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ORIGINAL ARTICLE

The visual and haptic contributions to hand perception

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Abstract Previous research has found that the perception of our hands is distorted. The characteristics of this distortion are an overestimation of hand width and an underestimation of finger length. The present study examined the role that different sensory modalities (vision and/or haptics) play in the perception of our hands. Participants pointed to their concealed hand in one of three groups: Vision+Haptics, Vision-only, or Haptics-only. Participants in the Vision+Haptics group had vision (non-informative) of the experimental setup and of the pointing hand, but no vision of the hand being estimated. They also experienced haptic feedback as the palm of the hand was in contact with the undersurface of a tabletop, where the estimations were made. Participants in the Vision-only group, instead of placing the hand to be estimated underneath the tabletop, they placed it behind their backs. Participants in this group were asked to imagine as if the hand was under the table when making their estimations. In the Haptics-only group, participants completed the task with the hand underneath the tabletop (as in the Vision+Haptics group) but did so while wearing a blindfold (no vision). All participants estimated the position of ten landmarks on the hand: the fingertip and the metacarpophalangeal joint of each digit. Hand maps were constructed using a 3D motion capture system. Participants in the Haptics-only group produced the most accurate hand maps. We discuss the possibility that vision interferes with somatosensory processing.

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Introduction

An accurate representation of the body is necessary to interact effectively with our surroundings. This is because we use our bodies as a guide to perform actions. For example, tasks such as reaching out to grab a glass of water, stepping over an obstacle, or reaching to a high shelf would be impossible without an accurate representation of the length of one's arms and legs. Body representation is defined as representations of body dimensions stored in the brain (Dijkerman & de Haan, 2007; Gallagher, 2005; Haggard & Wolpert, 2005; Paillard, 1999; Serino & Haggard, 2010). Body representation can be measured by both explicit and implicit methods. Explicit methods refer to tasks in which participants must actively assess their own body size (e.g., how long is my arm). Whereas, implicit methods are concerned with how participants perceive landmarks on their body (e.g., where is my elbow). Many studies on body representation have shown that it is accurate (Bolognini, Casanova, Maravita, & Vallar, 2012; Guardia et al., 2010; Sposito, Bolognini, Vallar, & Maravita, 2012; Sposito, Bolognini, Vallar, Posteraro, & Maravita, 2010). However, most of these studies have used explicit methods. For example, a study investigating perceived reaching capabilities asked participants to instruct the experimenter to raise or lower an object to the maximum height that the participant thought it could reach. The results showed that estimates were consistently within 90% of the participant's real maximum reachability (Wagman, Thomas, McBride, & Day, 2013). Similarly, another study found that participants were able to accurately identify the size of their bodies as well as of their body parts (Henninghausen, Enkelmann, Wewetzer, & Remschmidt, 1999). In this study, participants had to assess a series of photographs of their whole bodies and indicate which photo best reflected their body size. They also assessed the size of individual body parts like their lower leg, thigh, chest, and head. Participants were accurate in all their estimations. Other research using implicit methods, however, has shown inaccurate representation of body parts, specifically of the hands (Longo & Haggard, 2010). In this study, participants placed a hand under a tabletop, so it was hidden from view. Participants then referenced ten landmarks on their hands [the tips and metacarpophalangeal joints (mp joints) of each finger] by pointing on the tabletop to the location where they thought these landmarks were. The results showed a distorted hand featuring consistent greater hand width and shorter finger length. These findings have been replicated several times (Longo, 2014; Longo & Haggard, 2012a, 2012b; Longo, Long, & Haggard, 2012; Saulton, Dodds, Bulthoff, & de la Rosa, 2015). One interpretation for the distorted hand is that its representation reflects underlying tactile receptive field geometry (Longo & Haggard, 2011). In this study, two pairs of tactile stimuli were presented on the back of a participant's hand. Participants then judged which of the pairs of stimuli felt further apart. One of the stimuli was presented across the hand and the other was presented along the hand. Across the hand, stimuli were constantly perceived as being longer than along the hand stimuli. The authors argued that the reason why hand width is constantly overestimated and finger length underestimated, because the tactile receptive fields are anisotropic, or oval shaped.

A different possibility as to why the perception of the hands has been shown to be distorted is because during testing, visual information modified somatosensory processing, specifically haptic information. Haptic feedback refers to both tactile information from the skin receptors and proprioceptive information from the receptors in the joints, ligaments, and muscles (Grunwald, 2008; Keysers, Kaas, & Gazzola, 2010; Lederman & Klatzky, 1990). For example, on the aforementioned study by Longo and Haggard (2010), participants were asked to point on a table to where they believed their mp joints and fingertips were located, while their hand rested underneath a tabletop. Participants, therefore, had no visual information of the hand that they were estimating, but they had haptic feedback from this hand. They also had vision of the setup including the tabletop and of their free hand executing the pointing movements. This visual information, although not informative with respect to the hand being estimated, could have influenced the results. Previous research has shown that vision interferes with tactile perception. For example, in one study, participants were asked to indicate when they felt a pulse delivered to the left index finger. The results showed that there were significantly more false alarms (the participant reported a pulse when there was none) when participants had vision of their hands, suggesting that vision interferes with the tactile perception of the stimuli (Mirams, Poliakoff, Brown, & Lloyd, 2010). Another study found that when participants were blindfolded, they produced more accurate hand maps than when they had vision (Longo, 2014) suggesting again that vision could interfere with somatosensory processing. As the haptic information that the participant receives is accurate (it reflects the true location of the landmarks), whereas the visual information provides no relative cues to where the participants hand is located, this is a possible explanation for why vision may produce larger distortions in body perception.

Alternatively, it could be that haptic information interferes with visual information during the estimates of hand size. For example, a study examined if objects that resembled the shape of the human hand would also be perceived inaccurately (Saulton, Longo, Wong, Bülthoff, & de la Rosa, 2016). Participants were asked to estimate the size and shape of their own hand, a rubber hand, and a rake (using similar methods as that of Longo & Haggard, 2010). It was noted that the only condition that provided haptic feedback was when participants estimated their own hand. The results showed that the maps from the rubber hand and the rake, although distorted, were more accurate than those from the participant's hand. This finding suggests that haptic feedback could interfere with body perception.

A final possibility is that the interaction of vision and haptics leads to the inaccurate representation of hand size. If vision and haptics are interfering with one another (Mirams et al., 2010), then testing each of these sensory modalities independently should produce more accurate hand estimates. As previous research by Longo has found that when completed under one sensory modality (haptics), perception of the hand was significantly less distorted (Longo, 2014); this could suggest that the distortion is a result of conflicting sensory modalities. However, no study has investigated the implicit representation of the hand with visual but no haptic information (in healthy participants). Therefore, in the present study, a condition was added, where participants estimated the size of their hands using only visual feedback. We predicted that like haptics when vision was the only sensory modality available, hand perception would improve.

The purpose of the present study was to conduct a comprehensive examination of the role that vision and haptics play on the perception of the human hand. To investigate how different sources of sensory information shape hand perception, we designed a task, wherein participants were assigned to one of three groups: (1) Vision+Haptics; (2) Vision-only; and (3) Haptics-only. The participants in each of the three groups were required to point to where they believed that ten different landmarks on their hands were located, while their hands were hidden from view. The Vision+Haptics group completed the task while seated in front of a Plexiglas desk with one hand placed palm up against the undersurface of the Plexiglas (haptic feedback available). The Plexiglas was covered by a black tablecloth to prevent vision of the hand being estimated (only non-informative visual information was available). The participants in the Vision-only group were instructed to imagine as if their hands were placed underneath the tabletop, but instead, they rested behind their backs (no tactile feedback and no relevant proprioceptive feedback). Participants in the Haptics-only group completed the task just like the Vision+Haptics group, but they wore a blindfold to prevent non-informative visual information from playing a role in the estimations. We hypothesized that the Vision+Haptics group would yield distorted maps [as in Longo & Haggard, (2010)], whereas the Vision-only and the Haptics-only groups would show better accuracy, as they would not have conflicting sources of sensory information to rely on when making the judgements.

Methods

Participants

Fifty-one university students (45 females) participated in the study in exchange for course credit. All but two participants were right-handed. Handedness was evaluated using modified version of the Edinburgh (Oldfield, 1971) and Waterloo (Brown, Roy, Rohr, & Bryden, 2006) handedness questionnaires. Statistics were run with the inclusion of the two left-handed individuals, because their exclusion did not influence any of the statistical results and it allowed for a more inclusive sample. All participants gave written consent prior to participating.

Materials

An Optotrak Certrus sensor (Northern Digital, Waterloo, ON, Canada) recorded the position of an infrared emitting diode that was attached to the end of a wooden stylus (19.5 L × 0.5 W × 0.3 H cm). The location of the diode was recorded for 1000 ms at 100 Hz for each trial.

Procedure

Participants were divided into three equal groups: Vision+Haptics group, Vision-only group, and the Haptics-only group (17 participants per group). Participants in the Vision+Haptics group placed one of their hands palm up underneath a Plexiglas desk (41.0 L × 86.5 W cm) with a wooden shelf placed 12 cm below the Plexiglas (see Fig. 1). Their forearm was supported by a thin pillow. The table was then covered by a black tablecloth, occluding vision of the participant's hand (the occluded hand trials). Although the tablecloth prevented the participant from viewing their hand, they were still able to see the table top and the rest of the experimental setup. As in Longo & Haggard, (2010), participants estimated the location of ten different hand landmarks (the metacarpal phalangeal joints and tips of each of the five fingers; order of the landmarks was pseudorandomized between participants). They did so using a stylus to touch the top of the glass table (directly above where the hand was located). After each trial, the participant returned the stylus to a home spot that was located directly above the participant's forearm. After the participant completed the occluded hand trials, they repeated the task but with full vision of their hands (the non-occluded hand trials). The non-occluded hand trials were conducted, so the estimation trials could be compared to the real size of the participant's hand. The task was then repeated using the other hand. Starting hand was counterbalanced across participants. The Vision-only group completed the same task, but participants were asked to rest the dorsum of the hand behind their back. In this way, the palm of the hand was free from any tactile feedback. Participants then were asked to imagine as if their hand was placed palm up underneath the glass table before starting their estimations. The Haptics-only group completed the task identically to the Vision+Haptics group, but they did while wearing a blindfold (no vision).

Analyses

Participants completed a total of 200 trials: 50 occluded hand trials and 50 non-occluded hand trials per hand. In both conditions (occluded and non-occluded hand trials), participants pointed to each of the ten locations on the hand five times (for a total of 50 trials per condition). Two main analyses were conducted on the data. The first analysis consisted of a series of a priori comparisons between the real and estimated hand dimensions. These raw values were obtained by taking the distance between each average landmark location for each measure used in the analyses. These a priori comparisons were modeled after the analysis used by Longo & Haggard, (2010). The second analysis (investigating the effects of Group and Hand) consisted of a 3 × 2 repeated measures ANOVA that included groups (Vision+Haptics, Vision-only, and Haptics-only) as a between factor and Hand (left, right) as a within factor. For this analysis, the data were normalized by expressing the estimated values as a percentage of the real hand values (occluded hand − non-occluded hand)/(non-occluded hand × 100). This normalization was done to account for

Fig. 1 Setup of the experiment for the non-occluded hand condition, and then the occluded hand conditions for each of the three groups (Vision+Haptics, Vision-only, and Haptics-only). Picture **a** is the setup of the real condition for each of the three groups. Picture **b** is the estimation trial setup of the Vision+Haptics group. Picture **c** is the setup of the Vision-only group's estimation trials. Picture **d** is the setup of the Haptics-only group estimation trials

individual hand size differences or postural variability between participants (Coelho et al., 2016).

The two analyses were repeated for five dependent variables: great span, little span, finger length, thumb length, and opposition (see Fig. 2). The great span was defined as the summed distance between the tip of digit 1 and the tip of digit 5. The little span was defined as the summed distance between the tip of digit 2 and the tip of digit 5. Finger length was calculated by averaging the distance between the tip and the mp joint for each of the five digits. Thumb length was determined as the distance from the mp joint of digit 1 to the tip of digit 1. Thumb opposition was determined as the distance between the tip of digit 1 to the tip of digit 2. We included the two analyses of width as the great span includes the thumb (which is the distance that would be used to perform a power grasp), whereas the little span covers the same distance (from the index finger to the pinky) which had been previously reported (Longo & Haggard, 2010). We also included measures about the thumb (length and distance to the index finger) due to their evolutionary importance, because thumb opposition was not reported in earlier studies.

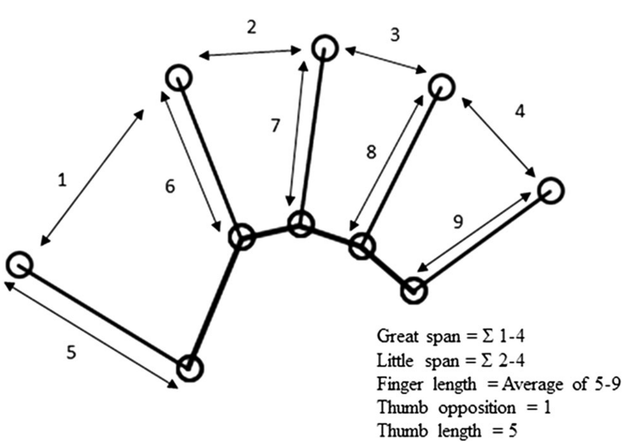

Fig. 2 Representation of the measures used in the experiment

Data processing

All trials were visually inspected, and extreme outliers were removed from the analysis (<1% of all trials). Visual inspection involved determining whether a given point was greater than 10 cm away from the mean of the other points for the same location.

Results

Table 1 summarizes the findings. Statistics are only reported for significant results.

Analysis one: occluded vs. non-occluded hand

Vision+Haptics group

Great span: hand width was overestimated in both hands [Left hand $t(16) = 2.6$, $p = .02$, $d = 1.3$; occluded hand 220.8 ± 7.5 mm, non-occluded hand 197.3 ± 5.2 mm; Right hand $t(16) = 2.7$, $p = .02$, $d = 1.4$; occluded hand 221.1 ± 8.6 mm, non-occluded hand 191.6 ± 4.9 mm].

Little span: this distance was overestimated in both hands [Left hand $t(16) = 3.7$, $p = <.01$, $d = 1.9$);

Table 1 List of distortion seen by group

	Vision+Haptics		Vision-only		Haptics-only	
	LH	RH	LH	RH	LH	RH
Great Span	↑	↑	–	–	–	↑
Little span	↑	↑	↑	–	–	↑
Finger Length	↓	↓	↓	↓	–	–
Thumb Opposition	–	–	↓	↓	–	–
Thumb Length	–	–	↓	↓	–	–

A ↑ indicates a significant overestimation, a ↓ indicates a significant underestimation, and a— no change. Arrows in grey represent measures that were approaching significance

occluded hand 125.6 ± 13.0 mm, non-occluded hand 102.4 ± 8.1 mm; Right hand $t(16) = 4.8$, $p < .01$, $d = 2.4$; occluded hand 152.2 ± 6.7 mm, non-occluded hand 110.9 ± 4.5 mm].

Finger length: participants underestimated the length of their fingers in both hands [Left hand: $t(16) = -2.7$, $p = .02$, $d = 1.4$; occluded hand 47.6 ± 1.9 mm, non-occluded hand 58.6 ± 3.0 mm; Right hand: $t(16) = -4.4$, $p = <.01$, $d = 2.4$; occluded hand 46.9 ± 1.8 mm, non-occluded hand 55.6 ± 0.8 mm].

Thumb opposition: no significant differences were found.

Thumb length: no significant differences were found.

Vision-only group

Great span: no significant differences were found.

Little span: the left hand was overestimated [$t(16) = 2.8$, $p = .01$, $d = 1.4$ occluded hand 147.5 ± 9.6 mm, non-occluded hand 119.3 ± 3.9 mm].

Finger length: participants underestimated finger length in both hands [Left hand: $t(16) = -5.8$, $p < .01$, $d = 2.9$ occluded hand 40.7 ± 1.7 mm non-occluded hand 52.2 ± 1.6 mm; Right hand: $t(16) = -6.2$, $p < .01$, $d = 3.1$ occluded hand 42.1 ± 1.15 mm, non-occluded hand 53.4 ± 1.1 mm].

Thumb opposition: the distance between the thumb and index finger was significantly underestimated for both hands [Left hand: $t(16) = -4.3$, $p < .01$, $d = 2.2$ occluded hand 51.5 ± 4.7 mm, non-occluded hand 74.3 ± 2.6 mm; Right hand: $t(16) = -4.9$, $p < .01$, $d = 2.6$ occluded hand 55.9 ± 4.0 mm, non-occluded hand 78.1 ± 2.8 mm].

Thumb length: underestimation of thumb length approached significance in both hands [Left hand: $t(16) = -2.085$, $p = .05$, $d = 1.0$ occluded hand 43.3 ± 3.4 mm non-occluded hand 50.4 ± 2.77 mm; Right hand: $t(16) = -2.068$, $p = .06$, $d = 1.0$ occluded hand 40.71 ± 3.11 mm non-occluded 47.91 ± 1.48 mm].

Haptics-only group

Great span: this distance was overestimated only for the right hand [$t(16) = 2.7$, $p = .02$, $d = 1.3$ occluded hand 208.3 ± 7.4 mm, non-occluded hand 186.5 ± 4.6 mm].

Little span: this distance was also overestimated for the right hand only [$t(16) = 2.4$, $p = .03$, $d = 2$ occluded hand 138.2 ± 7.0 mm, non-occluded hand 116.2 ± 6.5 mm].

Finger length: no significant differences were found.

Thumb opposition: no significant differences were found.

Thumb length: no significant differences were found.

Analysis two: group and hand comparisons

Great span: no main effect of group or hand was found, but the interaction approached significance [$F(2,48) = 2.909$, $p = .06$]. Follow-up paired samples t tests revealed that the values of the right hand were greater (marginally) than those of the left hand in the Haptics-only group (12.24 ± 4.4%) compared to their left hands (3.05 ± 5.67%) $p = .06$. No differences were found between the hands in the Vision+Haptics and Vision-only groups.

Little span: there was a main effect of hand [$F(1, 48) = 5.068$, $p = .03$ partial $\eta^2 = .095$], indicating that participants overestimated the width of their right hands (27.57 ± 5.56%) more than of their left hands (17.63 ± 4.57%). There was also a group by hand interaction [$F(2,48) = 5.401$, $p = <.01$ partial $\eta^2 = .184$] (see

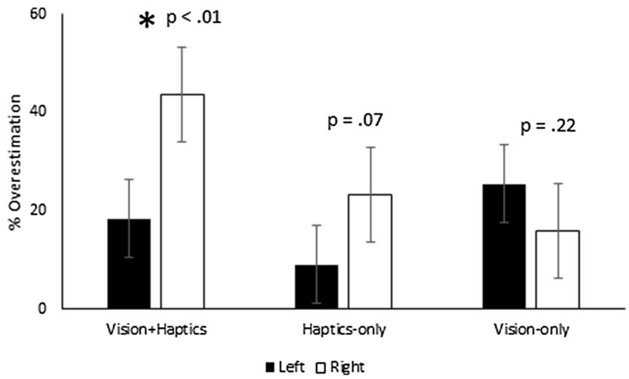

Fig. 3 Results of the group by hand interaction for the little span. The *black bars* represent the left hand and the *white bars* represent the right hand. Note the significant difference between the left and right hands in the Vision+Haptics group, but not for the other groups. *Error bars* represent the standard error of the mean

Fig. 3). Follow-up paired samples t tests revealed that the participants in the Vision+Haptics group overestimated the width of their right hands (43.67 ± 12.23%) more than of their left hands (18.39 ± 6.38%; $t(17) = -3.07, p = <.01$). The Haptics-only group showed a trend in this same direction (right hand = 23.15 ± 8.1%, left hand = 9.05 ± 7.4%); $t(17) = -1.96$, $p = .07$. There was no difference between the hands in the Vision-only group ($p = .221$).

Finger length: there was a main effect of group [$F(2,48) = 6.6$, $p = <.01$ partial $\eta^2 = .215$]. Follow-up pairwise comparisons revealed that the Haptics-only group was significantly different from the other two groups (compared to the Vision-only group $p < .01$, compared to the Vision+Haptic group $p = .05$). The Haptics-only group made more accurate estimations than the other two groups.

Thumb opposition: there was a main effect of group [$F(2,48) = 6.4$, $p < .01$, partial $\eta^2 = .211$]. Follow-up pairwise comparisons revealed that participants in the Vision-only group (−28.5 ± 5.2%) underestimated thumb opposition significantly more ($p < .04$ for all comparisons) than the participants in the Vision+Haptics group (−6.9 ± 5.2%) and the Haptics-only group (−7.9 ± 5.2%).

Thumb length: no significant main effects or interactions were found.

Discussion

The present study aimed to examine the contributions of vision and haptics separately and in conjunction to the perception of our hands. To this end, participants were asked to point-to-indicate certain landmarks of their unseen hands in one of three groups: Vision+Haptics, Vision-only, or Haptics-only. Participants in the Vision+Haptics group had vision (non-informative) of the experimental setup and of the pointing hand, but no vision of the hand being estimated. They also experienced haptic feedback as the palm of the hand was in contact with the undersurface of the tabletop, where the estimations were made. Participants in the Vision-only group placed their hand behind their backs (instead of under the table). They were asked to imagine as if the hand was under the table (no tactile feedback) when making their estimations. In this way, participants had vision of the experimental setup, but not tactile feedback at the visually attended location. Participants in the Haptics-only group completed the task with the hand underneath the tabletop (as in the Vision+Haptics group) but did so while wearing a blindfold (no vision). Participants in all groups were asked to estimate the position of ten landmarks on the hand: the fingertip and the mp joint of each digit. Comparisons between the occluded vs. the non-occluded hand maps were examined. In addition, effects of group (Vision+Haptics, Vision-only, and Haptics-only) and hand (left, right) were investigated for hand width (great span and little span), finger length, thumb opposition, and thumb length.

For participants in the Vision+Haptics group, both the left and right hands were significantly overestimated in terms of hand width, and significantly underestimated with regards to finger length (see Table 1). The findings of the Vision+Haptics group replicate what was reported by Longo & Haggard, (2010) as well as several other studies (Coelho, Zaninelli, & Gonzalez, 2016; Longo, 2014; Longo & Haggard, 2012a, 2012b; Longo et al., 2012; Saulton et al., 2015). Similar to Longo & Haggard, (2010) who found that the thumb was the least distorted digit, we found no significant differences between real and perceived thumb opposition and thumb length for this group. The finding from the Haptics-only group, however, did not completely replicate the pattern of the distortion seen in these previous studies. As it can be appreciated in Table 1, except for a slight overestimation of width in the right hand, all other estimations were accurate. This finding is consistent with our hypothesis that at least part of the distortion seen in previous studies is the result of visual and haptic information interfering with one another. Our prediction that participants in the Haptics-only group would produce more accurate representations than those participants in the Vision+Haptics group was, therefore, supported. A previous report also found a decrease in the magnitude of hand distortion when participants were blindfolded, although in that study hand perception was still inaccurate (Longo, 2014). Nevertheless, it is clear that non-informative vision interferes with perceptual judgements of hand size. Contrary to our hypothesis, however, participants in the Vision-only group produced distorted hand maps. These distorted hand maps featured several different characteristics than the Vision+Haptics group as well as the Longo & Haggard, (2010) study. The Vision-only group underestimated finger length, thumb opposition, and thumb length (marginally) of both hands, and overestimated hand width (little span) of the left hand. Since the Haptics-only group had more accurate judgments than the other two groups, but the Vision-only group produced distorted measures (just as the Vision+Haptics group did), the results cannot be fully explained by interfering sensory modalities; otherwise, the Vision-only group would have been more accurate than the Vision+Haptics group. This suggests that the observed distortion in hand representation is not as a result of two different sensory modalities interfering with one another, but that instead, visual information interferes with an accurate representation of the hands (in particular the left hand). This could be because the visual information that participants do have is irrelevant and it might even be distracting to the task (Mirams et al., 2010; Longo & Sadibolova, 2013; Beck et al., 2016; Longo, 2014). Whereas the Haptic-only and the Vision+Haptics groups could rely on the information arising from mechanoreceptors on the hand as it is pressed against the tabletop. A puzzling question remains as to why participants do not use only the haptic information to create their mental representations. It is possible that participants still use vision (given that it is the primary sensory modality used by primates to organize behaviour) to estimate the distance between landmarks.

Previous research has also found that visual information interferes with somatosensory processing. Non-informative vision has been associated with higher false alarms in a somatic detection task (Mirams et al., 2010), altering touch perception (Longo & Sadibolova, 2013), reducing information about stimulus intensity (Beck, Làdavas, & Haggard, 2016), and more distorted body perception (Longo, 2014). Specifically, Longo (2014) found that when participants were wearing a blindfold, they had significantly less distorted representation of their hands than when they had vision during the task. Our results are in agreement with Longo's, as we found that participants in the Haptics-only group made many accurate estimations, and overall, their maps were less distorted (i.e., produced many accurate measures) than those of the other two groups.

A possible explanation for the very different patterns of distortion seen between the Vision-only and Haptics-only groups is that vision and haptics are weighed differently depending on the task. For example, if we reach out to grasp a cup of coffee without a handle, we would rely more on haptic feedback to decipher if the cup was hot or cold and whether to pick it up. Haptic information about the cup's temperature would be irrelevant if the cup had a handle, and instead, visual information would guide the movement. In addition, it has been suggested that remembered haptic information is more reliable than visual information (Bellan et al., 2015). In a vision–haptic mismatch, task participants had to rely on vision or on haptics to make estimates of the position of their hand. At the beginning of the task, participants tended to use visual information to report the location of their hand, even though this information was inaccurate. As the task progressed, however, participants relied more on haptic information and reported the physical position of their hand. It is possible that our Haptics-only group produced the most accurate hand maps (in terms of how many measures were not distorted), because it had only proprioceptive and tactile information to rely upon.

The pattern of distortion amongst the three groups is most similar between the Vision+Haptics group and the Haptics-only group. A recent review highlights the lack of studies investigating the unique contributions of vision or haptics to body perception and argues that both are equally likely to be the dominant modality for body estimates (Azañón et al., 2016). Our results (as can be appreciated by Table 1 and Fig. 3) showed similarities in the pattern of distortion between the Vision+Haptics group and the Haptics-only group. This suggests that haptics dominates during body perception tasks, because when haptics is taken away (and therefore cannot be relied upon), the produced hand maps feature very different patterns of distortion. Nevertheless, visual information still influences hand representation given that some patterns were consistent between the Vision+Haptics and the Vision-only groups but not the Haptics-only group (e.g., underestimation of finger length).

The differences between the groups could also stem from vision and haptics having different representations of space. It has been suggested that visual information is more accurate in estimates of lateral space, whereas haptic information is more accurate in estimates of depth (Van Beers, Sittig, & van der Gon, 1998; Van Beers, Sittig, & van Der Gon, 1999). For example, in one study, participants had to match the position of a target with or without vision (Van Beers et al., 1998). The results showed that in the visual condition, participants were more accurate at estimating the horizontal position of the target, and in the proprioceptive condition, they were more accurate at estimating the vertical position. Interestingly, in the present study, we found that participants in the Vision-only group were more accurate in estimating width (horizontal dimension given the position of the hand underneath the tabletop), whereas the Haptic-only group was accurate at estimating length (vertical dimension). This result aligns with the previous studies (as in Van Beers et al., 1998, 1999) that suggested different spatial representations for different sensory modalities. This could explain the different patterns of distortion between the Vision-only and Haptic-only groups.

A final possibility is that visually-guided tasks produce underestimation errors whereas haptically-guided tasks produce overestimations (regardless of spatial orientation). A previous study on target-matching found just this result (Goble & Brown, 2008). In this study, participants completed both a visual and proprioceptive task. In the visual task, participants were briefly presented with a visual target, and once the target disappeared, they were required to indicate using a laser, where the target had been presented. During the proprioceptive task, the participants were blindfolded and their arm was passively moved to a specific elbow angle, and then returned to the start position. The participants were required to match the elbow angle that they experienced during the manipulation. The results from the visual task indicated that participants underestimated the target position. For the proprioceptive task, participants overestimated the distance between where the position was and where they perceived it to be. This result also aligns with the notion of different sensory modalities having different representations of space (Van beers et al., 1998, 1999). Thus, as a result of these differing spatial representations, it is possible that hand perception relying on haptic feedback overestimates width, and hand perception relying on visual feedback underestimates length.

Interestingly, participants in the Haptics-only group accurately estimated their left hands for all measures. This result could suggest a left-hand advantage for haptic-only processing. Previous studies have found that the left arm may in fact be better at haptically-driven actions (Colley, 1984; Goble, Lewis, & Brown, 2006). For example, elbow-matching tasks have been shown to be more accurate in the left arm than in the right (Goble & Brown, 2007, 2008). Other research has also suggested a left hand (right hemisphere) specialization for haptic processing (Butler et al., 2004; Cormier & Tremblay, 2013; Fontenot & Benton, 1971; Franco & Sperry, 1977; Harada et al., 2004; Kumar, 1977; Loayza, Fernández-Seara, Aznárez-Sanado, & Pastor, 2011). For example, a study from our lab has found an increase in left-hand use for grasping when vision is occluded and an increase in right-hand use when haptic feedback is minimized (Stone & Gonzalez, 2014). This study supports the suggestion of a left-hand right-hemisphere specialization for haptic processing.

Another finding of the present study concerns hand differences. Participants in the Vision+Haptics and in the Haptics-only group overestimated their right hands as being wider than their left hands. This asymmetry has been found before (Coelho et al., 2016; Linkenauger, Witt, Bakdash, Stefanucci, & Proffitt, 2009), wherein the right hand is perceived as larger than the left. Furthermore, it has been shown that participants estimate their right hands (when compared to their left) as being more capable of grasping objects (Linkenauger et al., 2009). Participants in that study were asked to estimate if they were able to grasp different sized blocks that were presented in front of them. The results indicated that with their right hands participants overestimate their grasping abilities, suggesting that they view their right hands as more capable. This bias in perception may be explained by a couple of imaging studies showing larger cortical representations for the right hand when compared to the left (Buchner, Kauert, & Radermacher, 1995; Soros et al., 1999). It remains unclear why the Vision-only group did not show hand differences with respect to width. Perhaps, the right-hemisphere specialization for haptic processing (Butler et al., 2004; Cormier & Tremblay, 2013; Fontenot & Benton, 1971; Franco & Sperry, 1977; Harada et al., 2004; Kumar, 1977; Loayza et al., 2011) allowed more accurate estimates of left hand in the Vision+Haptics and the Haptics-only groups.

One last consideration regarding the results from the Vision-only group is that perhaps, their estimations were erroneous, because visual and haptic information conflicted with each other. Although we removed tactile feedback to the palm of the hand by preventing participants from touching the undersurface of the tabletop (or any other surface), participants still received proprioceptive information. This proprioceptive information was non-informative, as the hand was behind the participant's back, but it could have produced a sensory mismatch. In other words, having the hand behind the back could have produced proprioceptive information that interfered with the visual feedback of where the estimations were taking place. Future research will aim to investigate this possibility. Also possible is that participants used haptic imagery to complete the task. A recent study by Ganea & Longo (2017) investigated if haptic imagery produced the same characteristic distortion as in the original study (Longo & Haggard, 2010). They found that the representation of the hand remained consistently distorted, regardless if the hand was underneath the table or not (Ganea & Longo, 2017). It seems unlikely that the participants in the Vision-only group used haptic imagery to complete the task, however, as our results differ from those of Ganea and Longo. Our participants must have relied on different strategies. Research has shown that both allocentric and egocentric reference frames govern the perception of our bodies (Galati et al., 2000). Egocentric frames of reference rely on perceptual information, whereas allocentric frames of reference utilize the long-term memory of the body (Burgess, 2006). It has been suggested that when one of these two frames of reference is not available, the result is a distorted representation of the body (Riva, Gaudio, & Dakanalis, 2015). For the Vision+Haptic and Haptic-only groups, both reference frames were available to the participants (egocentric information from the haptic feedback, and allocentric information from the remembered metrics of their hands). However, participants in the Vision-only group were limited to using allocentric information exclusively, and this may have resulted in a more distorted representation.

To conclude, the present study examined the role of vision and haptics, both separately and in conjunction, to hand perception. The study found that when participants completed the task using both visual and haptic information, the characteristic distortion was still present. However, those participants who completed the task with only haptic information (i.e., without vision) had a more accurate representation of their hands. Conversely, when the task was completed with only visual information, the representation of the hand remained distorted. These results suggest that visual- but not haptic-feedback interferes with the metric representation of the hand.

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Compliance with ethical standards

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Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All procedures performed in studies involving human participants were in accordance with the ethical standards of the institutional and/or national research committee and with the 1964 Helsinki declaration and its later amendments or comparable ethical standards.

Informed consent Informed consent was obtained from all individual participants included in the study.

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