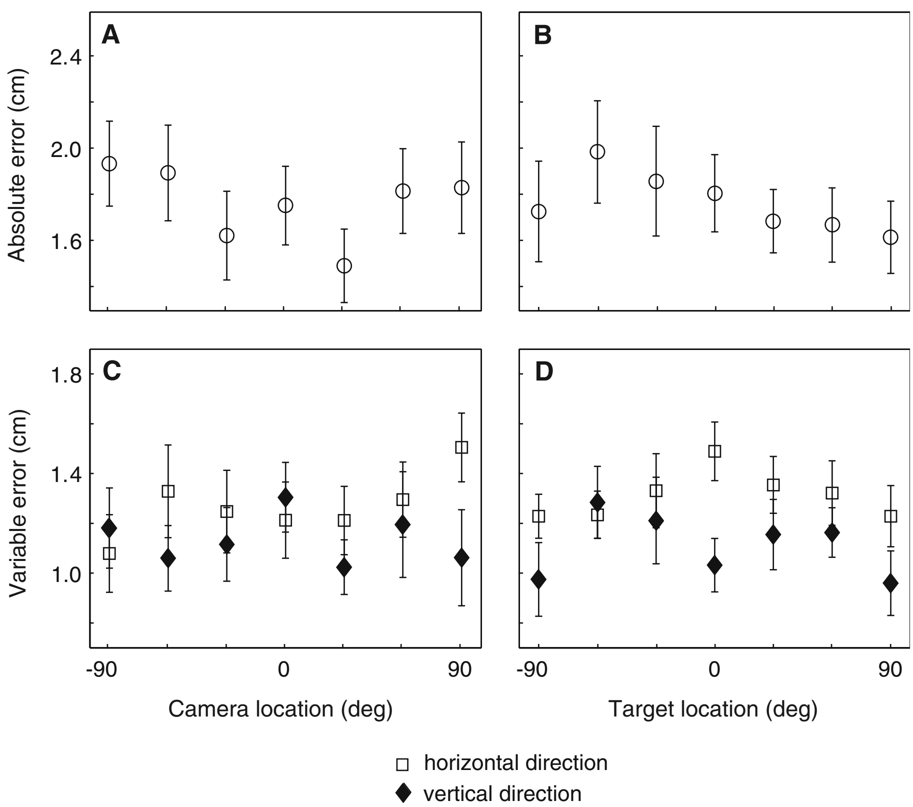

Fig. 8 Absolute error (**a**, **b**) and variable error (**c**, **d**) for each camera location (**a**, **c**) and each target location (**b**, **d**) in Experiment 1a, when the left hand was used. *Error bars* represent standard errors of the mean

shortest tapping times, was not directly opposite the participant but rather slightly shifted toward the direction of the hand used to perform the task. Another finding was a characteristic dependency of tapping time on target location with participants taking longer to reach a target in an oblique direction compared with a target in the direction along one of the cardinal axes (the M-effect).

Experiment 2: planning

In this experiment, we eliminated information about the moving hand and thereby forced participants to use only static information about the initial layout of the scene for visuo-motor remapping. Although online adjustment to errors is not possible in this experiment, the information about the layout of the scene should, in principle, suffice for making a ballistic movement toward the target.

Methods

Participants

Eight new right-handed participants from the Tübingen community volunteered to take part in Experiment 2 for payment, after being informed about what they would be required to do.

Apparatus

The same setup and stimuli as in Experiment 1 were used with the exception that a mouse was fixed to the Finger-Start Position. Participants used this mouse button to initiate each trial.

Design and procedure

The design of this experiment was identical to Experiment 1 but the experimental procedure was different. On each trial, participants started the trial with their eyes closed and their right index finger pressing the mouse button. A tone signaled that they could open their eyes to view the scene with the target present. They were instructed to plan an accurate movement to the target while keeping the mouse button pressed and not moving their hand. When they finished planning the movement, they first closed their eyes and then moved toward the target. They were instructed to tap the remembered target as quickly and as accurately as possible. After that, they returned their hand to the mouse button to end the trial, still keeping their eyes closed. Thus, in this experiment, participants never saw their hand moving. They did not need to touch a position within 7.2 cm of the target (as in Experiment 1); we simply measured the location of the first touch. There was no feedback about how close their touch was to the target.

For this experiment, we were interested in the time that the participants needed to plan the movement rather than the time they needed to move their hand because the latter happened without visual online control. Thus, our main dependent variable here was the viewing time from the onset of the tone to the release of the mouse button. We also measured the movement time from the release of the mouse button to the first touch.

Results and discussion

We used three criteria to remove outliers in Experiment 2: first, the viewing time had to be shorter than 5,000 ms; second, the movement time had to be between 200 and 1,500 ms; and finally, the error had to be smaller than 10.8 cm from the center of the target. In total, 132 of 1,568 trials were discarded. Of these, only 37 discarded trials were removed because of positional errors.

Figure 9 shows the tapped locations relative to the target for each camera location (a) and each target location (b). Figure 10 shows the viewing time (black open symbols) and the movement time added to the viewing time (which is equivalent to tapping time, gray filled symbols) as a function of camera location (a) and target location (b). The absolute and variable errors are shown in Fig. 11.

Figure 15 summarizes the main results across all experiments. Clearly, in this experiment participants needed more time to reach the target than in Experiment 1. A repeated measures ANOVA performed on our main measure of viewing time indicated an effect of target location ($F_{(6,\ 42)}$=6.56, P<0.01). There was no effect of camera location ($F_{(6,\ 42)}$=1.43, P=0.23) and no interaction between target and camera location ($F_{(36,\ 252)}$=0.81, P=0.77). Consistent with the lack of effect of camera location, a (M = -0.019, SEM=0.012) was not significantly different from zero (t_7 = -1.68, P=0.13), and there was no significant quadratic trend in the data ($F_{(1,\ 7)}$=2.15, P=0.19). Similar statistical results were obtained when total tapping time (i.e., viewing time plus movement time) was analyzed. Thus, in contrast to Experiment 1, performance was not affected by camera location. By comparison, viewing time depended on target location in the characteristic M-shaped way as found in Experiment 1 (Fig. 10b). This was supported by a post-hoc contrast with weights of -4 for the target locations -90, 0, and +90° and weights of three for the targets at -60, -30, +30, and +60° ($F_{(1,\ 7)}$=10.70, P=0.01, similar results for tapping time). This systematic effect on viewing time shows that viewing time is a sensitive measure that was

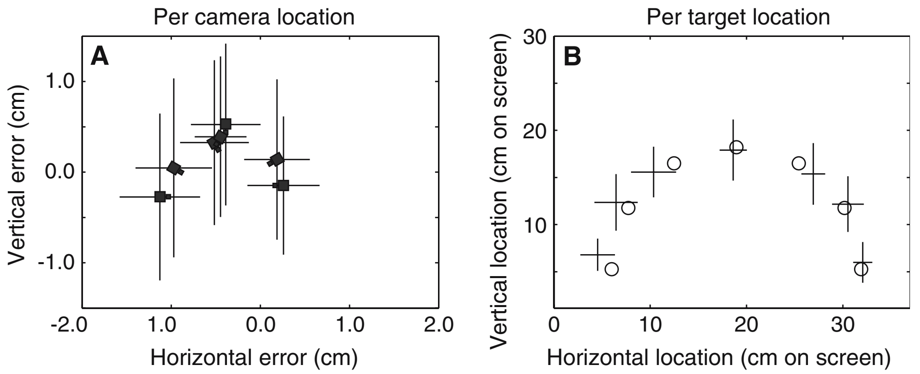

Fig. 9 Tapping locations relative to target locations in Experiment 2. Further, conventions as in Fig. 2

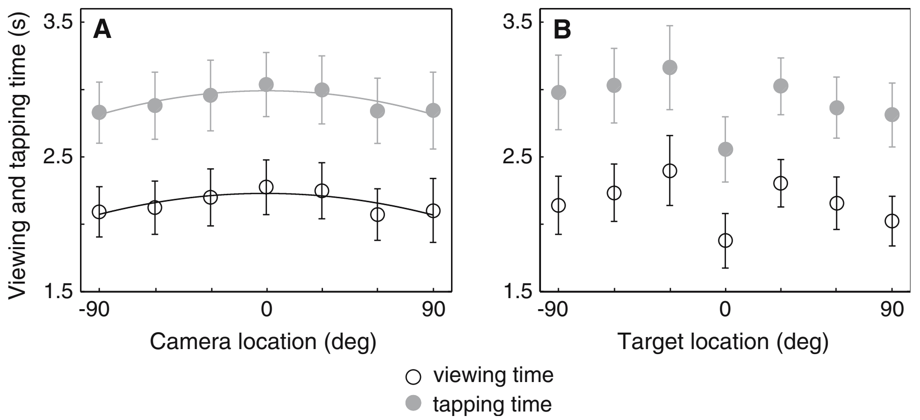

Fig. 10 Viewing time (*black curve* and *empty symbols*) and movement time added to viewing time (i.e., *tapping time*; *gray curve* and *filled symbols*) as a function of camera location (**a**) and target location (**b**) in Experiment 2. *Error bars* represent standard errors of the mean

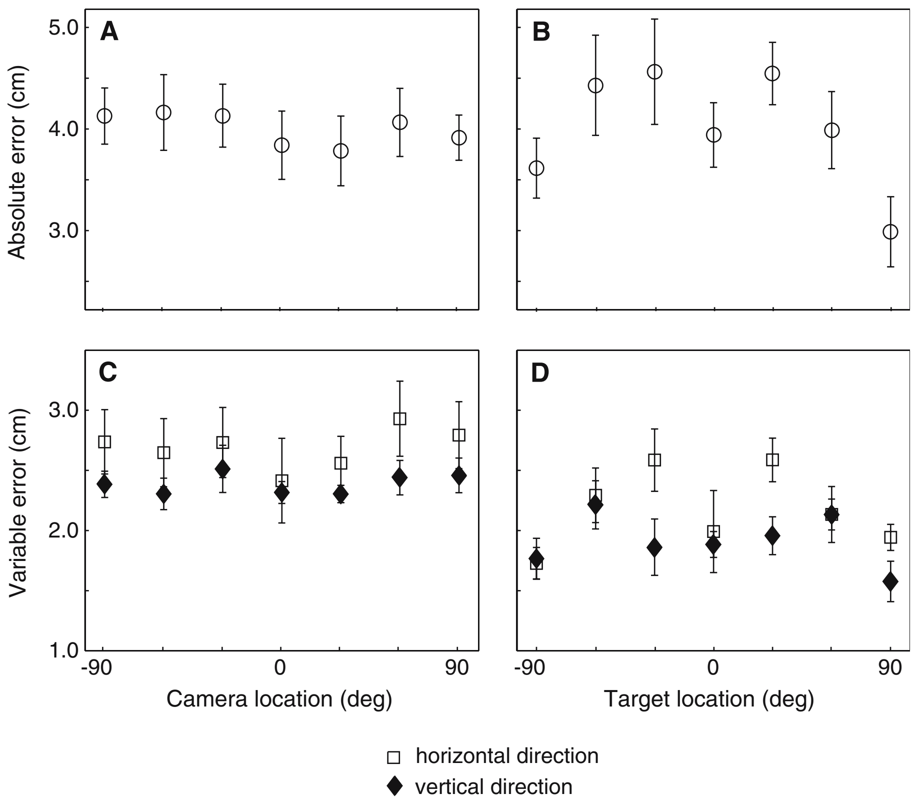

Fig. 11 Absolute error (**a**, **b**) and variable error (**c**, **d**) for each camera location (**a**, **c**) and each target location (**b**, **d**) in Experiment 2. *Error bars* represent standard errors of the mean

precisely controlled by the participants, and that the lack of effect of camera location is not an artifact of using a different variable to measure performance.

A repeated measures ANOVA performed on movement time showed no effect of camera location ($F_{(6, 42)}$=1.47, P=0.21; the filled symbols are a constant distance above the open symbols in Fig. 10). There was an effect of target location ($F_{(6, 42)}$=5.03, P<0.01) with shorter movement times for targets at 0° and progressively longer movement times for targets toward larger azimuths. There was no interaction between camera and target location ($F_{(36, 252)}$=1.19, P=0.22).

In sum, the effect of camera location on performance as we found in Experiment 1 disappeared when participants performed visuo-motor remapping during the planning phase of the movement, for which they could only use information about the initial static view of the scene, and moved in an open loop. However, we replicated the M-effect under these conditions.

Experiment 3: online control

In Experiment 1, participants could perform visuo-motor remapping during both the planning of the goal-directed movement and the online control phase of the movement. In Experiment 2, they could only perform this remapping during planning. In Experiment 3 the setup was adapted so that there was initially no information available about the location of the camera. Only after their hand started moving could participants use visual feedback to guide the movement. This procedure thus forced participants to perform visuo-motor remapping during the online control phase of the movement.

Methods

Participants

Eight right-handed participants from the Tübingen community volunteered to take part in Experiment 3 for payment, after being informed about what they would be required to do.

Apparatus

The experimental setup and task was similar to Experiment 1. In order to remove any information about the camera location at the start of the trial, we changed the setup in four respects. First, we placed a circular aperture over the screen to remove orientation cues provided by the edge of monitor. The aperture was placed over the center of the screen and had a radius of 26.5 cm. Second, the experiment was conducted in a dark room. To reduce the amount of light emitted by the screen, we also inverted the color of the targets and the background (gray targets on a black background). Third, the participants started each trial with their right hand on their lap so that the hand could not be seen at the beginning of the trial. Finally, there were 12 possible target locations instead of seven positions so that there was no positional cue provided by the location of the targets. These positions were equally spaced in 30° steps along the edge of the circular aperture at a fixed distance of 12.6 cm from the center of the screen. Because of these changes, the outline of the hand was visible only when it was above the circular aperture.

Design

As in Experiment 1, there were two within-subjects factors: camera location and target location for a total of 84 conditions (seven camera locations × 12 target locations). Each participant was run in two blocks with the 84 trials presented in random order on each block. There was a short break between blocks.

Procedure

Participants started each trial with their eyes closed and their hands on their lap. A tone was played to signal to them that they could open their eyes and move their hand to the target. As in Experiment 1, when they touched the target within 7.2 cm of the center, the trial ended. Participants were instructed to try to touch the center the target as quickly and as accurately as possible. After they responded, they returned their hand to their lap and closed their eyes.

In Experiment 3, the tapping time was measured from the onset of the tone to the offset of the target (i.e., the time that the target was tapped).

Results and discussion

We discarded 41 of 1,344 trials with extraordinary long tapping times (>10,000 ms).

Figure 12 shows the tapped locations relative to the target for each camera location (a) and each target location (b). Figure 13 shows tapping time as a function of camera location (a) and target location (b). The absolute and variable errors are shown in Fig. 14.

As in Experiment 2, tapping times were longer than in Experiment 1 (Fig. 15). A repeated measures ANOVA indicated that tapping time depended on camera location ($F_{(6, 42)}$=25.70, P<0.01) but not on target

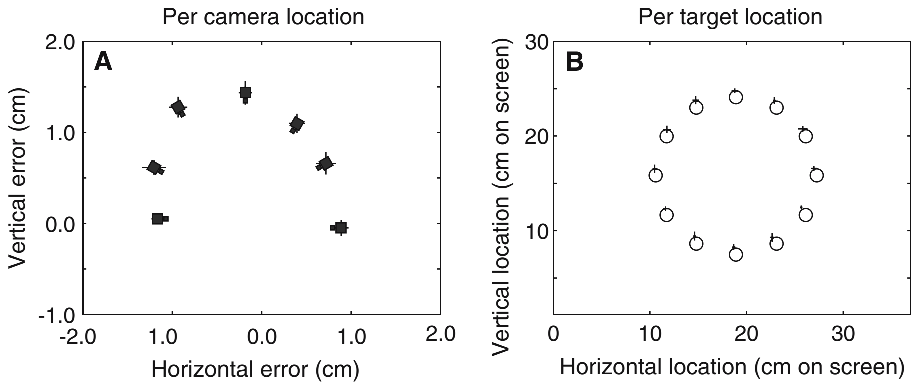

Fig. 12 Tapping locations relative to target locations in Experiment 3. Further, conventions as in Fig. 2

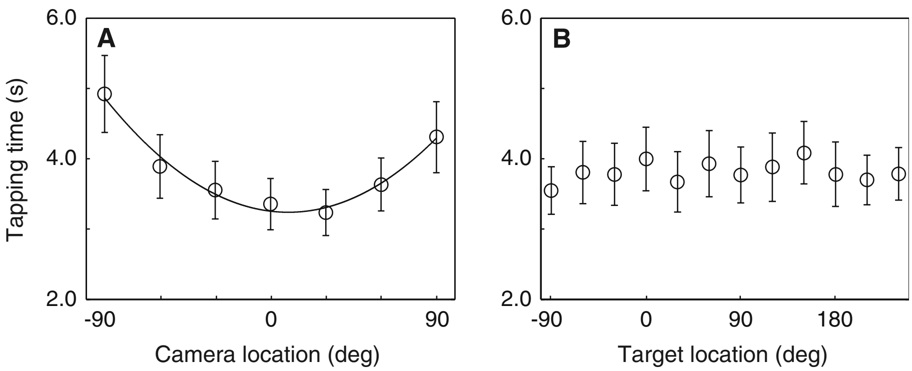

Fig. 13 Tapping time as a function of camera location (**a**) and target location (**b**) in Experiment 3. *Error bars* represent standard errors of the mean

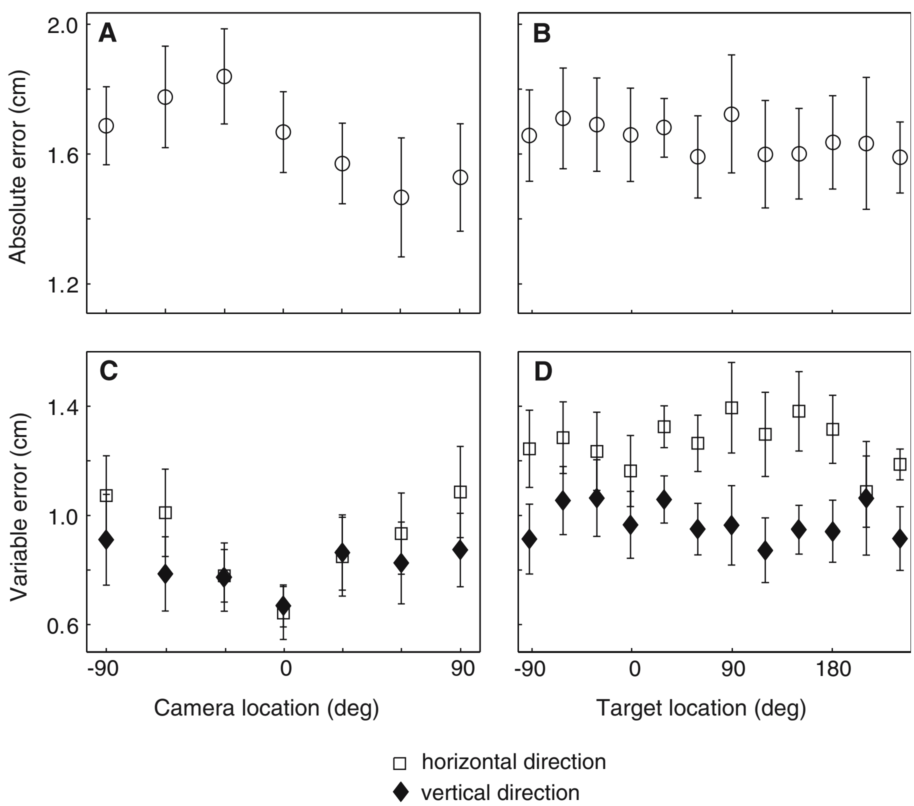

Fig. 14 Absolute error (**a**, **b**) and variable error (**c**, **d**) for each camera location (**a**, **c**) and each target location (**b**, **d**) in Experiment 3. *Error bars* represent standard errors of the mean

location ($F_{(11, 77)}$=1.36, P=0.21), and that there was no interaction between these variables ($F_{(66, 462)}$=0.83, P=0.82). Again, tapping time followed a U-shaped curve when plotted as a function of camera location (quadratic trend $F_{(1, 7)}$=39.17, P<0.01). After fitting the quadratic function, we found a large mean value of *a*

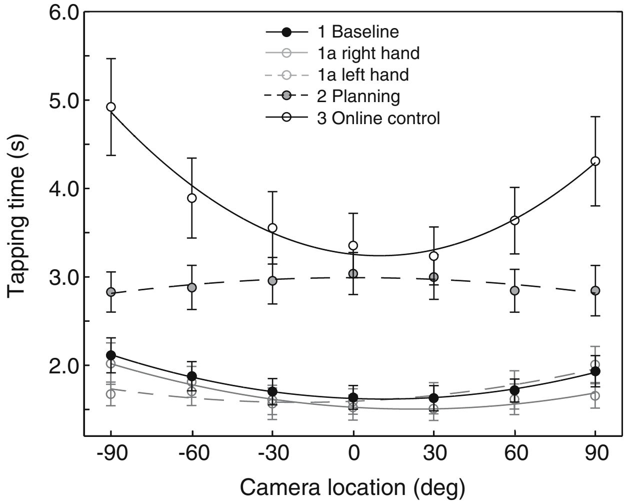

Fig. 15 Tapping time for all experiments as a function of camera location. *Error bars* represent standard errors of the mean

(M=0.163, SEM=0.027) that was significantly different from zero (t_7=6.13, P<0.01). The large value of a suggests that the U-effect was stronger in this experiment than in Experiment 1 (see also Fig. 15). This observation was supported by an independent sample t-test between the fitted values of a across participants in this experiment compared with the values obtained in Experiment 1 (t_{14} = -4.05, P<0.01). Because of the different experimental procedures across experiments, we also normalized the tapping time in both experiments by dividing them by the average tapping time for each participant separately, and fitting quadratic functions through these normalized data. After this procedure, we still found a stronger curvature for Experiment 3 than for Experiment 1 (t_{14} = -2.40, P=0.03). As in Experiment 1, we found a shift of the optimal camera location to the side of the used hand (M=9.72° to the right, SEM=1.93°, t_7=5.02, P<0.01).

In sum, the effect of camera location on tapping time became more pronounced when participants performed visuo-motor remapping during the control phase of the movement, when information about the moving hand was available. In contrast to the previous experiments, the tapping time did not depend on target location.

General discussion

Across three experiments, we varied the visual information that participants could use to perform a task in which they had to tap targets seen from different viewpoints. To successfully accomplish this task, participants had to remap their visual input to appropriate motor commands. In Experiment 1, participants could perform this visuo-motor remapping by using static information during the planning phase and by using dynamic information during the online control phase. We found that performance progressively improved when the camera approached a location approximately opposite the participants (the U-effect). Performance also depended on target position in the sense that targets along the cardinal axes were reached more quickly than those along the oblique axes (the M-effect). In Experiment 2, participants were forced to do the visuo-motor remapping during the planning phase, when only static information about the layout of the scene with their hand and target was available. In this experiment, performance was independent of camera location, though it still depended on target location in the same way as in Experiment 1. Lastly, in Experiment 3, participants could only start the visuo-motor remapping when their moving hand came into view, forcing them to do the remapping during the control phase when dynamic information was available. This condition resulted in a more pronounced effect of camera location on performance than in Experiment 1 (i.e., a stronger U-effect). There was no effect of target location in Experiment 3. The different effects of camera location on performance during planning, when only static information is available, than during control, when participants could use dynamic information, suggests that visuo-motor remapping happens differently during these two phases with these different kinds of information present. As the effect of camera location on performance for Experiment 1 falls between the effect of camera location for the planning experiment and that for the control experiment, it appears that, given the opportunity, participants perform visuo-motor remapping during the whole movement.

A question raised by the current results is what visuo-motor remapping strategies can account for the effects of camera and target location on performance. Although our study was not designed to investigate this question directly, the pattern of data suggests ways in which the participants could or could not have used the available visual information.

One possible strategy is to use the (static) visual information to infer camera location, and thus the location of the target. This inference may be possible using mental rotation. Participants could mentally rotate the scene or oneself until the two matched, and subsequently make the movement (Creem et al. 2001; Wraga 2003; Wraga et al. 2004). Using this strategy would cause an increase in processing time with the amount that the camera was rotated away from the participants' eyes, i.e., the amount of mental rotation that would be necessary for a match (Rieser 1989; Easton and Sholl 1995). As this strategy would typically be used in the planning phase, this pattern should be especially clear in Experiment 2. However, there was no effect of camera location in this experiment. In the other experiments, we observed the opposite of the pattern predicted by mental rotation.

It is more likely that participants used static information to code the movement direction towards the target relative to parts of the hand, for which they also have proprioceptive information. For example, participants perceive the target to be in the direction of where the little finger is and use proprioception to transfer this information into a movement in the correct direction. Similarly, the movement direction toward the target may be coded relative to the known orientation of the edges of the screen. For example, participants may follow the direction of the vertical edge in order to arrive at the target straight in front of them. The use of this information is consistent with the M-effect, which indicated that targets oriented along the vertical and horizontal edges of the screen were reached more quickly than other target locations (see Lhuisset and Proteau 2002, for a similar finding in a video-aiming task). It is also consistent with the results of Experiment 3, in which the M-effect was eliminated when the edges of the screen were circular. Coding the hand's movement direction relative to proprioceptively felt parts of the body or known parts of the environment should not depend on camera location, which is what we observed in Experiment 2 in which participants were required to perform visuo-motor remapping during the planning phase.

In Experiment 3, visuo-motor remapping happened during the control phase, when information about the moving hand was available. In this experiment (and to a lesser degree in Experiment 1), performance improved when the camera location approached a location close to 0° (i.e., opposite the participant). This pattern of results may arise because of the degree to which different camera locations disrupt the relative alignment of observers' visual and motor reference frames. For example, when the camera is facing the participant, rightward movements produce leftward movements in the visual image. Although the direction of motion is flipped, the orientation of the axes remains the same. In contrast, when the camera is located to the right side (90°), the visual reference frame is rotated relative to the motor reference frame. Rightward movements result in forward movement in the image. This misalignment could be harder to control than in the first case. Similar results were found by Boy et al. (2005) and Hellmann and Huber (2005). Their participants performed a pointing task on a horizontal surface while visual feedback was given on a vertically oriented monitor via a camera overhanging the workspace. When the camera was rotated, the movement time was substantially longer compared with when the camera was not rotated (for the first few trials).

The misalignment between visual and motor reference frames does not clarify why the optimal camera location is not exactly at 0°, but shifted 10–25° to the side of the used arm. This bias may be caused by occlusion. An important role of occlusion in performing the task is suggested by the plots of horizontal and vertical errors as a function of camera location (Figs. 2a, 5a, 9a, 12a). The tapped locations are attracted toward the camera. This finding is especially clear in Experiment 3 when feedback about the moving hand was particularly important (Fig. 12a). It suggests that participants considered the target to be reached when they occluded it with the hand. If participants are more likely to approach the target from the right side when using their right hand and from the left side when using their left hand, they would occlude (and reach) the target sooner when the camera is slightly shifted in the direction of the hand used. This would result in a bias in the optimal camera location to the side of the used arm, as we found.

Overall, our results suggest that participants may have initially determined the movement direction by relating the seen target to seen and felt features of their hand or to seen and known features of the environment, and subsequently controlled their movement by using information about the moving hand until the finger occluded the target. Coding the movement direction relative to features of the hand or the environment does not depend on viewpoint, whereas using visual feedback about the moving hand probably does. This could explain our finding of different visuo-motor remapping during planning and online control.

A short note on learning

If we had not varied the camera location from trial to trial, participants would probably have learned to move to the target fast and accurately for the different camera locations (as participants quickly learned to make goal directed movements with visual information being provided by rotated cameras, Boy et al. 2005). However, also with varying camera locations, participants showed some evidence for learning, as indicated by regression analyzes performed on tapping time as a function of trial number. For Experiment 1, 15 of 16 participants had negative slopes, indicating that they were improving over trials. Not all individual regressions were significant but across participants, the average slope was significantly different from zero. In Experiments 2 and 3, the average slopes were not significantly different from zero. In addition, only five of eight participants showed a negative slope in Experiment 2, and only six of eight participants showed a negative slope in Experiment 3. It is likely that more trials would be needed for the more difficult experiments to observe learning.

It may be surprising that making goal-directed movements while viewing the world through a camera was not easy for participants as indicated by the long tapping times and modest learning effects because all information for making a correct movement was available at the first glance (except in Experiment 3). Also, the camera locations at ±90° were not so far off from possible eye positions. Indirectly, our results suggest that in every day situations, proprioceptive, efferent, or vestibular information about the location of the eyes play an important role.

Conclusions

We found a systematic effect of viewpoint on remapping visuo-motor space when participants could perform the remapping both during planning and controlling the movement, with the best performance for a camera location nearly opposite the participants. As the effect of camera location was qualitatively different between the planning phase and the online control phase of the goal-directed movement, we conclude that visuo-motor remapping happens differently during these two phases. We suggest that this is due to the use of different visual information, such as the relative positions of the target and hand in the seen and known environment during planning, and the movement of the hand during control.

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