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The effects of rapid versus controlled actions on perceptual hand maps

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Abstract

Perceiving the location of body parts in external space using position sense requires that proprioceptive signals coming from the body be combined with stored information about the size and shape of body parts. A widely used paradigm to investigate this metric representation of the body involves having participants judge the location of different landmarks on the hand. By comparing the relative location of different landmarks, perceptual maps of the hand can be constructed and compared to actual hand structure. These maps show large distortions that are highly stereotyped, and consistent across people. In this study, we investigated whether judgements in this paradigm are modulated by whether pointing responses are made in a controlled manner versus rapidly. In the controlled condition, participants were asked to make localisation judgements in a precise and deliberate way. In the rapid condition, in contrast, they were asked to make judgements quickly and intuitively. Highly similar distortions were apparent in both conditions. These results provide further evidence that the distortions of perceptual hand maps are not strongly dependent on the manner of response.

Keywords Perception and Action · Spatial cognition · Spatial localization

Introduction

Several classes of sensory signal provide information about the location of body parts in space (Proske & Gandevia, 2012). These include receptors in joints (Ferrell et al., 1987), in the skin (Edin & Johansson, 1995), and in muscle spindles (Goodwin et al., 1972), as well as efferent-copies of motor commands (Gandevia et al., 2006). Each of these signals provides information about joint angles, or the degree of flexion and extension at each joint. In order to calculate the absolute spatial position of part of the body, however, such angular information needs to be combined with metric information about the length of body segments between joints (Longo, 2025; Longo et al., 2010).

Longo and Haggard (2010) developed a procedure to measure this metric representation of hand size and shape. Participants are asked to judge the location in external space of multiple landmarks on their occluded hand. By comparing the relative location of these judgements, an implicit perceptual map of hand structure can be constructed and then compared to the actual, physical structure of the hand. These maps show consistent and highly stereotyped distortions, including: (1) Overall underestimation of finger length, (2) A gradient across the hand with increasing underestimation from the thumb to the little finger, and (3) Overestimation of hand width. These distortions have been replicated many times, both in our own lab (Longo, 2015b; Longo & Haggard, 2012a, b; Tamè et al., 2017) and in other labs (Cocchini et al., 2018; Coelho et al., 2017, 2019; Hidaka et al., 2023; Lopez et al., 2012; Matsumiya, 2022; Mora et al., 2021; Peviani & Bottini, 2018; Saulton et al., 2015, 2016; Stone et al., 2018).

While the existence of these distortions is well established, their interpretation remains controversial. Longo and his colleagues have interpreted these maps as reflecting a central body model, and the distortions as relating to low-level features of somatosensory maps (Longo, 2017, 2022; Longo & Haggard, 2010). For example, the pattern

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of underestimation across fingers mirrors the tactile acuity and cortical magnification of digits (Duncan & Boynton, 2007; Vega-Bermudez & Johnson, 2001). Similarly, the overestimation of hand width versus length parallels the elongated shape of tactile receptive fields on the hand and arm, which are longer in the proximo-distal than in the medio-lateral axis (Alloway et al., 1989; Brooks et al., 1961). Other researchers, however, have emphasized the potential role of more general factors. For example, Saulton and colleagues (2015, 2016) have found that qualitatively similar distortions can be found for non-body objects, such as a rake. Similarly, underestimation of finger length may relate to conceptual misunderstanding of where knuckles are located within the hand (Longo, 2015a; Saulton et al., 2017). Medina and Duckett (2017) have argued that some aspects of the distortions may relate to carry-over effects across trials, with repulsion of subsequent judgements away from the location of previous responses. Finally, Peviani and colleagues (2024) suggest that distortions arise from a process of Bayesian integration of noisy finger geometry and posture in the act of localising body parts.

One approach to investigating the factors underlying distorted perceptual body maps has been to study the effects of different modes of responding. Another approach has been to compare responses with the mapped hand in different orientations relative to the rest of the body (Longo & Haggard, 2010; Matsumiya, 2022). Any biases related to the control of the hand doing the pointing responses should reverse in these conditions. Nevertheless, highly similar maps have been found in the two postures. Yet another approach has been to manipulate the stimulus information on which responses are based. Similar maps are found whether participants can see where they are pointing or are blindfolded (Longo, 2014), indicating that real-time visual feedback is not critical. Similar distortions are also found whether the location being judged is cued verbally (Longo & Haggard, 2010), by touch (Longo et al., 2015; Mattioni & Longo, 2014), or by a visual cue on a hand silhouette (Hidaka et al., 2020; Longo et al., 2015).

Another approach has been to eliminate the motor act of pointing entirely. For example, Longo and colleagues compared maps produced by active pointing by the participant to a situation where participants gave verbal instructions about how to move the baton to an experimenter who implemented that actual movement. Similar distortions were apparent in these two conditions, both in a woman born without a left arm (Longo et al., 2012) and in a group of control participants (Longo, 2018). Similarly, Matsumiya (2022) recently compared active pointing with a task in which participants used a trackball to move a cursor to the desired location, again finding broadly consistent results in the two cases. Matsumiya further compared manual pointing responses to responses made with eye movements, finding that eye-movement maps showed substantially smaller (though qualitatively similar) distortions to active reaching. These results, however, are difficult to interpret, as the smaller distortions for eye-movement maps only occurred when participants also saw a virtual hand superimposed over the occluding board in a head-mounted display. When no such virtual hand was present, very similar distortions were present for manual reaching and eye movements. Other studies have shown similar distortions when no localisation judgement is made at all, but participants make judgements of size (Cardinali et al., 2019) or length (Longo & Haggard, 2012b).

A large neuropsychological literature has emphasised important differences between the mechanisms underlying overt motor behaviour and conscious perceptual experience (Milner & Goodale, 2006). Double dissociations have been reported between the ability to explicitly describe objects and to act on them effectively (Carey et al., 2006; Goodale et al., 1991, 1994). While this distinction was drawn originally within vision, it has been elegantly extended to the somatosensory system by Dijkerman and de Haan (2007). Indeed, dissociations between perception and action have been reported for a variety of somatosensory abilities, including tactile size perception (Anema et al., 2008; Westwood & Goodale, 2003), tactile localisation (Anema et al., 2009; Cardinali et al., 2011; Paillard et al., 1983; Rossetti et al., 1995), and proprioceptive localisation (Jones et al., 2010, 2012; Kammers et al., 2009). For example, Kammers and colleagues (2009) showed that proprioceptive biases induced by the rubber hand illusion were eliminated when participants responded by active pointing to the perceived location of their finger.

While our own studies of proprioceptive hand maps have mostly involved manual pointing movements (e.g., Longo & Haggard, 2010), it is not clear that these involve the sort of fast and rapid movements that might be expected to differ from purely perceptual judgements. Indeed, in these studies participants have been instructed to respond in a slow and deliberate manner, rather than to point rapidly or 'ballistically'. Some evidence suggests that these types of pointing movements may differ fundamentally. For example, Króliczak and colleagues (2006) investigated the role of response modality in producing the hollow-face illusion, in which the concave interior of a face mask is seen as a convex face. They found that rapid 'flicking' movements of the fingers appeared to be immune to the hollow-face illusion. In striking contrast, when participants made slow and deliberate pointing movements, the illusion affected responses just as much as in a purely perceptual task. These results indicate that slow and precise pointing responses may not involve the dorsal-stream mechanisms for real-time action seen with rapid or ballistic responses.

In the present study, we therefore compared perceptual hand maps obtained with different types of manual pointing responses. The *controlled* condition was similar to that used in previous studies using this paradigm in our lab (e.g., Longo & Haggard, 2010). Participants were asked to respond in a precise and deliberate way, and to feel free to adjust their response until they were satisfied. In the *rapid* condition, in contrast, participants were asked to respond immediately, using whichever location seemed immediately intuitive, and without adjusting their initial response.

Methods

Participants

Twenty members of the Birkbeck community (15 women, mean age: 31.4 years, *SD*: 10.3 years) participated. All were right-handed as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971) (*M*: 85.7, range: 30.4–100). Participants gave written informed consent before participating. Procedures were approved by the School of Psychological Sciences Research Ethics Committee at Birkbeck, and were consistent with the principles of the Declaration of Helsinki.

A weighted average of effect sizes from 15 previous experiments in our lab using this paradigm (total $N = 283$) produced an average Cohen's d of 1.78 for underestimation of finger length and 1.89 for overestimation of hand width. These studies differed in a variety of ways, including the laterality of the hand mapped and hand posture, but all used the hand-mapping paradigm developed by Longo and Haggard (2010). A power analysis using G*Power 3.1 software (Faul et al., 2007) on the smaller of these effects with alpha of.05 and power of.95 indicated that six participants were needed. Even for an effect size only half as large as in these previous studies (i.e., $d = 0.89$), the present sample size would have power greater than.95. Thus, the study was well powered to detect distortions in the rapid condition, even if they were substantially smaller than found in previous studies using more controlled responses.

Procedure

The procedure was similar to our previous experiments using this paradigm (Ganea & Longo, 2017; Longo & Haggard, 2010, 2012a, b; Mattioni & Longo, 2014). Participants sat at a table with their left hand resting palm down on a board, and approximately aligned with their body midline. The participant's hand was covered by an occluding board (40 x 40 cm) which rested on four pillars (6 cm in height). Participants judged the perceived location of ten landmarks on their occluded left hand by indicating the location on the occluding board directly above each landmark. The location of each judgement was recorded by a Logitech Webcam Pro 9000, which saved a JPEG image (1,600 x 1,200 pixels) for offline coding. Data collection was controlled by a custom MATLAB script (Mathworks, Natick, MA, USA).

At the beginning and end of each block, a photograph was taken without the occluding board to allow coding of the actual position and size of the participant's left hand. A 10-cm ruler on the table allowed conversion between distances in pixels and cm. At the start of the experiment, a small black mark was made on each knuckle of the participant's left hand using a felt tip pen, to facilitate coding from photographs. The ten landmarks judged were the tip of each finger (i.e., the most distal bit of skin) and the knuckle of each finger (i.e., the centre of the metacarpophalangeal joint). At the start of each trial, participants were given a verbal instruction about which landmark to judge, using a long baton (35 cm in length; 2 mm in diameter).

The main manipulation in this study was the manner in which participants were asked to respond. The *controlled* condition was similar to previous studies using this paradigm in that participants were asked to respond deliberately and precisely, to avoid ballistic pointing, and to avoid strategies such as tracing the outline of their hand. In the *rapid* condition, in contrast, they were asked to respond quickly, by immediately pointing. The difference between the two conditions was described to participants as follows:

> "In different blocks, I'll ask you to approach the way you respond in different ways. Sometimes, I'll ask you to indicate whichever location seems immediately intuitive. In this case, please move the baton to the board immediately, without adjusting your response after your first movement. Other times, I'll ask you to be deliberate and precise in your responses. In this case, please take your time in adjusting your response until you are comfortable with your judgement."

At the end of each trial, the participant was asked to move the tip of the baton to the side of the occluding board to make responses as independent of each other as possible. There were four blocks of 30 trials each, two blocks of the controlled condition and two blocks of the rapid condition. The blocks were presented in ABBA order, with the initial condition counterbalanced across participants. Each block was comprised of three mini-blocks of ten trials each. Each mini-block included one trial of each landmark, presented in random order.

Raw data are available on the Open Science Framework at: https://osf.io/m2sh6/

Analysis

The analysis was similar to previous studies using this paradigm in our lab. The x/y pixel coordinates of each judgement were coded from photographs using a custom MATLAB script and averaged across the three repetitions of each landmark within a block. Distances between pairs of landmarks were calculated and converted from pixels into cm. We calculated the length of each finger (i.e., the distance between the knuckle and fingertip) as well as the overall width of the hand (i.e., the distance between the knuckles of the index and little fingers). The same distances were calculated for each hand size from the photographs taken before and after each block. For each distance, we calculated percent overestimation as: 100 × (judged length – actual length)/actual length.

To visualise grand average perceptual maps, we placed maps from each condition into Generalized Procrustes alignment across participants. Procrustes alignment translates, rotates, and scales maps of homologous landmarks to place them into optimal alignment (Bookstein, 1991; Gower, 1975; Rholf & Slice, 1990). As the fingers can rotate independently, differences in hand posture could be conflated with differences in hand shape (Adams, 1999). We therefore rotated each finger to a common posture, defined as the angle formed by the intersection of the line running through the knuckles of the index and little fingers. These angles were the same as in our original study (Longo & Haggard, 2010), specifically 44.4°, 64.4°, 77.4°, 86.8° and 106.1° for the thumb to the little finger. For each map in each participant the tip of each finger was rotated to produce these angles, while preserving the distance between the knuckle and fingertip. As there were two experimental blocks of each condition, the two maps for each participant were first put into Procrustes alignment to produce a single average perceptual map for each participant for each condition. The four maps of actual hand shape for each participant were similarly placed into Generalized Procrustes alignment to construct an average hand map. Then, a second group-level Generalized Procrustes alignment was used to place the judged maps from each condition into alignment across participants.

Results

Figure 1 shows perceptual maps in Procrustes alignment with actual hand shape in the controlled condition (left panel) and the rapid condition (right panel). Clear and well-organized maps were present in both conditions. Both conditions also clearly showed the characteristic pattern of distortions we have described previously, including: (1) overall underestimation of finger length, (2) a progressive increase in this underestimation from the thumb to the little finger, and (3) overestimation of hand width.

The left panel of Fig. 2 shows underestimation of finger length for each finger in the two conditions. Collapsing across the five fingers, there was overall underestimation in both the controlled condition (*M*: 28.0%), $t(19) = -8.57$, $p < .0001$, $d = 1.92$, and the rapid condition (*M*: 29.3%), $t(19) = -7.72$, $p < .0001$, $d = 1.73$. The difference between conditions was investigated using a repeated-measures analysis of variance (ANOVA) with factors condition (controlled, rapid) and finger (thumb, index, middle, ring, little). There was a strong main effect of finger, $F(2.39, 45.45) = 42.77$, $p < .001$, $\eta_p^2 = .692$. However, there was no main effect of condition, $F(1, 19) = 0.50$, $p = .487$, $\eta_p^2 = .026$, nor an interaction between condition and finger, $F(2.42, 45.88) = 0.38$, $p = .722$, $\eta_p^2 = .020$. Collapsed across fingers, there was a strong correlation between the magnitude of underestimation in the two conditions, $r(18) = .908$, $p < .0001$.

We quantified the change in underestimation across the hand using least-squares regression, regressing percent overestimation on finger number (i.e., thumb = 1 to little finger = 5). There were clear gradients across the hand in both the controlled condition (*M*: 3.6% per finger), $t(19) = -3.89$, $p < .001$, $d = 0.870$, and the rapid condition (*M*:

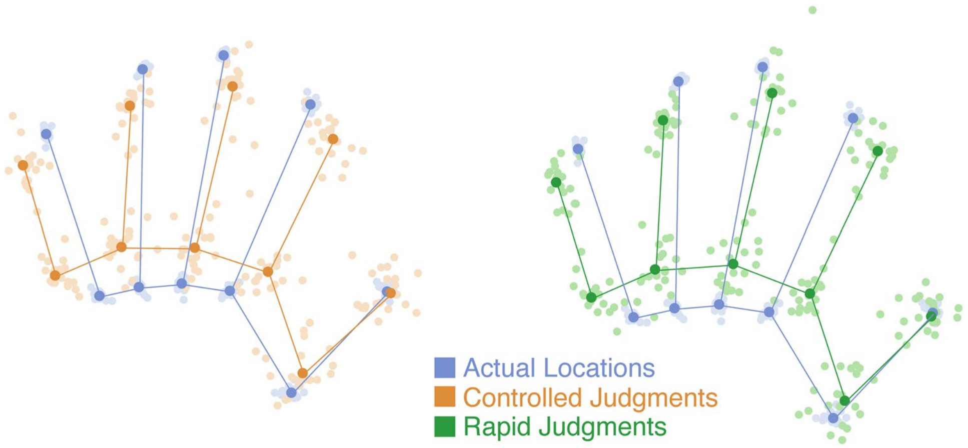

Fig. 1 Generalized Procrustes alignment of hand maps of the actual hand (blue) and perceptual maps in the controlled condition (orange) and rapid condition (green). The pale dots indicate maps from individual participants. The darker dots and lines indicate grand-average maps

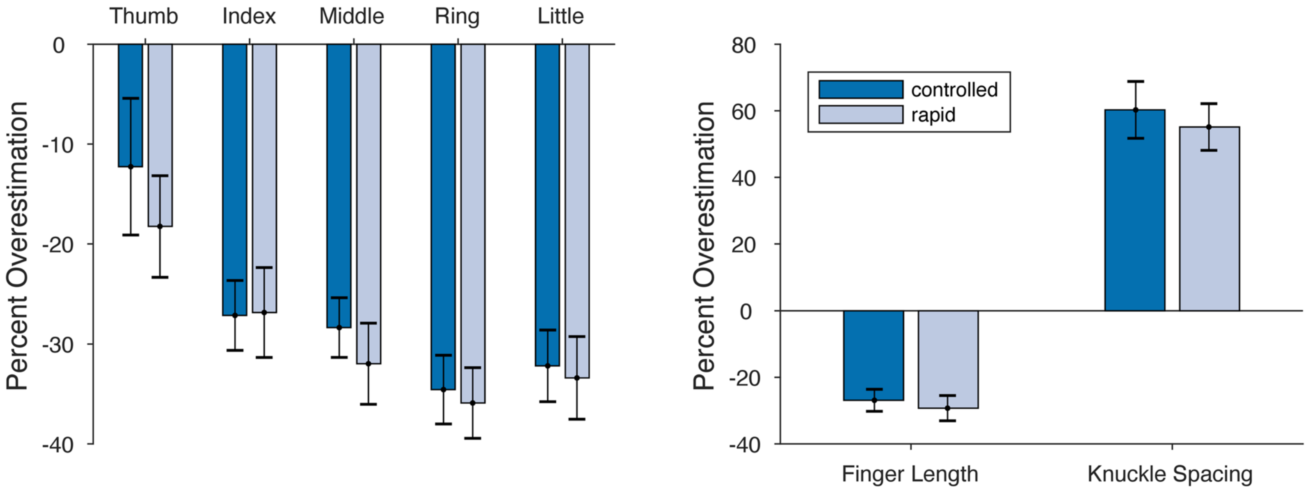

Fig. 2 ***Left panel:*** Underestimation of finger length across the five fingers in the controlled and rapid conditions. In both conditions, there was clear underestimation, which increased from the thumb to the little finger. ***Right panel:*** Underestimation of finger length (averaged across the five fingers) and overestimation of hand width in both conditions. Error bars are one standard error

3.9% per finger), $t(19) = -5.08$, $p < .001$, $d = -1.136$. The magnitude of slopes did not differ between conditions, $t(19) = 0.41$, $p = .687$, $d_z = 0.092$. There was a significant correlation in regression slopes between conditions, $r(18) = .585$, $p < .01$.

We took the distance between the knuckles of the index and little fingers as an overall measure of hand width. As shown in the right panel of Fig. 2, there was substantial overestimation of hand width in both the controlled condition (M: 60.3%), $t(19) = 7.06$, $p < .0001$, $d = 1.578$, and the rapid condition (M: 55.1%), $t(19) = 7.86$, $p < .0001$, $d = 1.758$. There was no significant difference in the magnitude of overestimation in the two conditions, $t(19) = 1.50$, $p = .151$, $d_z = 0.335$. There was a strong correlation in the magnitude of overestimation across conditions, $r(18) = .921$, $p < .0001$.

As an overall measure of the aspect ratio of the hand, we used an adaptation of Napier's (1980) shape index, which we defined as: SI = 100 X (width/length). We used the distance between the knuckles of the index and little fingers as the measure of width and the length of the middle finger as the measure of length. Large values of the shape index indicate a squat, fat hand, while small values indicate a long, slender hand. On average, participants' actual hands had a shape index of 56.63. Shape indices were significantly larger than actual hands, both in the controlled condition (M: 129.61), $t(19) = 8.96$, $p < .0001$, $d = 2.004$, and in the rapid condition (M: 136.89), $t(19) = 8.33$, $p < .0001$, $d = 1.863$. There was no significant difference in shape index between the two conditions, $t(19) = 0.94$, $p = .359$, $d_z = 0.210$. Shape indices in the two conditions were significantly correlated, $r(18) = .615$, $p < .01$.

A concern about the manipulation of controlled versus rapid pointing is that participants may not actually be approaching the task differently in the two conditions. We therefore measured the time that participants took to make their responses, as rapid judgements should be made more quickly than controlled judgements. The time that participants took to respond on each trial was quantified from the timestamps on each image file specifying the time they were created. Because this time includes the time required for the experimenter to give the verbal instruction and for the webcam to save the file, the experimenter completed 12 blocks with no participant, to estimate the amount this added on average to each trial. This gave a value of 2.82 s, which was subtracted from the mean values in both conditions. On average, participants took longer to respond on controlled trials (3.53 s) compared to rapid trials (2.27 s), $t(19) = 4.66$, $p < .0005$, $d_z = 1.043$. This provides a manipulation check that participants were approaching the task in a different way in the two conditions.

We also quantified how noisy responses were in the two conditions. For each landmark in each block, we calculated the centroid size of the three judgements. The centroid size is the root-mean-squared of the distance from each judgement from the centre-of-mass of all three judgements (Bookstein, 1991), and is essentially a generalisation of the standard deviation to multidimensional data. On average, the centroid size was modestly larger in the rapid condition (M: 2.15 cm) than in the controlled condition (M: 1.96 cm), but this difference was not statistically significant, $t(19) = 1.59$, $p = .127$, $d_z = 0.357$.

Discussion

Perceptual maps of hand size and shape were highly similar whether localisation responses were made in a controlled or a rapid manner. In both cases, the stereotyped pattern of distortions described previously (e.g., Longo & Haggard, 2010) was clearly apparent. Maps showed underestimation of finger length, which increased from the thumb to the little finger, and overestimation of hand width. There was no evidence for any difference between the conditions, and thus no evidence that rapid, real-time hand actions are immune to these distortions.

The present results complement other studies showing similar distortions for controlled pointing responses and verbal instructions given to an experimenter (Longo, 2018; Longo et al., 2012), responses made by using a trackball to move a cursor (Matsumiya, 2022), and eye movements (Matsumiya, 2022). Thus, across a wide variety of response methods, similar distortions are found. This provides evidence that these distortions are not an artefact of any specific method of responding. Some quantitative differences have been found between these conditions, however. For example, overestimation of hand width was somewhat smaller for controlled pointing responses than for verbal instructions (Longo, 2018). Similarly, Matsumiya (2022) reported that distortions were quantitatively smaller (though qualitatively similar) for responses made with eye movements or trackball responses than for active pointing movements. Curiously, however, as noted above, these differences between response methods were only found when a virtual hand was simultaneously seen by the participant. When that hand was absent, the magnitude of distortions was virtually identical for all three response types.

It is interesting that the opportunity to adjust localisation responses in the controlled condition did not improve the accuracy of maps. While people are obviously to some extent aware of the posture of their body, perception of posture is believed to be mediated by a sensorimotor representation known as the *postural schema* (Head & Holmes, 1911) or *body schema* (de Vignemont, 2010; Longo, 2016). As this representation may be inaccessible to conscious introspection, the opportunity to reflect on one's response may not provide additional useful information.

Similarly, the lack of any difference between controlled and rapid pointing in the present study provides an interesting contrast to visual illusions, in which controlled pointing appears to be influenced by illusions such as the hollow-face illusion, whereas rapid pointing does not (Króliczak et al., 2006). This suggests that these distortions are not a result of purely perceptual processes in proprioception, which would not affect real-time, skilled action. This is consistent with recent research by Peviani and colleagues (2020; Peviani & Bottini, 2018), which shows that these distortions affect active movements of the hand. In these studies, participants are shown a visual landmark and asked to move different landmarks of their unseen hand to that location. This allowed Peviani and her colleagues to build implicit maps of hand shape based on active movements of the measured hands. These maps showed similar distortions to those seen in other studies using perceptual judgements, though of somewhat smaller magnitude.

One limitation of the present study is that while participants were asked to approach the task differently in the two conditions, it is difficult to tell exactly how these instructions affected the way in which they responded. By quantifying the duration of each trial, we were able to estimate the reaction time of responses, which showed that rapid responses were indeed made more quickly than controlled responses. However, it is true that even in the rapid condition, responses still took a considerable amount of time (2.82 s on average). While it is worth noting that this time includes time needed for linguistic processing of the instruction, it is still not extremely rapid. It is possible that participants may have felt constrained from responding more quickly by factors such as not wanting to make obviously incorrect responses, or not wanting to damage the experimental equipment.

In conclusion, the present results provide further evidence for the presence of large and systematic distortions in proprioceptive hand maps, which generalise across a wide range of response types. We found no apparent difference in these maps depending on whether pointing responses were made in a controlled or a rapid fashion.

Open practices statement The raw data from the study are available via the Open Science Framework at https://osf.io/m2sh6/. The study was not pre-registered.

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Availability of data and materials The raw data from the study are available via the Open Science Framework at: https://osf.io/m2sh6/

Code availability The MATLAB code used for data collection is available via the Open Science Framework at: https://osf.io/m2sh6/

Declarations

Conflicts of interest/Competing interest The authors declare no conflicts of interest.

Ethics approval Procedures were approved by the School of Psychological Sciences Research Ethics Committee at Birkbeck, University of London.

Consent to participate Participants provided written informed consent before participating.

Consent for publication Not applicable.

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