Reaching and grasping actions and their context shape the perception of object size

Annalisa Bosco
Department of Pharmacy and Biotechnology, University of Bologna, Bologna, Italy

Fabio Daniele
Department of Pharmacy and Biotechnology, University of Bologna, Bologna, Italy
Department of Biomedical, Metabolic and Neuroscience Sciences, University of Modena and Reggio Emilia, Modena, Italy

Patrizia Fattori
Department of Pharmacy and Biotechnology, University of Bologna, Bologna, Italy

Humans frequently estimate the size of objects to grasp them. In fact, when performing an action, our perception is focused towards the visual properties of the object that enable us to successfully execute the action. However, the motor system is also able to influence perception, but only a few studies have reported evidence for action-induced visual perception modifications. Here, we aimed to look for a feature-specific perceptual modulation before and after a reaching or a grasping action. Human participants were instructed to either reach for or grasp two-dimensional bars of different size and to perform a size perceptual task before and after the action in two contexts: in one where they knew the subsequent type of movement and in the other where they did not know. We found significant modifications of perceived size of stimuli more pronounced after grasping than after reaching. The mere knowledge of the subsequent action type significantly affected the size perception before the movement execution, with consistent results in both manual and verbal reports. These data represent direct evidence that, in natural conditions without manipulation of visual information, the action type and the action context dynamically modulate size perception, by shaping it according to relevant information required to recognize and interact with objects.

Introduction

The perception and action relationship usually supports the idea that a primary goal of perception is action. In this framework, traditional information-processing perspectives aimed at defining motor response as separate from and consequent to perception. In the last years, several behavioral studies have shown evidence for an "action-modulated perception" mechanism that automatically enhances relevant object features during action preparation (Bekkering & Neggers, 2002; Craighero, Fadiga, Rizzolatti, & Umiltà, 1999; Fagioli, Hommel, & Schubotz, 2007; Hannus, Cornelissen, Lindemann, & Bekkering, 2005). Several theories proposed a weighting mechanism for processing visual features of objects (Bundesen, 1990; Found & Muller, 1996; Muller, Reimann, & Krummenacher, 2003; Wolfe, 1994). In this view, the cognitive system assigns weights to information that is particularly relevant, so that information belonging to the dimension with the highest weight is prioritized. According to the dimensional weighting theory proposed by Muller et al. (Muller, Heller, & Ziegler, 1995), the visual field is represented in separate maps, such as color, orientation and size. Saliency signals are sent from these maps to a master map of saliency that computes the sum of dimension-specific signals. For example, if the target-defining dimension in a visual search task is known in advance, participants can increase the weights of that dimension before the target presentation so that features can be processed more efficiently.

The effect of motor preparation on visual perception has been extensively studied for the oculomotor system suggesting that, shortly before the actual execution of an eye movement, spatial perception greatly improves at the eye movement target location (Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995;

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Neggers et al., 2007). In the skeletomotor domain, some authors found that a relevant feature like orientation perception is enhanced during preparation of a grasping action, compared with a pointing action, for which object orientation is not important (Gutteling, Kenemans, & Neggers, 2011; Gutteling, Park, Kenemans, & Neggers, 2013). This "enhanced perception" is triggered by the intention to grasp and is important in order to examine objects with the maximum possible accuracy. This action effect is in line with the common coding approach that predicts perceptual effects on action planning and assumes a bidirectional relationship between perception and action. This notion implies the possibility of action-induced effects on perception (Hommel, Musseler, Ascersleben, & Prinz, 2001). Because visual objects and motor actions are assumed to be represented by shared feature codes, it is expected that action planning affects perceptual processing by biasing the cognitive system toward feature dimensions that are relevant for the preparation of the intended response (Hommel et al., 2001). More specifically, several studies showed that perceptual processes are affected by anticipated effects of action plans (Jordan & Hershberger, 1994; Jordan & Hunsinger, 2008), and that perception can be biased by particular action plans (Craighero et al., 1999; Fagioli et al., 2007; Memelink & Hommel, 2005, 2006; Musseler & Hommel, 1997). For example, Fagioli et al. (Fagioli et al., 2007) demonstrated that preparing a grasping movement facilitated the detection of the size of oddballs, whereas preparing a pointing movement facilitated the detection of the location of oddballs. In the studies by Wykoswska et al. (Wykowska, Hommel, & Schubö, 2011; Wykowska, Schubö, & Hommel, 2009), a size-defined visual target was detected more easily while preparing for a grasping movement, and a luminance-defined target was better detected in the preparation of a pointing movement. This is because size is a relevant perceptual dimension for grasping control, whereas luminance is particularly relevant for pointing control (Anderson & Yamagishi, 2000; Graves, 1996).

All these studies defined the effects of action on perception in the detection ability of relevant features of objects, measuring the reaction time by playing with the presence/absence of prior knowledge of relevant information (i.e., the object size, during the preparation of different action types). However, the direct influence of preparation and execution of different action types on the amount of changes in size perception was not fully investigated. Moreover, the weighting mechanism described above was related to the advanced knowledge of stimulus information, but how varying the knowledge in advance of the subsequent action type influenced size perception of a stimulus was never investigated.

The size processing for action and perception was extensively studied by the Ebbinghaus illusion that was used to identify differences between the visual processing mediating perceptual judgments and visually guided actions, such as grasping in different visual contexts. In the pivotal study by Aglioti and colleagues (Aglioti, DeSouza, & Goodale, 1995), the effect of the illusion on grip scaling during grasping movement was significantly smaller with respect to manual responses in perceptual judgements (Aglioti et al., 1995). This suggested that visual illusions affected perception but not action, as predicted by the "two-visual-systems" hypothesis proposed by Milner and Goodale (1995). However, other studies revealed a consistent illusion effect on grasping (de Grave, Hesse, Brouwer, & Franz, 2008; Franz & Gegenfurtner, 2008; Kopiske, Bruno, Hesse, Schenk, & Franz, 2016), suggesting an important interaction between perceptual and motor systems. One of the principal variables that can have an impact on the response functions of size perceptual measures is the manual size estimation used in all the cited studies. When performing manual estimation, participants indicate the size of an object using their index finger and thumb. Haffenden and Goodale (1998) interpreted this as a manual read-out of what participants perceived or a form of cross-modal matching (Stevens, 1959). However, manual estimation typically exaggerates a physical change of object size (Haffenden & Goodale, 1998).

On the basis of these studies, it would be logical to expect that, when preparing and executing different types of actions such as reaching or grasping, the perception of object size would be affected. Here, we provide a measure of visual size estimation of objects before and after hand action was executed. We did this without visual illusion or haptic feedback, so as to evaluate the effect of preparation and execution of different action types on the perceived object size. Then, we aimed to assess the action modulation effect on size perception when participants knew or did not know in advance the type of subsequent movement in order to investigate the size perception when the weighting information is related to action and not to object features. And finally, we used both manual and verbal estimations to define a general effect not influenced by the response modality used. We demonstrated that size perception is influenced at two levels. Before the action execution, the knowledge of action type modulated the size perception without differences between perceptual responses preceding a reaching and a grasping movement. After the movement, the perceptual responses were modified according to the type of action executed. These results reveal similarities between verbal and manual perceptual responses.

Materials and methods

Participants

A total of 37 right-handed participants (24 females and 13 males, aged 21–40 years; with normal or corrected-to-normal vision) took part in the experiments. Experiment 1 was the *Constant size manual report*: It was performed by two groups of participants. One group of 10 participants performed the Prior knowledge of action type experiment, and the other group (10 participants) performed the No prior knowledge of action type. Experiment 2 was the *Constant size verbal report*: It involved another group of 10 participants in which each participant was tested with both Prior Knowledge and No Prior Knowledge conditions performed on separate days. Experiment 3 was a *control experiment*: We tested seven participants in the *different size manual report* in which each participant was tested with both Prior Knowledge and No Prior Knowledge conditions performed on separate days. The participants had no history of musculoskeletal or neurological disorders. All participants were naive to the experimental purpose of the study and gave informed consent to participate in the experiments. Procedures were approved by the Bioethics Committee of the University of Bologna and were in accordance with the Ethical standards of the 2013 Declaration of Helsinki.

Apparatus and setup

Participants in Experiments 1, 2, and 3 were seated in an environment with dim background lighting and viewed a touchscreen monitor (ELO IntelliTouch, 1939L) which displayed target stimuli within a visible display of 37.5 × 30.0 cm as is shown in lateral view in Figure 1A. To stabilize the head position, the participants placed their heads on a chin rest. The display had a resolution of 1152 × 864 pixels and a frame rate of 60 Hz (15,500 touch points/cm^2). For stimulus presentation, we used MATLAB (The MathWorks) with the Psychophysics toolbox extension (Brainard, 1997). The stimuli were white and red and green dots with a radius of 1.5 mm and 10 differently sized white and red and green bars, all 9 mm wide. The bars differed in length and were 30, 33.6, 37.2, 40.8, 44.4, 48, 51.6, 55.2, 58.8, and 62.4 mm.

Hand position was measured by a motion capture system (VICON, 460; frequency of acquisition 100 Hz), which follows the trajectory of the hand in three dimensions by recording infrared light reflection on passive markers. Markers were placed on the index finger and thumb, respectively. The hand was kept on the table at 34 cm from the screen (Figure 1A) within a square on the table marked with tape and detectable by touch. Before the start of estimation and movement phases, the hand was kept at rest and opened with the palm facing the table and within the marked square at a constant distance from the monitor. All markers were held in place on the participant's skin with small pieces of adhesive tape that allowed freedom of movement of the hand and fingers.

Experiment 1: Constant size manual report

In the Constant size manual report (Experiment 1), participants performed 10 blocks of 10 trials each. Each trial consisted of three successive phases: *Presize perception*, *Reaching or Grasping movement*, *Postsize perception* (Figure 1B). In Presize perception (phase 1), a white or green central fixation target stayed on the screen for 1 s; then, a white or green bar was presented for 1 s, 12° on the left or on the right side of the central fixation target and, after an acoustic signal, it disappeared. The participants were required to manually indicate the perceived horizontal size of the bar. During the manual report, participants indicated the bar sizes by extending their right thumb and index fingers within the marked square on the table. While indicating the size of the bar, participant received no instructions for the posture to be assumed by the hand, so the posture of the hand was unrestricted. The distance between the participant's eyes and the screen was 43 cm (Figure 1A) that created a visual field of 50° × 40°. This distance was kept constant from participant to participant to avoid any effect of distance on the estimation of size (Sousa, Smeets, & Brenner, 2012). In the Reaching or Grasping movement phase (phase 2), after 1 s, the white or green central fixation point was followed by a bar identical in position and size to that of phases 1 and 3. Participants were required to perform a reaching (closed fist) or grasping action (extension of thumb and index finger to "grasp" the extremities of the bar) towards the bar after the acoustic signal, respectively. The type of action was instructed by the colors of the stimuli (fixation point and bar). In half of the participants, if the color of the stimuli was white, participants were required to perform a reaching movement whereas, if the color was green, they were required to perform a grasping movement. The colors were inverted in the other half of participants so, if the color was green, they performed reaching and, if it was white, they performed grasping. In the Prior knowledge of action type, the color of fixation points and bars was white or green in all three phases of trial and so the participants knew in advance (from phase 1) which action type was required in the movement phase (phase 2), as is shown

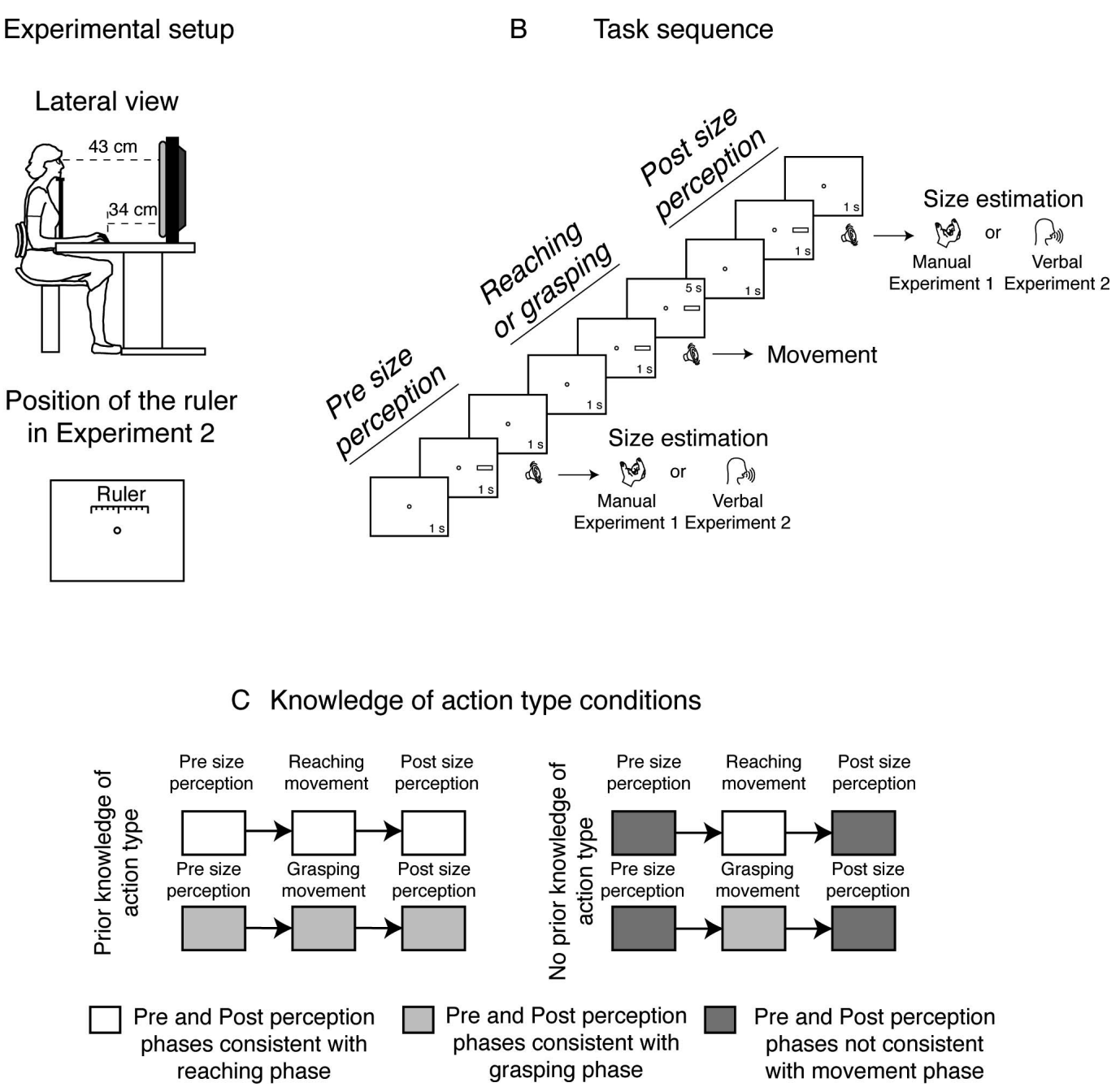

Figure 1. Experimental setup and task sequence. (A) Top row: Lateral view of the experimental setup. An optical motion capture system recorded the 3D positions of the thumb and index fingertips. Stimuli were projected on a computer monitor at 43 cm from the subject's eyes and hand position was at 34 cm from the monitor. Bottom row: Position of the ruler in Experiment 2 showed in the central upper part of the screen at the beginning of each session of trials. (B) From bottom to top: Presize perception phase of Constant size manual report or Constant size verbal report. Participants were instructed to fixate on the central fixation target shown as a small circle. After 1 s, a bar was presented for 1 s; following an acoustic signal, participants had to indicate the perceived size of the bar by grip aperture in Experiment 1 and verbal report in Experiment 2 (as indicated by the sketch at the right). The colors of stimuli could be red for NPK condition and white or green for PK condition according to reaching and grasping instructions. Reaching or Grasping execution phase (identical for Experiment 1 and 2). A central fixation target was presented, and after 1 s a bar appeared, but participants had to wait 1 s before executing a reaching or grasping movement when an acoustic signal sounded. If the stimuli were white, participants had to execute a reaching action whereas if they were green, participants had to execute a grasping action (inverted colors in half the participants). Postsize perception phase. It was structured in the same way as the Presize perception phase. (C) Left: distribution of the three trial phases as colored blocks in the Prior knowledge of subsequent action type condition. →

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The colors of the squares correspond to color of the stimuli: white for reaching and light gray for grasping movement. In both trial types, the color of the stimuli was always in accordance with the color of the stimuli in the movement phase (phase 2). Right: distribution of the three trial phases in the No prior knowledge of subsequent action type condition. The colors of the squares correspond to color of the stimuli: white for reaching, light gray for grasping movement, and dark gray for stimuli in the perception phases. In both trial types the color of the stimuli was not in accordance with the color of the stimuli in the movement phase (phase 2).

in Figure 1C-left. In the No prior knowledge of action type, the sequence of the three phases was structured in the same way as in the Prior knowledge of action type condition, but the colors of fixation points and bars were changed from white/green to red in phases 1 and 3, as depicted in Figure 1C-right in gray scale. The color of the stimuli during phase 2 remained white or green according to the movement type, reaching or grasping, respectively. Phase 3 was structured in the same way as phase 1: It was a postsize perception phase. With this color manipulation, participants could not know in advance the successive action type. Figure 1C represents a scheme of the sequence of color stimulus in the Prior and No prior knowledge of action type conditions.

Experiment 2: Constant size verbal report

The Constant size verbal report was performed to check whether the size estimation effect was specific to the manual report or more generally related to size perception. In this experiment, participants had to indicate the perceived size of the bars verbally as a number in millimeters. The stimuli and structure of the experiment were identical to the aforementioned Experiment 1, except for the two estimation phases that consisted of a verbal report of the estimated size of the bars presented (Figure 1B). Each of the 10 participants was required to perform two experimental sessions with both experimental conditions separately. In one session they performed the Prior knowledge of action type condition, and in the other one they performed the No prior knowledge of action type condition (as Experiment 1). Experiments were executed with at least one day between them. During the Presize perception and Postsize perception phases, an acoustic signal requested the participant to provide a verbal judgement in millimeters about the bar presented on the screen. At the beginning of each session, participants were presented with a ruler in the top-central part of the screen to remind them of the scale (Figure 1A, bottom). White and green colors of the stimuli indicated the movement required in each trial, reaching or grasping respectively, as reported for Experiment 1. The number of trials was the same as in Experiment 1.

Experiment 3: Different size manual report

To support the previous results and generalize the action-induced effect, we performed Experiment 3 (Different size manual report) as a control experiment. In this experiment, participants had to indicate the perceived size of the bars by manual estimation. The structure and the task sequence of the experiment were identical to Experiment 1. The Presize perception consisted in the manual indication of a bar presented on the screen after the acoustic signal, and the Reaching and Grasping phases (phases 1 and 2) consisted in performing a reaching or a grasping movement towards the bar according to the color of the stimuli (see Experiment 1). In these two phases the size of the bars presented was the same and three different sizes (37.2, 48, and 58.8 mm) could be presented in each trial. In the Postsize perception phase, the size of each stimulus was changed; we randomly presented bars 7.2 mm smaller or larger than the bars shown in phases 1 and 2. In other words, if the bar presented in phases 1 and 2 was 37.2 mm, in phase 3, the bar could be 30 mm (smaller) or 44.4 mm (larger). If it was 48 mm in phases 1 and 2, it could be 40.8 mm (smaller bar) or 55.2 mm (larger bar), and if it was 58.8 mm, it could be 51.6 mm (smaller) or 66 mm (larger). Each of the seven participants was required to perform the Prior knowledge of action type condition in one session and the No prior knowledge of action type condition in the other one. They were not informed about the change in the bar size occurring between phase 2 and phase 3.

From here on, we refer to No prior knowledge of action type as NPK condition and to Prior knowledge of action type as PK condition, respectively. All participants received the same instructions. In all experiments, the sequences of bar sizes and conditions were randomly created by MATLAB code.

Data analysis

After data collection, finger position data were interpolated at 1000 Hz; then data were run though a fifth-order, Butterworth low-pass filter (cutoff frequency, 30 Hz; Bosco, Lappe, & Fattori, 2015). For data processing and analysis, we wrote custom software

in MATLAB to compute the distance between index and thumb markers during the pre- and postmanual estimation phases (Experiments 1 and 3). Grip aperture was calculated considering trial intervals in which the velocities of the index and thumb markers remained $<$ 5 mm/s (Bosco et al., 2015). Grip aperture was defined as maximum distance within this interval. We calculated the maximum grip aperture (MGA) during the grasping movement and it was defined within a search window beginning at the onset of the movement and ending at the end of the movement. The onset of the movement was defined as the time at which the index and thumb velocity exceeded a threshold velocity of 5 mm/s for 200 ms and the end as the time at which the velocity became less than 5 mm/s. For all experiments, the amount of shift in size perception after reaching or grasping movement was computed as the difference of size reports between postsize and presize estimation phases (phases 1 and 3) averaged across sizes and participants. We tested for significance by using two-tailed t test with independent samples to compare reaching and grasping deviations and by using one-sample t test to compare the single deviation against zero.

For the estimation accuracy, we realized that the participants estimated the sizes from the fingertip. As the perceived sizes of the manual experiment were extracted by the distance between the two markers on the thumb and index fingers placed on the nails, we used a caliber to measure the thickness of the two fingers with the markers attached. Thus, to obtain more efficient matching with the real sizes and to make the accuracies of the manual experiment comparable with those of the verbal experiment, we considered the true thickness of the thumb and index finger of each participant and we subtracted it from the perceived sizes. Then, we averaged the difference values of the distances across sizes and participants. This allowed us to obtain the mean real distance between the fingertip. We assessed the linear relationship between perceived and real sizes before and after the reaching and grasping movements by performing a linear regression analysis. In particular, we evaluated whether there was similar or different correlation between perceived sizes before the two movements and the real sizes and between the perceived sizes after the movements and the real sizes. This analysis allowed us to assess differences across reaching and grasping movements and conditions. Then, we tested the significance of linear regression applying the R^2 formula.

A two-way Anova was employed to evaluate the effect of NPK and PK conditions (Factor 1) and the effect of reaching and grasping (Factor 2) on deviations of perceptual responses. For all statistical analyses the significant criterion was set to $p < 0.05$.

Analysis of the effect of knowledge of action type

To evaluate the magnitude of the effect of NPK and PK conditions on perceptual responses before the movement, we calculated the average difference between the two responses, and we compared this difference and the perceptual responses between the two conditions by a t-test analysis in manual and verbal experiments. We then applied the Signal Detection Theory (SDT) to study the strategy used by participants to respond in PK and NPK conditions, respectively. We applied this analysis because it gives a measurement of the discrimination ability between the PK and NPK condition. It thus makes it possible to have smaller responses in PK condition or vice versa, focusing on the frequency of responses across trials.

In our case, the perceptual responses before the movement in PK condition correspond to *signals,* and the perceptual responses before the movement in NPK condition correspond to *noise*. We considered the perceptual responses smaller than the responses of the noise trials as hits in the signal trials and the responses of the noise trials smaller than those of the signal trials as false alarms. The goal of SDT is to estimate two main parameters from the experimental data. The first parameter, called d', indicates the strength of the *signals*; the second parameter, called β, reflects the strategy of response of the participants. We calculated hit (H) and false alarm (F) rates and the two z scores corresponding to those rates. Then, we computed the Φ function that converts z scores into probabilities and we obtained two normal distributions centered on the two computed z scores corresponding to hit and false alarm rates, respectively. The d' value was calculated as follows (Macmillan, 1993; Stanislaw & Todorov, 1999):

$$d' = \Phi^{-1}(H) - \Phi^{-1}(F),$$

where $\Phi^{-1}(H)$ is the z score of the hit rates and $\Phi^{-1}(F)$ is the z score of the false alarm rates; d' is the distance between the signal distribution and the noise distribution. A value of 0 indicates an inability to distinguish the signals from the noise, whereas larger values indicate a corresponding greater ability to distinguish between the two. β was calculated with the equation (Macmillan, 1993; Stanislaw & Todorov, 1999):

$$\beta = e^{\left\{\frac{[\Phi^{-1}(F)]^2 - [\Phi^{-1}(H)]^2}{2}\right\}},$$

where $\Phi^{-1}(H)$ is the z score of the hit rates and $\Phi^{-1}(F)$ is the z score of the false alarm rates. β reflects the strategy of response of the participants and it is called criterion. For our data, if β was set at the midpoint between the two distributions, the criterion is neutral and it is called the ideal observer. If β was different from the ideal observer, the criterion indicates a bias in

favor of smaller perceptual responses in PK condition compared to NPK condition. The likelihoods of hit and false alarm rates are given by the intersection of the criterion (β) with the signal and noise curves, respectively. We performed this analysis for reaching and grasping actions as well as for the verbal and manual responses.

Finally, to evaluate whether the perceptual responses in the two conditions were correlated to the movement, we calculated the correlation coefficients between perceptual responses before the grasping and MGA, and we tested them for significance.

Results

We performed manual and verbal size perceptual reports and evaluated the change in size perception before and after a reaching or a grasping movement for objects of different sizes. We tested two experimental conditions called No prior knowledge and Prior knowledge of action type (NPK and PK, respectively) where we evaluated the effects of prior knowledge of the subsequent action type on the perceptual responses.

Experiment 1: Action plan and action execution modulates size perception by manual reports

In the Constant size manual report (Experiment 1), we assessed the effects of action plan and action execution on perceptual responses comparing the single participant responses before the movement with those after the movement. Figure 2A on the left shows perceptual responses in the NPK condition shown with different colors before and after a reaching movement (white dots) and responses before and after a grasping movement (black dots). In particular, they were plotted as perceptual responses before the movement (x axis) against the perceptual responses after the movement (y axis). The majority of responses fell below the diagonal, suggesting an adjustment of perceptual estimation after both reaching and grasping movements. To evaluate whether this adjustment was different after the two types of movements, we calculated the amount of perceptual adjustment as the difference between the size manual reports before and after the movement. Figure 2A-right displays a negative adjustment for the NPK condition after both reaching (white) and grasping (black) movements (reach = −1.14 mm ± *SEM* 0.95 mm; grasp = −2.71 mm ± *SEM* 1.14 mm). Only the grasping adjustment significantly deviated from zero (reach, $p = 0.075$; grasp, $p < 0.001$) and the difference between the adjustments in the two movement types was significant (two-tailed t test, $p = 0.0161$).

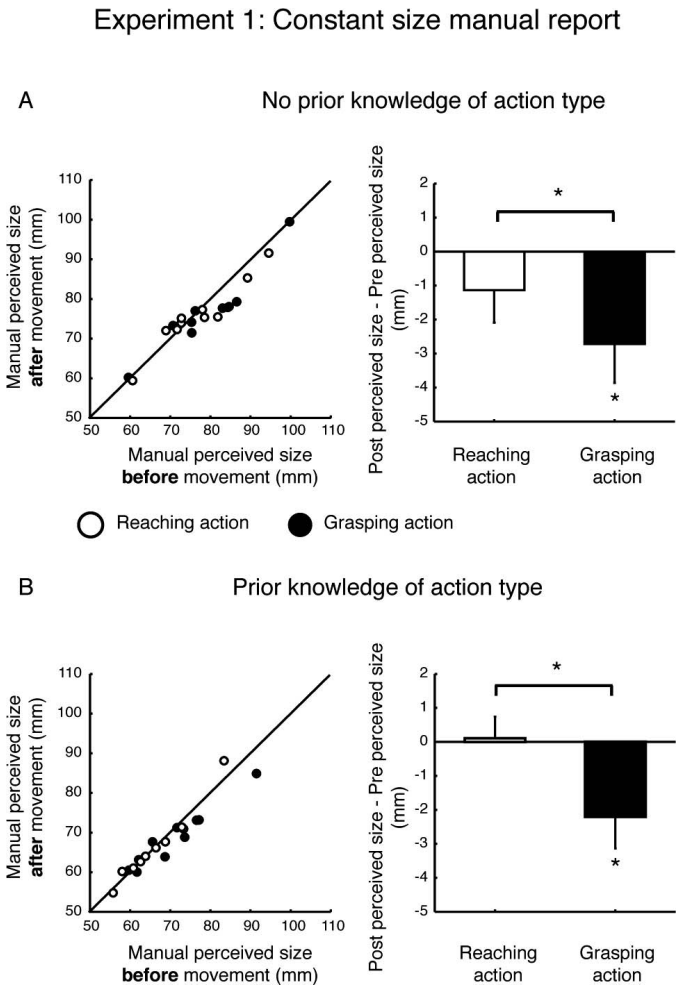

Figure 2. Manual perceptual responses before and after the reaching and grasping movements. (A) Left: The manual responses before and after the reaching (white dots) and the grasping actions (black dots) were plotted one against the other for each subject in NPK condition. Right: mean deviation of perceptual responses for manual experiment for reaching (white column) and grasping (black column) averaged across participants and sizes. (B): Left: manual perceptual responses before and after the reaching (white dots) and grasping movements (black dots) in PK condition. Right: mean deviation of perceptual responses for the Experiment 1 for reaching (white column) and grasping (black column) averaged across participants and sizes in PK condition. Error bars indicate standard errors of the mean (*SEM*). Asterisks with brackets indicate two-tailed t test, single asterisks indicate one-sample t test against zero. *$p < 0.05$, significant level.

In the PK condition, we found that the majority of participants' responses after the grasping movement were located below the diagonal whereas after the reaching movement they mainly remained on the diagonal, as is shown in Figure 2B-left. In the PK condition, the negative adjustment was maintained only for the grasping movement (−2.2 mm ± *SEM* 0.93 mm) and presented a significant difference (two-tailed t

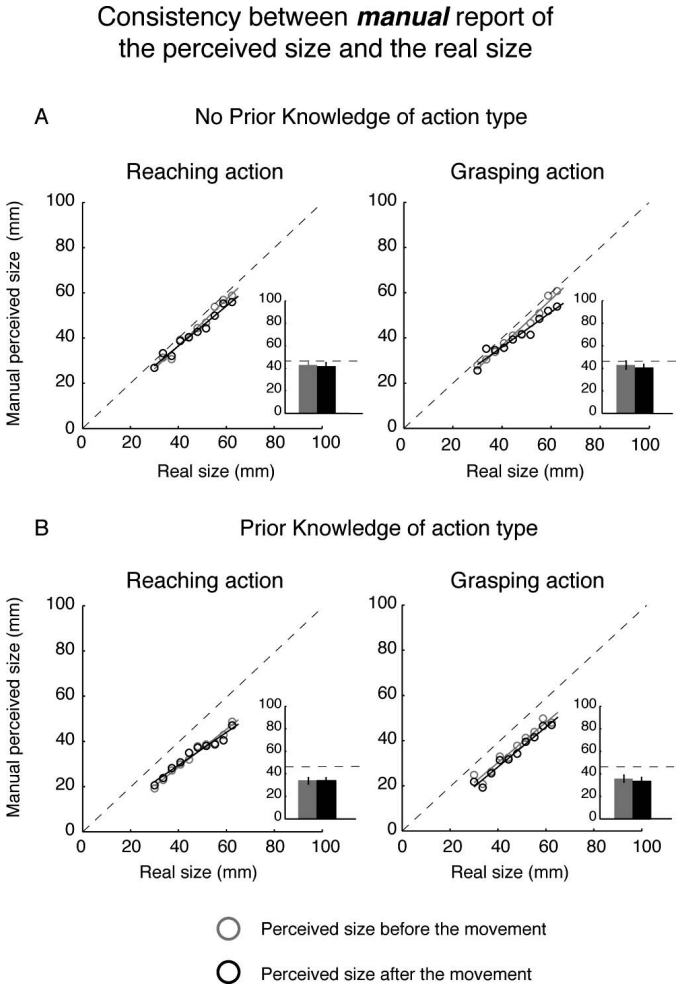

Figure 3. Correspondence between perceived and real sizes in Constant size manual report. (A) Left. Scatter plot of manual perceived size (mm) as function of real size of the ten bars in NPK condition before (gray, empty dots) and after a reaching action (black, empty dots). Gray and black lines represent linear regression for manual perceived sizes before and after a reaching movement, respectively. The equation lines are $y = x - 4.4$ (before reaching movement, $R^2 = 0.98$, $^*p < 0.001$) and $y = 0.88x + 1.2$ (after reaching movement, $R^2 = 0.97$, $^*p < 0.001$). Right: scatter plot of manual perceived size (mm) as function of real size of the ten bars before and after a grasping movement in NPK condition. The equation lines are $y = x - 4.2$ (before grasping movement, $R^2 = 0.98$, $^*p < 0.05$) and $y = 0.78x + 4.9$ (after grasping movement, $R^2 = 0.94$, $^*p < 0.001$). (B) left: scatter plot of manual perceived size (mm) as function of real size of the ten bars before and after a reaching movement in the PK condition. The equation lines are $y = 0.84x - 4.9$ (before reaching movement, $R^2 = 0.98$, $^*p < 0.001$) and $y = 0.73x + 0.38$ (after reaching movement, $R^2 = 0.96$, $^*p < 0.001$). Right, Scatter plot of manual perceived size (mm) as function of real size of the ten bars before and after a grasping movement in the PK condition. The equation lines are $y = 0.89x - 5.3$ (before grasping movement, $R^2 = 0.95$, $^*p < 0.001$) and $y = 0.88x - 6.9$ (after grasping movement, $R^2 = 0.97$, $^*p < 0.001$). →

test, $p < 0.001$) compared with the reaching adjustment (0.1 mm ± *SEM* 0.64 mm) as is shown in Figure 2B-right. In this condition, only the manual estimation after grasping showed a significant deviation from zero (one-sample t test: reach, $p = 0.6801$; grasp, $p < 0.001$). This means that, after a grasping movement and in both conditions, participants perceived the bars to be significantly smaller than after a reaching movement.

Figure 3 shows the accuracy of estimations reporting the manual perceptual responses before (gray empty dots) and after the movement (black empty dots) on the y axis as function of the 10 real sizes of the bars tested on the x axis. We performed the regression analysis to evaluate whether the perceptual responses before and after the movement (gray and black lines in Figure 3, respectively) linearly fitted with the real sizes. In the inset of each scatter plot of Figure 3, we reported the mean of the 10 perceived sizes represented as gray and black columns (before and after the reaching, respectively) and the mean real size represented as horizontal dotted line. Figure 3A-left shows the 10 perceptual responses before and after the reaching movement in NPK condition and the mean of perceived sizes (gray and black columns). The perceived sizes show a significant linear fit with the real sizes both before and after the reaching movement indicating a good ability of participants in discriminating the sizes of the bars. In both cases, the R^2 values were higher than 0.9 ($p < 0.001$). The regression lines corresponding to perceived sizes before and after the reaching movement were superimposed (Figure 3A-left, gray and black lines, respectively) presenting intercepts equal to –4.4 before the reaching and 1.2 after the reaching. The mean values showed that, before and after the reaching movement, participants underestimated the real sizes (mean perceived size before reaching: 42.90 mm ± *SEM* 3.56 mm; mean perceived size after reaching: 41.95 mm ± *SEM* 3.08 mm; real mean size: 46.2 mm ± *SEM* 3.45 mm). Figure 3A-right displays the same analysis for perceived sizes before and after the grasping movement (gray and black dots and columns, respectively) again in NPK condition. Before and after the grasping movement, we found significant linear fit between perceived and real sizes (R^2 values > 0.9, $p < 0.001$). Although the regression analysis showed a good correspondence between perceived and real sizes in grasping too, there were differences between perceived sizes before and after the grasping movements. The regression line corresponding to perceived sizes after

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The histograms on the right of each scatter plot represent the mean perceived size of the 10 bars before (gray) and after the movement (black). Dotted lines represent the mean real size of the 10 bars. Error bars indicate *SEM* and all color details are as in Figure 3A.

the grasping movement (Figure 3A-right, black line) was more shifted below the diagonal for larger bars with respect to the regression line corresponding to the perceived sizes before the movement (Figure 3A-right, gray line). The two intercepts were −4.2 and 4.9, respectively. Also in this case, there was underestimation of the real sizes (histogram in Figure 3A-right, mean perceived size before grasping: 42.96 mm ± *SEM* 3.56 mm; mean perceived size after grasping: 40.75 mm ± *SEM* 2.76 mm; real mean size: 46.2 mm ± *SEM* 3.45 mm). All these results suggest that, in NPK condition, after the grasping movement, the participants tended to underestimate the real sizes more than after the reaching movement.

Figure 3B shows the same analysis performed for the PK condition. Figure 3B-left shows significant linear fit between perceptual responses and real sizes in PK condition both before and after reaching ($R^2 > 0.9$, $p < 0.001$). The two regression lines were overlapped with intercepts corresponding to −4.9 before the reaching and 0.38 after the reaching. As is displayed in the gray and black columns in the inset, the participants underestimated the real sizes (mean perceived size before reaching: 33.82 mm ± *SEM* 2.92 mm; mean perceived size after reaching: 33.97 mm ± *SEM* 2.56 mm; real mean size: 46.2 mm ± *SEM* 3.45 mm). Figure 3B-right shows significant linear fit both before and after grasping ($R^2 > 0.9$, $p < 0.001$) but the regression line after the grasping (black line) was more shifted below the diagonal with respect to the line before the grasping (gray line). The two intercepts were −5.3 and −6.9, respectively. Also in this case, participants underestimated the real sizes (mean perceived size before grasping: 35.78 mm ± *SEM* 3.15 mm; mean perceived size after grasping: 33.80 mm ± *SEM* 3.09 mm; real mean size: 46.2 mm ± *SEM* 3.45 mm). These results suggest that participants underestimated the real sizes mainly in the PK condition (see the dots more underdeviated in Figure 3B) and, globally, after the grasping movement in both NPK and PK conditions (see the histograms for comparisons).

Experiment 2: Action plan and action execution modulates size perception by verbal reports

The scheme of grasping modulation on size perception for the Constant size verbal report (Experiment 2) is shown in Figure 4. Figure 4A-left shows the perceived sizes before and after the reaching (white dots) and grasping (black dots) movements for each participant in the NPK condition. The majority of participants perceived the bars to be smaller after the grasping compared to the reaching movement, as the black dots fell below the diagonal in Figure 4A. The amount of adjustment averaged across participants is

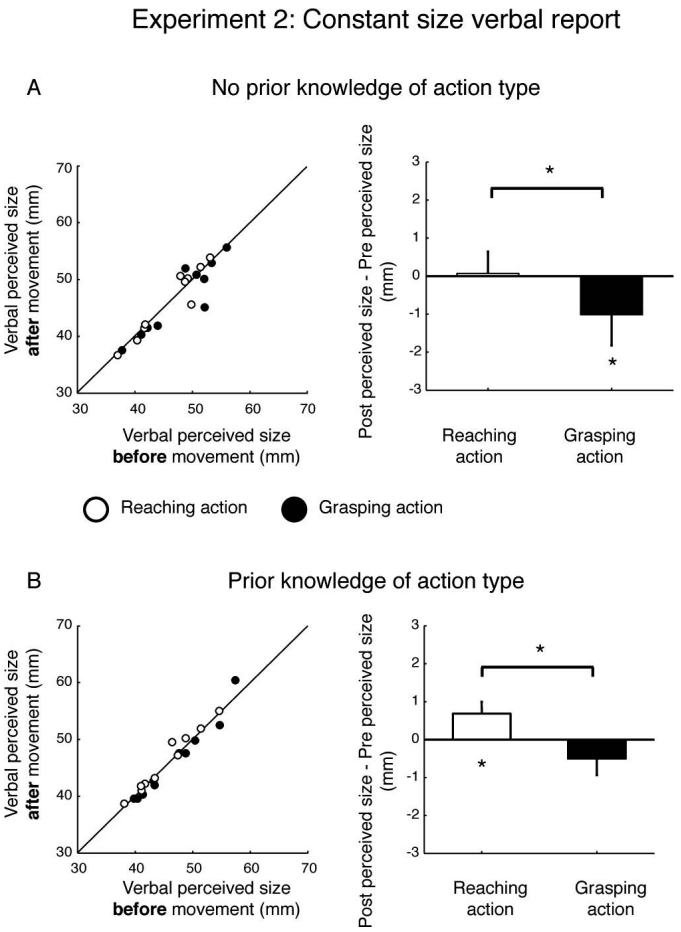

Figure 4. Verbal perceptual responses before and after the reaching and grasping movements. (A) Verbal perceptual responses before and after the movement in NPK condition. Left: The verbal responses before and after the reaching (white dots) and the grasping actions (black dots) were plotted one against the other for each participant. Right: mean deviation of perceptual responses for verbal experiment for reaching (white column) and grasping (black column) averaged across participants and sizes. (B) Left: verbal perceptual responses before and after the reaching (white dots) and grasping movements (black dots) in PK condition. Right: mean deviation of perceptual responses for reaching (white column) and grasping (black column) averaged across participants and sizes. Error bars indicate *SEM*. All symbols are as in Figure 4. *$p < 0.05$, significant level.

reported in Figure 4A-right and it was negative in grasping (−1.02 mm ± *SEM* 0.57 mm) and positive in reaching (0.07 mm ± *SEM* 0.57 mm). The difference between the amount of adjustment after a reaching and a grasping movement was significant (two-tailed *t* test, $p = 0.005$). Only grasping adjustment showed a significant deviation from zero (one sample t test: reach, $p = 0.6944$; grasp, $p = 0.0037$). Figure 4B-left shows the perceived sizes in PK condition. In this condition, participants' verbal reports fell below the diagonal after the grasping movement with respect to

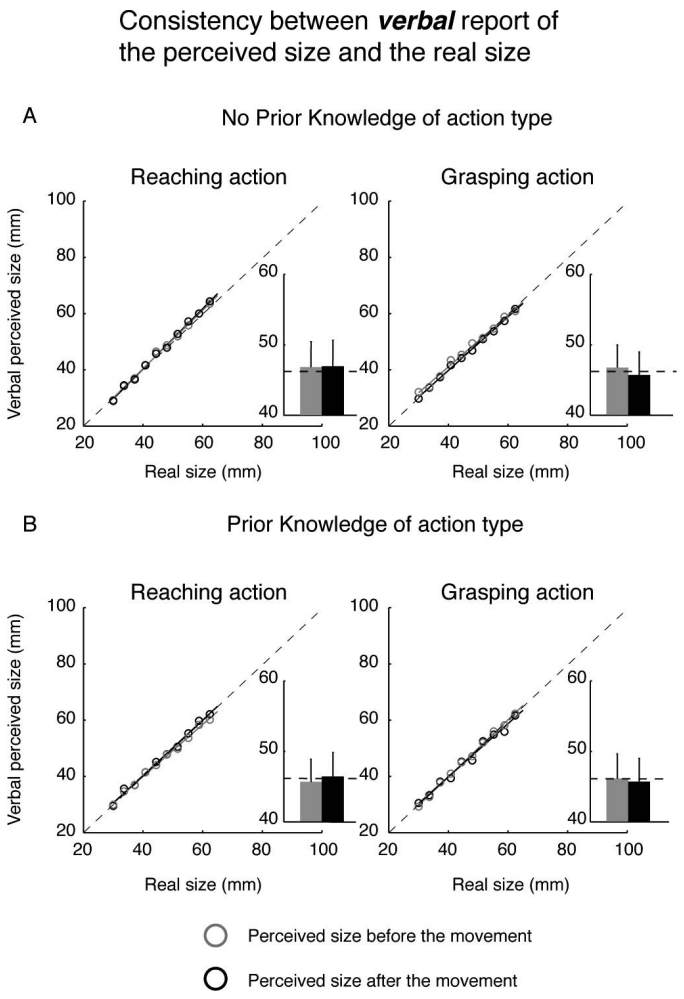

Figure 5. Correspondence between perceived and real sizes in Constant size verbal report. (A) Left: scatter plot of verbal perceived size (mm) as function of real size of the 10 bars before (gray, empty dots) and after a reaching movement (black, empty dots) in NPK condition. Gray and black lines represent linear regression for verbal perceived sizes before and after a reaching movement, respectively. The equation lines are $y = x - 1.1$ (before reaching movement, $R^2 = 0.99$, $^*p < 0.001$) and $y = 1.1x - 2.5$ (after reaching movement, $R^2 = 0.99$, $^*p < 0.001$). Right: scatter plot of verbal perceived sizes (mm) as function of real size of the 10 bars before and after a grasping movement in NPK condition. The equation lines are $y = 0.92x + 4.3$ (before grasping movement, $R^2 = 0.99$, $^*p < 0.001$) and $y = 0.95x + 1.7$ (after grasping movement, $R^2 = 0.99$, $^*p < 0.05$). (B) Left: Scatter plot of verbal perceived sizes (mm) as function of real size of the 10 bars before and after a reaching movement in the PK condition. The equation lines are $y = 0.93x + 2.9$ (before reaching movement, $R^2 = 0.99$, $^*p < 0.001$) and y $= 0.98x + 1$ (after reaching movement, $R^2 = 0.99$, $^*p < 0.001$). Right: scatter plot of verbal perceived sizes (mm) as function of real size of the 10 bars before and after a grasping movement in the PK condition. The equation lines are $y = x - 0.7$ (before grasping movement, $R^2 = 0.99$, $^*p < 0.001$) and $y = 0.95x + 2$ (after grasping movement, $R^2 = 0.98$, $^*p < 0.001$). →

the reaching movement. The averaged amount of adjustments displays a negative deviation for grasping (−0.5 mm ± *SEM* 0.44 mm) and a positive deviation for reaching (0.68 mm ± *SEM* 0.31 mm) as is reported in Figure 4B-right (two-tailed *t* test, $p < 0.001$). In this condition, only the reaching adjustment significantly deviated from zero (one sample *t* test: reach, $p < 0.001$; grasp, $p = 0.0694$). In both conditions, the adjustment after a grasping movement was significantly smaller with respect to manual experiments (Experiment 1, two-tailed *t* test, $p < 0.001$), but the direction of the deviations was the same in both experiments. These results of the effects of grasping on size perception were congruent between the manual and the verbal reports.

Figure 5 shows the analysis of accuracy of the verbal perceived sizes similarly to what was performed in Figure 3 for the manual report. Figure 5A shows a significant linear relationship between perceived and real sizes before and after reaching and grasping movements in NPK condition. The R-squared values were higher than 0.9 ($p < 0.001$). The intercepts of regression lines before and after reaching were −1.1 and −2.5, respectively whereas those before and after grasping were 4.3 and 1.7. The participants' perceptions when executing reaching and grasping were very accurate before and after the movement, as is shown in the gray and block columns representing the mean perceived sizes (mean perceived size before reaching: 46.84 mm ± *SEM* 3.59 mm; mean perceived size after reaching: 46.95 mm ± *SEM* 3.70 mm; mean perceived size before grasping: 46.77 mm ± *SEM* 3.18 mm; mean perceived size after grasping: 45.70 mm ± *SEM* 3.28 mm; real mean size: 46.2 mm ± *SEM* 3.45 mm). However, participants underestimated more after a grasping than after a reaching movement, as a slight shift of regression line after grasping (black line, Figure 5A-right) was present. This is highlighted by the mean values in the histograms of Figure 5A-right.

As done for the manual report, we analyzed the accuracy for perceived size in PK condition also for the verbal report (Figure 5B). We found significant linear fit between perceived and real sizes before and after reaching and grasping movements (R^2 values > 0.9, $p < 0.001$) and high mean accuracy for both movements, as is reported in the histograms of mean perceived sizes (mean perceived size before reaching: 45.69 mm ± SEM 3.20 mm; mean perceived size after reaching: 46.44 mm ± *SEM* 3.40 mm; mean perceived size before grasping: 46.15 mm ± *SEM* 3.50 mm; mean perceived size after grasping: 45.73 mm ± *SEM* 3.28 mm; real

←
The histograms on the right of each scatter plot represent the mean perceived size of the 10 bars before (gray) and after the movement (black). Dotted lines represent the mean real size of the 10 bars. Error bars indicate *SEM* and all color details are as in Figure 3A.

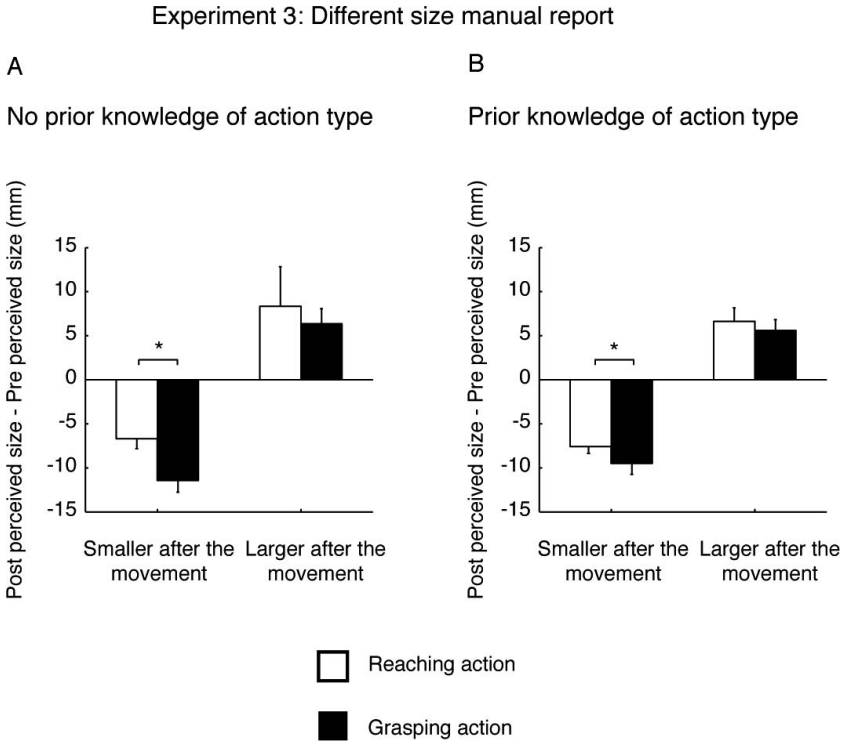

Figure 6. Mean deviations of perceptual responses when the size of bars changes after the movement in the Different size manual report experiment. (A) Mean deviations of perceptual responses for reaching (white column) and grasping (black column) averaged across participants and sizes in NPK condition. The deviations are reported for presentation of smaller sizes after the movement (on the left) and for presentation of larger sizes after the movement (on the right). (B) Mean deviations of perceptual responses for reaching (white column) and grasping (black column) averaged across participants and sizes in PK condition. The deviations are reported for presentation of smaller sizes after the movement (on the left) and for presentation of larger sizes after the movement (on the right). In both size changes and conditions, the estimations decreased after grasping movement. Error bars indicate *SEM*. *$p < 0.05$, significant level.

mean size: 46.2 mm ± *SEM* 3.45 mm). The overlapping of regression lines before and after reaching was high with intercepts equal to 2.9 and 1 before and after the reaching, respectively. For grasping, the overlapping of regression lines was evident too. Intercepts were equal to −0.7 and 2 before and after the movement, respectively. In this case, participants maintained a high correspondence between perceived and real sizes before and after the two movements, but they presented more underestimation after the execution of grasping as the mean values on the histograms show.

Experiment 3: Size perception is modulated by action plan and action execution when size changes after the movement

In the previous experiments, we tested the effect of action plan and action execution on size perception when the size of the bars presented was identical in the pre, postperception, and movement phases (phase 1, 2 and 3, see Materials and methods). We observed a significant reduction of size perception after the grasping movement compared with the reaching movement. However, in order to generalize these results we performed a similar experiment where we changed the size of the bars in the postperception phase (phase 3). In this case, the participants had to indicate by manual response, as in Experiment 1, the perceived size of bars that could be smaller or larger with respect to bars shown in phases 1 and 2. Each participant was tested in NPK and PK conditions in separate sessions.

Our hypothesis was that, if a real effect of action plan and action execution on size perception existed, the perceived size of a smaller and a larger bar after the grasping movement should be more reduced if compared with the size perception after the reaching movement. Figure 6A shows the results of NPK condition and it displays negative adjustments when we presented the smaller bar for both reaching and grasping movements. The negative adjustment was significantly higher when participants performed the grasping action (reach: −6.697 mm ± *SEM* 1.13 mm; grasp: −11.435 mm ± *SEM* 1.32; two-tailed *t* test, $p < 0.001$) suggesting that they perceived smaller sizes after the grasping action with respect to the reaching action,

again as seen in Experiments 1 and 2. When a larger bar was presented, the adjustments were positive, but the participants perceived smaller bars after the grasping action compared with the reaching movement although the difference was not significant (reach: 8.33 mm ± *SEM* 4.48 mm; grasp: 6.35 mm ± *SEM* 1.70; two-tailed *t* test, $p = 0.5005$).

Figure 6B shows the same results in PK condition. When the smaller bars were presented, the adjustments were negative, but the participants perceived significantly smaller bars after the grasping movement (reach: −7.575 mm ± *SEM* 0.78 mm; grasp: −9.497 mm ± *SEM* 1.23; two-tailed *t* test, $p = 0.0019$). When the larger bars were presented, the adjustments were positive and the participants perceived smaller bars after the grasping movement (reach: 6.629 mm ± *SEM* 1.53 mm; grasp: 5.600 mm ± *SEM* 1.22; two-tailed *t* test, $p = 0.64$), although not significant.

Overall effects of action plan and action execution on size perception

Collectively, these data suggest that participants perceived the stimuli to be smaller after a grasping action than after a reaching action. Although the adjustments after a grasping movement were significantly different in manual and verbal experiments (two-tailed *t* test: NPK, $p < 0.001$; PK, $p < 0.001$), the trend was the same independently of the response modality used. However, this modification of size perception due to action execution is not directly correlated with a significant improvement of size estimation after a grasping movement. We performed a two-way ANOVA to describe the effects of knowledge conditions (NPK and PK conditions) and action type on the adjustments of manual and verbal perceptual reports after the movement. The statistical analysis described only a significant main effect of action type on size perception adjustments in Experiment 1: knowledge condition, $F(1, 1) = 3.8$, $p = 0.0514$; and action type, $F(1, 1) = 17.66$, $p < 0.001$. However, the effect of knowledge condition was very close to significance ($p = 0.0514$). In Experiment 2, we found significant main effects of knowledge condition and action type: knowledge condition, $F(1, 1) = 4.8$, $p < 0.05$; and action type, $F(1, 1) = 19.39$, $p < 0.001$. We did not find a significant interaction between the two factors in either experiment: $F(1, 1) = 0.13$, $p = 0.72$, Experiment 1; $F(1, 1) = 0.04$, $p = 0.848$, Experiment 2. The lack of a significant interaction between the two factors could suggest that the modulation exerted by PK and NPK condition and that exerted by the type of action originated from two different processes.

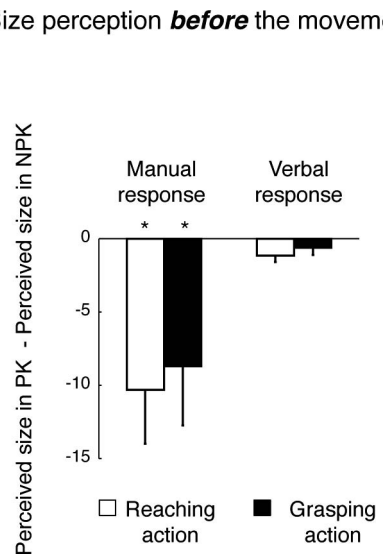

Figure 7. Mean differences of perceptual responses between PK and NPK conditions in reaching (white column) and grasping (black column) for Experiments 1 and 2, respectively. Error bars indicate *SEM*. *$p < 0.05$, significant level.

Size perception before movement execution: Role of the knowledge of the type of action

To analyze the effect of the NPK and PK conditions on size perception in more depth, we focused the analyses on manual and verbal size reports before the movement execution (Presize perception phase). We computed the difference between the Presize perception reports in PK condition and the Presize perception reports in NPK condition. This difference made it possible to highlight the amount of change in size perception in the two conditions tested. We found a significant difference between the PK and NPK conditions for the perceptual responses before the reaching and the grasping, respectively (two-tailed *t* test, reach: $p < 0.001$; grasp: $p < 0.001$). As is shown in Figure 7, we found that in Experiment 1 the amount of change in reaching was −10.54 mm ± *SEM* 3.67 mm and in grasping −8.71 mm ± *SEM* 4.04 mm, but, in both cases, they significantly deviated from zero (*t* test one sample, $p < 0.001$).

In the Experiment 2, the values of size reports were not significantly different from zero for both reaching and grasping (*t* test one sample, $p = 0.37$, reaching; $p = 0.30$, grasping) but they deviated to negative values (−1.15 mm ± *SEM* 0.44 mm and −0.62 mm ± *SEM* 0.49 mm, respectively). The change in reaching was more shifted to negative values with respect to the change in grasping for both manual and verbal experiments, but neither of the two comparisons was statistically different (two-tailed *t* test, $p = 0.34$, Experiment 1; $p = 0.91$, Experiment 2). In this experiment, the direct comparison between the PK and

NPK conditions resulted not significant for reaching and grasping (two-tailed t test, reach: $p = 0.21$; grasp: $p = 0.3$). Generally, participants tended to perceive the sizes presented in the condition where they were aware about the subsequent action (PK condition) as smaller compared with the condition where they were uncertain about the subsequent movement (NPK condition). The knowledge about the subsequent movement type revealed a greater influence on manual perceptual responses with respect to verbal ones. This may be due to different design of the two experiments (between-subjects design of Experiment 1 vs. within-subjects design of Experiment 2, Figure 7).

We applied the Signal Detection Theory (SDT) analysis to measure the ability of participants to distinguish between the two conditions (d' value) and the strategy used by participants to respond (β value, see Materials and methods). Figure 8 illustrates the distribution of z scores of signal and noise trials represented as black and gray curves, respectively. In the previous analysis, we observed that perceptual responses in PK condition were smaller than those in NPK conditions. Based on this, we considered the perceptual responses smaller than the responses of the noise trials (trials in NPK condition) as hits in the signal trials (trials in PK condition) and the responses of the noise trials smaller than those of the signal trials as false alarms. Figure 8A reports the two distributions for manual perceptual responses before the reaching movements (Figure 8A-left) and for those before the grasping movements (Figure 8A-right). We calculated d' as the measurement of the distance between the mean of the signal distribution and the mean of the noise distribution (i.e., the distance between the peaks of the two distributions in Figure 8) in standard deviation units. For manual perceptual responses, the two d' values were similar and corresponded to 1.022 for responses before the reaching movement and 1.070 for responses before the grasping movement, respectively (Figure 8A, left and right, respectively). This suggests that the participants showed the same ability in discriminating the two conditions both before the reaching and before the grasping movement. Then, we calculated the two β values for reaching and grasping, and they are reported in Figure 8A as the shaded portions of the distributions. The β value in reaching trials was 1.19 and corresponded to signal and noise likelihoods of 0.3105 and 0.01, respectively (Figure 8A-left). In the grasping trials, we found a β value of 1.21 that corresponded to signal and noise likelihoods of 0.3102 and 0.08, respectively (Figure 8A-right). These results in grasping overlap with those in reaching (compare left versus right of Figure 8A). These data indicate that participants judged the objects to be smaller more frequently in PK condition with respect to NPK condition and used the same strategy for reaching

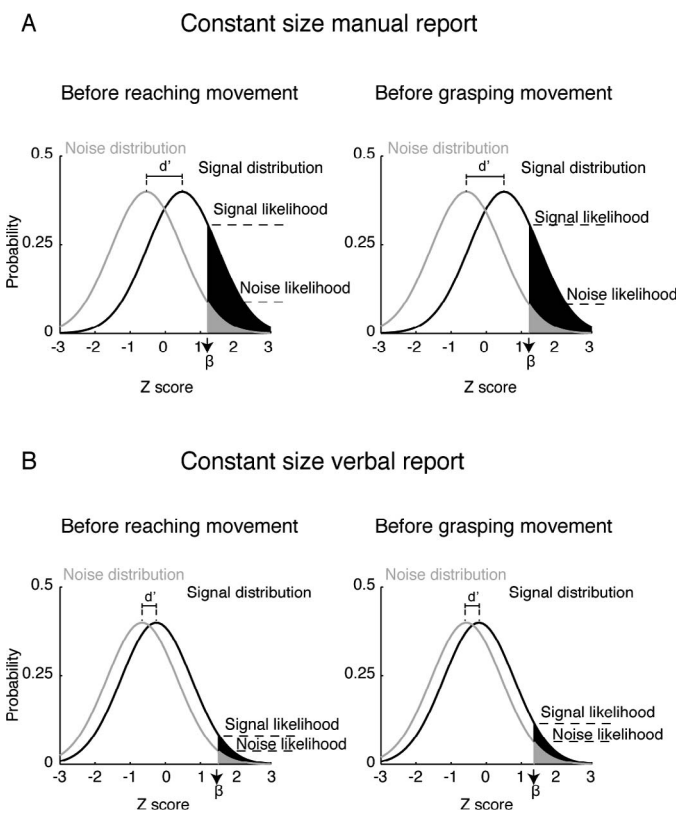

Figure 8. Signal detection theory analysis. (A) Distribution of signal (trials of PK condition) and noise trials (trials of NPK condition) in black and gray colors, respectively in the Constant size manual report experiment. The two distributions are reported for manual responses before the reaching movement (on the left) and for manual responses before the grasping movement (on the right). Each diagram shows d', the distance between the mean of the two curves, and β, representing the corresponding criterion used by participants to respond. The shaded portions of the curves indicate the likelihoods on which β is based. (B) Distribution of signal and noise trials in black and gray colors, respectively, in the Constant size verbal report experiment. The two distributions correspond to verbal responses before the reaching action (on the left) and to verbal responses before the grasping action (on the right). d', β, and the corresponding likelihoods are as in Figure 8A.

and grasping trials. Figure 8B reports the same analysis for verbal perceptual responses. We found that in reaching trials the d' was 0.41 (Figure 8B-left) and in grasping trials it was 0.36 (Figure 8B-right). In this case, the distances between the signal and the noise distributions decreased, demonstrating a weaker ability in discriminating the PK and the NPK conditions with respect to the manual experiment in both reaching and grasping movements. The β value in reaching trials was 1.501 and corresponded to signal and noise likelihoods of 0.08 and 0.03, respectively (Figure 8A-left). In grasping trials, we found similar values compared with reaching, corresponding to a β value of 1.35 and to

signal and noise likelihoods of 0.11 and 0.06, respectively (Figure 8A-right). When the participants responded verbally in Experiment 2, they showed a slight tendency to judge the objects to be smaller in the PK condition with respect to the NPK condition, but they were less able to discriminate the two conditions compared to the results of the manual experiment (Experiment 1). The SDT analysis suggested that the ability in discriminating the PK and NPK condition was significantly higher for perceptual responses given manually.

Finally, we investigated how the NPK and PK conditions affect the correlation between the MGA of grasping movement and the perceptual responses before the movement. In Experiment 1, the manual experiment, we found that the correlation coefficient between MGA and the perceptual responses before the grasping movement was 0.41 ($p = 0.23$) in the NPK condition, and it was 0.85 ($p < 0.001$) in the PK condition. In Experiment 2, the verbal experiment, the values of correlation coefficient were 0.85 ($p = 0.0016$) in the NPK condition and 0.94 ($p < 0.001$) in the PK condition. In both experiments, the analysis showed an increasing correlation between perception and motor responses when participants knew in advance the type of movement they were required to execute. The difference between the correlation coefficients relative to NPK and PK conditions was higher in the manual report experiment compared to the difference in the verbal report experiment (0.41 vs. 0.85, Experiment 1; 0.85 vs. 0.94, Experiment 2).

Discussion

In the current study, we found direct evidence for a perceptual modification of a relevant feature such as object size before and after the execution of two types of hand movement. This was demonstrated using manual and verbal estimates of object size. These changes depended on two factors: the type of action executed and the knowledge of the subsequent action type. Changes in perception were sharpened after a grasping action compared with a reaching action, in both manual and verbal reports. In both cases, all participants perceived objects to be smaller after a grasping movement than after a reaching movement. This effect is supported by the control experiment (Experiment 3: Different size manual report) where we used different sizes of bars in the phase after the movement (phase 3) compared to the previous phases (phases 1 and 2). In this experiment, we found that the estimated size after the grasping was reduced with respect to reaching for either smaller or larger bars presented after the movements. All together, these data suggest a generalization of perception tuning given by the planning and execution of different types of action on object size perception.

The study of action effects exerted by the skeletomotor system on perception has been focused on the evidence that relevant features of objects, such as size or orientation, prime the perceptual system in order to execute a more accurate subsequent grasping movement. Indeed, Gutteling et al. (2011) demonstrated an increased perceptual sensitivity to object orientation during a grasping preparation phase. The effect of action-modulated perception has also been shown to facilitate visual search for orientation. Bekkering and Neggers (2002) analyzed the performance of participants that were required to grasp or point to an object of a certain orientation and color among other objects. They demonstrated that fewer saccadic eye movements were made to wrong orientations when participants had to grasp the object than to point to it (see also Hannus et al., 2005).

Considerable evidence of oculomotor and skeletomotor systems has demonstrated the action-modulation effect on perception during the preparation phase of movement (Deubel & Schneider, 1996; Gutteling et al., 2011; Hoffman & Subramaniam, 1995; Neggers et al., 2007). Our study suggests a modulation effect also *after* the execution when information is no longer necessary for a successful action. In fact, our findings suggest that the perceived sizes of objects are scaled by the type of action. For example, it was demonstrated that the perceived distance of reachable objects is scaled according to the use or not of a hand tool when performing a reaching action. In fact, objects appeared closer when participants reached with a tool than when they did without one (Witt & Proffitt, 2008; Witt, Proffitt, & Epstein, 2005). More specifically for grasping, a study by Linkenauger and colleagues (Linkenauger, Witt, & Proffitt, 2011) about size object perception suggests an interdependence of perceived sizes of objects with the action-capabilities. Linkenauger and coworkers found that objects looked smaller when placed in or judged relative to their right hand compared to their left. They interpreted these results as demonstrating that perceivers use the extent of their hands' grasping abilities as perceptual rulers to scale the apparent size of graspable objects. In other words, the perceived sizes of graspable objects are scaled by the action capabilities of the hand relevant to the intended action. In our experiments, there are some differences. Participants perceived the bars to be smaller after a grasping than after a reaching action performed with the same right hand. In our case, we cannot refer to action capabilities of the hand used for the movement, but to the type of action from which we can directly extract size information. The execution of grasping tuned the perceptual system and defined the

ruler through scaling the size of graspable objects by the use of visual and proprioceptive sensory feedbacks given by the grasping execution.

Other evidence suggests that experienced-induced changes in visual processing near used tools (Reed, Betz, Garza, & Roberts, 2010) and the hands of other actors (Sun & Thomas, 2013) occur. Additionally, acting with the hands introduces action-specific shifts in the way in which visual information near the hands is processed (Thomas, 2015, 2017). These findings may be aligned with our results because they support the idea that specific actions have an impact on visual processing also in tasks that measure the amount of changes in size perception and not only the detection of a certain stimulus.

The use of two-dimensional objects in the present study represents an important aspect that could have an impact on the results. Recent evidence showed that, during action planning and execution, the neural representations of real three-dimensional objects versus two-dimensional ones differed more for grasping movements than for reaching movements (Freud et al., 2017). This is because grasping three-dimensional objects involves fine-grained planning and anticipation of the consequences of a real interaction. In other words, it means that if the grasping action is affected by the realness of the target objects, this requires more elaborated planning based on visual cues to predict the consequences and execute the movement successfully. Our results demonstrated that the planning and execution of a grasping movement influences the size perception but not in terms of increased accuracy (see Figures 3 through 5). The main reason could be attributed to the use of two-dimensional objects that did not require a fine elaboration of visual properties. Moreover, grasping two-dimensional objects does not benefit from tactile feedback that can be used to optimize manipulation for better performance in subsequent trials (Safstrom & Edin, 2008) and this may be a critical factor in the observed behavioral performance. So, the use of three-dimensional objects could affect the visual perception after a grasping movement differently from a reaching movement, but these changes may be beneficial for a better matching of the perceived sizes with the real sizes. We found also that verbal perceptual responses were more veridical in both reaching and grasping with respect to manual perceptual responses where the participants typically underestimated the object sizes. We can postulate that the rescaling effect given by the planning and execution of the movement could be stronger and additive on manual responses compared with verbal responses, as the same movement effector was used to indicate the object size. However, future studies must be addressed to clarify these aspects.

To summarize, we demonstrated that the planning and execution of grasping movement rescaled the size perception of two-dimensional objects following a mechanism that could be dependent on the visual and/or proprioceptive matching of the fingers with the outer border of objects. Then, this is integrated with the prior knowledge about object properties gained through former experience (Bayesian theory, Körding & Wolpert, 2006; Van Beers, Wolpert, & Haggard, 2002). Bayesian theory has been applied to formalize processes of cue and sensorimotor integration (Körding & Wolpert, 2006; Van Beers et al., 2002). According to this view, the nervous system combines prior knowledge about object properties gained through former experience (prior) with current sensory cues (likelihood), to generate appropriate object property estimations for action and perception (Hirsiger, Pickett, & Konczak, 2012).

Effect of Knowledge of subsequent action type on size perception

In the present study, we found an effect of the knowledge of the subsequent action type on object size perception not specific for movement type. Behavioral (Baldauf, Wolf, & Deubel, 2006; Deubel & Schneider, 1996; Gutteling et al., 2011) and electrophysiological (Baldauf & Deubel, 2009; Eimer, Forster, Van Velzen, & Prabhu, 2005; Eimer, Van Velzen, Gherri, & Press, 2006; Gherri, Van Velzen, & Eimer, 2009) studies demonstrated that preparation of reaching or grasping movements alters the sensory processing at—or near to—the goal location, such that visual perception is facilitated. This suggests a tight coupling between action and perception because sensory perception is facilitated by the action that is being planned. In Gutteling's study (Gutteling et al., 2011) the orientation, and not the luminance, was a relevant feature to correctly configure fingers to grasp. Then, the correlation between selection of relevant information for action and programming of correct movement could constitute a single process and such a model might represent an extension of the premotor theory of attention (Rizzolatti, Riggio, Dascola, & Umiltá, 1987), which was initially used to explain the link between ocular movements and reorienting of attention and successively was extended to the skeletomotor system. In this view, the premotor theory of attention claims that programming of a motor act coincides with the attentive preparation that facilitates it.

Our tasks presented a perception phase before and after movement where in the first case (before) participants could know or not the type of movement to subsequently execute. We found that the knowledge of action type was a factor modulating size perception.

In fact, participants perceived the bars to be smaller during the condition where they knew the subsequent action (PK) compared with the other condition where they did not know the subsequent action (NPK) for both reaching and grasping and in both verbal and manual experiments (Figures 7 and 8). Interestingly, we found that the perceptual responses before the grasping movement were more correlated to the maximum grip aperture in the PK condition with respect to the NPK one. The significance of these results is in line with the evidence from behavioral research suggesting that motor planning processes do increase the weight of visual inputs. Hand visual feedback has been found to have a greater impact on movement accuracy when participants prepare their movements with prior knowledge that vision will be available during their reaches (Elliott & Allard, 1985; Zelaznik, Hawkins, & Kisselburgh, 1983). Moreover, motor preparation facilitates the processing of visual information related to the target of movement. Similarly to Gutteling et al. (2011) for object orientation, Wykowska and colleagues (Wykowska, Schubö, & Hommel, 2009) reported that the detection of target size was facilitated during the planning of grasping but not during the planning of pointing. All these studies show the ability of the brain to modulate the weight of visual inputs and provide an illustration of the importance of the context in visual information processing. Increasing the sensitivity of the visual cortical network could be the neural mechanism underpinning the greater impact of vision in circumstances where vision is critical for controlling movements. In line with all these studies, our findings suggest that the knowledge or not of the subsequent movement type defines a context that modulates the perceptual system. When participants knew the subsequent movement, the perceptual system was within a definite context, and the perceived object was smaller and more correlated to action, scaling the measures according to hand motor abilities. In the other case, participants were in an uncertain context about the subsequent action, and the perceptual system used different rules to scale the size. In both cases, the results of the defined and undefined context were present in different magnitudes in verbal and manual reports, suggesting a general effect not driven by modality response. Another hypothesis can be that the participants detected only the colors of the stimuli to decide how to respond in the PK condition and paid less—or different—attention to the size.

Figure 9 generalizes the principal findings of this study. Here, perception is represented by arrows passing throughout two modulation levels: the context represented by the knowledge of action type and the action represented by reaching and grasping movements. The arrow thickness is proportional to size estimations. The first level of modulation, the context, was not specific for the action type since it modulated the responses in a similar way before reaching and grasping. This could suggest two different representations of object size that depend on the knowledge or non-knowledge of the subsequent action type. The second level, the action, specifically shaped the perceptual responses according to the type of movement executed. This level significantly reduced the size perception after the grasping movement. No statistical interaction between knowledge condition and action type execution was found, suggesting that the two levels of modulation were not jointly processed by the brain. Thus, they were present in both modality responses used but the extent of modulation was different in the two (weaker for verbal responses).

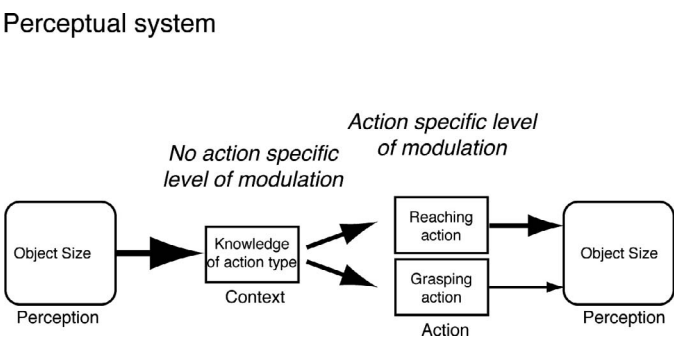

Figure 9. Summary of size perception modulation by the knowledge of action type and by the execution of the reaching and grasping actions. The thickness of the arrows is proportional to size perceptual responses. The perceptual responses are modulated by the context and by the reaching and grasping actions. The knowledge of subsequent action type decreased the responses, and they were further decreased passing throughout the action channel, particularly the grasping action.

Conclusions

In summary, we found that after the execution of a grasping movement, the perception of object size is modulated, revealing a tendency to perceive the object to be smaller after the movement than before. This modification of perceptual responses was consistent with the view that perceivers scaled and recalibrated the extents of graspable objects using visual and proprioceptive feedback of the finger boundaries of their hand for grasping.

Beyond the action-modulation effect, the knowledge of subsequent action type influences the object perception. In fact, the defined or undefined context generates different perceptual responses not specific for movement type. More generally, the present findings are in line with the view that the brain dynamically modulates the weight of sensory information during the preparation and execution of movements (Blouin,

Saradjian, Lebar, Guillaume, & Mouchnino, 2014; Lebar, Bernier, Guillaume, Mouchnino, & Blouin, 2015) and, in this view, the perceived sizes of objects are seen in terms of the action that the object affords.

Keywords: perceptual behavior, motor behavior, object size processing, knowledge of action type

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Commercial relationships: none.
Corresponding author: Annalisa Bosco.
Email: annalisa.bosco2@unibo.it.
Address: Department of Pharmacy and Biotechnology, University of Bologna, Bologna, Italy.

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