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RESEARCH ARTICLE

The visibility of contact points influences grasping movements

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Abstract When humans grasp an object, the thumb habitually contacts the object on the visible part, whereas the index finger makes contact with the object on the occluded part. Considering that the contact points play a critical role in object-oriented actions, we studied if and how the visibility of the points of contact for the thumb and index finger affects grasping movements. We adapted reach-to-point movements (visual feedback displacement: 150 mm in depth) performed with either the thumb or the index finger to measure how a newly learned visuomotor mapping transfers to grasping movements. We found a general transfer of adaptation from reach-to-point to reach-to-grasp movements. However, the transfer of adaptation depended on the visibility of contact points. In the first experiment, in which only the thumb's contact point was visible during grasping, the transfer of adaptation was larger after thumb than after index finger perturbation. In the second experiment, in which both contact points were equally visible, the transfer of adaptation was of similar magnitude. Furthermore, thumb trajectories were less variable than index trajectories in both experiments weakening the idea that the less variable digit is the digit that guides grasping movements. Our findings suggest that the difficulty in determining the contact points imposes specific constraints that influence how the hand is guided toward the to-be-grasped object.

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Introduction

Grasping is generally conceived as a combination of two more or less synchronized components: transporting the hand toward the object and shaping the hand to enclose the object (Jeannerod 1984; Hoff and Arbib 1993). For a stable grasp, positioning the thumb and the index fingers on the opposite sides of an object is essential. Inevitably, not all contact points on the surface of the object are simultaneously visible. Most commonly, the thumb contacts the object on the visible part, whereas the other digits enclose the object on the occluded part. Given this functional asymmetry, it has been hypothesized that the thumb may play a preferential role in guiding the hand during reach-to-grasp actions. In fact, several studies support the idea that the major concern of the motor system during hand transport is the control of the thumb position (Wing and Fraser 1983; Haggard and Wing 1997; Galea et al. 2001; Melmoth and Grant 2012).

Wing and Fraser (1983) analyzed the grasping performance of a single subject with congenital absence of her left arm below the elbow that was fitted with a functional artificial hand. Although the mechanics of the artificial hand made it equally easy to control the thumb or the index finger, the thumb maintained a straighter path to its contact point, whereas the index finger was responsible for the reduction of grip aperture as the hand approached the object. The control of the artificial hand thus mimicked natural grasping movements. Their conclusion was that the relative invariance of the thumb trajectory is a consequence of the role the thumb has in guiding the hand during grasping movements. Similar conclusions were reached by Galea et al. (2001). Analogously, Haggard and Wing (1997) studied the role of the thumb in guiding grasping movements by focusing on the consistency of the thumb's path. The thumb showed lower variability than the wrist did, and the variability decreased throughout the movement suggesting an active visual control process of the digit's approach to the object. Unfortunately, no comparison was made with the variability of the index path.

More recently, Melmoth and Grant (2012) compared the consistency of thumb and index finger trajectories. The path of the thumb was more direct and less variable. Importantly, these features were preserved even when vision of the whole hand was excluded or when vision of either the thumb or the index finger was selectively prevented. These results are thus consistent with the idea that only the thumb is primarily guiding the hand during grasping actions.

However, the directness and consistency of thumb trajectories might simply result from the very different approach paths toward the near side (straight trajectories) and the back side (curved trajectories) of an object (Smeets and Brenner 2001). According to this alternative view on grasping, the thumb and the index finger have an equivalent role and they move independently to the contact points on the object (Smeets and Brenner 1999; Verheij et al. 2012). Therefore, if a grasping task has the same mechanical constraints for both digits, the movements of the digits will be the same. Or, if the movement constraints are harder for the thumb, the movement of the index finger should be more direct and less variable. In fact, Cavina-Pratesi and Hesse (2013) tested whether the trajectory variability is dependent on the starting position of the hand relative to the object. When the hand was placed in front of the object, the trajectory variability was higher for the index finger than for the thumb, in accordance with the previous results. On the contrary, when the hand was placed behind the object, the variability pattern reversed, with the variability being higher for the thumb than for the index finger. The directness and consistency of thumb trajectories were thus a direct result of the grasping tasks used.

In the current study, we wanted to deepen the understanding of the role of the digits in guiding grasping movements. Unlike previous studies that have mainly focused on the directness and consistency of trajectories, we adopted a different approach. We selectively perturbed reach-to-point movements made with either the thumb or the index finger to promote the learning of a new visuomotor mapping through adaptation. We then tested the impact of these perturbations on grasping performance. Depending on the role that the different digits play in grasping, learning to perform reaching movements with either the thumb or the index finger under visuomotor incongruence should differentially affect the subsequent grasping behavior.

The perturbation during reach-to-point movements was induced by misaligning the visual and proprioceptive locations of the effector digit by 150 mm in depth. Offsetting the visual location of the effector in virtual environments or with prism goggles is a widely used perturbation paradigm for studying a wide range of phenomena related to visuomotor control (von Helmholtz 1867; Ghahramani et al. 1996; Martin et al. 1996; Cressman and Henriques 2009; Volcic et al. 2013). Typically, the perturbation of the normal congruence between vision and proprioception disrupts visuomotor coordination. However, subjects quickly adapt to the new sensory arrangement and produce appropriate motor commands to guide the hand to the target. Once visual feedback is removed, the newly learned visuomotor mapping is essentially preserved until the normal sensory congruence is reintroduced, although drifting effects are sometimes present (Wann and Ibrahim 1992; Desmurget et al. 2000; Smeets et al. 2006).

After the reach-to-point perturbation session, subjects were asked to grasp differently sized objects positioned at eye height at different distances. In two experiments, we varied the grasp type. In a first experiment, they were required to perform a precision grip along the depth axis of the object. In a second experiment, subjects were required to perform the precision grip along the vertical axis of the object. Aside from the different approach orientations, the main difference between the two experiments consists in the visibility of contact points. While grasping an object along the depth axis, only the thumb's contact point is directly visible, whereas the contact point for the index finger is positioned on the invisible part of the object. On the other hand, while grasping an object along the vertical axis, both contact points are equally visible.

Contact points play an important role in object-oriented actions. Eye movements briefly precede hand movements in a highly predictive manner and fixations are close to the site of action (Ballard et al. 1992; Johansson et al. 2001). When grasping, people tend to look at the contact points of the digits, in particular in the direction of the index finger (de Grave et al. 2008; Brouwer et al. 2009; Desanghere and Marotta 2011; Cavina-Pratesi and Hesse 2013). This asymmetry is generally explained by a preference to fixate the location where visual feedback is needed more (Brouwer et al. 2009) or by a preference to fixate the location at which the hand makes first contact with the object (Cavina-Pratesi and Hesse 2013). In cases in which contact points are not visible due to occlusion, the occluder influences fixation locations, but it does not prevent fixations on occluded object parts (de Grave et al. 2008). Moreover, altough there is a preference to look at grasping points, people do not always and necessarily aim at visible contact points (Voudouris et al. 2012).

According to the different views on grasping, different effects of the reach-to-point perturbation sessions on subsequent grasping behavior might be expected. If grasping is a combination of the transport and grip components (Jeannerod 1984; Hoff and Arbib 1993), we would predict that independently of which digit is adapted and which grasp type is then used, only the transport component should be affected and the transfer of adaptation should be equal in all conditions in both experiments. Instead, if it is the thumb that primarily guides the hand during grasping actions (Wing and Fraser 1983; Haggard and Wing 1997; Galea et al. 2001; Melmoth and Grant 2012), we would predict in both experiments a larger transfer of adaptation after thumb perturbation than after index finger perturbation. Another possibility would be that the grasping movements follow from the movement of individual digits (Smeets and Brenner 1999; Verheij et al. 2012), but the specific task requirements constrain how grasping is executed. Therefore, we could expect that the difficulty in determining the contact points might play a relevant role. In the case in which the contact point for the index finger is hard to resolve due to occlusions and has thus to be extrapolated, we would predict that the thumb perturbation should influence the grasping behavior more heavily. In contrast, in the case in which the contact points of both digits are equally easy to resolve, we would predict an equivalent effect of both thumb and index finger perturbation.

Methods

Participants

Sixteen undergraduate students (8 females) participated in this study. All had normal or corrected-to-normal vision. All of the subjects were naïve to the purpose of the experiments and were paid for their effort. Half of them participated in Experiment 1, and the other half in Experiment 2. Experiments were undertaken with the understanding and written consent of each subject, with the approval of the Comitato Etico per la Sperimentazione con l'Essere Vivente of the University of Trento, and in compliance with national legislation and the Code of Ethical Principles for Medical Research Involving Human Subjects of the World Medical Association (Declaration of Helsinki).

Apparatus

Subjects were seated in a dark room in front of a high-quality, front-silvered 400 × 300 mm mirror (see Fig. 1a). 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. To present visual stimuli in 3D, we used a frame interlacing technique in

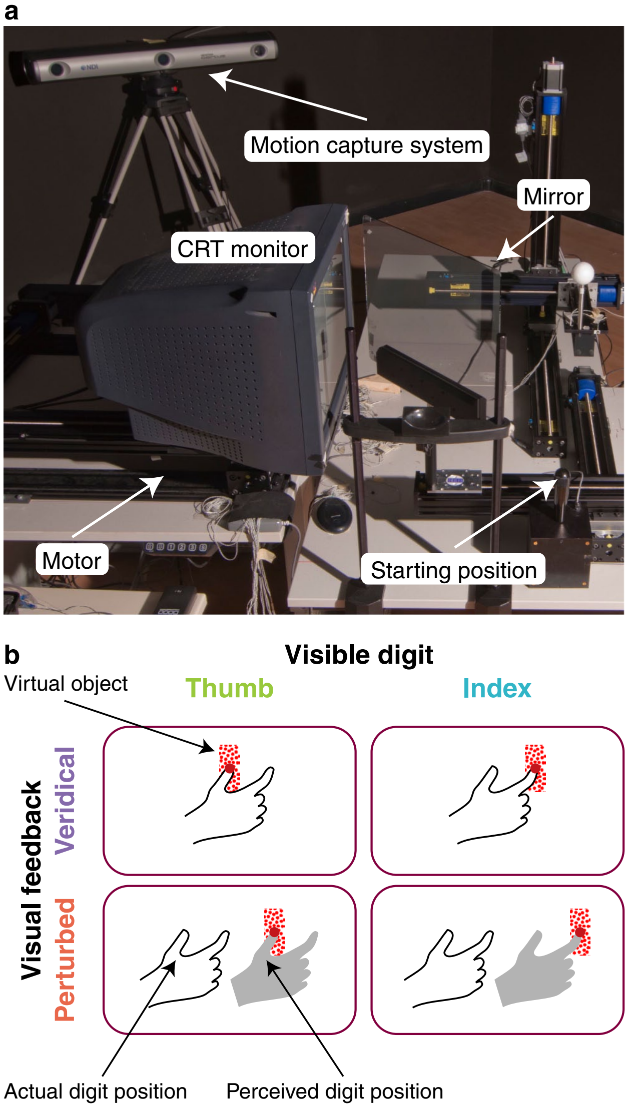

Fig. 1 **a** A picture of the setup showing the arrangement of the motion capture system (one of the two position sensors), the mirror in front of the monitor, the motors for moving the monitor, and the pole used as the starting position. **b** Reach-to-point blocks from the combination of the factors visible digit and visual feedback. Subjects had to align the tip of the visible digit (*red dot*) with the center of the virtual object (vertically oriented cylinder). The visible digit could either be the index or the thumb, and the visual feedback could either be veridical (i.e., coincident with the actual position of the fingertip) or perturbed (i.e., displaced by 150 mm in depth). The range along which the object was positioned was identical irrespective of whether the visible digit was the thumb or the index finger. A reach-to-grasp block was measured after each of these reach-to-point blocks (color figure online)

conjunction with liquid crystal FE-1 goggles (Cambridge Research Systems, Cambridge, UK) synchronized to the frame rate of the monitor. A custom C++ program was used for stimulus presentation and response recording.

Head, wrist, index and thumb movements were acquired on-line at 100 Hz with sub-millimeter resolution by using an Optotrak Certus motion capture system with two position sensors (Northern Digital Inc., Waterloo, Ontario, Canada). Head movements updated the subjects' viewpoint to present the correct geometrical projection of the stimulus in real time. Subjects' head position and orientation was tracked with three infrared-emitting diodes worn on the back of the head. The position of the tip of each digit was calculated during the system calibration phase with respect to three infrared-emitting diodes attached on each distal phalanx. Additional details about the experimental setup are available in Nicolini et al. (2014).

High-contrast random-dot visual stimuli were rendered in stereo simulating: a vertically oriented cylinder (height: 70 mm, radius: 6.5 mm) during reach-to-point blocks, 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) during reach-to-grasp blocks in Experiment 1, or a vertically oriented cylinder (height: 20 or 40 mm, radius: 6.5 mm) during reach-to-grasp blocks in Experiment 2. These differently shaped stimuli during reach-to-grasp blocks resulted in slightly different end constraints for the two digits in the two experiments. The visual surface in Experiment 1 was curved and relatively larger than the flat surface in Experiment 2. However, the main difference was relative to our principal variable of interest, i.e., the visibility of the contact points. In reach-to-point blocks, stimuli were simulated at a random position along the line of sight (range of distances: 420–520 mm during veridical visual feedback and 570–670 mm during perturbed visual feedback to perfectly match the range of hand movements in the two visual feedback conditions). In reach-to-grasp blocks, stimuli were simulated at two distances (440 and 500 mm). Virtual instead of real objects were used to avoid proprioceptive/tactile feedback that would inform subjects about the correctness of their movements in reach-to-grasp blocks.

The setup allowed subjects to comfortably reach behind the mirror to perform reaching and grasping movements with their right hand. The hand starting position (a pole) was shifted relative to the body of the observer by about 250 mm to the right from the coronal plane, 150 mm from the sagittal plane and 300 mm lower than the subjects' line of sight. Thus, to perform the grasping movement, subjects needed to move their hand in leftward, forward and upward direction. During reach-to-point blocks, visual feedback of either the index finger or the thumb was provided by means of a dot representing the tip of the digit and was constantly visible during the execution of the movement. No visual feedback about the digits or hand position was available during reach-to-grasp blocks.

Design

Each reach-to-point movements block consisted of 60 trials resulting from a sequence of pointing movements toward the virtual cylinder randomly positioned along the line of sight. There were four kinds of reach-to-point blocks obtained by the combination of two factors: *visible digit* and *visual feedback* (see Fig. 1b). During reach-to-point movements, the visible digit could either be the *index finger* or the *thumb* and the visual feedback could either be *veridical* (i.e., coincident with the actual position of the digit tip) or *perturbed* (i.e., displaced by 150 mm in depth). The visible digit was the digit used to perform the actual reach-to-point movements. The range along which the virtual cylinder was positioned was identical irrespective of whether the visible digit was the thumb or the index finger. These blocks were used to let subjects interact with the environment either with congruent visuomotor information or to adapt them to a new visuomotor contingency.

After each block of reach-to-point movements, a block of reach-to-grasp movements was measured. Reach-to-grasp blocks consisted of 40 trials resulting from two depth magnitudes × 2 distances × 10 repetitions. These trials were in pseudo-randomized order with the constraint that the same combination could not be presented on two consecutive trials. Each subject thus performed four sequences of reach-to-point and reach-to-grasp blocks for a total of 400 trials.

Procedure

Each subject was tested in a dark room with his/her head positioned on a chin rest to maintain the same head position during all blocks. Before starting the experiment, subjects were tested for stereo vision and were subsequently presented with a set of practice trials to get accustomed to the tasks. Subjects started each trial of the experiment with their thumb and index fingertips in contact and resting on the top of a pole. During reach-to-point blocks, subjects had to align their visible digit with the center of the vertically oriented cylinder. To keep the posture of the hand invariant in all reach-to-point blocks, subjects were instructed to hold their hand with the thumb and index fingers spread apart (see Fig. 1b). On average, the distance between the thumb and index finger at the end of the reaching movement was 64.3 mm and did not differ among conditions. The visual feedback of the digit was provided as soon as the digit entered in the subject's visual field and

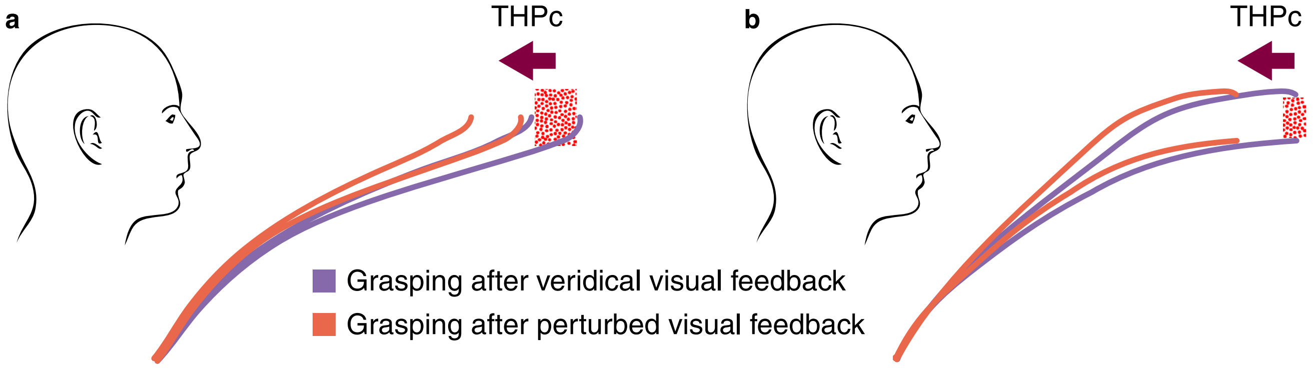

Fig. 2 **a** Experiment 1: Subjects were asked to grasp virtual objects along the depth axis by positioning the thumb and index finger on the front and back sides, respectively. **b** Experiment 2: Subjects were asked to grasp virtual objects along the vertical axis by positioning the thumb and index finger on the *bottom* and *top sides*, respectively. THPc (*left-pointing arrow*) and TGAc were calculated by comparing the difference in grasping behavior after veridical and perturbed visual feedback blocks. Example trajectories show the grasping behavior after veridical (*purple lines*) and after perturbed (*red lines*) visual feedback reach-to-point blocks (color figure online)

remained visible for the whole duration of the trial. At the end of each trial, the monitor turned black and the subject returned with his/her hand to the starting position. Then, the monitor moved to the new position ready for the start of the next trial.

Once all trials of a reach-to-point block were completed, an auditory signal introduced a reach-to-grasp block. Subjects were asked to make a natural movement as if grasping a physical object with a precision grip. In Experiment 1, subjects were asked to grasp virtual objects along the depth axis by positioning the thumb and index finger on the front and back sides, respectively (Fig. 2a). In Experiment 2, on the other hand, subjects were asked to grasp virtual objects along the vertical axis by positioning the thumb and index finger on the bottom and top sides, respectively (Fig. 2b). Trials in which the markers were occluded were discarded and repeated later in the experiment (<1%). All the other aspects of these blocks were identical to the reach-to-point blocks, except that no feedback of any kind was provided.

The experiment was completed in two testing sessions on separate days. Each testing session consisted of two sequences of blocks interrupted by a short pause. The first block of each sequence was always a reaching block, whereas the second block of each sequence was a grasping block.

Data analysis

The raw positional data were processed and analyzed offline using custom software. The raw data were smoothed and differentiated with a 2nd-order Savitzky-Golay filter with a window size of 41 points. These filtered data were then used to compute velocities and accelerations in three-dimensional space for each fingertip and the wrist, the Euclidean distance between the fingertips of the thumb and the index finger (grip aperture), and the velocity and acceleration of the change in grip aperture.

The dependent measures in the reach-to-grasp blocks were the terminal hand position (THP) and the terminal grip aperture (TGA). We defined the end of the grasping movement on the basis of the Multiple Sources of Information method proposed by Schot et al. (2010), in which different sources of information are transformed into either binary or continuous objective functions with values between zero and one and then multiplied together to obtain a combined objective function. Continuous objective functions were based on the velocities of the index, thumb, and wrist and on the distance from the starting position. Binary objective functions were based on the velocity and acceleration of the change in grip aperture. The maximum of the combined objective function identified the point of interest, i.e., in our case the end of the grasping movement. Trials in which the end of the grasping movement could not be identified correctly (e.g., the hand kept drifting) were discarded (4.22 and 2.5% of the trials in experiments 1 and 2, respectively). In both experiments, the THP was defined as the mean position along the z-axis (depth component) calculated between the fingertips of the thumb and index finger at the end of the grasping movement. Similarly, the TGA was defined as the Euclidean distance between the fingertips at the end of the grasping movement.

We considered the responses after veridical visual feedback blocks as baseline performance. We computed a mean for each subject, each digit exposure, each depth/height magnitude, and each distance separately, and we subtracted these baselines from the corresponding responses that were measured after perturbed visual feedback blocks. We thus obtained the actual changes in THPc and the actual changes in TGAc that reflect the difference in grasping behavior after veridical and perturbed visual feedback blocks.

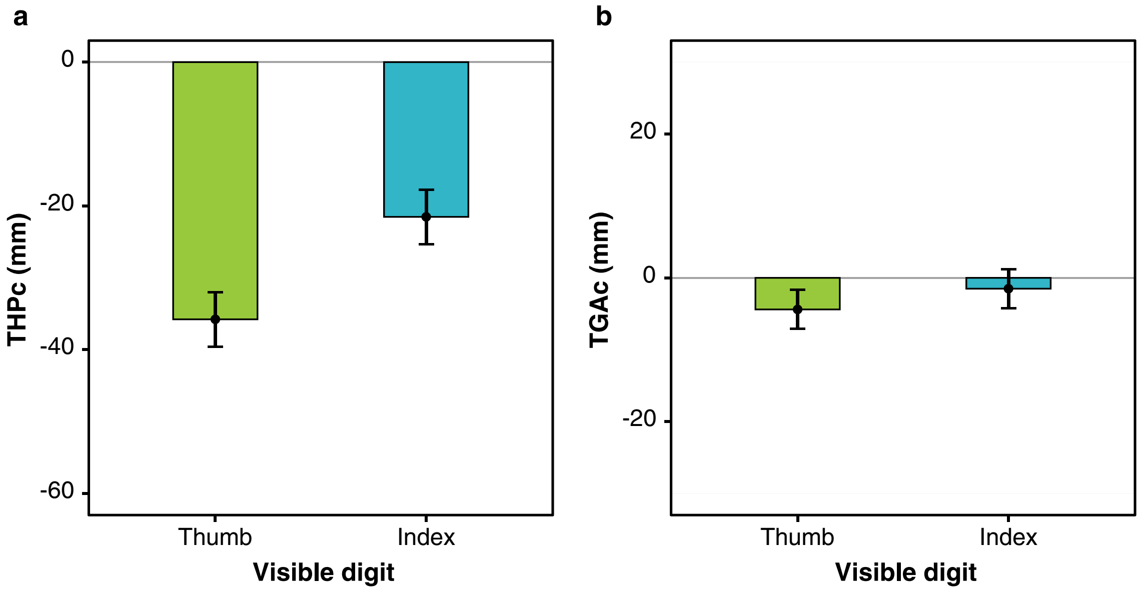

Fig. 3 Experiment 1: **a** Terminal hand position change (THPc) in reach-to-grasp blocks after thumb and index visual feedback exposure. **b** Terminal grip aperture change (TGAc) in reach-to-grasp blocks after thumb and index visual feedback exposure. *Error bars* denote standard errors based on fixed-effects uncertainty

Negative THPc values would indicate that the hand during reach-to-grasp blocks is positioned at a closer distance after perturbed than after veridical visual feedback (see Fig. 2). Negative TGAc values would indicate that the grip aperture during reach-to-grasp blocks is smaller after perturbed than after veridical visual feedback.

We analyzed the THPc and the TGAc data using linear mixed-effects models which included as fixed effects the variables: visible digit (grasping behavior after being exposed to reaching with either the thumb or the index), depth/height magnitude (20 or 40 mm), and distance (440 and 500 mm). The optimal structure of the random component was determined using likelihood ratio testing by comparing nested models fitted with restricted estimate maximum likelihood. The most parsimonious models in both Experiment 1 and Experiment 2 for the analysis of both THPc and TGAc included independent random intercept and random slope terms for subjects. A comparison of models with nested fixed effects showed that neither THPc nor TGAc was affected by neither depth/height magnitude nor Distance; therefore, the final fixed structure contained the visible digit variable only. In this and all subsequent analyses, the denominator degrees of freedom were adjusted for the F tests by using the Kenward-Roger method (Kenward and Roger 1997).

In addition, to check whether the hand position slowly changed over the course of the experiment due to drift between vision and kinesthesia when vision of the hand was prevented, we analyzed the data as a function of the number of movements made in the reach-to-grasp blocks. We ran a linear mixed-effect model which included as fixed effect the trial number and independent random intercept and random slope terms for subjects.

To analyze the variability of the thumb and index finger trajectories, we normalized the movement trajectories in 100 time frames. For each normalized time frame, we used the x, y and z positions to calculate the standard deviation error ellipsoid for each digit, each participant, and each experimental condition. The semi-principal axes that correspond to the unit eigenvectors of the covariance matrix scaled by the square root of the corresponding eigenvalue were used to calculate the volume of each ellipsoid. The values of these volumes were cumulated across the normalized time frames to obtain a measure of trajectory variability. Cumulative volumes were analyzed using a linear mixed-effect model which included as fixed effects the variables Digit (thumb or index) and Experiment (grasping along the depth or vertical axis), and independent random intercept and random slope terms for subjects.

Results

Experiment 1: grasping along the depth axis

Subjects placed their hand at a closer distance while grasping after the exposure to perturbed visual feedback than after the exposure to veridical visual feedback [Fig. 3a, $F(1, 7.005) = 88.8$, $p < 0.001$]. Simple t tests with Bonferroni correction showed that THP changed significantly both after thumb [$t(7) = -8.35$, $p < 0.001$] and after index

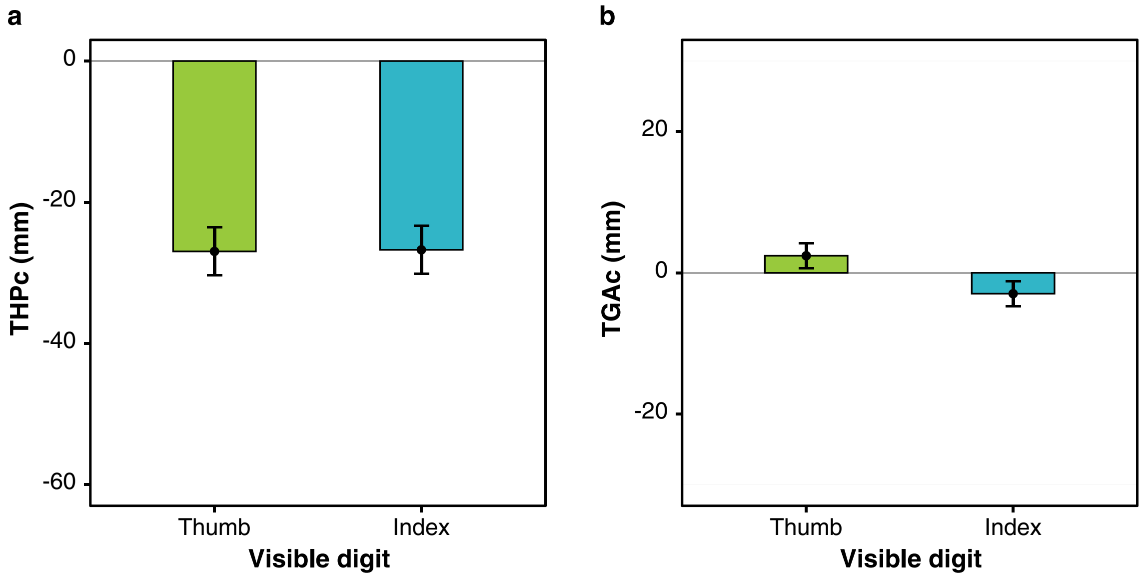

Fig. 4 Experiment 2: **a** Terminal hand position change (THPc) in reach-to-grasp blocks after thumb and index visual feedback exposure. **b** Terminal grip aperture change (TGAc) in reach-to-grasp blocks after thumb and index visual feedback exposure. *Errors bars* denote standard errors based on fixed-effects uncertainty

[$t(7) = -5.96$, $p < 0.001$] reaching sessions. However, the effect on THPc depended on which digit was used during reach-to-point blocks. THPc was on average 14.3 mm larger after the thumb than after the index reaching session [$F(1, 6.993) = 7.88$, $p = 0.026$], that is, subjects performed shorter grasping movements after thumb than after the index reaching session.

After being exposed to veridical visual feedback, subjects did not show a significant drift in the subsequent reach-to-grasp blocks [$F(1, 7) = 0.6$, $p = 0.462$]. On the other hand, subjects drifted slowly in a direction contrary to the adaptation direction after being exposed to perturbed visual feedback both after thumb and after index reaching sessions [$F(1, 7) = 10.82$, $p = 0.013$].

The aperture between the thumb and the index finger at the end of the grasping movement was not modulated by the exposure to veridical and perturbed visual feedback [Fig. 3b, $F(1, 7.002) = 1.36$, $p = 0.281$]. Simple t tests with Bonferroni correction showed that TGAc was not significantly different from zero neither after thumb [$t(7) = -1.35$, $p = 0.436$] nor after index [$t(7) = -0.61$, $p \approx 1$] reaching sessions. No significant difference was found in TGAc after the thumb and after the index reaching session [$F(1, 6.994) = 1.12$, $p = 0.326$].

Experiment 2: grasping along the vertical axis

As in Experiment 1, subjects placed their hand at a closer distance while grasping after the exposure to perturbed visual feedback than after the exposure to veridical visual feedback [Fig. 4a, $F(1, 7.002) = 120.32$, $p < 0.001$]. Simple t tests with Bonferroni correction confirmed that THP changed significantly both after thumb [$t(7) = -15.54$, $p < 0.001$] and after index [$t(7) = -5.65$, $p = 0.002$] reaching sessions. Importantly, and in contrast to Experiment 1, the effect on THPc did not depend on which digit was used during reach-to-point blocks. THPc was very similar after the thumb and after the index reaching session [$F(1, 6.99) = 0.002$, $p = 0.965$].

After being exposed to veridical visual feedback, subjects did not show a significant drift in the subsequent reach-to-grasp blocks, as in Experiment 1 [$F(1, 7) = 0.11$, $p = 0.745$]. On the other hand, subjects drifted slowly in a direction contrary to the adaptation direction after being exposed to perturbed visual feedback both after thumb and after index reaching sessions [$F(1, 7) = 23.72$, $p = 0.002$].

The terminal aperture between the thumb and the index finger was not significantly affected by the exposure to veridical and perturbed visual feedback, just as we found in Experiment 1 [Fig. 4b, $F(1, 7.002) = 0.03$, $p = 0.875$]. TGAc after the thumb and after the index reaching session was found to be significantly different [$F(1, 6.997) = 6.64$, $p = 0.037$], yet simple t tests with Bonferroni corrections showed that TGAc was not significantly different from zero neither after thumb [$t(7) = 0.99$, $p = 0.354$] nor after index [$t(7) = -2.41$, $p = 0.093$] reaching sessions.

Experiments 1 and 2: trajectory variability

The variability of thumb trajectories was on average lower than the variability of the index finger trajectories [1,610.9 ± 143 vs. 1,835.2 ± 178 cm^3;

$F(1, 14) = 7.11$, $p = 0.018$]. No difference was found between the two experiments [$F(1, 14) = 0.04$, $p = 0.849$]. Importantly, the interaction between the digit trajectories and experiments was also not significant [$F(1, 14) = 0.61$, $p = 0.448$] indicating that the type of grasp (along the depth axis or along the vertical axis) did not influence the trajectory variability of the two digits.

Discussion

This study investigated the role of the visibility of contact points on grasping movements. We adapted reach-to-point movements (visual feedback displacement: 150 mm in depth) performed with either the thumb or the index finger to measure how a newly learned visuomotor mapping transfers to grasping movements. Moreover, in two separate experiments, we varied the type of grasp. In the first experiment, subjects grasped virtual objects positioned at eye height along the depth axis by positioning the thumb and index finger on the front and back sides, respectively. In the second experiment, subjects' grasps were made along the vertical axis by positioning the thumb and index finger on the bottom and top sides, respectively. Hence, the visibility of the contact points changed depending on grasp type. Only the thumb's contact point was directly visible when objects were grasped along the depth axis, whereas the contact points for both the thumb and index finger were equally visible when objects were grasped along the vertical axis.

We found a general transfer of adaptation from reach-to-point movements to reach-to-grasp movements. After reach-to-point sessions with perturbed visual feedback, subjects positioned their hand at a closer location than normally while grasping. However, the effector digit used during reach-to-point movements and the type of required grasp modulated differentially the magnitude of the transfer. In the first experiment, in which only the thumb's contact point was visible, the transfer of adaptation was larger after thumb than after index finger perturbation. In other words, the terminal hand position of the grasping action was more strongly affected by the adaptation of thumb reach-to-point movements than by the adaptation of index finger reach-to-point movements. In the second experiment, in which both contact points were equally visible, the transfer of adaptation was, however, of the same magnitude after thumb or index finger perturbation.

Concurrently, we measured whether the TGA was influenced by the perturbation of reach-to-point movements. No difference in the grip aperture was observed in the two experiments. Although the hand position consistently changed after perturbed reach-to-point movements, TGA remained unaffected. These results are consistent with the idea that the positioning of the hand and the enclosure of the digits can be altered independently (Marotta et al. 2005; Coats et al. 2008).

Our results are difficult to be explained in terms of the classical description of grasping as a combination of transport and grip components (Jeannerod 1984; Hoff and Arbib 1993). No matter which effector digit was perturbed during the reach-to-point blocks, we should have observed an equivalent transfer of adaption on the following movements in the reach-to-grasp blocks. But this was clearly not the case. Similarly, our results are incompatible with the view that it is the thumb that always guides the hand during grasping actions (Wing and Fraser 1983; Haggard and Wing 1997; Galea et al. 2001; Melmoth and Grant 2012). Interestingly, despite that the transfer of adaptation differed depending on the available visual input, the variability of thumb trajectories was consistently lower than the variability of the index finger trajectories in both experiments. This evidence casts doubt on the proposition that the less variable digit is the digit that guides grasping movements.

It is interesting, instead, to consider our findings in light of the view that specific task constraints influence the movement of individual digits (Smeets and Brenner 1999, 2001). According to this view, the differences in the directness and consistency of thumb trajectories are considered a product of the way the digits need to make contact with the object. We propose that the difficulty in determining the contact points, e.g., due to occlusions, imposes additional constraints that, in turn, affect grasping movements. This aspect might have important implications on models for the control of grasping movements.

Taken together, these results provide good evidence that the visibility of contact points affects grasping behavior and influences how the digits are directed toward the to-be-grasped object. Determining the most suitable grasping points on the object surface is an essential part of the grasp planning and execution (Smeets and Brenner 1999; Verheij et al. 2012). In fact, contact points attract the majority of gaze fixations during grasping (de Grave et al. 2008; Brouwer et al. 2009; Desanghere and Marotta 2011; Cavina-Pratesi and Hesse 2013), although people do to necessarily aim at those contact points (Voudouris et al. 2012). However, direct visual information about certain contact points is frequently absent due to self-occlusions of the object or to occlusions by other objects in the scene. In these circumstances, the most efficient and reliable grasps are certainly those guided by the digit that aims toward the visible contact point. From a behavioral standpoint, this aspect makes a lot of sense, in that it would mean that grasping actions are always steered by the maximal amount of available information.

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