Available online at www.sciencedirect.com

ScienceDirect

Journal homepage: www.elsevier.com/locate/cortex

Letter to the Editor

Typical biomechanical bias in the perception of congenitally absent hands

Gilles Vannuscorps [a,b,c,*] and Alfonso Caramazza [a,b]

[a] Department of Psychology, Harvard University, Cambridge, MA, USA
[b] Center for Mind/Brain Sciences, Università degli Studi di Trento, Rovereto, Italy
[c] Institute of Psychological Sciences, Université catholique de Louvain, Belgium

ARTICLE INFO

Article history:
Received 18 November 2014
Reviewed 19 December 2014
Revised 9 February 2015
Accepted 24 February 2015
Published online xxx

There is compelling evidence that our perception of others' bodies and movements is shaped by several rules and constraints, such as the biomechanics of body movement, originally thought to affect only the control and execution of actual movements (Grosjean, Shiffrar, & Knoblich, 2007; Parsons, 1987; Shiffrar & Freyd, 1993). For numerous authors, this demonstrates that the perception of others' bodies and movements is supported by somatosensory and motor representations of our own body (Grush, 2004; Hommel, Müsseler, Aschersleben, & Prinz, 2001; Wilson & Knoblich, 2005). Accordingly, the presence or absence of effects of body constraints on body perception is increasingly used as an index of, respectively, the integrity or impairment of covert stages of action production in patients with motor execution disabilities (e.g., Conson et al., 2013; Conson, Pistoia, Sarà, Grossi, & Trojan, 2010; de Lange, Roelofs, & Toni, 2008; Fiorio, Tinazzi, & Aglioti, 2006; Helmich, de Lange, Bloem, & Toni, 2007; Munzert, Lorey, & Zentgraf, 2009; Nico, Daprati, Rigal, Parsons, & Sirigu, 2004). For example, because the response latencies of patients with left cerebral palsy in judging the laterality of presented hand drawings are positively correlated with biomechanical difficulty of the hand configurations, but not those of patients with right cerebral palsy, it was concluded that only the latter group of patients suffer from a motor planning deficit (Mutsaarts, Steenbergen, & Bekkering, 2007).

However, these biomechanical constraints biases might simply reflect how the visuo-perceptual system processes and represents human bodies (Shiffrar & Freyd, 1993; Tessari, Ottoboni, Symes, & Cubelli, 2010; Vannuscorps, Pillon, & Andres, 2012). Evidence for this alternative comes mainly from the observation that two individuals born with severely reduced upper limbs (congenital bilateral upper limb dysmelia) also showed biomechanical biases when asked to provide perceptual judgments about hand postures and upper limb movements (A.Z.: Brugger et al., 2000; Funk & Brugger, 2008; Funk, Shiffrar, & Brugger, 2005; D.C.: Vannuscorps et al., 2012). The evidence from those studies, however, could be challenged on the ground that D.C. and A.Z. had upper limb stumps and, therefore, were not totally deprived of motor experience with the upper limbs (and motor representations thereof). In addition, A.Z. presented with a rare profile of very vivid phantom sensations of the missing body parts that she was able to intentionally “move”, making her case difficult to interpret.

Here, to overcome the ambiguity of the previous studies with dysplasic individuals and test these alternative accounts, we asked a 27 year-old woman (P.M.) born without upper limbs *at all* (bilateral upper limb amelia, i.e., no arm, no forearm, no hand) and no history of upper limb prosthetics or phantom limb sensations to judge as fast as possible the laterality of successively presented drawings of left and right hands displayed in 2 different postures and 7 angles of

* *Corresponding author*. Centre for Mind/Brain Sciences (CIMeC), University of Trento, Via Delle Regole 101, 38122 Mattarello, TN, Italy.
E-mail address: gilles.vannuscorps@unitn.it (G. Vannuscorps).
http://dx.doi.org/10.1016/j.cortex.2015.02.015
0010-9452/

rotation (see Fig. 1a). In this Hand Laterality Judgment (HLJ) task (Parsons, 1987) the influence of body constraints on perception is typically unveiled by three features of participants' response latencies. First, response latencies are characterized by a three-way interaction between LATERALITY, POSTURE, and ANGLE of rotation of the hand, reflecting the different clockwise rotational range of movement of left and right hands in different hand postures. Second, response latencies are shorter for hands oriented in medial (stimuli rotated toward the mid–sagittal plane) than lateral (away of the mid–sagittal plane) directions (the Medial-Over-Lateral-Advantage effect), in congruence with the fact that it is easier to orient one's own hand in medial than lateral directions (see Fig 1a). Third, response latencies are positively correlated with estimates of the awkwardness of the different hand positions (i.e., the difficulty to place the appropriate limb into the orientation of the stimulus) even after controlling for the part of variance explained by the effect of visual familiarity with the stimuli (Vannuscorps et al., 2012). We reasoned that if the influence of body biomechanical constraints on perception reflects the recruitment of participants' somatosensory and motor representations of their own body, then, these features should not characterize P.M.'s performance. If, however, this bias reflects a property intrinsic to how the visuo-perceptual system processes observed body parts, then, P.M.'s response profile should be analogous to that of typically developed participants.

During the experiment, P.M. was seated at about 60 cm of a computer screen. She performed 5 blocks of 28 trials (2 sides × 2 postures × 7 angles). In each block, stimuli were mixed in different orders. The first block included 10 practice trials. Each trial started with the presentation of a central cross for 200 msec followed by a hand drawing displayed until a response was recorded. Trials were separated by a blank screen of random duration between 500 msec and 1000 msec. The experiment was controlled with the E-Prime software (Psychological Software, 2002, Pittsburgh, PA). PM responded verbally ("right" or "left") and the post-stimulus onset latency of the subject's vocalization was recorded by a voice-key. The accuracies of responses and of the voice-key vocalization detection were monitored on-line by the experimenter. The study was approved by the biomedical ethics committee of the Cliniques Universitaires Saint-Luc, Brussels, Belgium.

P.M.'s results are shown in Fig. 1. There were no voice key failures. Response errors (10%) were discarded from response latency analyses. PM's response latencies showed the three typical indexes of an influence of the body biomechanical constraints: a three-way interaction between LATERALITY, ANGLE (30–150° *vs* 210–330°), and POSTURE [F (1, 100) = 10.62, p < .01] (Fig. 1a) of the hand (data from the angles 30–150 and 210–330 were collapsed and then log transformed to satisfy the homoscedasticity and normality assumptions of ANOVA); shorter response latencies for hands oriented in medial (stimuli rotated toward the

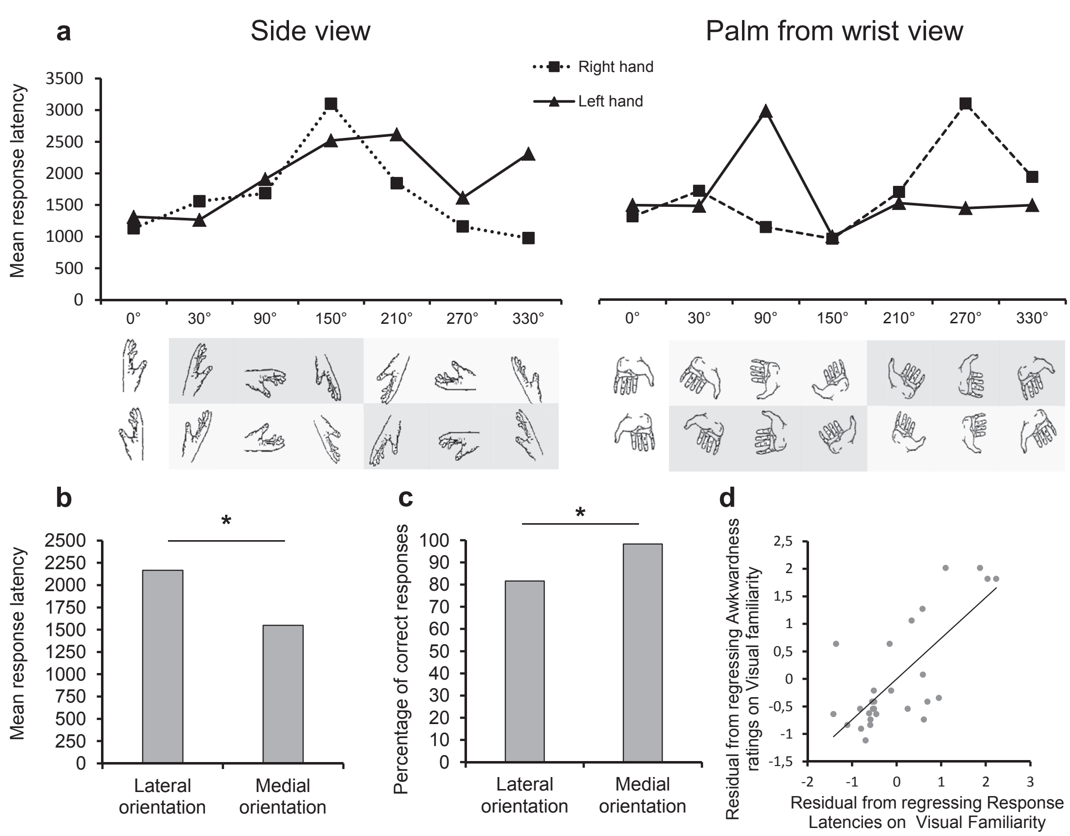

Fig. 1 – Results. (a) Mean response latency for left and right hand drawings rotated clockwise viewed from the side (left) and from the wrist (right). On dark grey: medial orientations; on light grey: lateral orientations. (b, c) Mean response latency (b) and mean percentage of correct responses (c) as a function of hand orientation (Lateral *vs* Medial). (d) Partial correlation between response latency and motor awkwardness rating controlling for visual familiarity.

Please cite this article in press as: Vannuscorps, G., & Caramazza, A., Typical biomechanical bias in the perception of congenitally absent hands, Cortex (2015), http://dx.doi.org/10.1016/j.cortex.2015.02.015

mid–sagittal plane) than lateral (away of the mid–sagittal plane) directions [medial: 1549 msec ± 445 msec; lateral 2166 msec ± 742; t (18) = 2.46, p = .02] (Fig. 1b); and response latencies positively correlated with estimates of the awkwardness of the different hand positions (extracted from Parsons, 1987) after controlling for the effect of P.M.'s visual familiarity with the stimuli [P.M. was asked to rate how often she sees each of the stimuli in everyday life; partial correlation: r (25) = .74, p < .001] (Fig. 1d). In addition, PM made significantly more errors on lateral than medial hand orientations [chi^2 (1) = 9.26, p < .01] (Fig. 1c).

In sum, P.M.'s speed and accuracy at judging the laterality of hand drawings was influenced by the biomechanical complexity of the different hand postures and orientations, despite her impossibility to simulate motorically hand postures and orientations. This finding is consistent with the results obtained previously with two other individuals with congenital bilateral upper limb abnormalities (A.Z.: Brugger et al., 2000; Funk & Brugger, 2008; D.C.: Vannuscorps et al., 2012). The present study goes beyond the previous evidence, however, by demonstrating the presence of a typical biomechanical bias in an individual totally deprived of upper limbs and who has never experience phantom limb sensations. It allows the conclusion that the influence of body constraints on body perception is not necessarily a consequence of an automatic recruitment of the observer's representation of her/his own body and can be a natural consequence of how the *visuo-perceptual system* processes and represents human bodies.

This interpretation of our results may be open to three criticisms. A first objection that could be raised is that a congenital absence of upper limbs does not prevent the dysplasics from using (innate) motor representations of the upper limb movements to support their judgment of hand laterality. The existing evidence, however, suggests that the dysplasics' motor cortex does not contain a representation of the missing limbs (Funk et al., 2008; Reilly & Sirigu, 2011; Stoeckel, Seitz, & Buetefish, 2009). Rather, the specific parts of their somatosensory and motor cortices that would normally represent the "absent" limbs are allocated to the representation of adjacent body parts (Funk et al., 2008; Stoeckel, Pollok, Witte, Seitz, & Schnitzler, 2005, Stoeckel et al., 2009).

A second possibility is that P.M.'s response profile may arise from her imagining moving her lower limbs to the position of the hand drawings. The very different skeletal and muscular features and degrees of freedom of the arms and legs and hands and feet make it virtually impossible to imitate all the observed hand postures with the feet, however. For example, while the medial rotation of the palm of the hand viewed from the back can easily reach 180°, the corresponding rotation with the foot is limited to approximately 30° (Nordin & Frankel, 2001). The observation that A.Z. also showed the same effect despite the fact that she had no feet (Brugger et al., 2000; Funk & Brugger, 2008) and that D.C. was slower at judging the laterality of feet in comparison to hands (Vannuscorps et al., 2012) are also incompatible with this account.

A last objection that could be raised against our interpretation is that we cannot discard the possibility that the effect of the biomechanical constraints in P.M and in typically developed participants might be supported by different strategies or computations. This is true. However, our conclusion seems reasonable in the light of the evidence from the neuropsychological and transcranial magnetic stimulation literature showing that the effect of the biomechanical constraints can be observed even after transient lesions to the motor system (Ganis, Keenan, Kosslyn, & Pascual-Leone, 2000; Pelgrims, Michaux, Olivier, & Andres, 2010; Sauner, Bestmann, Siebner, & Rothwell, 2006) and in patients suffering from diverse conditions preventing the normal execution of hand movements (e.g., Fiorio et al., 2006; Helmich et al., 2007; de Lange et al., 2008). It is also in agreement with the observation that occipito-temporal regions of the human cortex are sensitive to violations of the biomechanical constraints in observed movements (Costantini et al., 2005; Stevens, Fonlupt, Shiffrar, & Decety, 2000). In any case, our results constitute existence proof that using one's own body motor and somatosensory representations is not needed to obtain the performance profiles that have been used to support theories claiming that our perception of others' bodies and movements is supported by somatosensory and motor representations of our own body (Grush, 2004; Hommel et al., 2001; Wilson & Knoblich, 2005). As a corollary, they also suggest that our visuo-perceptual system is endowed with a representation of human bodies that specifies the biomechanical constraints imposed by the body musculoskeletal structure (Shiffrar & Freyd, 1993; Tessari, et al., 2010; Vannuscorps et al., 2012).

This conclusion does not conflict with previous evidence showing that the performance in the HLJ task can be delayed, and the effect of the biomechanical constraints hindered, in patients suffering from motor disorders. Evidence for the influence of motor disorders in the HLJ task are compelling and have been found in different populations of patients (Conson et al., 2013, 2010; Fiorio et al., 2006; Helmich et al., 2007; de Lange et al., 2008; Munzert et al., 2009; Nico et al., 2004). Within the classical interpretation of the HLJ task, it is hypothesized that performance in the HLJ task is supported by both a perceptual analysis of the hand shape providing a first estimate of the hand laterality and then by a verification strategy involving an implicit simulation of this hand posture and orientation (Parsons, 1987). On this theoretical account, motor disorders interfere with the verification process, thereby affecting participant's performance. In contrast, participants, such as P.M., who cannot use a motor verification strategy judge the hand laterality based only on visuo-perceptual processes.

In sum, our finding encourages a shift in the focus of future research away from motor simulation as a necessary component of human movement perception and toward the interesting question of how the visuo-perceptual system represents and processes articulated objects and their movements. In addition to its theoretical significance, this finding also serves as a cautionary note in the use of the Hand Laterality Task as a tool to study the integrity of covert stages of action production in neurological and psychiatric conditions.

Acknowledgements

We are very grateful to Lawrence Parsons who kindly provided us with the hand drawings used in this study. This research was supported in part by an *Additional Postdoctoral Grant* (Fonds Spécial de Recherche, Université catholique de Louvain) to Gilles Vannuscorps. We declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

REFERENCES

Brugger, P., Kollias, S. S., Müri, R. M., Crelier, G., Hepp-Reymond, M. C., & Regard, M. (2000). Beyond re-membering: phantom sensations of congenitally absent limbs. *Proceedings of the National Academy of Sciences of the United States of America, 97*, 6167–6172.

Conson, M., Mazzarella, E., Frolli, A., Esposito, D., Marino, N., Trojano, L., et al. (2013). Motor imagery in Asperger syndrome: testing action simulation by the hand laterality task. *PLoS One, 23*, e70734.

Conson, M., Pistoia, F., Sarà, M., Grossi, D., & Trojano, L. (2010). Recognition and mental manipulation of body parts dissociate in locked-in syndrome. *Brain and Cognition, 73*, 189–193.

Costantini, M., Galati, G., Ferretti, A., Caulo, M., Tartaro, A., Romani, G. L., et al. (2005). Neural systems underlying observation of humanly impossible movements: an FMRI study. *Cerebral Cortex, 15*, 1761–1767.

Fiorio, M., Tinazzi, M., & Aglioti, S. M. (2006). Selective impairment of hand mental rotation in patients with focal hand dystonia. *Brain, 129*, 47–54.

Funk, M., & Brugger, P. (2008). Mental rotation of congenitally absent hands. *Journal of the International Neuropsychological Society, 14*, 81–89.

Funk, M., Lutz, K., Hotz-Boendermaker, S., Roos, M., Summers, P., Brugger, P., et al. (2008). Sensorimotor tongue representation in individuals with unilateral upper limb amelia. *NeuroImage, 43*, 121–127.

Funk, M., Shiffrar, M., & Brugger, P. (2005). Hand movement observation by individuals born without hands: phantom limb experience constrains visual limb perception. *Experimental Brain Research, 164*, 341–346.

Ganis, G., Keenan, J. P., Kosslyn, S. M., & Pascual-Leone, A. (2000). Transcranial magnetic stimulation of primary motor cortex affects mental rotation. *Cerebral Cortex, 10*, 175–180.

Grosjean, M., Shiffrar, M., & Knoblich, G. (2007). Fitts' law holds in action perception. *Psychological Sciences, 18*, 95–99.

Grush, R. (2004). The emulation theory of representation: motor control, imagery, and perception. *Behavioral and Brain Sciences, 27*, 377–442.

Helmich, R. C., de Lange, F. P., Bloem, B. R., & Toni, I. (2007). Cerebral compensation during motor imagery in Parkinson's disease. *Neuropsychologia, 45*, 2201–2215.

Hommel, B., Müsseler, J., Aschersleben, G., & Prinz, W. (2001). The theory of event coding (TEC): a framework for perception and action planning. *Behavioral and Brain Sciences, 24*, 849–937.

de Lange, F. P., Roelofs, K., & Toni, I. (2008). Motor imagery: a window into the mechanisms and alterations of the motor system. *Cortex, 44*, 494–506.

Munzert, J., Lorey, B., & Zentgraf, K. (2009). Cognitive motor processes: the role of motor imagery in the study of motor representations. *Brain Research Reviews, 60*, 306–326.

Mutsaarts, M., Steenbergen, B., & Bekkering, H. (2007). Impaired motor imagery in right hemiparetic cerebral palsy. *Neuropsychologia, 45*, 853–859.

Nico, D., Daprati, E., Rigal, F., Parsons, L., & Sirigu, A. (2004). Left and right hand recognition in upper limb amputees. *Brain, 127*, 120–132.

Nordin, M., & Frankel, V. H. (2001). *Basic biomechanics of the musculoskeletal system* (3rd ed.). Philadelphia: Lippincott Williams and Wilkins.

Parsons, L. M. (1987). Imagined spatial transformations of one's hands and feet. *Cognitive Psychology, 19*, 178–241.

Pelgrims, B., Michaux, N., Olivier, E., & Andres, M. (2010). Contribution of the primary motor cortex to motor imagery: a subthreshold TMS study. *Human Brain Mapping, 32*, 1802–1810.

Reilly, K. T., & Sirigu, A. (2011). Motor cortex representation of the upper-limb in individuals born without a hand. *PloS One, 6*, e18100.

Sauner, D., Bestmann, S., Siebner, H. R., & Rothwell, J. C. (2006). No evidence for a substantial involvement of primary motor hand area in handedness judgements: a transcranial magnetic stimulation study. *The European Journal of Neuroscience, 23*, 2215–2224.

Shiffrar, M., & Freyd, J. J. (1993). Timing and apparent motion path choice with human body photographs. *Psychological Science, 4*, 379–384.

Stevens, J. A., Fonlupt, P., Shiffrar, M. A., & Decety, J. (2000). New aspects of motion perception: selective neural encoding of apparent human movements. *NeuroReport, 11*, 109–115.

Stoeckel, M. C., Pollok, B., Witte, O. W., Seitz, R. J., & Schnitzler, A. (2005). Shrinkage of somatosensory hand area in subjects with upper extremity dysmelia revealed by magnetoencephalography. *Journal of Neurophysiology, 93*, 813–818.

Stoeckel, M. C., Seitz, R. J., & Buetefisch, C. M. (2009). Congenitally altered motor experience alters somatotopic organization of human primary motor cortex. *Proceedings of the National Academy of Sciences of the United States of America, 106*, 2395–2400.

Tessari, A., Ottoboni, G., Symes, E., & Cubelli, R. (2010). Hand processing depends on the implicit access to a spatially and bio-mechanically organized structural description of the body. *Neuropsychologia, 48*, 681–688.

Vannuscorps, G., Pillon, A., & Andres, M. (2012). The effect of biomechanical constraints in the hand laterality judgment task: where does it come from? *Frontiers in Human Neuroscience, 6*, 299.

Wilson, M., & Knoblich, G. (2005). The case for motor involvement in perceiving conspecifics. *Psychological Bulletin, 131*, 460–473.

Please cite this article in press as: Vannuscorps, G., & Caramazza, A., Typical biomechanical bias in the perception of congenitally absent hands, Cortex (2015), http://dx.doi.org/10.1016/j.cortex.2015.02.015