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RESEARCH ARTICLE

Grasping in absence of feedback: systematic biases endure extensive training

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Abstract Reach-to-grasp movements performed without visual and haptic feedback of the hand are subject to systematic inaccuracies. Grasps directed at an object specified by binocular information usually end at the wrong distance with an incorrect final grip aperture. More specifically, moving the target object away from the observer leads to increasingly larger undershoots and smaller grip apertures. These systematic biases suggest that the visuomotor mapping is based on inaccurate estimates of an object's egocentric distance and 3D structure that *compress the visual space*. Here we ask whether the appropriate visuomotor mapping can be learned through an extensive exposure to trials where haptic and visual feedback of the hand is provided. By intermixing feedback trials with test trials without feedback, we aimed at maximizing the likelihood that the motor execution of test trials is positively influenced by that of preceding feedback trials. We found that the intermittent presence of feedback trials both (1) largely reduced the positioning error of the hand with respect to the object and (2) affected the shaping of the hand before the final grasp, leading to an overall more accurate performance. While this demonstrates an effective transfer of information from feedback trials to test trials, the remaining biases indicate that a *compression of visual space* is still taking place. The correct visuomotor mapping, therefore, could not be learned. We speculate that an accurate reconstruction of the scene at movement onset may not actually be needed. Instead, the online monitoring of the hand position relative to the object and the final contact with the object are sufficient for a successful execution of a grasp.

Keywords Grasping · Visual feedback · Haptic feedback · Calibration · Visuomotor learning

Introduction

To reach for an object and grasp, it seems to be an effortless action that is rarely unsuccessful, but the mechanisms involved in this common task are still unclear. One possible explanation of this skill is that the brain represents accurately and precisely the location and shape of a target object and maps this information onto the appropriate motor program. This would imply that vision for action is veridical and therefore not influenced by inaccuracies that frequently characterize perceptual tasks. For example, perceptual judgments of an object distance and 3D structure are often systematically biased. These biases are thought to be the result of processes that ignore the visual information potentially available for a veridical metric reconstruction of the environment (Domini and Caudek 2013). Another explanation is that when we grasp an object, the visual system overcomes biases in the initial reconstruction of the scene by making use of the information provided by (a) the vision of the hand in relation to the object and (b) the physical presence of the object detected through haptic feedback. Growing empirical evidence seems to support this second explanation, since the precision and accuracy of grasping actions are critically dependent on the availability of visual feedback of the hand and target (Carlton 1981; Jakobson and Goodale 1991; Westwood et al. 2003)

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and the presence of haptic feedback at the end of the movement (Bingham et al. 2007; Schenk 2010, 2012). When the presence of feedback is reduced or removed (e.g., memory-guided movements), grasping and reaching movements are compromised, both in terms of their accuracy (e.g., undershooting a target, Flanders et al. 1992) and precision (e.g., high variability in endpoint estimation, Carlton 1981; Westwood et al. 2003). In the absence of any feedback from the hand, reaching and grasping are subject to systematic biases even when vision of the object is available throughout the grasping action (Bingham et al. 2007; Bozzacchi et al. 2014: Campagnoli et al. 2012).

An open question is whether training participants with feedback trials can teach the visuomotor system the correct mapping necessary for the accurate execution of reach-to-grasp actions performed without feedback.

In a previous study, we addressed this question with a blocked-design experiment in which participants executed front-to-back grasps of objects located along the line of sight and only specified by binocular disparities (see Fig. 1). Objects were always visible throughout the grasping action. First, we assessed the presence of systematic biases in a block of trials in which grasping was executed without feedback. A first important result of this condition is that participants were consistently unable to correctly position their hand at the object egocentric distance and to separate their index and thumb to accurately reproduce the depth of the object. More importantly, in spite of the large inter-subject variability present in these tasks, a systematic bias affecting all participants' reach-to-grasp behavior indicated a consistent *compression of visual space*. For instance, the difference in terminal hand position (THP) when reaching the farthest distance (520 mm) with respect to the shortest distance (420 mm) was on average 75 mm, i.e., 25-mm short of the actual distance span (Bozzacchi et al. 2014). In other words, the visual estimate of a distance interval of 100 mm appears to be subject to a 25 % compression. This systematic bias in egocentric distance estimate has predictable consequences on the estimate of the object depth: the same object should seem deeper at closer distances than at further distances. Indeed, larger grasps are executed for closer objects than for further objects, both in terms of final grip aperture (FGA) and maximum grip aperture (MGA) (Bozzacchi et al. 2014; Bozzacchi and Domini 2015). Remarkably, these results are in perfect quantitative agreement with previous data on perceptual tasks (Volcic et al. 2013, but see also Hecht et al. 1999), indicating that visual estimates for action are the outcome of the same mechanisms underlying our perceptual experience.

In a second phase of the experiment, participants executed 60 grasps with feedback in a training block and were tested afterward in a battery of test trials where feedback was no longer available. We found only a partial improvement of the average final position of the hand, whereas errors in grip aperture remained unchanged. A closer look at the temporal evolution of the subject's THP error exposed a more accurate performance on the test trials that immediately followed the training block. The performance, however, quickly deteriorated toward baseline levels of accuracy (but see also Smeets et al. 2006). Strikingly, biases revealing a compression of visual space persisted, indicating a failure of calibration.

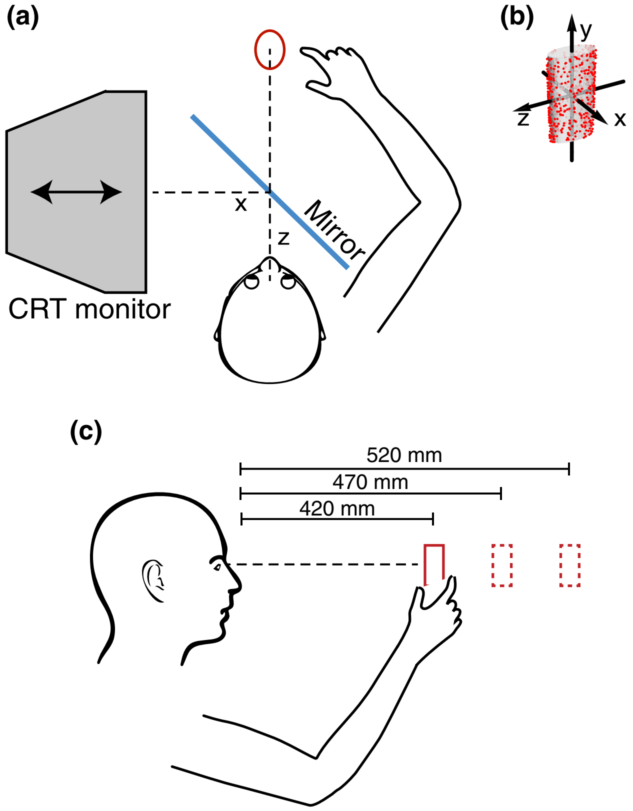


Fig. 1 Experimental apparatus and feedback conditions. **a** Schematic top view of the experimental apparatus. Subjects reached behind the mirror to grasp the 3D object they could see reflected on the mirror. The monitor distance was adjusted to match the simulated distance of the object. **b** Schematic representation of the stimulus. The dimension of the cylinder with an elliptic cross section could vary along the *z*-axis that was oriented along the viewing direction. **c** Sagittal representation of a grasp at one of three possible distances at which the object could be located (420, 470, 520 mm)

These seemingly conflicting results may suggest that training with a blocked design was ineffective, for at least two reasons. First, the repetition of several feedback trials within a training block may not have a cumulative effect on learning. It could be the case that the "memory" of what taught by feedback trials is only short-lived, and that test trials must be temporally contiguous to feedback trials for an effective transfer of the correct visuomotor mapping. Therefore, a cumulative effect leading to a correction of the compression of visual space may need several alternations of feedback trials with test trials, as if the visuomotor system must be continuously "reminded" of what the correct visuomotor mapping is. Second, the awareness of the absence of feedback during test trials may have a detrimental influence on the calibration process. If the participant knows in advance that no object will be encountered at the end of the grasping action, then he/she may adopt a different strategy in programming that action.

For these reasons, in the present study, we investigated the effect of the random and intermittent presence of feedback trials, which allowed to (a) maximize the temporal contiguity of test and feedback trials and (b) eliminate the possible effect of predictability, since during the planning phase participants did not know whether an actual physical object was going to be present at the end of the grasp.

In summary, this experimental paradigm was intended to maximize the likelihood that the brain learns the correct visuomotor mapping for performing those reach-to-grasp actions executed without the aid of feedback. If biases still persist, then we can speculate that the compression of visual space is the outcome of hardwired mechanisms that can be hardly modified, and that visual and haptic feedback of the effector is a necessary condition for successful goal-directed actions.

Materials and methods

Subjects

Nineteen undergraduate and graduate students from the University of Trento (mean age 23.2; 10 females) with no neurological or psychiatric diseases took part in the study. All participants were naive to the purpose of the experiment and were paid eight euros for their participation. The total duration of the experiment was 1 h. Participants were all right-handed based on a self-report of hand preference. The experiment was approved by the Comitato Etico per la Sperimentazione con l'Essere Vivente of the University of Trento and in compliance with the Declaration of Helsinki. After full explanation of the procedures, all participants provided written informed consent.

Apparatus and design

Participants were seated in a dark room in front of a high-quality, front-silvered 400 × 300 mm mirror. The mirror was slanted at 45° relative to the subjects' sagittal body midline and reflected the image displayed on a ViewSonic 9613, 19″ CRT monitor placed directly to the left of the mirror. For consistent vergence and accommodative information, the position of the monitor, attached to a linear positioning stage (Velmex Inc., Bloomfield, NY, USA), was adjusted on a trial-by-trial basis to equal the distance from the subjects' eyes to the virtual object and did not move during the trial (Fig. 1a). All experimental sessions started with the calibration procedure. The position of the head, eyes, wrist, the thumb and index finger pads was calculated with respect to infrared-emitting diodes. For the head, three diodes were located on a band surrounding the head of the participants. For the wrist, a single diode was located on the ulnar styloid. Finally, for the thumb and index finger, three diodes were placed on metal plates and fixed on the nail of each finger. This allowed to calculate the actual position of the pad of each finger (Nicolini et al. 2014). Head, wrist, index and thumb movements were acquired online at 100 Hz with submillimeter resolution by using an Optotrak 3020 Certus motion capture system with two position sensors (Northern Digital Inc., Waterloo, Ontario, Canada). To present visual stimuli in 3D, we used a frame interlacing technique in conjunction with liquid crystal FE-1 goggles (Cambridge Research Systems, Cambridge, UK) synchronized to the monitor frame rate. Stimuli presentation and response recording were controlled by a C++ program. The interocular distance (IOD) measured before starting the experiment, in conjunction with the measured head pose, was used online to generate the correct image to the two eyes. The subjects' viewpoint was thus constantly updated to present the correct geometrical projection of the stimulus in real time. Visual feedback of the thumb was rendered by means of a disk representing the thumb pad. The correct position of the thumb pad for the presentation of the virtual disk was calculated during the calibration process at the beginning of the experiment (see above). Disparity-defined high-contrast random-dot visual stimuli were rendered in stereo simulating a vertically oriented cylinder with an elliptic cross section (height: 70 mm, minor axis: 30 mm, major axis oriented along the viewing direction: 20 or 40 mm, Fig. 1b). Stimuli were simulated at three distances along the line of sight (420, 470 and 520 mm, Fig. 1c). The starting point of the hand was shifted in respect of the center of the body of the subject by 200 mm to the right, 300 mm lower than the line of sight and 150 mm from the coronal plane. Therefore, the object was simulated at about 475, 505, 538 mm with respect to the hand. All participants performed two different blocks in a fixed order, including the different combinations of the three distances and two object depths presented in a randomized order. Participants were required to reach-to-grasp the virtual object shown in front of them, which was not visible before they moved. An auditory cue was the signal for participants to initiate the movement. At movement onset (when the fingers were 15 mm from the starting position), the object appeared and remained visible for 2500 ms, corresponding to the trial duration. We decided to present the target immediately after movement onset and keep it visible during the entire movement execution in order to let participants rely on real-time visual information only.

After this interval, a second auditory cue was provided in concomitance with the disappearance of the stimulus to indicate the end of the trial. Participants were required to perform and complete their movement within this interval and move back to the starting point only after the second auditory cue.

Procedure

Each participant was tested in a dark room with his/her head stabilized by a chin rest. Before running the experiment, participants were tested for stereo vision and were allowed to perform some practice trials to get accustomed to the virtual environment. All participants underwent two consecutive blocks: a *baseline* and a *test*, involving two different conditions presented in random order. The first block (*baseline*) was composed of 60 trials in which they performed the reach-to-grasp toward a virtual object visible for the total duration of the trial but without the visual feedback of their hand and without feeling the object at the end of the movement. The *test* block was composed of 120 trials. In all trials, the vision of the object was constantly provided for the total duration of the trial. Sixty trials were performed with the visual feedback of the thumb throughout the movement and the final haptic feedback of the object (*mixed-F* condition). This feedback was chosen on the basis of previous studies in which we found that the feedback of the thumb was sufficient to correctly guide the movement and induce motor adjustments (Bozzacchi et al. 2014; Volcic and Domini 2014). The haptic feedback was provided by physical cylinders located at the same distance and having the same size and shape as the virtual cylinders. The physical cylinders were fixed on a moving mechanical arm (Velmex Inc., Bloomfield, NY, USA) adjusted on a trial-by-trial basis to move the physical object to the correct position. The mechanical arm was controlled by a C++ program, and its position was calibrated at the beginning of the experiment. These trials were randomly intermixed with other 60 trials performed without visual feedback of the hand and final haptic feedback (*test* trials), as in the *baseline* condition. In order to avoid a long sequence of the same type of trial, we generated a blocked randomization as a sequence of blocks in which all the 12 combinations of condition, distance and object depth were presented.

During the *test* block, participants were unaware about the kind of trial they were going to initiate before they started the action. The visual feedback of the thumb became visible as soon as the hand entered the subject's visual field and remained visible for the whole trial duration. The presence of the visual feedback informed the participants about the condition they were performing. Participants started each trial of the experiment with their thumb and index fingertips touching each other and resting on the top of a pole. They were required to grasp the virtual cylinder along the depth axis. Trials in which the markers were occluded were discarded and repeated later in the experiment.

Data analysis: variables of interest

Data were processed and analyzed offline using custom software. The raw data were smoothed and differentiated with a second-order Savitzky–Golay filter with a window size of 41 points. These filtered data were then used to compute (1) velocities and accelerations in 3D space for each fingertip and the wrist, (2) the Euclidean distance between the fingertips of the thumb and the index finger (grip aperture), and (3) the velocity and acceleration of the change in grip aperture. The dependent measures were the terminal hand position error (THPerr), the maximum grip aperture (MGA) and the final grip aperture (FGA). We defined THPerr and FGA on the basis of the multiple sources of information method as proposed by Schot et al. (2010). The parameters used in order to implement this method were the velocities of the index, thumb and wrist, the distance from the starting position, and the velocity and acceleration of the change in grip aperture. The THPerr was defined as the difference along the *z-axis* between the position of the thumb fingertip at the end of the movement with respect to the anterior surface of the object, considered as the thumb contact point. The MGA and the FGA were defined as the maximum and final distance between the fingertips, respectively.

Data analysis: statistical analysis

The statistical analyses were performed on the data collected in the present study, termed *mixed-feedback experiment*, in conjunction with a subset of data from our previous work (22 subjects; mean age 24.3; 17 females from Bozzacchi et al. 2014), in which participants performed three separate blocks (*baseline*, *training* and *test)*. In this investigation, which we will name *blocked-design experiment*, only in the *training* block subjects were provided with visual feedback of the hand and haptic feedback of the object (Bozzacchi et al. 2014). The only difference between the previous and the present study lies in the training procedure (i.e., blocked-design vs. mixed-feedback), whereas the *baseline* conditions (pre-training in the previous study) are identical. Statistical analysis included a type III mixed ANOVA with experiment (*blocked-design* vs. *mixed-feedback*) as between-participants variable and block (*baseline* vs. *test*) and distance as within-participants factors for the THPerr variable, and the factor depth was also considered in the analysis of the FGA and MGA. To study the effect of feedback exposure on these variables, we also analyzed the temporal evolution of calibration. To this end, we divided the 60 *test* trials in both experiments into 10 temporally consecutive bins of 6 trials each that we analyzed with a mixed ANOVA with experiment as between-participants factor and trial bin as within-participants factor. Finally, because of our specific interest in testing the calibration of the compression of the visual space, we specifically tested the effect of distance on all these variables by fitting for each subject, variable, experiment and block, a linear regression model as function of distance centered on the mean value of this variable (470 mm), to be tested with a mixed ANOVA with experiment and block as between- and within-participants factors, respectively.

Results

In the *baseline* condition, where visual feedback of the effector and haptic feedback of the object are absent, three systematic biases characterize the reach-to-grasp actions: (1) Individual average THPerr is consistent with respect to the physical position of the object, resulting in a large absolute error that varies greatly across participants, with a general tendency of undershooting the object (Fig. 2a, b, left panels); (2) the negative slope of the position error as function of distance, since the average error is smaller at the closest distance than at the farthest distance (Fig. 2a, b, black lines); (3) the FGA and MGA decrease with the object distance (Figs. 5a, b, 7b). The last two biases are compatible with a compression of visual space, since the difference between the average THPerr at the farthest distance and at the closest distance is smaller than the actual distance interval. The underestimation of the distance interval yields an incorrect scaling of binocular disparities affecting the FGA and MGA.

Terminal hand position error

Figure 2 shows the individual averaged thumb position error as function of viewing distance in the *baseline* block and the first and last bin of *test* trials. A first glance at the results reveals that participants corrected their error in hand position during the first 6 *test* trials in both experiments. Thus, participants who had large undershoots or overshoots of the target object corrected considerably their reach.

The overall effect of training was the reduction in the average undershoot of the target object with respect to the *baseline* condition (Fig. 2a, b, right panels, black lines), as revealed by the main effect of block [$F(1, 37) = 13.15$; $p = 0.0008$] in a mixed ANOVA on THPerr with experiment as between-participants factor and block and distance as within-participants factors. Not surprisingly, there was a main effect of distance [$F(2, 74) = 80.03$; $p < 0.0001$], indicating a compression of visual space and an interaction effect between experiment, block and distance [$F(2, 74) = 3.21$; $p = 0.04$]. In a subsequent analysis, we considered the two experiments separately and run a repeated-measures ANOVA with block and distance as within-participants factors. For the mixed-feedback experiment, we observed a main effect of block [$F(1, 18) = 7.99$; $p = 0.01$], distance [$F(2, 36) = 6.45$; $p = 0.004$] and their interaction [$F(2, 36) = 6.45$; $p = 0.004$], showing

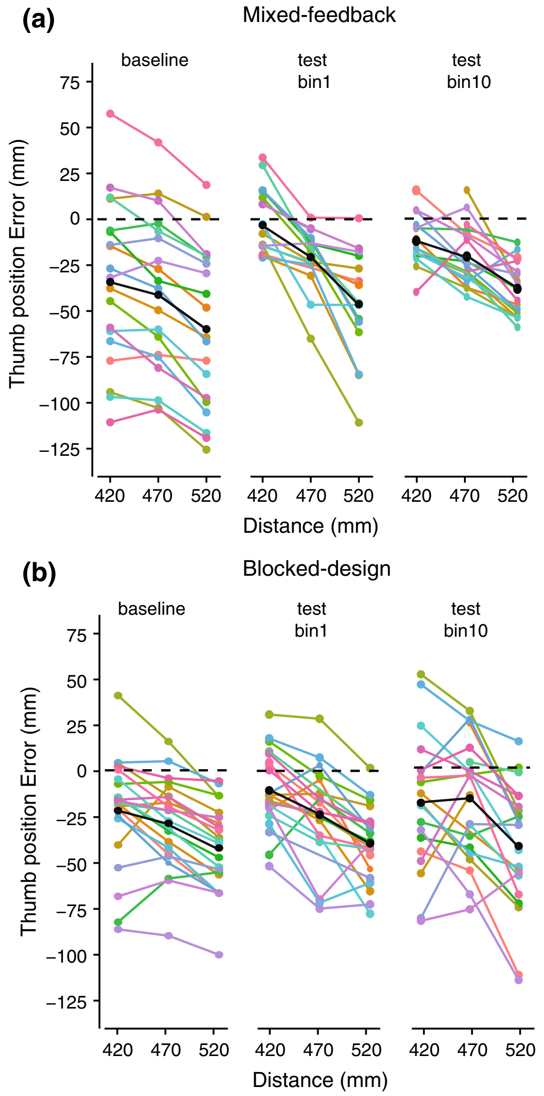


Fig. 2 Terminal hand position error. Terminal hand position error for the *baseline* condition (*left panels*), the first 6 trials (*central panels*) and last 6 trials (*right panels*) of the *test* condition as function of object distance. The performance of each participant is coded with a *different color*, whereas *black lines* represent the averaged THP error. **a** Mixed-feedback experiment; **b** blocked-design experiment (data from Bozzacchi et al. 2014) (color figure online)

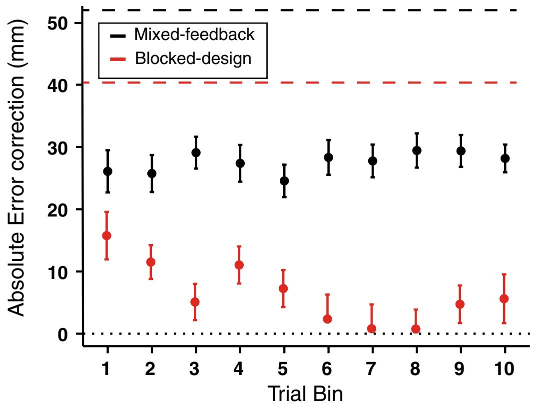


Fig. 3 Time course of absolute error correction. Absolute error correction in the *test* condition with respect to the *baseline* condition as function of trial bin for the mixed-feedback experiment (*black marks*) and blocked-design experiment (*red marks*). Each trial bin comprises 6 trials (3 distances × 2 sizes). Zero correction means lack of calibration. *Dashed lines* represent full correction for the mixed-feedback (*black*) and blocked-design (*red*) experiments. For the mixed-feedback experiment, a sizeable calibration effect can be noticed right at the beginning of the intermixed block (trial bin = 1), only after six feedback trials. Note how this level of calibration persists throughout the block. For the blocked-design experiment, a calibration effect can be noticed right after the training block (trial bin = 1) that subsequently fades away. *Error bars* represent standard error of the mean (color figure online)

that in the *test* condition, the effect of distance was much stronger than in the *baseline* condition. On the other hand, for the blocked-design study, a main effect of block [$F(1, 21) = 9.83$; $p = 0.005$] and distance [$F(2, 42) = 23.72$; $p < 0.0001$] was present, but no interaction between them.

As shown in Fig. 2, there was an overall effect of training in both experiments on the THP error. Its average value, which in the *baseline* condition determined an overall undershoot of the target, was partly corrected after training, to a larger extent in the mixed-feedback experiment. Instead, the negative relationship of THP with distance remained the same after training or became even stronger in the mixed-feedback experiment. The effect of distance on the THPerr will be better investigated in the further analysis.

Terminal hand position: absolute position error correction

In Fig. 3, we plot the average absolute error correction in THP with respect to the *baseline* condition as function of trial bin. The mixed ANOVA showed a strong effect of experiment [$F(1, 36) = 7.44$; $p = 0.009$] and an interaction effect of experiment and trial bin [$F(9, 324) = 2.76$; $p = 0.004$]. As it can be clearly noticed, the initial correction observed in the first bin of *test* trials of the blocked experiment quickly tends to the *baseline* level, whereas for the mixed-feedback experiment, it holds constant throughout the block. Comparison between the first bins revealed no difference between the two experiments [$t(38) = -1.37$; $p = 0.34$], whereas the two experiments clearly diverged in the last bin [$t(38) = -2.84$; $p = 0.01$].

Terminal hand position: compression of visual space

The strong effect of distance as found in the previous analysis denoted a consistent underestimation of the position of the target, which persisted regardless of the training. An index of the compression of visual space is given by the slope of the linear function interpolating the data, relating distance and error in THP. Therefore, in order to better investigate this specific phenomenon, we fitted a linear regression model for each subject, block and experiment as function of distance, after centering this variable at the mean distance of 470 mm. Figure 4a, b shows that in the *test* condition, the slope is negative, and that in the mixed-feedback experiment, its magnitude is even larger than in the *baseline* condition. Indeed, a mixed ANOVA with experiment as between-participants factor and block as within-participants factor showed an effect of block [$F(1, 37) = 4.14$; $p = 0.05$] as well as a marginal interaction of experiment and block [$F(1, 37) = 3.43$; $p = 0.07$]. Figure 4a suggests that in the mixed-feedback experiment, the slope in the *test* condition increases with respect to the *baseline* condition, a pattern not evident in the blocked-design experiment.

Figure 4b shows how the slope magnitude changes as function of trial bin. What is important to note is that in the mixed-feedback experiment, the compression of visual space is initially very pronounced (slope = −0.4) and then tends to become smaller, but it is always larger (in absolute value) than in the *baseline* condition. In the blocked-design experiment, the slope in the *test* condition never changes significantly from the magnitude observed at *baseline*. Accordingly, the mixed ANOVA on slope with experiment as between factor and trial bin as within factor, showed a significant effect of experiment [$F(1, 30) = 5.56$; $p = 0.02$] and interaction between experiment and trial bin [$F(9, 270) = 2.43$; $p = 0.01$]. A subsequent analysis considering the two experiments separately confirmed that the interaction is due to the change in slope with trial bin in the mixed-feedback experiment [$F(9, 126) = 2.30$; $p = 0.02$], whereas this change is absent in the blocked-design experiment [$F(9, 153) = 1.33$; $p = 0.22$].

Final grip aperture

In Fig. 5a, we plotted the FGA as function of distance for the two object depths in the baseline and test blocks. Importantly, no significant effects of experiment [F(1,

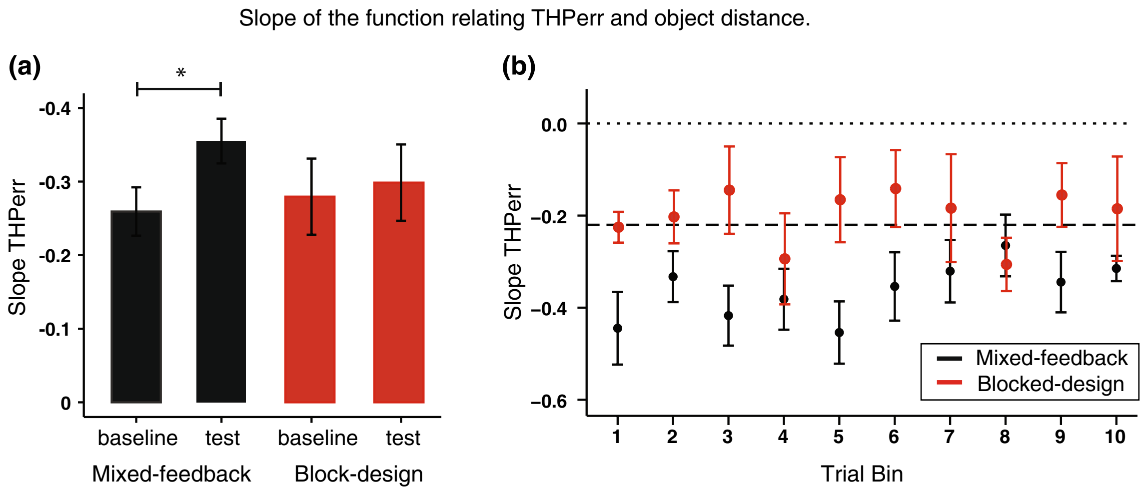


Fig. 4 Distance effect on terminal hand position error (THPerr). **a** Slope of the function relating THPerr to distance in the baseline and test conditions of the two experiments. No significant change in slope was present after training for the blocked-design experiment (*red bars*), whereas a stronger effect of distance is visible for the *test* condition with respect to the *baseline* condition in the mixed-feedback experiment (*black bars*). *Error bars* represent standard error of the mean. **b** Temporal evolution of the slope of the THPerr in the *test* condition of the mixed-feedback experiment (*black marks*) and blocked-design experiment (*red marks*). *Dashed line* represents the average slope of the *baseline* conditions (note that the slopes in the *baseline* conditions of the two experiments overlap). *Error bars* represent the standard error of the mean (color figure online)

37) = 0.30; $p = 0.56$], block [$F(1, 37) = 0.01$; $p = 0.88$] or interaction [$F(1, 37) = 1.07$; $p = 0.30$] between these two variables were found in the mixed ANOVA. The analysis showed a strong effect of distance [$F(2, 74) = 18.11$; $p < 0.0001$], depth [$F(1, 37) = 41.97$; $p < 0.0001$] and their interaction [$F(2, 74) = 7.59$; $p = 0.0009$]. In fact, the effect of distance was more pronounced for the big [$F(2, 76) = 25.44$; $p < 0.0001$] than for the small object [$F(2, 76) = 4.98$; $p = 0.009$].

Figure 6 shows that there is not a clear pattern of change of FGA as function of trial bin, even though a mixed ANOVA with experiment as between-participants factor and bin as within-participants factor showed a main effect of bin [$F(9, 333) = 2.09$; $p = 0.02$].

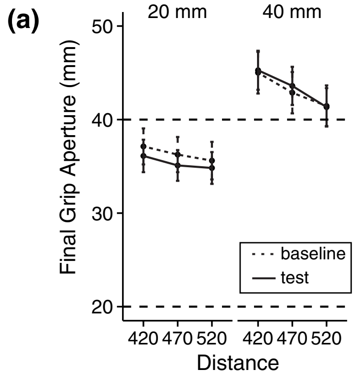
Final grip aperture: compression of visual space

The negative slope relating FGA to object distance is an index of visual space compression. Therefore, as for THP, we fitted the FGA with a linear regression model for each subject, block and bin as function of distance, after centering this variable at the mean distance of 470 mm. Figure 5b shows how the slope was significantly different from zero in all conditions. A first mixed ANOVA with experiment and block as within and between factor on the slope of the FGA revealed a strong effect of block [$F(2, 74) = 8.73$; $p = 0.0004$] and a marginal interaction effect [$F(2, 74) = 2.66$; $p = 0.07$] (Fig. 5b). A following mixed ANOVA with experiment as between-participants factor and bin as within-participants factor did not show any significant effect of experiment [$F(1, 30) = 2.80$; $p = 0.1$], bin [$F(1, 30) = 3.32$; $p = 0.08$] or interaction between them [$F(1, 30) = 1.51$; $p = 0.22$].

Maximum grip aperture

Figure 7a shows the MGA as function of depth in the *baseline*, *test* and feedback conditions. For sake of clarity, we present the MGA values averaged over the three target distances, since the effect of distance did not interact with any other factor, as revealed by a mixed ANOVA with experiment as between-participants factor and block (*baseline*, *test*, *feedback*), depth and distance as within-participants factors. The analysis showed a significant effect of block [$F(2, 74) = 10.34$; $p = 0.0001$], depth [$F(1, 37) = 33.46$; $p < 0.0001$], distance [$F(2, 74) = 14.16$; $p < 0.0001$], an interaction between block and experiment [$F(2, 74) = 3.96$; $p = 0.02$] and experiment, block and depth [$F(2, 74) = 3.60$; $p = 0.03$]. A mixed ANOVA with experiment and bin as factors did not reveal any temporal evolution of the MGA ($p = 0.88$).

The first clear result emerging from this analysis is the similar performance between feedback (*mixed-F*) and *test* trials in the mixed-feedback experiment [$t(18) = -1.16$; $p = 0.25$], which was significantly different from the *baseline* condition [$t(18) = -2.68$; $p = 0.04$]. Instead, in the blocked-design experiment, *test* and *baseline* conditions lead to the same performance [$t(21) = -0.51$; $p = 0.61$], which, in turn, differed significantly from the feedback trials of the training block [$t(21) = 3.86$; $p = 0.002$ and



(b) Slope of the function relating FGA and distance.

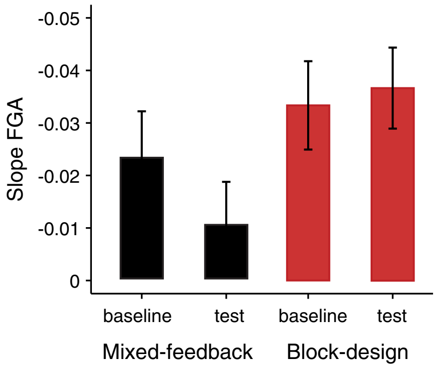


Fig. 5 Final grip aperture and distance effect on FGA. **a** FGA for the two object sizes (20 and 40 mm) as function of distance performed in the baseline (*dashed line*) and test (*continuous line*) blocks averaged across experiments. The negative relationship between FGA and object distance is consistent with a compression of visual space. *Dotted lines* represent the veridical depth of small (20 mm) and big (40 mm) objects. **b** Slope of the FGA as function of distance in the *baseline* and *test* conditions of the two experiments. None of the apparent differences among conditions and experiment was significant. Due to the absence of bin effect, data are represented in *block charts*. *Error bars* represent the standard error of the mean

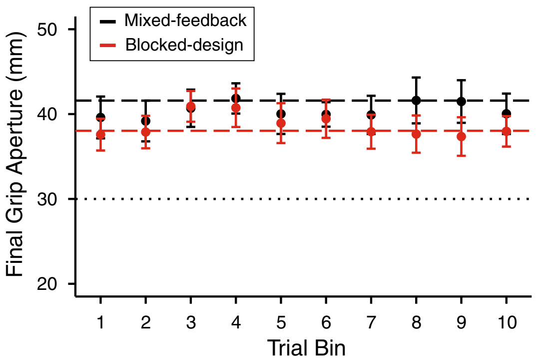


Fig. 6 Time course of FGA. The FGA of the *test* blocks for the mixed-feedback (*black*) and blocked-design (*red*) experiments are plotted as function of trial bin. *Dashed lines* represent the average FGAs performed at *baseline*. *Error bars* represent the standard error of the mean (color figure online)

$t(21) = 3.71$; $p = 0.003$, for the *baseline* and *test* block, respectively]. This finding suggests that in the mixed-feedback experiment, the pre-shaping of the hand was the same for the *test* and feedback trials, eliminating the possibility that in the *test* trials, participants behaved differently from feedback trials, because they did not expect a final contact with a physical object.

Maximum grip aperture: compression of visual space

The second important result is the effect of distance on the MGA, providing further converging evidence of a compression of visual space. As for the THPerr and FGA, there is a negative relationship between MGA and distance, resulting in a negative slope for both the blocked-design experiment (mean $= -0.038 \pm 0.13$) and the mixed-feedback experiment (mean $= -0.014 \pm 0.08$). Figure 7b shows the average slope, found with the same fit as for the FGA, in each condition of the two experiments. A mixed ANOVA with experiment as between-participants factor and trial bin as within-participants factor did not show any effect of experiment [$F(1, 30) = 1.56$; $p = 0.22$], bin [$F(1, 30) = 2.91$; $p = 0.09$] or any significant interaction [$F(1, 30) = 0.46$; $p = 0.50$].

Discussion

In theory, binocular information is sufficient for an accurate estimate of an object depth and egocentric distance (Foley 1980). However, as also shown in previous studies on reach-to-grasp actions (Bozzacchi et al. 2014; Hibbard and Bradshaw 2003), we found that this information alone does not give rise to a precise visual space representation, and, more specifically, that in the absence of visual feedback of the hand and haptic information of an object, participants are seldom accurate. Specifically, the analysis of the THP shows that participants fail to place their hand at the correct object location, indicating an incorrect estimate of the object egocentric distance. Moreover, the FGA does not correspond to the actual depth of the object. Whereas different participants show distinct magnitudes of THP and FGA absolute errors, they all expose systematic biases compatible with a compression of visual space, as if the distance between object locations along the line of sight is underestimated.

A possible explanation for these systematic biases is that under these unusual viewing conditions—where a luminous object is floating in the dark at the participant's eye height—the brain cannot extrapolate the necessary information to generate the appropriate motor program. If so, the intermittent availability of the visual feedback of the hand and haptic feedback of the object should be sufficient

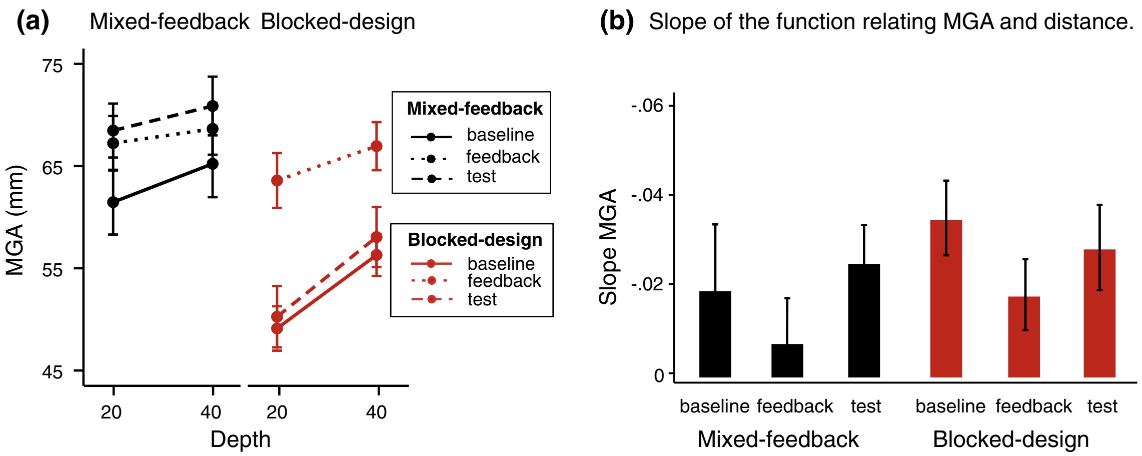


Fig. 7 Maximum grip aperture and distance effect on MGA. **a** MGA as function of object depth for the mixed-feedback experiment (*black lines*) and blocked-design experiment (*red lines*). In the mixed-feedback experiment (*left panel*), the MGA in the *test* condition (*dashed line*) is wider than in the *baseline* condition (*continuous line*) and similar to the feedback condition (*dotted line*). A different pattern can be noticed in the blocked-design experiment (*right panel*), where the MGAs in the *test* and baseline conditions are the same and significantly smaller that the MGA in the feedback trials. **b** Slope of the linear function relating MGA and object distance in each condition of the mixed-feedback (*black*) and blocked-design (*red*) experiments. The negative slope found in the baseline conditions is not subject to any significant correction. Due to the absence of bin effect, data are represented in *block charts*. *Error bars* represent the standard error of the mean (color figure online)

to calibrate the system, also when feedback signals are not longer provided. Alternatively, if the system cannot be calibrated, we could speculate that correct reach-to-grasp actions can be performed *only if* visual feedback of the hand is present throughout the action and terminal haptic feedback is provided.

In a previous study, we explored these alternatives and found that prolonged training had only a marginal effect on reach-to-grasp in depth, with errors remaining basically unchanged (Bozzacchi et al. 2014). Right after the training phase, there was a substantial correction of absolute error in THP, but this calibration effect quickly faded away (Figs. 2, 4, bin 1). Nevertheless, the compression of visual space observed at *baseline* persisted and it was never subject to any correction for THP, FGA and MGA.

Here we asked whether the constant presence of feedback trials randomly intermixed with *test* trials allows the learning of a more correct visuomotor mapping, which reduces or even eliminates biases associated with a compression of visual space. Remarkably, we actually found the opposite result for the THP. The compression of visual space observed in the *baseline* trials (25 %) is overall even larger in the *test* trials (35 %) (Fig. 4a). Therefore, and somehow paradoxically, a strong correction of absolute error in THP, which persists throughout the mixed block (Fig. 3), is accompanied by a worsening of the visual space compression bias (Fig. 4a). The analyses on FGA and MGA in the *test* trials provide converging evidence that distance estimates are not subject to any correction. Instead, they affect the scaling of stereo depth information, leading to a systematic lack of depth constancy, since the same object is grasped with smaller apertures at larger distances than at closer distances (Figs. 5, 7b).

One possible explanation of the different amount of position error observed at different distances might be related to biomechanical constraints or decrease in end-state comfort. However, this possibility is likely implausible since, on the one hand, the range of distances to be reached was very small (100 mm) and therefore could not have induced increased contractile forces. On the other hand, the calibration in hand position achieved in the *test* block shows that participants had no difficulty in reaching closer to the target than in the *baseline* condition (see also Graham et al. 1998; Heath and Binsted 2007). One could also speculate that in the *baseline* condition, participants pantomimed their responses due to the absence of haptic feedback from a real object (see Milner et al. 2012; Schenk 2012). Even though this interpretation could explain part of the results, it cannot account for the observed compression of visual space that remains unchanged in the *test* block, where haptic feedback is unpredictably available in half of the trials.

Additionally, a different strategy in the execution of grasps during feedback and *test* trials cannot explain the fact that a correct visuomotor mapping could not be learned. Instead, two results suggest that feedback trials and non-feedback trials were identical in terms of motor program and execution, until the very last moments of the reach-to-grasp movement. First, it is important to note that when *test* trials were intermixed with feedback trials, there was a rapid correction in terms of THP absolute error, achieved during the very first six *test* trials. Second, the MGA in *test* trials was the same as in feedback trials and significantly larger than in the *baseline* condition (Fig. 7a, left panel). On the contrary, data from the previous study showed no adjustment of the MGA, since performance in the *baseline* and *test* blocks was identical (Fig. 7a, right panel). These findings, therefore, suggest that analogous mechanisms and strategies were adopted by participants in the execution of feedback and no feedback trials. In particular, being the MGA in the *test* block wider than in the *baseline* condition, we can infer that participants decided to adopt a *default* safety margin of error in order not to collide with the physical object, regardless of its actual physical presence. This explanation is also in agreement with other studies reporting a wider MGA for grasping physical objects than objects that were physically removed (e.g., memory-guided pantomime) (Goodale et al. 1994; Fukui and Inui 2013; Bozzacchi et al. 2014).

It is interesting to note that feedback training affected the MGA but not the FGA. Thus, whereas feedback trials cause a modification of the hand pre-shaping phase, at least up to the point of MGA, their effect does not propagate to the very last phase of the grasping movement. A possible explanation of this result is that when the hand is about to enclose an object, the visuomotor system relies almost entirely on visual online control, provided by the mutual relationship between hand and target and its physical presence to secure a stable grip. Therefore, we speculate that during the very last phase of the movement, the visuomotor system does not benefit from a refined motor execution, since any distortion in the metric estimate of the object structure does not hinder the successful completion of the grasp.

The absolute error correction observed in this study corroborates findings about the short-term effects of sensory information on the accuracy of grasping performance (Goodale et al. 1994; Whitwell et al. 2008). For example, Bingham et al. (2007) showed that the intermittent availability of haptic feedback was sufficient for grasping without feedback to be as accurate in both object distance and size estimate as grasping with feedback. Nevertheless, in Bingham et al. (2007) study, the object distance along the depth dimension covaried with its lateral position and, therefore, did not directly address the compression of visual space along the sagittal plane.

The interesting dissociation found here between the strong correction of the THP and MGA performance, and the persistent compression of visual space can be reconciled the hypothesis that adaptation consists of a specific change in the felt position of the adapted arm (limb position sense) relative to the body and does not imply any change in visual processing (Harris 1965, 1974). As such, the feedback provided in our experiment might have induced participants to stretch their arm further from the body (if they initially overshoot the target), but could not modify the estimate of egocentric distances caused by the compression of visual space.

In conclusion, these findings illustrate that in the absence of visual and haptic feedback, actions have a tendency to show systematic biases, demonstrating the fundamental role of online sensory information (Goodale et al. 1994; Smeets et al. 2006; Bozzacchi et al. 2014; Westwood et al. 2003; Whitwell et al. 2008). In particular, the final phase of grasping movements is subject to online control, which guides and refines the movement to its completion (Jeannerod 1984; Connolly and Goodale 1999) until the hand makes contact with the object (Schenk 2012). Indeed, previous studies showed that binocular vision of the effectors is critical for efficient online control (Hu and Knill 2011) and that vision of the hand plays a role even after the target has disappeared before the end of the movement (Ma-Wyatt and McKee 2007). Such online control may not require accurate metric information (Bradshaw et al. 2000), because low-level image information, like the relative disparities between fingers and object contact points, is sufficient for the grasping action to be completed successfully.

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