Adaptation of pointing and visual localization in depth around the natural grasping distance

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Abstract

Vision in depth is distorted. A similar distortion can be observed for pointing to visual targets in depth. It has been suggested that pointing errors in depth reflect the visual distortion. Alternatively, pointing in depth might be guided by a prior that biases movements toward the natural grasping distance at which object manipulation is usually performed. To dissociate whether pointing is guided by distorted vision only or whether it takes into account a natural grasping distance prior, we adapted pointing movements. Participants received visual feedback about the success of their pointing once the movement was finished. We distorted the feedback to signal either that pointing was not far enough or in separate sessions that pointing was too far. Participants adapted to this artificial error by either extending or shortening their pointing movements. The generalization of pointing adaptation revealed a bias in movement planning that is inconsistent with pointing being guided only by distorted vision but with the involvement of knowledge about the natural grasping distance. Adaptation was strongest for pointing movements to a middle position that corresponds to the natural grasping distance and it was weakest for movements leading away from it. It has been demonstrated that pointing adaptation in depth changes visual perception (Volcic R, Fantoni C, Caudek C, Assad JA, Domini F. J Neurosci 33: 17081–17088, 2013). We also wondered how effects of pointing adaptation on visual space would generalize in depth. We found that adaptation changed visual space, but that this change was independent of the adaptation direction.

NEW & NOTEWORTHY Which information guides pointing in 3D space? Inaccuracies of vision in depth generate the need for the sensorimotor system to rely on other information sources to optimally plan movement trajectories. Here, we implemented pointing adaptation experiments that could dissociate if the generalization of adaptation follows visual distortions or if it is informed by a “natural grasping distance” prior. Adaptation was strongest for movements toward the natural grasping distance, suggesting the latter hypothesis to be true.

adaptation; pointing; 3D vision

INTRODUCTION

How do we determine the locations of objects in three-dimensional space? The primary visual cues to depth—in the absence of motion parallax—are binocular cues. Although monocular cues can in principle guide movements, reaching performance in one-eyed vision drops down dramatically, suggesting the dominance of binocular cues in natural depth vision (1, 2). However, depth information provided by binocular disparity can only be interpreted ambiguously such that a small object that is close produces the same cues as a large object that is far away. When compensating this ambiguity through ocular convergence, the brain generates systematic errors in depth perception: Objects near to an observer are overestimated and objects far away are underestimated (3, 4).

Pointing in depth is similarly distorted: We overshoot close objects and undershoot far objects (5). This distortion in 3D pointing has been termed “specific distance tendency” and was interpreted as a behavioral preference for a distance of a general magnitude (6). As the underlying cause for this preference, Owens and Leibowitz (7) assumed the resting state of vergence in the absence of visual stimulation to be responsible. Others suggested that a regression to the average of the stimulus population, a phenomenon they called “contraction bias” (8), determined these results. Regression
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...to the mean usually is considered a strategy to reduce uncertainty about stimulus features and should therefore be strongest when information about these features is weak. Consistent with this explanation, studies found a contraction bias when the amount goes to distance is limited (9, 10).

However, these biases in pointing might also be a signature of optimizing sensorimotor performance by weighing prior knowledge with sensory information (e.g., 11–13). In the absence of precise visual information, consulting prior knowledge supports the choice of a movement that maximizes utility (14). For sensorimotor decisions, utility is a weighed comprise between the likely visual target position and the cost of the movement. In case visual information is weak, movements will be guided stronger by priors about movement costs that have been built up over the lifetime (15). The distance that is usually chosen for manual interaction has been termed the “natural grasping distance” (16). It has been demonstrated that depth estimates are most accurate at a distance that corresponds to this average distance where persons conveniently manipulate objects (17). This finding indicates that binocular depth perception is calibrated to the “natural grasping distance” at which precise depth estimation is most crucial for object interactions. Indeed, reaching and grasping movements are involved in the calibration of binocular depth perception (16). In a visuomotor adaptation task resulting in a change in perceived arm length, the authors show that participants quickly adapted the “new” natural grasping distance, changing the distance at which estimates of relative distance are most accurate.

Here, we asked if humans compensate the 3D ambiguity in visual depth perception by employing a “natural grasping distance” prior. To this end, we implemented two pointing adaptation experiments that could dissociate whether the generalization of adaptation follows visual distortions or if it is informed by a “natural grasping distance” prior. In both experiments, observers pointed to visual targets in a virtual environment without seeing their hands and received distorted feedback about the success of the movement when they reached the target. To place the targets around the natural grasping distance, the target positions were adjusted according to the arm length of the participants. In shortened reach adaptation sessions, the visual feedback suggested that participants did not point far enough as if they had a shortened reach. In these adaptation sessions, participants had to point farther in depth to bring the visual feedback onto the target. In adaptation sessions with a virtual extended reach, participants had to point closer to their body to match the position of the targets with the feedback. The visual distortion hypothesis and the natural grasping prior make opposite predictions for the two adaptation directions. Under the visual distortion hypothesis, participants should adapt stronger for far targets than for close targets in shortened reach adaptation, since due to the distortion, the feedback would be exaggerated for far targets and shrunk for close targets. The opposite holds true for extended reach. The adaptation blocks were identical between experiments. We also measured how pointing adaptation might affect visual space. Volcic et al. (16) have provided evidence that pointing adaptation can shift the point where visual accuracy for relative depth is maximal, suggesting that motor coordinates are constitutive for the calculation of object relations. Hence, in both experiments a visual localization task was presented before and after pointing adaptation to estimate the putative effect of motor signals on visual space. In experiment 1, participants had to estimate the distance of a probe stimulus in an adjustment task, and in experiment 2, distances were estimated in a two alternative forced-choice task. Measuring purely visual adaptation aftereffects with a psychophysical task requires presenting a probe in an adapted region and a comparison stimulus in a nonadapted region of the visual field. We used a dual adaptation method, where pointing to the right was followed by wrong visual feedback about the movement and pointing to the left by correct feedback. It has been shown that humans are able to adapt identical movements to two (or more) perturbations simultaneously if a contextual cue differentiates between the two (18–27). Gahramani and Wolpert (28) demonstrated that it is possible to produce a dual adaption field where rightward movements are adapted in one direction and leftward movements in the opposite direction.

METHODS

Experiment 1

Participants.

Forty-five participants (28 females, ages 18–47, average 25, 4 left-handed), including the second author, took part in the experiments. In separate sessions, we tested two different adaptation directions. Participants were randomly assigned to one of these two session types. In shortened reach adaptation, 23 participants took part and in extended reach 22. All participants had normal or corrected-to-normal vision. All participants gave their written informed consent before participation and subsequently received either monetary compensation or course credits. All experiments were approved by the ethics committee of the Faculty of Mathematics and Natural Sciences of the Heinrich-Heine-University Düsseldorf, Germany, and the study procedures were in line with the declaration of Helsinki.

Apparatus and stimuli.

Participants were sitting in a chair wearing a head-mounted display (HMD) and holding a VR controller in their right hand. Stimuli were delivered by an Intel i7-based PC (Intel, Santa Clara, CA) with an NVIDIA GTX 1080 connected to an HTC Vive HMD (HTC Corporation, Taoyuan, Taiwan). The HMD presents stimuli on two low-persistence organic light-emitting diode (OLED) displays with a resolution of 1,080 × 1,200 pixels per eye and a refresh rate of 90 Hz. Additionally, participants received a Vive motion-controller for their right hand. The virtual environment was rendered using a custom-made program created in the Unity game engine, version 2019.1.8f1 (Unity Technologies, San Francisco, CA). Head and hand movements were tracked via the HMD and controller using the standard SteamVR tracking system. According to previous research (29), this tracking system
provides a robust tracking of head and hand motion with a 360° coverage provided tracking loss is prevented. Tests of Verdelet et al. (30) demonstrated a submillimeter precision (0.237 mm) and an accuracy of 8.7 mm for static and 8.5 mm for dynamic objects. Although the system can update the user’s pose (position and orientation) at a higher rate (up to 1,000 Hz for the HMD and 250 Hz the controllers), in this study the sampling rate for both HMD and controllers was limited by the HMD’s refresh rate of 90 Hz.

In the present study, participants always responded to stimuli in front of them and we did not need the full coverage around the participants. Hence, to minimize the change of occlusions of the HMD or controller and thereby avoiding tracking loss, our setup had both base stations facing the participant. Throughout the experiment, participants held the controller with an outstretched index finger placed on top of the controller with the fingertip matching the tracking origin of the controller as close as possible.

**Target positions.**

Stimuli were presented in an empty midgray space maximally reducing monocular cues. To ensure that the locations of the stimuli relative to the observer were the same across participants, all stimuli were positioned relative to the location of the HMD at the start of the experiment. Participants were instructed to stay in the same position throughout the experiment (see Fig. 1A). A visual and acoustic error signal appeared when the participants left their predetermined head position.

A white sphere (diameter: 10 cm) was placed centrally 5 cm in front of their chest. This sphere served as a starting position where participants had to place their right hand between trials. Pointing targets were presented in red and visual targets in black color (diameter: 3 cm). The distance between the participant and the pointing targets was adjusted according to the arm length of the participants. This was done to match targets around the natural grasping head position.

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In adaptation trials, a target appeared randomly in one of four possible target locations (with two on the left and two on the right side). The four target positions were spaced 15 cm in z-direction and 30 cm in x-direction. Each target location was repeated 40 times. The feedback on the left side was always veridical, and on the right side distorted to shorten or extend participant’s reach, depending on the session (shortening or extending the reach). The 10-cm distortion was introduced gradually over three quarters of the whole amount of trials to minimize conscious adjustments of pointing (recalibration).

In visual localization trials, observers saw two targets in front of them, a static reference and a probe whose location in z-direction could be controlled with their thumb using the controller’s trackpad. In half of the trials, the reference sphere was presented on the left side and the probe on the right and vice versa. In total 10 probe positions were tested (five on each side), one per trial. The distance between the probe positions in z-direction was set to 6.25 cm. Participants were instructed to adjust the position of probe along the z-axis until it matches depth of the reference stimulus. Each position of the reference was repeated 5 times.

Targets in deadaptation trials were the same as in adaption trials. However, in deadaptation trials, participants always received veridical feedback.

**Trial structure experiment 1.**

Before the experiments started, participants were trained for 40 trials to execute a pointing movement to a peripherally

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**Figure 1.** A: side view of the possible stimulus positions relative to the observer along the z-axis in pointing trials of experiments 1 and 2. Only one target was shown per trial. B: trial structure for experiments 1 and 2. C: locations of all pointing targets in experiment 1. In experiment 2, only two of these targets were presented. D: locations of all visual localization targets in experiment 1. In experiment 2, a different procedure was used (see METHODS section for more information). E: locations of all pointing adaptation targets in experiments 1 and 2. On the left side the feedback was accurate, on the right it was distorted such that to hit the target observer should either point closer than the target (extended reach) or further than the target (shortened reach). Green dot shows the pointing feedback resulting from respective hand positions.
flashed target with their right index-finger. In each trial, a single red sphere appeared for 500 ms in front of the participant. The pointing was registered when the tracked finger crossed the table level in \( y \)-direction, which was signaled to the participant as a short vibration of the controller. Participants were instructed to point to the targets from below. During piloting, we tested both pointing from above or from below. The latter turned out to be more comfortable for participants, since they were not required to hold their hand above table level between trials. During the training, the participants received an accurate visual feedback of their landing position in form of a green sphere (1 cm in diameter).

The experiments consisted of five phases (see Fig. 1B). In 120 pointing trials, participants had to point to one of 12 possible target locations, nine on the right and three on the left (see Fig. 1C). Each position was tested 10 times. In all trials except pre- and postadaptation pointing trials, participants also received a visual feedback of their landing position, accurate or distorted depending on trial type and pointing side. When participants returned their hand to the starting position, another short vibration was emitted, and the next trial started after a fixed intertrial interval of 1,000 ms.

Then, a block of 50 visual localization trials followed. In a visual localization trial, observers saw two black spheres. One of them served as reference and the other as probe whose position along the \( z \)-axis could be controlled via the trackpad of the controller. The observers were asked to adjust the position of the probe sphere until it matched the location of the reference sphere in \( z \)-direction.

In 160 adaptation trials (see Fig. 1E), participants received wrong feedback about their terminal pointing location. In shortened reach sessions, the feedback appeared closer in depth relative to the actual pointing position, whereas in extended reach sessions the feedback was shown farther in depth. The displacement of the feedback shown on the display was increased gradually across trials until it reached the maximum value of 10 cm. In an adaptation trial, a target appeared in one of four possible positions with two target positions on the left and two on the right side of the screen. After pointing to the targets on the left side, participants always received veridical visual feedback about their terminal pointing location, whereas in adaptation trials, pointing to targets on the right side was followed by systematically shifted feedback.

After the adaptation block was finished, participants performed four visual localization blocks again, each consisting of 16 trials, except the last block, which contained only two trials, resulting in 50 visual localization trials in total. A trial started with the presentation of a fixation point for 1,000 ms, to which participants had to direct their gaze. Between each block, participants had to perform a block of eight readaptation trials. Then seven blocks of 16 pointing trials were conducted, again was each block separated by a block of eight readaptation trials. Following the last readaptation block, another pointing block of eight trials was performed, resulting in 120 pointing trials in total. Finally, 20 deadaptation trials were conducted, without any distorted feedback. Experiment 1 contained 640 trials and took on average around 37 min.

### Experiment 2

**Participants.**

Fifty-one participants (31 females, ages 18–47, average 25, 2 left-handed), including two of the authors, participated in experiment 2. All participants had normal or corrected-to-normal vision. Each subject participated in two adaptation sessions (shortened reach and extended reach adaptation). All participants gave their written informed consent before participation and subsequently received either monetary compensation or course credits.

**Target positions.**

Target positions in experiment 2 were the same during adaptation as in experiment 1 and differed only in pre- and postadaptation pointing and visual localization trials.

In pointing trials, the number of possible target positions was reduced to two (one on the left and one on the right). The positions corresponded to the central target position in the left group of targets shown in Fig. 1C and the central target position of the group of targets shown on the right. The closer pointing target positions were positioned 30 cm from the headset for shortened reach adaptation sessions and 40 cm for extended reach adaptation sessions to attend for the distances that observers needed to reach. With this change we aimed to have the final adapted movements comparable in shortened reach and extended reach adaptation.

In visual localization trials, two stimuli were presented (one on the left side and one on the right) with an interstimulus interval of 250 ms. The stimulus on the right side was the probe stimulus that was always presented in the same location, i.e., the central location on the right side (see Fig. 1C). On the left side, the reference stimulus was presented in one of seven possible, equiprobable and equidistant (2 cm) locations.

**Trial structure experiment 2.**

The procedure of experiment 2 followed the trial structure of experiment 1 (Fig. 1B). After the training block, participants performed 20 pointing trials without visual feedback toward two target locations with 10 repetitions per location.

Then, a block of 98 visual localization trials was presented. A trial started with the presentation of a fixation point for 1,000 ms, to which participants had to direct their gaze. Then, the left black sphere was flashed at one of the seven positions on the left for 10 ms. After 200 ms, the right sphere was flashed for 10 ms. Participants were asked to indicate which sphere was closer to their body by moving the controller to the left or right side of the starting position. A vibration on the controller indicated that they choice has been accepted. A psychometric function was measured for two probe locations. For each psychometric function, seven different comparison stimuli were presented, each repeated seven times.

Following adaptation, participants performed visual and blind testing blocks again, mixed with readaptation blocks to maintain the adaptation effect. After 10 testing trials, participants performed eight readaptation trials (2 repetitions per adaptation target position). Finally, participants made five deadaptation trials per target in which they received an accurate pointing feedback on both sides. Target presentations in the pointing and the visual trials were randomized. Altogether, the experiment contained 544 trials and took around half an hour to complete.
Each participant performed two sessions (shortened reach and extended reach adaptation), separated by at least a few hours, and for most participants (37 of 41) were separated by a day and more.

Data Analysis

The free statistical software R (R Foundation for Statistical Computing, Vienna, Austria; www.r-project.org) and RStudio (RStudio Team, 2020) were used to analyze the behavioral data. For statistical analysis, a nonparametric repeated measures ANOVA was calculated, using the Aligned Rank Transform (31).

We determined the terminal pointing coordinates in the x- and z-direction for a given target position once they crossed the table level in the y-direction. We included all trials in the analysis, in which the pointing movement did not start before or too late after target onset. To this end, we defined pointing trajectories as valid if they lasted longer as 100 ms and were shorter than the mean plus two standard deviations of the path length for the respective observer. In experiment 1, we included 95.4% in the shortened reach adaptation sessions and 94.6% in the extended reach adaptation sessions.

For the analysis of experiment 2, we excluded again trials from pre- and postadaptation pointing trials, using the same criteria as in experiment 1. We included 94.5% of the data in the shortened reach adaptation sessions and 96.4% in the extended reach adaptation sessions.

RESULTS

Experiment 1

Preadaptation pointing error.

We first checked the pointing performance of the 120 preadaptation pointing trials in which participants received no visual feedback about their terminal pointing position. In each trial, participants pointed to a target in one of 12 possible positions. Three target positions where on the left side and nine on the right. Targets presented on the right side served as probe targets to investigate generalization of pointing adaptation. For the probe targets, we analyzed pointing errors in the z-direction by averaging for each participant across all three targets in x-direction. Figure 2A shows average preadaptation pointing errors from sessions with shortened reach adaptation. Positive errors for the close targets indicate that participants overshot the physical target location with their pointing. The opposite holds true for the far targets. These were undershot by participants. A nonparametric repeated measures ANOVA revealed a significant effect of target depth on pointing error size [$F(2,44) = 21.972$, $P < 0.001$]. For each pointing target position in z-direction, we correlated the variable (root mean square) error with the constant error (see Fig. 2B). For the close and the medium positions, we found a positive correlation between the variable and the constant error, indicating that those participants with the highest variable error also showed the highest constant error, i.e., overshoot of the target toward the middle position. For the far location, we found a negative correlation. Since participants undershot the far position, the direction is now reversed: Those participants with the highest variable error, also showed the highest undershoot.

Average preadaptation pointing errors from sessions with extended reach adaptation are shown in Fig. 2C. Similarly, participants overshot the close and undershot the far targets. Pointing error size differed significantly between targets in depth [$F(2,42) = 9.11$, $P = 0.0005$].

Pointing to the average stimulus location could also be explained by a regression to the mean of all stimuli. By necessity, several repetitions of all stimuli will be needed for the brain to calculate the average of the stimulus population. To test the regression of the mean hypothesis, we performed the same analysis of the preadaptation trials as before but only for the first trial for each stimulus for each observer. A nonparametric repeated measures ANOVA revealed a

![Figure 2](https://example.com/figure2.png)

**Figure 2.** A: pointing errors for all three target distances in z-direction averaged within participants across all targets in x-direction and averaged across observers. Data derive from shortened reach adaptation sessions. Error bars represents SE across observers. B: mean pointing errors in z-direction against root mean square error of pointing for all observers in shortened reach adaptation sessions. The black line indicates the linear regression. C: pointing errors for all three target distances in z-direction averaged within participants across all targets in x-direction and averaged across observers. Data derive from extended reach adaptation sessions. Error bars represents SE across observers. D: mean pointing errors in z-direction against root mean square error of pointing for all observers in extended reach adaptation sessions. The black line indicates the linear regression. RMS, root mean square error.
significant effect of target depth on pointing error size in shortened reach \(F(2,44) = 275.96, P < 0.001\) and in extended reach \(F(2,42) = 297.07, P < 0.001\) adaptation sessions. As for the shortened reach sessions, we found negative correlations between variable and constant error for the close and the medium position and positive correlations for the far position (see Fig. 2D).

**Adaptation trials.**

After the preadaptation trials, 50 preadaptation visual localization trials were presented, which will be analyzed below, together with the postadaptation visual localization trials. Then, in 160 adaptation trials (40 trials of each of the two targets on the left and on the right side), participants received visual feedback about their terminal pointing position once their pointing movement was finished. The location of the feedback was gradually distorted over trials, i.e., it was displayed shifted from the physical terminal position. The distortion reached a maximum of 10 cm. Feedback was only distorted for the targets on the right but not for those on the left side. Figure 3A shows average pointing performance in the shortened reach adaptation trials for each of the two targets on the left side. Although no distorted feedback was provided for pointing to targets on the left side, one can see that across trials, participants pointed closer to their bodies, thus undershooting the physical target location. In shortened reach adaptation sessions, feedback was presented closer to the body of the observers. In attempting to reduce the error between their desired pointing location and the visual feedback, participants pointed farther away from to their bodies. As feedback was distorted only on the right side, adaptation likely overlapped to the left side, generating the small trend of adaptation seen in Fig. 3A. Terminal positions for pointing to targets on the right side is shown in Fig. 3B. For both targets, a strong adaptive shift in pointing terminal positions was generated by the distorted feedback.

In sessions with feedback that suggested an extended reach, participants should point closer to their bodies, trying to reduce the error between their terminal position and the feedback location. Similar as in shortened reach sessions, adaptation was very weak on the left side (see Fig. 3C). Only a small amount of adaptation over the course of trials is visible. However, on the right side a strong adaptation magnitude can be seen (see Fig. 3D).

To estimate whether adaptation took place at the movement planning stage, we analyzed the peak velocities of the movement trajectories. Figure 4A shows average peak velocities from shortened reach adaptation sessions for the left and the right side from preadaptation pointing trials (shown in white) and postadaptation pointing trials (shown in black). Peak velocities of pointing movements to targets on the left were virtually identical. However, peak velocities of pointing movements to targets on the right side were higher before than after adaptation. This difference is consistent with the larger movements, i.e., pointing further away from the body, that was performed after shortened reach adaptation. A nonparametric repeated measures ANOVA revealed a significant main effect for pointing direction [left/right: \(F(1,21) = 33.23, P = 8.45 \times 10^{-8}\) and for adaptation phase [pre/post: \(F(1,22) = 11.73, P = 0.002\)]. The interaction between pointing direction and adaptation phase was not significant \(F(1,22) = 4.26, P = 0.051\). In extended reach adaptation session, peak velocities did not differ much on the left side (see Fig. 4B). On the right side, peak velocities were higher before adaptation than after adaptation, consistent with movements that were farther in the z-direction. A nonparametric repeated measures ANOVA revealed a significant main effect for pointing direction [left/right: \(F(1,21) = 7.03, P = 0.015\) and for adaptation phase [pre/post: \(F(1,21) = 4.99, P = 0.037\)] and a significant interaction effect \(F(1,21) = 29.13, P = 2.35 \times 10^{-5}\).

**Postadaptation pointing error.**

After adaptation trials were finished, postadaptation pointing trials alternated with readaptation trials. We defined pointing aftereffects as the difference between pointing before and after adaptation. Figure 5A shows aftereffect magnitudes for each of the 12 probe targets as arrows. The starting point of each arrow is given by the average preadaptation pointing location and the tip of the arrow represents the average postadaptation pointing location. Circles show the physical target positions.

**Figure 3.** A–D: adaptation curves averaged over participants, one curve for each target position. Horizontal gray lines mark the target position. Black arrows on the right of the curves connect the average values of first and last five trials of respective curve. Vertical dashed line represents the end of the distortion adjustment. Error bands represent 95% confidence intervals.
For all arrows on the right side, participants pointed farther in z-direction, indicating that shortened reach adaptation successfully increased pointing movements in depth. One can also see that before and after adaptation, pointing to targets close to the body overshot the physical target position while pointing for the targets farthest in z-direction were closer to the physical target locations. The tendency to overshoot the close targets was already analyzed for preadaptation trials (see Fig. 2). Due to the adaptation direction in shortened reach sessions, this tendency increased after adaptation. No systematic pointing aftereffects were found for pointing to targets on the left side. When comparing aftereffect magnitudes on the right side for shortened and extended reach adaptation, one can see that for shortened reach adaptation aftereffects are stronger for the closer targets than for the farthest targets in z-direction. In extended reach adaptation, the opposite holds true. Pointing to the farthest targets shows the strongest adaptation aftereffects. For statistical analysis we used pointing errors, defined as the difference between each pointing terminal position and the physical target location.

For shortened reach adaptation, a nonparametric repeated measures ANOVA with the factors target position in x-direction (three levels), target position in z-direction (three levels), and adaptation phase (pre/post) revealed a significant main effect of target position in z-direction \( [F(2,44) = 31.63, P = 3.06 \times 10^{-9}] \) and a significant main effect of adaptation phase \( [F(1,22) = 23.86, P = 6.97 \times 10^{-5}] \).

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**Figure 4.** A: average peak velocity of pointing movements from preadaptation (bright gray) and postadaptation trials (dark gray) in the shortened reach adaptation sessions. Error bars represent SE. B: average peak velocity of pointing movements from preadaptation (light gray) and postadaptation trials (dark gray) in the extended reach adaptation sessions. Error bars represent SE.

**Figure 5.** A: average pointing aftereffects in shortened reach sessions shown as arrows. The x-direction of the pointing trajectory is shown on the abscissa and the z-direction on the ordinate. Gray circles mark the positions of targets. The starting point of the arrows indicate the average preadaptation pointing location and the tips the average postadaptation pointing location. B: average pointing aftereffects in extended reach sessions. Same conventions as in A.
The main effect for target position in x-direction was not significant \(F(2,44) = 0.08, P = 0.919\). The interaction between adaptation phase and target position in x-direction was significant \(F(2,44) = 3.57, P = 0.037\). These results confirm that adaptation changed pointing terminal positions and that adaptation magnitude was modulated by the target position in z-direction. Furthermore, the interaction also indicated a modulation of the adaptation magnitude by the target location in x-direction. Neither the interaction between target position in x-direction and target position in z-direction \(F(4,88) = 2.28, P = 0.067\) nor the interaction between target position in z-direction and adaptation phase \(F(2,44) = 2.55, P = 0.089\) were significant. However, pairwise comparisons using Tukey’s HSD revealed significant differences of pointing errors when comparing the aftereffects for the closest target (M = 2.48 cm, SD = 3.45 cm) and the farthest target (M = 2.17 cm, SD = 4.28 cm); \(t(44) = 2.015, P = 0.05\), confirming the assumption that the aftereffects were stronger for closer targets after shortened reach adaptation. The three-way interaction was not significant \(F(4,88) = 0.64, P = 0.639\).

For extended reach adaptation, a nonparametric repeated measures ANOVA with the factors target position in x-direction (three levels), target position in z-direction (three levels), and adaptation phase (pre/post) revealed a significant main effect of target position in x-direction \(F(2,42) = 18.19, P = 2.12 \times 10^{-6}\), a significant main effect of target position in z-direction \(F(2,42) = 16.48, P = 5.21 \times 10^{-6}\), and a significant main effect of adaptation phase \(F(1,21) = 59.88, P = 1.40 \times 10^{-7}\).

The interaction of adaptation phase and target position in x-direction was also significant \(F(2,42) = 4.84, P = 0.013\) as well as the interaction of adaptation phase and target position in z-direction \(F(2,42) = 8.28, P = 0.0009\). Pairwise comparisons using Tukey’s HSD revealed a significant differences of pointing errors when comparing the aftereffects of the closes target (M = 3.59 cm, SD = 2.70 cm) and the middle target (M = 5.40 cm, SD = 3.95 cm); \(t(44) = 3.741, P = 0.0005\), as well as between the closest target and the farthest target (M = 4.92 cm, SD = 3.52 cm); \(t(44) = 3.256, P = 0.002\), confirming the assumption that the aftereffects are stronger for farther targets after extended reach adaptation, as one would expect according the natural grasping distance hypothesis.

The interaction between target position in x-direction and target position in z-direction was not significant \(F(4,84) = 0.87, P = 0.48\). Similarly, the three-way interaction between target position in x-direction, target position in z-direction, and adaptation phase was not significant \(F(4,84) = 1.11, P = 0.36\). For shortened reach adaptation, these results confirm that adaptation successfully changed pointing behavior and that adaptation magnitude depended on x-direction and z-direction of the targets.

**Postadaptation effects on the nonadapted side.**

Pointing to targets on the left side always received correct feedback. We tested whether pointing on the left side was changed by the distorted feedback on the right side. For each target location on the left side, we calculated a paired t test. There was no significant difference for any of the targets (shortened reach: \(t(22) = 1.056, P = 0.419\); \(t(22) = 1.42, P = 0.292\); \(t(22) = -4.209, P = 0.052\); and extended reach: \(t(21) = -0.478, P = 0.680\); \(t(21) = -0.727, P = 0.543\); \(t(21) = 0.269, P = 0.813\).

**Visual localization.**

In the visual localization task, participants matched the position of a visual reference by adjusting the position of a visual stimulus presented on the opposite side of the visual field. Visual localization was measured before and after adaptation.

**Figure 6A** shows visual localization aftereffects for all 10 target locations from shortened reach adaptation sessions. As for pointing, visual aftereffects were defined as the difference between pre- and post-adaptation and are represented by the lengths of the arrows. For all positions except one, after adaptation targets were localized to be farther in z-direction. A nonparametric repeated measures ANOVA with the factors positions (five), adaptation phase (pre/post), and adaptation side (left/right) revealed a significant main effect for the factor positions \(F(4,88) = 14435, P = 2.22 \times 10^{-16}\). The...
main effect for the factor adaptation phase was also significant \( [F(1,22) = 4.55, P = 0.044] \). The factor adaptation side did not result in a significant effect \( [F(1,22) = 0.63, P = 0.437] \). The interaction between positions and adaptation phase was significant \( [F(4,88) = 3.55, P = 0.009] \). Neither the interaction between positions and adaptation side \( [F(4,88) = 1.92, P = 0.114] \) nor the interaction between adaptation phase and adaptation side \( [F(1,22) = 1.33, P = 0.262] \) were significant. Similarly, the interaction between positions, adaptation phase, and adaptation side was not significant \( [F(4,88) = 0.48, P = 0.745] \).

Aftereffects measured in extended reach adaptation sessions are shown in Fig. 6B. Visual localization of targets on the right side is generally shifted into the z-direction after adaptation. Visual localization of targets on the left side is not systematically shifted for all positions. A nonparametric repeated measures ANOVA revealed a significant main effect for the factor positions \( [F(4,84) = 1.30, P = 2.0 \times 10^{-16}] \) and a significant main effect for the factor adaptation phase \( [F(1,21) = 6.06, P = 0.02] \). The main effect for the factor adaptation side was not significant \( [F(1,21) = 0.16, P = 0.696] \). The analysis revealed no significant interactions between positions and adaptation phase \( [F(4,84) = 0.32, P = 0.864] \), positions and adaptation side \( [F(4,84) = 0.37, P = 0.831] \), or adaptation side and adaptation phase \( [F(1,21) = 0.46, P = 0.504] \). The interaction between positions, adaptation phase, and adaptation side was not significant \( [F(4,84) = 0.49, P = 0.75] \).

The absence of a significant interaction effect for both adaptation directions leaves it open whether the pointing shift in z-direction was triggered by adaptation. Distorted visual feedback was only provided on the right side. If adaptation was responsible for the pointing shift in z-direction, one would have expected a stronger shift on the right than on the left side. To investigate this hypothesis with a more sensitive visual localization task, we conducted a second experiment.

**Experiment 2**

**Pointing trials.**

Experiment 2 aimed at testing visual localization after pointing adaptation with a more sensitive method. We tested pointing adaptation with only two target positions. In the visual task, we flashed one target on the unadapted left side and one on the adapted right side to implement a psychometric spatial discrimination task. The trial structure was identical to experiment 1 (see Fig. 1B); only the number of trials was changed for certain blocks. Since we measured only two target positions before and after adaptation, 20 trials were tested in each, the pre- and the postadaptation pointing blocks. The adaptation block contained 160 trials as in experiment 1 with pointing to four different target locations. Pointing aftereffects are shown in Fig. 7.

In shortened reach adaptation sessions, pointing to the target on the left side, where visual feedback was veridical during adaptation, remained unchanged after adaptation. However, pointing to the target on the right side was shifted in z-direction after adaptation. A nonparametric repeated measures ANOVA with the factors positions (left/right) and adaptation phase (before/after) revealed a significant main effect for the factor positions \( [F(1,50) = 245.78, P = 2.22 \times 10^{-16}] \), a significant main effect for the factor adaptation phase \( [F(1,50) = 100.64, P = 1.44 \times 10^{-13}] \), and a significant interaction between positions and adaptation phase \( [F(1,50) = 141.57, P = 3.38 \times 10^{-16}] \). These results confirm that distorted visual feedback successfully adapted pointing behavior.

The same holds true for extended reach sessions, except that the direction of the aftereffect for pointing on the right side reversed its direction. A nonparametric repeated measures ANOVA revealed a significant main effect for the factor positions \( [F(1,50) = 84.17, P = 2.68 \times 10^{-13}] \), a significant main effect for the factor adaptation phase \( [F(1,50) = 8.66, P = 0.005] \), and a significant interaction between positions and adaptation phase \( [F(1,50) = 81.23, P = 4.71 \times 10^{-12}] \). The size and direction of the aftereffects for both, the shortened reach and the extended reach adaptation, replicate the findings from experiment 1.

**Visual localization.**

In 98 visual localization trials, tested before and after adaptation, participants estimated which target, the one on the left or the one on the right, was located farther in z-direction. Figure 8A shows example psychometric functions from two observers from shortened reach adaptation sessions.
Psychometric functions measured before adaptation are shown in gray and those measured after adaptation are shown in black. The slope of the curves reveals that participants were well able to perform the localization task. However, there is no difference in localization before and after adaptation for these two participants. On average, localization was almost veridical with no difference before and after adaptation [see Fig. 8A, paired t test, t(50) = −1.29, P = 0.19]. Figure 8C shows example psychometric functions from two observers from extended reach adaptation sessions. The results were almost identical to those of shortened reach adaptation. Localization was nearly veridical and did not differ between adaptation states. The same holds true for the average performance, as can be seen in Fig. 8D [paired t test, t (50) = −0.67, P = 0.50].

**DISCUSSION**

In this study, we asked whether the distortions in visual 3D space, which are commonly observed in human perception, are compensated for pointing by involving prior knowledge about the natural grasping distance. To this end, we investigated the spatial generalization of pointing adaptation. We first looked at pointing errors before adaptation. We found that participants estimated close targets to be further in depth and far targets to be nearer than they really are. This bias might have two origins: On the one hand, participants might produce these motor errors because they are guided by distorted space perception, on the other hand, movement planning might be biased toward the “natural grasping distance.” The analysis of preadaptation pointing data showed that those participants with the highest variable errors showed the strongest constant errors in their pointing. A possible explanation for this finding could be that participants with higher variable errors compensate the uncertainty about the true target location by biasing their movement toward the middle position. We conducted adaptation experiments to investigate whether this bias might be produced by a natural grasping distance prior. We used pointing adaptation to find causal evidence that might distinguish between both hypotheses. First, we applied visual pointing feedback that suggested a shortened reach. This artificial error led participants to extend their movements further into depth. We found a significant difference in adaptation strength in depth. After shortened reach adaptation we found the strongest adaptation effects for targets closest to the participant. After extended reach adaptation this pattern reversed, and we observed stronger adaptation effects for targets farther away. This result is inconsistent with adaptation following the visual distortion. Since vision is overestimated for targets being closer to the body, the distorted feedback would appear to be closer to the actual hand position and therefore induce weaker adaptation. Under the “natural grasping distance prior” hypothesis, adaptation should be strongest when leading toward the “natural grasping distance” and weakest when leading away from it. The results from extended reach adaptation are also clearly in favor of the latter view. Adaptation was weakest for close targets and strongest for targets farthest in depth. In summary, adaptation generalization in depth for both adaptation directions is biased by an urge toward the “natural grasping distance.”

In two experiments, we tested visual adaptation in an adjustment task and in a two alternative forced-choice task before and after adaptation. Both tasks involved a purely visual task that estimated the perceived position of a probe stimulus. To compare a visual probe against a visual reference stimulus, we used a dual adaptation field, in which pointing movements to one region of the visual field were adapted and movements to the opposite field were left unadapted. Any effect of motor adaptation on visual perception should have manifested as a shift in apparent location of the probe stimulus. We found a significant change in visual localization after pointing adaptation only in experiment 1, in which participants had to slide a stimulus to match the position in depth of a comparison stimulus. After shortened reach adaptation, participants localized stimuli further in depth. This finding is consistent with a study by Priot et al. (33), in which participants pointed to targets with their right hand while wearing prims goggles. When in pre- and postadaptation trials, they used the left (unexposed) hand, their pointing movements to visual targets were shifted by adaptation, indicating an overestimation of the visual target position. Similar results were found by van Beers et al. (34) who
asked participants to point with the left index finger to the position of the right index finger. A projection of the visual finger position—that could be seen through a mirror—was distorted in adaptation trials. Before and after adaptation, the authors tested pointing either to the seen visual or to the felt proprioceptive right index finger position. They found adaptive shifts in pointing with the finger to visual targets, indicating an overestimation of the visual target position.

We also tested visual localization after extended reach adaptation which adapted participants to point closer to their body. In this condition, the visual localization results again indicated an overestimation of target distance. This result is surprising, as one would expect the visual shift to follow the adaptive shift. Volcic et al. (16) induced pointing adaptation with an extended reach feedback. They found that pointing adaptation shifted the position where the object size is estimated accurately toward the adapted location. The direction of their perceptual shift is consistent with our results from extended reach adaptation. However, as we found the same effect in shortened reach adaptation, a simple explanation such as “vision follows pointing adaptation” is not available.

A possible explanation for these findings is that visual distortions are generated by the mere pointing movements, irrespective of the visual feedback. During the experiment, participants pointed repeatedly away from their body, and this repetitive pointing might result in a shift of the perceived distance of the target in the direction of pointing. Future research needs to investigate whether repeatedly pointing in a certain direction shifts the perceived distance in that direction. Alternatively, the observed visual aftereffects in experiment 1 might be explained by eye-muscle potentiation (EMP). Sustained convergence results in changes of extraocular muscle tone and previous research has demonstrated that an altered vergence effort following sustained convergence induced by a telestereoscope or by prisms can result in a distance overestimation (33, 35). However, this explanation appears to be unlikely considering that changes in extraocular muscle tone should affect the perceived distance of the probe and test stimulus equally.

We did not find any effect of pointing adaptation on vision in the second experiment. In experiment 2, we used a task in which two absolute spatial positions had to be compared. A limitation of this task, as well as of the localization task of experiment 1 was that the tasks could also have been solved by using monocular cues such as stimulus size or height in the visual field. However, this would not explain why we found differences in localization before and after adaptation in experiment 1, making it unlikely that the task was solely solved by using monocular cues. In contrast to the localization task of experiment 2, in the tasks used in experiment 1 and the study by Volcic et al. (16) the target position had to be actively matched. Thus, a possible explanation for the different findings could be that active localization and passive observation are differently affected by sensorimotor adaptation. An important aspect in this reasoning concerns the status of adaptation. Does it really occur on a motor stage or is it rather a conscious strategy to induce compensation to the artificial feedback error. We strived to make our adaptation procedure to invoke realignment (“true adaptation”) and not the strategic recalibration. First, to avoid stereotypic movements, we created two adaptation targets at each side. Second, we introduced the distortion gradually over 66% of the adaptation trials, because previous studies demonstrated that gradual exposure increases the level of adaptation compared to a single-step introduction of the shift (36). We found that peak velocities were increased after shortened reach adaptation and decreased after extended reach adaptation. Although this finding does not represent irrevocable evidence for true adaptation, it does at least show that we successfully altered movement plans of participants. In an attempt to reduce the error, participants could have consciously replanned their pointing movements. However, this hypothesis would predict a uniform generalization of adaptation which stands in stark contrast to our findings. In pioneering work on the spatial generalization of visuomotor adaptation, Bedford (37–39) demonstrated that distorted pointing feedback provided at a focused location in space transfers to other locations where they received correct feedback. From these findings, she concluded that spatially specific visuomotor adaptation is not possible. However, in her studies the pointing targets and the distorted feedback were presented in the same dimension. In our study, we placed the pointing targets on which correct feedback was provided in the left field of the display and the targets on which distorted feedback was provided on the right. We did not find any significant pointing aftereffect at targets on the left side. However, pointing aftereffects for targets on the right side differed significantly in the horizontal direction, most likely reflecting an influence of the correct feedback for pointing on the left side.

Our dual field adaptation method was similar to that used in a previous study (28). They demonstrated a generalization of pointing adaptation that was decaying from the adapted region. In our case this holds true only for the z-direction dimension, whereas in x-direction the aftereffects increase further from the nonadapted field. This difference in generalization might be due to the different adaptation methods in both studies. During adaptation they registered the success of the trial and showed the cursor only if the fingertip was within 0.5 cm of the target. They report that it made pointing difficult and participants had to move their fingers around and received verbal aid in case it took them long. In our experiment we excluded most of the monocular depth cues. Early studies have shown that movement performance drastically decline if they are guided only by monocular cues (2); however others found that movement trajectories might be relatively unaffected by this restriction (40, 41). From the remaining binocular cues in our setup, only binocular disparity was a valid indicator of depth, as ocular convergence cannot covary with virtual stimulus depth in a head-mounted display. Vergence has measurable supportive effects on depth estimates, but binocular disparity clues play the major role (10).

In summary, our study suggests that pointing movements in depth are biased toward the natural grasping distance. Using pointing adaptation separately in opposite directions, we could dissociate the hypothesis that pointing follows vision from the hypothesis that pointing is biased by a natural grasping distance prior. Adaptation was strongest for those movements that went toward the natural grasping distance, clearly suggesting the latter hypothesis to be true.
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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

T.K. and E.Z. conceived and designed research; T.K. and E.Z. performed experiments; T.K. and E.Z. analyzed data; M.W., T.K., and E.Z. interpreted results of experiments; M.W., T.K., and E.Z. prepared figures; M.W., T.K., and E.Z. drafted manuscript; M.W. and E.Z. edited and revised manuscript; M.W. and E.Z. approved final version of manuscript.

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