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RESEARCH ARTICLE

Grasping in wonderland: altering the visual size of the body recalibrates the body schema

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Abstract Can viewing our own body modified in size reshape the bodily representation employed for interacting with the environment? This question was addressed here by exposing participants to either an enlarged, a shrunken, or an unmodified view of their own hand in a reach-to-grasp task toward a target of fixed dimensions. When presented with a visually larger hand, participants modified the kinematics of their grasping movement by reducing maximum grip aperture. This adjustment was carried over even when the hand was rendered invisible in subsequent trials, suggesting a stable modification of the bodily representation employed for the action. The effect was specific for the size of the grip aperture, leaving the other features of the reach-to-grasp movement unaffected. Reducing the visual size of the hand did not induce the opposite effect, although individual differences were found, which possibly depended on the degree of subject's reliance on visual input. A control experiment suggested that the effect exerted by the vision of the enlarged hand could not be merely explained by simple global visual rescaling. Overall, our results suggest that visual information pertaining to the size of the body is accessed by the body schema and is prioritized over the proprioceptive input for motor control.

Keywords Body schema · Body image · Body-size distortion · Reach to grasp · Vision · Proprioception

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Introduction

Visual modifications of the size of the body effectively impact the way we experience the world. For example, the perceived visual size of the body has been shown to modulate: tactile perception (de Vignemont et al. 2005); haptic perception (Bruno and Bertamini 2010); pain perception (Moseley et al. 2008; Mancini et al. 2011); the perceived size of objects, their distance from the observer (van der Hoort et al. 2011); and the rubber hand illusion (Pavani and Zampini 2007).

A recent study by Marino et al. (2010) showed that visually altering the perceived size of the body also affects motor control. In particular, viewing one's own enlarged hand while performing reach-to-grasp movements caused a decrease in maximum grip aperture (MGA), which persisted even after the visual feedback of the enlarged hand was removed. This result suggests that visual modifications of body size can significantly and persistently affect the internal model of the body used for motor planning and control. Interestingly, these changes were observed only for a visually enlarged hand, while no effects were found for a shrunken hand.

However, Marino et al.'s study (2010) left important questions open, which constitute the aim of the present investigation. The main unresolved issue pertains to whether the internal model of the body proposed by the authors can be related to the classic concept of *body schema* (Paillard 1999; Berlucchi and Aglioti 2010). The body schema is considered a sensorimotor map of the body and its parts mainly based on proprioception, and used to guide action in a bottom–up fashion. As such, it is classically distinguished from the *body image,* regarded as a pictorial description of the body which is mainly based on visual exteroception, it is capable of top–down influences, and it incorporates notions from phenomenological, subjective experience (Gallagher 2005; Head and Holmes 1911–1912; Kammers et al. 2010). The fact that visually enlarging the hand reliably changes the execution of grasping movements suggests that pictorial information pertaining to the body size could actually be accessed by the body schema and utilized for motor control. Moreover, this access would happen with reference to short-term representations and not with reference to long-term, previously stored records of the size of the body. In this way, if the visual appearance of the hand size changes, the control of movements should be updated accordingly. However, the study of Marino et al. (2010) did not provide conclusive evidence in this respect. In fact, when the image of the hand is optically enlarged or shrunken relative to a target of constant size, several issues in the control of the hand potentially arise, being possibly responsible for the observed result.

First, the visual position of the hand relative to the target changes, causing an increase or a decrease in the distance between the hand and the target in the case of the enlarged or shrunken hand, respectively. This happens as a consequence of the optical enlargement/shrinkage of the image, which expands/contracts concentrically not only the hand, but also the space between the hand and the target, so that the hand "drifts" farther away from/closer to the target. It is known that the hand-target distance does not affect the MGA (Paulignan et al. 1997). However, varying the hand-target distance has been shown to influence the movement time, the time to peak velocity of the wrist, and the time to maximum grip aperture (Paulignan et al. 1997). This factor could therefore influence the motor control of the hand under this hand-size visual manipulation.

Even more importantly, the change in the visual distance between the hand and the target is accompanied by a change in the visual speed of the hand movement, with movements being visualized on the monitor as faster in the case of the enlarged hand and as slower for the shrunken hand. It is known that a significant modification in the transport speed of reach-to-grasp movements induces changes in the kinematics, not only of the transport component, but also of the grasp component (Rand et al. 2006). If movements were perceived as significantly faster/slower, changes in movement kinematics would be expected in three interconnected parameters: wrist velocity, wrist acceleration and, crucially, grip aperture (Rand et al. 2006).

Another factor that could influence the control of the hand under the hand-size visual manipulations is the amount of precision required for accomplishing the task, which likely becomes higher for the enlarged hand as the object seems now relatively smaller. The analysis of the deceleration phase of the reaching component would be informative of whether this factor could play a role in this context as it is sensitive to changes in movement accuracy (Marteniuk et al. 1987).

More in general, it can be noted that the enlarged or shrunken hands are at least unusual effectors, compared to the real-size hand. This raises the possibility of differences in the control of the hand due to a greater margin of uncertainty. These differences could play a role in affecting kinematic parameters such as the time to reach peak velocity, the time to MGA and MGA itself (Jacobson and Goodale 1991). Since the study of Marino et al. (2010) focused only on the MGA and the time to MGA, their results cannot disambiguate between a specific manipulation of the body schema and these other potential confounding factors.

Another study also manipulated the visually perceived size of the hand in a reach-to-grasp task (Karok and Newport 2010). In addition to the MGA, these authors reported data for reach movement time, peak velocity, and deceleration profiles. The authors confirmed the reduction in MGA for the enlarged hand condition. Furthermore, they found an increase in reach peak velocity and a decrease in movement time. However, in this study, the size of the hand was progressively enlarged *throughout* each movement execution. Performing a movement while perceiving a progressive change in one's own body size might have generated peculiar kinematic patterns per se, making these results not directly informative about the relationship between the visual size of the body and the body schema.

The present study was primarily addressed at clarifying the nature of the kinematic effects previously reported under stable visual modification of the hand size. We employed a detailed kinematic description of the reach-to-grasp movements. If the experimental manipulations were to produce a change specifically attributable to the body schema, then a selective modulation of the MGA should be expected. If, otherwise, different or additional mechanisms are responsible for the change of the MGA, then pattern of changes in other components of the movement kinematic should be observed.

Marino et al. (2010) also described a carryover pattern such that the reduction in MGA under the enlarged hand condition was maintained even when the vision of the hand was removed in a subsequent block of trials. We maintained this aspect of the design, in order to observe the evolution in any of the aforementioned kinematic features when the visual feedback was removed.

In a second experiment, we investigated the possibility that the effects exerted by hand size on grasping are not direct, but mediated by a general visual rescaling of the objects toward which grasping is directed. The visual size of the body has been shown to act as an anchor to scale the visual size of the other objects in the visual scene (Linkenauger et al. 2010). From this perspective, grasping a target of a given dimension with an enlarged or shrunken hand could parallel grasping a correspondingly smaller or bigger target with a normal size hand. However, in this case, also changes in wrist movement timing should be expected. In fact, it is known that the duration of aiming movement is inversely proportional to the target size (Fitts 1954). To test whether hand size has direct or indirect effects on reach-to-grasp movements, we compared the results from Experiment 1 with a control experiment, in which we manipulated the target size, rather than the hand size. If the effect of hand size on grasping is indirect and mediated by a change of perceived object size, a modulation of reach duration and MGA should be observed both in Experiments 1 and 2. Alternatively, if the hand size exerts a direct effect on grasping, measurements of wrist movement time should show no change in Experiment 1 and the modulation of total reach duration should be observed in Experiment 2 only.

Finally, we explored the possible asymmetric effects exerted by visual modifications of hand size on these movements. Reports of the effects of shrinking the visual appearance of the hand are contradictory, with some studies showing effects in a direction opposite to the enlarged condition (Mancini et al. 2011; van der Hoort et al. 2011) and other studies showing no reliable effects (de Vignemont et al. 2005; Marino et al. 2010; Pavani and Zampini 2007). Such a lack of effect could be due to a reduced visual saliency of the shrunken images of the body as compared to the enlarged ones, with the result that observers are less sensitive to them despite the two conditions employ a physically symmetrical scaling factor. Here, we utilized a large sample size to enhance statistical power so to detect any potential effects, even though small, of shrunken-hand manipulation. Additionally, we created two clusters of subjects, with higher versus lower variability in the baseline measurements of MGA. We tested whether a reliable effect of the shrunken-hand manipulation could be evidenced in the subject with a lower amount of noise in the spontaneous control of the hand. Within such a large sample, we also employed an exploratory analysis to investigate whether individual differences in baseline motor control and in anthropometric factors such as subject's hand size, body height, and weight could predict individuals' sensitivity to the modifications of visual hand size.

Experiment 1

Materials and methods

Subjects

Forty neurologically unimpaired participants (31 females, age 22.2 ± 3.6 years) were recruited as unpaid volunteers. All participants were right-handed according to the Edinburgh Handedness Inventory (Oldfield 1971) and had normal or corrected-to-normal vision. The study was conducted

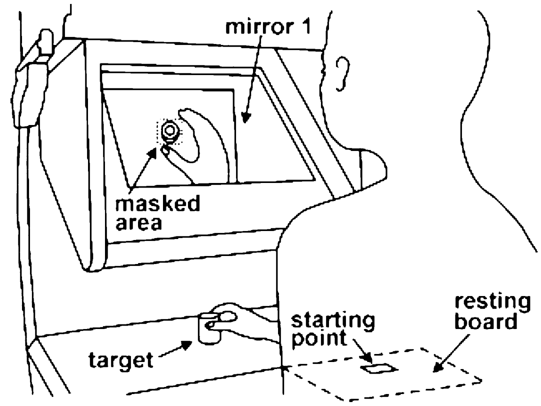

Fig. 1 A schematic sketch of the experimental apparatus

in accordance with guidelines established by the Declaration of Helsinki (1964).

Apparatus

Participants sat at a table (645 × 470 mm), in a dimly lit room, with their right hand resting on a board and their right thumb and index finger held in the pinch position over a piece of adhesive paper that indicated the starting point (Fig. 1). They looked at a 45° upward-tilted mirror (Mirror 1), suspended 180 mm above the table. The mirror completely prevented participants from directly seeing the table and their own hand throughout (see Marino et al. 2010 for a detailed description of the apparatus).

Participants were asked to reach and firmly grasp a plastic cylinder (diameter 40 mm), centrally positioned on the table and uniformly illuminated by three halogen lamps fixed behind the mirror. The task required participants to perform the grasping movement with the right hand using a precision grip (i.e., using the thumb and the index finger), without lifting the target. The cylinder was fixed to the table. A digital video camera (NV-GS17, Panasonic, 48 kHz), invisible to the subject, acquired real-time images of the table from the participants' perspective through a 45° downward-tilted mirror (Mirror 2) placed behind the upward-tilted mirror. These images were sent to a video mixer (MXPro Videonics), which extracted the image of the hand from the actual table and superimposed it on a fixed picture of the table and the target, sent through an alternative video channel (i.e., Chroma-key technique). This composed image was then sent to a CRT 22-inch color monitor (SyncMaster-1200nf Samsumg) suspended face down over the upward-tilted mirror, so that the participants could visually follow online (the actual delay of the video system was 94 ms; similar delays have been previously reported as being largely unnoticed, see Keetels and Vroomen 2012) their own grasping movements superimposed on the fixed image of the target cylinder. This setup creates a situation in which participants can see their own hand enlarged or shrunken, by zooming in or out with the video camera, while the target object keeps a constant size (see Marino et al. 2010 for further details).

It should be noted that using this apparatus, two visual inconsistencies are generated as participants actually touch the object: when the hand is enlarged, the fingers are seen to be close to the target surface without touching it, whereas when the hand is shrunken, the fingers are seen to enter inside the target. We therefore masked the grasp contact point to avoid interference effects by these inconsistencies by centrally sticking a squared piece of paper (60 mm^2) on Mirror 2. This paper was of the same color of the table top, so that it could be filtered away by the video mixer, while hiding the hand as it made contact with the target.

An optoelectronic motion analyzer (SMART system BTS, sampling rate of 120 Hz, accuracy <0.2 mm) recorded the 3D spatial position of three passive reflective markers fixed on the tip of the right thumb (marker 1), the tip of the right index finger (marker 2), and the styloid process of the ulna (marker 3) of the participant. Markers 1 and 2 were used to compute the following kinematic parameters of the grasping component: total grasp time (GTotDur), maximum grip aperture (MGA), time to maximum grip aperture (TMGA), peak velocity of finger opening (GOpenPVel), time at peak velocity of finger opening (TGOpenPVel), peak velocity of finger closing (GClosePVel), time at peak velocity of finger closing (TGClosePVel). Marker 3 was used to compute the following parameters of the reaching component: total reach time (RTotDur), reach peak velocity (RPVel), time to reach peak velocity (TRPVel), reach peak acceleration (RPAcc), time to reach peak acceleration (TRPAcc), reach peak deceleration (RPDec), time to reach peak deceleration (TRPDec).

Experimental design and procedure

Participants performed the reach-to-grasp task under four different visual feedback conditions: real-size hand (RH), no vision (NV), visually shrunken hand (SH), and visually enlarged hand (EH). Under the RH condition, participants could see both the target and their grasping hand at their actual size. Under the NV condition, participants could only see the picture of the target sent through the alternative video channel without receiving any visual feedback from their movements (open-loop grasping). Under the SH and the EH conditions, the image of the participants' hand was, respectively, shrunk or enlarged by zooming out or in with the video camera by a physically equivalent factor (magnification factor 0.65 and 1.35, respectively), while the picture of the target sent through the alternative video channel was kept constant. We tested both the direct effect of modified visual hand size on reach-to-grasp movements (exposure blocks) and any carryover effect on open-loop movements (post-exposure blocks) within a single experimental session consisting of seven blocks (comprising of 10 reach-to-grasp movements each, for a total of 70 trials). In blocks 1 and 2, the baseline measures for the RH and NV conditions were collected, respectively. Blocks 3 and 6 consisted of either the EH or SH conditions, in counterbalanced order across participants, each followed by a NV condition (post-exposure blocks 4 and 7). In block 5, participants again performed the task under the RH condition, as a washout from any influence following the previous exposure to the visual modification of the hand size, before being exposed to the opposite modification. On each trial, participants grasped the target with their right hand at a go-signal presented from the loudspeakers. At the end of the trial, they put their hand back to the resting board. Each trial lasted about 3 s with an inter-trial interval of about 8 s, during which they could relocate the fingers over the starting point by touching the adhesive tape stuck on the resting board and return to the closed pinch position.

Participants were given a brief training session under the RH condition in order to ensure that they could accomplish the task properly. At the end of the experiment, a measure of each participants' hand size was taken by recording their maximum possible finger aperture, by means of the opto-electronic system.

Results

Data were analyzed offline for each trial and then averaged across trials for each experimental condition and participant.

Effects of visual manipulation of hand size

Averaged values measured for each kinematic parameter were separately submitted to a mixed two-way analysis of variance (ANOVA) with Experimental Block as a three-level (RH, SH, and EH) within-subjects factor and Block Order as a two-level (EH/SH or SH/EH) between-subjects factor. Block Order was included as a factor to verify whether having seen the hand enlarged or shrunken could influence (e.g., interfere with) the subsequent opposite manipulation.

With respect to the grasping parameter MGA, the analyses revealed a main effect of Experimental Block ($F[2,39] = 5.09$, $p < .009$, $\eta_p^2 = .12$). No significant effect of Block Order or of their interaction was found. Paired sample t tests revealed that in the EH exposure block, MGA was significantly smaller compared to the RH block (MGA RH: 94.5 ± 9.5 mm, EH: 91.7 ± 9.9 mm, $t = 2.65$, $p = .012$). No significant differences in MGA were found between the RH and the SH blocks (SH: 93.5 ± 9.9 mm, $t = 1.17$, $p = .249$). With respect to the other grasp component parameters, as well as for all parameters of the reaching component, the analyses did not revealed any significant effects. The left

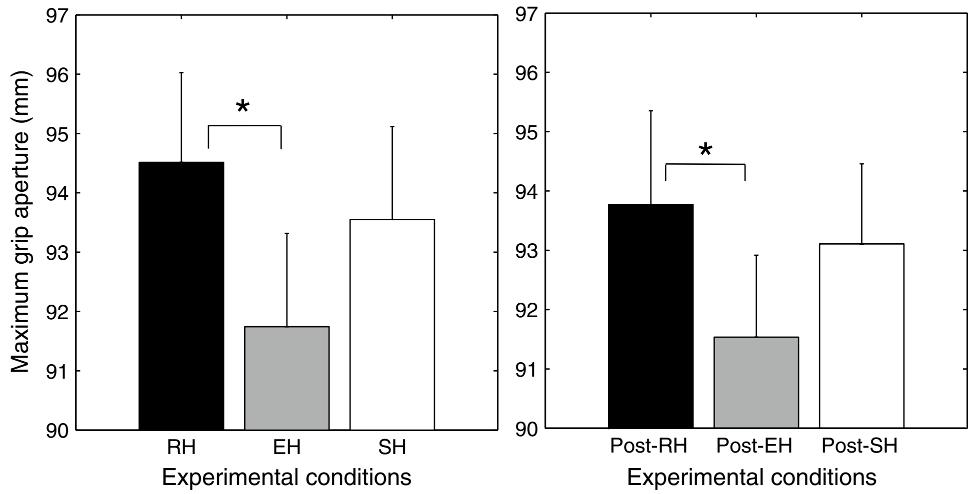

Fig. 2 Mean maximum grip aperture (±standard error) in the six experimental blocks. *RH* real hand, *EH* enlarged hand, *SH* shrunken hand; post = no-vision block. *Left Panel* The visual enlargement of the hand is associated with a significant reduction in maximum grip aperture as compared to the real-size hand condition. *Right Panel* This reduction is maintained even when the visual feedback of the hand is removed (10 trials under no-vision condition)

panel of Fig. 2 shows the modulation of MGA through the experimental blocks.

Carryover effects

Averaged values measured for each kinematic parameter were also separately submitted to a mixed two-way ANOVA with No-vision Block as a three-level (post-RH, post-SH, and post-EH) within-subjects factor and Block Order as a two-level (EH/SH or SH/EH) between-subjects factor. For the MGA parameter, the analyses revealed a main effect of No-vision Block ($F[2,39] = 4.1$, $p = .02$, $\eta_p^2 = .1$). No significant effect of Block Order or of their interaction was found. Paired sample t tests revealed that in the post-EH block, MGA was significantly smaller, compared to the post-RH block (MGA post-RH: 93.7 ± 9.9 mm, post-EH: 91.5 ± 8.7 mm, $t = 2.39$, $p = .022$). No significant differences in MGA were found between the post-RH and the post-SH block (post-SH: 93.1 ± 8.5 mm, $t = .77$, $p = .447$). No difference among the no-vision exposures was found for any other grasping or for any reaching parameter. The right panel of Fig. 2 shows the modulation of MGA through the no-vision bocks.

Response to the SH and variability

Participants were divided in two groups on the basis of their MGA standard deviation measured for the RH exposure block, using a median split procedure (split value: 4.6 mm). The two resulting groups comprised of 20 participants each. Independent t tests showed that the two groups were homogeneous with regard to both MGA in the RH block and to hand size (i.e., maximum possible finger aperture; both $p > .05$, see Table 1). To test the hypothesis that a reliable response to the SH manipulation was related to subject's baseline variability, MGA was submitted to a mixed two-way ANOVA with Experimental Block as a two-level within-subjects factor (RH and SH) and Group as a two-level between-subjects factor (low variability and high variability). The ANOVA revealed that none of the two factors yielded a significant main effect, but their interaction was statistically significant ($F = 4.35$, $p = .044$, $\eta_p^2 = .1$).

This interaction indicated that participants in the high-variability group showed a tendency to decrease their MGA in the SH block, which was near to significance ($t = 1.97$, $p = .063$), while the opposite behavior in the low-variability group was not statistically reliable ($t = -.8$, $p = .436$) (Table 1).

Table 1 Low- and high-variability groups have been created using a median split procedure on the standard deviation of maximum grip aperture from the baseline real-hand condition (StDev MGA real hand)

	Low-variability group	High-variability group
StDev MGA real hand (mm)	3.5	6.5
Mean MGA real hand (mm)	94.7	94.3
Mean MGA shrunken hand (mm)	95.4	91.7
Mean MGA enlarged hand (mm)	94.3	89.1
Hand size (mm)	143	143.7

Kinematic parameters as predictors of response to SH: an exploratory analysis

We calculated the MGA differential value between SH and RH blocks as: SHdeltaMGA = MGA(SH) − MGA(RH). Positive and negative values indicate an update of body schema, respectively, compatible (increase in MGA) or incompatible (decrease in MGA) with the SH manipulation. A stepwise

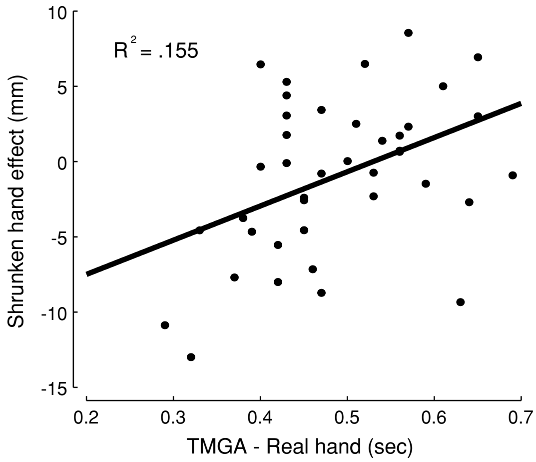

Fig. 3 *TMGA* time to maximum grip aperture for the baseline condition (real hand). Shrunken-hand effect is computed as the difference in maximum grip aperture (MGA) between the shrunken-hand condition and the real-hand condition (baseline). Participants that exhibited in the baseline a longer TMGA tended to increase the MGA under the shrunken-hand condition

linear regression analysis was run to identify whether the kinematic parameters of grasping measured in the RH block are reliable predictors of SHdeltaMGA. Anthropometric factors such as participants' weight, height, and hand size were also considered as potential reliable predictors. The procedure revealed a model predicting 15 % of the SH variance. The TMGA was the only reliable predictor (regression equation: SHdeltaMGA $= -11.8 + 0.42 \times$ TMGA; adjusted $R^2 = .155$, $p < .008$). Thus, participants that exhibited in the baseline a longer time to maximum grip aperture tended to increase the MGA in the shrunken-hand condition (Fig. 3).

Experiment 2

Experiment 1 showed that altering the visual size of the hand produced no effects on movement duration. This suggests that the effect on MGA is direct and that is not mediated by a general rescaling of the visual scene. Experiment 2 was intended to provide further evidence for the hypothesis that effects exerted by hand size on the kinematics of grasping are not due to a visual rescaling mechanism of object size relative to hand size: participants were presented with a setup that replicated the exact relative proportions between the hand and the object sizes as in the RH and EH conditions of Experiment 1. However, in this case, we manipulated the object size, leaving unaltered the size of the hand. Consistent with Fitt's law, according to which the time of aiming movements is inversely proportional to the target size and in contrast to the results obtained in the previous experiment, a significant modulation of movement duration should be observed here.

Materials and methods

Subjects

Twenty neurologically unimpaired participants (16 females, age 23.4 ± 2.6 years) were recruited as unpaid volunteers in accordance with the Declaration of Helsinki (1983). All participants were right-handed according to the Edinburgh Inventory and had normal or corrected-to-normal vision.

Apparatus

The apparatus was the same as in Experiment 1, with the exception that a modification of target size, rather than hand size was introduced. Two wooden cylinders served as target objects: one was exactly the same size of the object used in Experiment 1 and the other had a diameter of 26 mm, corresponding to the 65 % of the size of the original object. The size ratio between this cylinder and subject's hand exactly matched the hand/target size ratio of EH block in Experiment 1.

Experimental design and procedure

Participants performed a block of 10 reach-to-grasp movements with each of the two target objects. The order of the two blocks was counterbalanced across subjects. On each trial, participants grasped the target with their right hand at a go-signal presented from loudspeakers. Afterwards, they put their hand in a closed pinch position back to the resting board. Each trial lasted about 3 s with an inter-trial interval of about 8 s, during which they could relocate the fingers over the exact starting point by touching the adhesive tape stuck on the resting board. Participants were given a brief training session to ensure that they could accomplish the task properly, using a third wooden cylinder of 54 mm diameter.

Results

Data were analyzed offline for each trial and then averaged across trials for each target object and participant. MGA was submitted to a paired sample t test revealing that finger aperture was significantly smaller for the small object (90 ± 13 mm) as compared to the normal object (96 ± 9 mm; $t = 4.23$, $p < .001$). Mean total reach duration was submitted to a paired sample t test revealing that also movement time differed between the two conditions, being significantly higher for the small object (0.91 ± 0.16 s) as compared to the normal object (0.85 ± .14 s; $t = -3.13$, $p < .005$, see Fig. 4).

Fig. 4 Mean movement time (± standard error) and target size. Reducing the size of the target produced an increase in movement time, as predicted by the Fitt's law

Discussion

This study was designed to further investigate the effects of visual modification of body size on reach-to-grasp movements. We hypothesized that these changes reflect an update of the internal bodily representation, due to altered information from visual feedback.

The experiments yielded the following main findings: first, the visual enlargement of the hand induces a decrease of hand pre-shaping during grasping, in keeping with previous investigations (Karok and Newport 2010; Marino et al. 2010). Second, the effect of the hand-size manipulation is specific for hand pre-shaping; indeed, it does not affect either the reaching or grasping components other than maximum grip aperture. Third, this specificity is carried over in trials performed immediately after, under a no-vision condition. Fourth, visual shrinkage of the hand does not modulate any parameter of the reach-to-grasp movements. Finally, the effect of the enlarged hand cannot be explained by a general visual rescaling mechanism of object size relative to hand size.

Classical models have hypothesized a dual nature of the way the brain represents our body, namely *body schema* and *body image*. The body schema is a dynamic representation of the relative positions of body parts derived from multiple sensory and motor inputs, and serves the generation of actions. On the other side, the body image is a pictorial description of the body primarily derived from the visual input and includes a topological map of body parts locations as well as lexical-semantic representations (Head and Holmes 1911–1912; Schwoebel and Coslett 2005). Interestingly, it remains unclear whether the perceived size of the body should pertain to one, to the other, or to both of these concepts. Some views consider the body size as "archetypical" of the body image (e.g., Ehrsson et al. 2005), while others regard it as a central component of the body schema (e.g., de Vignemont 2010). While it is reasonable to think that at least the visual size of the body constitutes a component of the body image (e.g., Longo and Haggard 2010; Pavani and Zampini 2007), the question of whether the visual size of the body could also play a role in the body schema and the programming of action has not been experimentally addressed, until very recently. Importantly, if the visual body size is to be ascribed exclusively to the body image, no modifications of actual motor control should be expected when the body size is experimentally modified.

To our knowledge, only two previous investigations (Karok and Newport 2010; Marino et al. 2010) employed such an experimental manipulation. Interestingly, both these studies reported modification of movement kinematics as a result. The present investigation further tested the hypothesis that the visual size of body parts could be accessed for the construction of the body schema and employed for its implementation in motor control. Similarly to these previous studies, we presented participants with enlarged or shrunken visual feedback of their own hand while performing reach-to-grasp movements. To test our hypothesis, the modification of the visual size of the hand was held constant throughout the movement (differently from Karok and Newport 2010). Furthermore, a thorough analysis of movement kinematics was performed (differently from Marino et al. 2010). We found that under stable visual enlargement of the hand size, subjects decrease their maximum grip aperture, with *no other modifications* in several key parameters of the movement. This result excludes spurious effects due to changes across different exposure blocks in the visual position of the hand, its speed, the precision required for accomplishing the task, and the familiarity of subjects with the visual feedback, which are inevitably created when distorting the visual size of the hand. Our findings also confirm that the reduction in MGA following visual enlargement of the hand is not due to the aspects of previous designs such as a progressive visual enlargement throughout the movement (Karok and Newport 2010) or mismatches between the visual and somatosensory information at the point of contact with the object (Marino et al. 2010). This decrease in MGA appears to be relatively robust, considering in particular that: (1) it is not likely a strategy for managing the uncertainty possibly generated by the modification of the visual input; in fact, it is known that grip aperture *increases*, and not decreases, as a consequence of uncertainty (Schlicht and Schrater 2007); (2) the specific reduction in MGA is carried over in subsequent no-vision trials, thus showing resistance to somatosensory afferent feedback from ongoing movements.

MGA modifications under enlarged hand exposure condition could be alternatively explained also by a global visual rescaling effect. When presenting participants an enlarged hand and a target, it is not possible to know a priori that this situation will be correspondingly rendered perceptually. On the contrary, it is conceivable that the whole scene would be rescaled, so that the hand's size would appear normal and the target would appear correspondingly smaller. The power of these shifts in perception of relative size has been nicely shown in a recent study by Linkenauger et al. (2010): when graspable objects were magnified by magnifying goggles, they appeared to shrink back to about-normal size when one's hand (also magnified) was placed next to them. However, there are reasons to suggest that these effects are not responsible for our results. First, in Linkenauger et al.'s (2010) study, both the object and the hand changed size in each condition. Instead, in our experiment, the object was always the same size, both visually and with regard to somatosensory input, for all conditions, while the hand only was subjected to visual distortions. This method likely reduced the probability that modifications of the object size were perceived. Second, Linkenauger et al. (2010) described this rescaling effect in the domain of perception. This does not automatically imply that this influences the execution of actions, given that a dissociation between action and perception has been frequently reported for various bodily illusions (e.g., Kammers et al. 2006, 2009). Finally, in the domain of action when objects are perceived to be smaller, they are approached more slowly, according to the Fitts' law (1954). In fact, we showed that in our setup when the object size is reduced by 35 %, the grip aperture decreases and, crucially, the reaching time increases. However, the increase in reaching time is not seen when the hand is enlarged relative to the object under the same magnification factor. This suggests that what we find is related to perceived changes in the hand and not in the object.

Overall, our results are suggestive of an update of a short-term representation of the body metrics employed for motor control, namely the body schema. Together with the two previous investigations, they provide direct support to the notion that visual information pertaining to the size of the body is accessed and utilized by the body schema, in addition to the body image.

It is worth noticing that the distorted visual information provided in this study, showing an enlarged hand, is in stark conflict with the somatosensory information, which remains constant. Despite the somatosensory information remaining the same, subjects changed their behavior as if they trusted more the altered visual information. This result is reminiscent of a rich literature showing a general tendency of vision to dominate proprioception (Rock and Harris 1967; Welch and Warren 1986). Visual dominance has been shown before using different paradigms, such as prism adaptation (Harris 1965), visuo-proprioceptive conflicts of target size (Rock and Victor 1964), and the rubber hand illusion (Botvinick and Cohen 1998). However, subsequent studies have also shown that the relative weight of vision and proprioception is not fixed. Instead, the two modalities are optimally combined so that visual dominance occurs only when the variance associated with visual estimation is lower than that associated with haptic estimation (Burge et al. 2010; Ernst and Banks 2002). A few relevant examples of differential weighting are: (a) the proprioceptive weight is larger when the hand is moved actively than when it is moved passively (Mon-Williams et al. 1997); (b) the proprioceptive weight decreases with increasing availability of visual cues (Mon-Williams et al. 1997); (c) proprioception weighs more in evaluating the depth dimension, while vision dominates the evaluation of azimuth (van Beers et al. 2002); (d) the target's coordinate frame, visual versus proprioceptive, determines the preferred sensory modality, vision versus proprioception, used for motor planning (Sober and Sabes 2005); (e) the presence in the visual feedback of explicit information about joint angles determines a heavier weight on vision during motor command generation (Sober and Sabes 2005); (f) synchronicity of bimodal visual-proprioceptive stimulation facilitates visual capture (Botvinick and Cohen 1998). In the present investigation, participants had to perform an active reach-to-grasp movement, with full visual feedback of their hand as well as of the target, presented with minimal delay. Our outcome of a prominent weight of vision is in keeping with the reviewed literature, as almost all the conditions outlined above favor this sensory modality over proprioception. Moreover, in the present investigation, preventing participants to lift the object limited their possibility to make use of the visual mass of the object and to update their reaching of its weight. This could have further emphasized the perceptual, rather than motor side of the visually guided movements, increasing the possibility of the perceptual distortion to affect hand movements.

As mentioned before, the effect of the exposure to an enlarged hand on reach-to-grasp movements was limited to the size of the grasp pre-shaping component. This is what is to be expected if the manipulation we were inducing was specific for the body schema and not due to changes across experimental conditions of contextual factors such as target size, hand position, and velocity. In fact while grasping requires matching volumetric information about both hand size and target size, reaching mostly relies on positional information. The information about hand size would not be relevant for computing reaching movements, which therefore would remain unchanged by hand-size manipulations. This result is not in keeping with the findings of Karok and Newport (2010), who found a decrease in movement time and an increase in peak velocity for the reaching component of grasping movements when the visual size of the hand was enlarged. Several factors can account for this discrepancy, such as those related to differences in the goal of the two studies and consequently in their experimental designs. In fact, Karok and Newport (2010) were interested to assess the weighting of a constantly changing online sensory feedback on the execution of grasping movements, while the present investigation questioned the connection between body-size visual distortions and the concept of body schema. First, these authors employed an online, progressive visual enlargement of the hand throughout each movement. This novel situation might have created per se a peculiar kinematic pattern in the control of the wrist, regardless of whether a visually enlarged hand would itself result or not in changes of reaching movements. This might have been further enhanced by the fact that, in this previous study, the hand size was randomized across trials and therefore, on any given trial, participants did not know the size of the hand in advance. Another difference in the two studies is that in the case of Karok and Newport (2010), subjects were asked to lift the object after the grasping. It would be worth to explore in future investigations whether this might be in part responsible for the different outcomes, for example due to a different emphasis on the perceptual versus motor components, or grasping versus reaching components in the two designs.

Despite a considerable sample size and a reliable effect for the enlarged hand, a significant effect of visual shrinkage of the hand on motor control did not emerge overall. This finding replicates that collected by Marino et al. (2010) using the same motor task. It also parallels previous findings showing that well-established illusions such as the rubber hand illusion (Pavani and Zampini 2007) and the illusory alteration of limb size due to tendon vibration (de Vignemont et al. 2005) fail to produce any effect in the case of limb shrinkage. Instead, the same illusions hold when the limb is enlarged (Pavani and Zampini 2007), with tendon vibration also modulating tactile perception (de Vignemont et al. 2005). Altogether, these results suggest an anisotropy of the body representation, such that our body representation may be more likely to integrate enlargements than shrinkages of body parts.

In the present investigation, we further addressed the anisotropy of body representation in different ways. First, we tested whether changes in motor control that followed visual hand shrinking could be evidenced for participants who showed more stable motor parameters under the baseline condition. It was possible that the changes induced by the experimental manipulation could have been masked by excessive noise in the data, indeed. A detectable shrunken-hand effect was predicted for participants showing lower variability of baseline motor performance. We found only a moderate support for this prediction: a significant interaction between being classified as "high-variability" versus "low-variability" performer and the direction of the shrunken-hand effect was found, as expected. However, the tendency observed in the high-variability group to decrease the grip aperture under the shrunken hand was not mirrored by an opposite tendency in the online group. Second, we employed a complementary, exploratory approach to investigate whether individual differences in anthropometric factors and features of motor control in the real-hand condition were predictive of differential responses to the shrunken hand. While the participants' anthropometric features did not show to play any role, participants who take more time for controlling the opening of the fingers tended to respond to the shrunken-hand condition in a way compatible with an updating of the body representation (i.e., increasing finger aperture). Putting together these results, a low variability in finger aperture and a longer time to achieve such aperture are suggestive of a careful, online movement monitoring, as opposed to a relatively offline strategy of performance. It is therefore possible to surmise that relying more on the online visual feedback could enhance the effect of shrunken-hand exposure, as compared to executing the movement mainly on the basis of an offline, entirely preprogrammed information. While attractive, this tentative explanation of body-size anisotropy is based on little evidence and requires further investigation.

In conclusion, we have provided new evidence for the possibility to modulate motor control through the manipulation of the visual size of the body. This line of research is of significant interest for the field of motor control rehabilitation (e.g., following stroke), with particular regard to techniques that capitalize on the role of vision (e.g., Buccino et al. 2006). The effect of the enlarged hand on grasping behavior documented here could potentially help patients in reducing unnecessary, compensatory, and abnormal movements during fine motor control exercises. A better understanding of the mechanisms that could trigger shrunken-hand effects might lead in the future to help patients to move *more* following a manipulation of the visual input, in fact a fascinating perspective.

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