

# The origin of the biomechanical bias in apparent body movement perception



Gilles Vannuscorps<sup>a,b,c,\*</sup>, Alfonso Caramazza<sup>a,b</sup>

<sup>a</sup> Department of Psychology, Harvard University, Cambridge, MA 02138, USA

<sup>b</sup> Center for Mind/Brain Sciences, Università degli Studi di Trento, Mattarello 38122, Italy

<sup>c</sup> Institute of Psychological Sciences, Université catholique de Louvain, 1348, Belgium

## ARTICLE INFO

### Article history:

Received 24 March 2016

Received in revised form

18 May 2016

Accepted 25 May 2016

Available online 27 May 2016

### Keywords:

Biomechanical bias

Body perception

Biological motion

Action perception

Common coding

Motor simulation

Embodied cognition

## ABSTRACT

The perception of apparent body movement sometimes follows biologically plausible paths rather than paths along the shortest distance as in the case for inanimate objects. For numerous authors, this demonstrates that the somatosensory and motor representations of the observer's own body support and constrain the perception of others' body movements. In this paper, we report evidence that calls for a re-examination of this account. We presented an apparent upper limb movement perception task to typically developed participants and five individuals born without upper limbs who were, therefore, totally deprived of somatosensory or motor representations of those limbs. Like the typically developed participants, they showed the typical bias toward long and biomechanically plausible path. This finding suggests that the computations underlying the biomechanical bias in apparent body movement perception is intrinsic to the visual system.

© 2016 Elsevier Ltd. All rights reserved.

## 1. Introduction

There is abundant evidence that implicit knowledge of the human body biomechanical constraints influences not only the planning, control, and execution of one's own body movements, but also the perception of others' bodies and body movements (Grosjean et al., 2007; Parsons, 1987; Shiffrar and Freyd, 1990, 1993). One of the most striking examples of this influence is the biomechanical bias on the perceived path of apparent body movement (Heptulla-Chatterjee et al., 1996; Funk et al., 2005; Shiffrar and Freyd, 1990, 1993; Stevens et al., 2000). In the seminal study of this effect, Shiffrar and Freyd (1990) showed their participants photographs of a human model whose hand alternated between two positions at different frequencies and asked them to report the perceived path of body movement. If body movements were processed like any other object, then the body should be perceived moving back and forth over the shortest distance between these two postures (Burt and Sperling, 1981). Instead, the participant's perception of apparent body movement sometimes followed biologically plausible paths rather than paths along the shortest distance. This was the case, in particular, when the

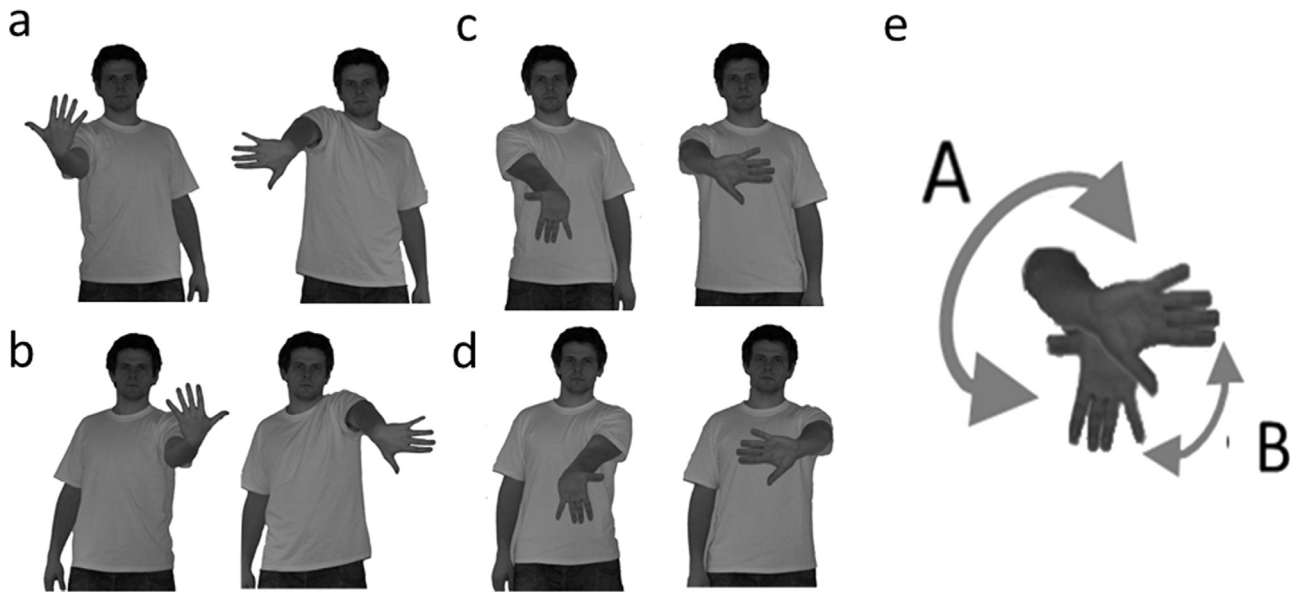
shortest path between the hand positions was biomechanically impossible (see for instance Fig. 1, a-d) and the interval between the two hand pictures (ISI) was long enough for the longer movement to be plausible. Follow-up studies have replicated and extended this finding (Heptulla-Chatterjee et al., 1996; Funk et al., 2005; Shiffrar and Freyd, 1993; Stevens et al., 2000). However, the nature of the representations and processes underlying this perceptual bias remains unclear.

According to a "visual hypothesis", the biomechanical bias in action perception reflects implicit knowledge ("internal model") of the body movement capabilities, accumulated in the course of perceptual learning and encoded in the visual system (Marr and Vaina, 1982; Tessari et al., 2010; Vannuscorps et al., 2012; Vannuscorps and Caramazza, 2015). According to a "motor hypothesis", this perceptual bias relies on the observer's own body somatosensory and motor representations, learned through movement execution (Knoblich, 2008; Thornton et al., 1998; Stevens et al., 2000). In accord with the latter view, it has been argued that the biomechanical bias constitutes compelling evidence that efficient perception of others' actions relies on a direct mapping process by which observed actions are mapped onto the corresponding motor representation in the observer's brain (Blakemore and Decety, 2001; Decety and Grèzes, 1999; Galantucci et al., 2006; Glenberg et al., 2013; Grossman, 2006; Thornton et al., 1998; Wilson, 2001, 2006).

The evidence in support of these two competing hypotheses

\* Correspondence to: Department of Psychology, Harvard University, Williams James Hall, 9th floor, 33 Kirkland Street, Cambridge, MA 02138, USA.

E-mail address: [gvannuscorps@wjh.harvard.edu](mailto:gvannuscorps@wjh.harvard.edu) (G. Vannuscorps).



**Fig. 1.** Material. (a, b, c, d) Pairs of pictures used to induce an apparent rotation of the right (a, c) or left (b, d) hand about the wrist with the palm oriented toward the body (a, b) or away from the body (c, d). (e) Example of a response diagram depicting both the shortest but biomechanically impossible (B) and a longer and biomechanically possible (A) path between the two hand positions.

remains ambiguous. The three main types of data that have been cited in favor of the motor hypothesis are: 1) that observing someone else's actions elicited activation in frontal and parietal areas (among others), which are also activated during action execution (e.g., Gazzola et al., 2009), 2) that this motor involvement is specific to biomechanically plausible actions (Stevens et al., 2000), and 3) that the biomechanical bias in apparent movement perception is modulated by the interstimulus interval (Shiffrar and Freyd, 1990, 1993). This latter effect, in particular, has been cited as evidence for the motor hypothesis on the ground that it would be a direct consequence of the time needed to motorically simulate the biomechanically plausible path. Therefore, participants would more likely perceive the longer and biomechanically possible path only when the interval is long enough for that long path to be motorically simulated (e.g., Stevens et al., 2000). However, these results are open to alternative explanations. The activation of the motor system during the observation of biomechanically plausible movements could result from, rather than constitute the source of the biomechanical bias in perception (e.g., Mahon and Caramazza, 2008). Likewise, the impact of the interstimulus interval can be interpreted within the framework of the visual hypothesis as an influence of implicit knowledge of the possible speed of body movement.

In favor of the visual hypothesis, we (Vannuscorps and Caramazza, 2015) recently reported the case of one individual born with no upper limbs, P. M., whose response latency when asked to judge the laterality of a visually presented hand (Parsons, 1987) was influenced by the biomechanical complexity of the hand posture and position, as found for typically developed individuals. For instance, P. M. was slower at recognizing a right hand pointing to the right side of the screen than the same hand pointing to the left side, reflecting the smaller degree of freedom associated with lateral than medial hand movements. This finding constitutes existence proof that the biomechanical bias on body part perception does not require motor involvement (see also Brugger et al., 2000; Funk and Brugger, 2008; Vannuscorps et al., 2012). It remains unclear, however, whether this finding can be generalized to the perception of body movements.

In an attempt to address this issue, Funk et al. (2005) presented an upper-limb apparent-movement task to two individuals, A. Z.

and C. L., born without fully developed upper limbs. If the motor hypothesis were true, they reasoned, A. Z.'s and C. L.'s response profiles should not be characterized by two typical indexes of the biomechanical bias in this task: (1) they should not perceive "long and plausible" rather than "short and impossible" paths and, (2) in any event, their path choice should not be modulated by the interstimulus interval (ISI). The results were ambiguous. On the one hand, and in support of the visual hypothesis, A. Z. showed the two typical features of the biomechanical bias. This finding cannot be considered as conclusive evidence in favor of the visual hypothesis, however, because A. Z. presented with a very rare profile of very vivid phantom sensations of her absent limbs including the ability to execute voluntary movements of her phantom arms. This makes her case very difficult to interpret since one cannot rule out the existence of limb representations, which could explain her response profile (Brugger et al., 2000; Funk and Brugger, 2008; Funk and Shiffrar, 2005). On the other hand, in favor of the possibility that A. Z.'s profile could be due to her feeling phantom upper limbs, and in favor of the motor hypothesis, the authors also reported that C. L., who had never felt any phantom sensations of the missing body parts, almost systematically perceived the short but biomechanically impossible path.

The empirical approach taken in this study constitutes an attempt to overcome this ambiguity. We presented an apparent upper limb movement perception task involving elbow and wrist movements to typically developed participants and to five individuals born with no elbow or wrist and who have no experience of phantom limbs movements or sensations (individuals with dysplasia, IDs, see Fig. 2). The existing evidence suggests that the motor cortex of the IDs who do not report phantom sensations of the absent limbs does not contain a representation of the missing limbs (Funk et al., 2008; Reilly and Sirigu, 2011; Stoeckel et al., 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 et al., 2005, 2009). Therefore, if the influence of the body biomechanical constraints on the perceived path of apparent body movement relies on somatosensory and motor representations of the observer's own body, then, the perception of apparent upper limb movement should be biased toward biomechanically

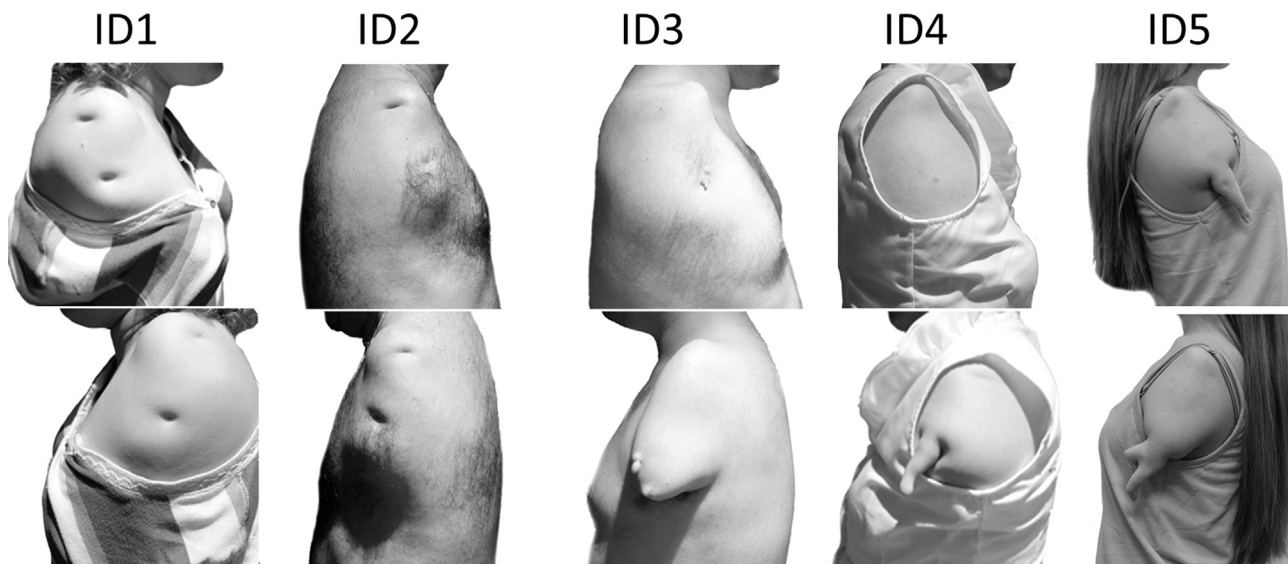


Fig. 2. Upper limb extremities of the participants ID1–5.

plausible movements in the controls but not in the IDs.

## 2. Method

### 2.1. Participants

We tested five individuals born without completely developed upper limbs (participants with bilateral upper limb dysplasia, IDs; 3 women; mean age=34; see Fig. 2) and 16 typically developed and able control participants (8 women; mean age=24). No participant had a history of psychiatric or neurological disorder. All had normal or corrected-to-normal vision. All participants except ID1 had normal lower limbs. ID1's right leg was  $\pm 7$  in. shorter than the left one. The presence of a history of phantom limb sensations or movements in the IDs was explored by asking them the question: "Often after amputation but also sometimes for congenitally absent limbs people report that they can feel the presence of the missing limb(s) or at least some parts of it. These experiences are known as "phantom" limbs. Phantoms may be extremely vivid and present almost all of the time, or they may be quite fleeting experiences, which occur every few months. The phantom may represent the entire missing limb (a complete forearm for instance) with all phantom parts being equally vivid or the phantom may, for example, be limited to the vague sensation of a hand with undifferentiated "finger-like" projections. The phantoms may manifest as voluntary movements, tingling feelings or even pain. Have you ever had any phantom limb experiences in/of the missing limb?". All the IDs included in this study responded without hesitation that they never felt any such experience. ID1, 4 and 5 have never used prosthetics. ID2 occasionally used a wood composite prosthetic with locking elbow and hooks controlled by cables attached to leg straps from 3 to 7 years old, a wood composite prosthetic with electronic elbow and three pronged hooks controlled by micro switches in shoulder harness from 7 to 11 years old and a composite prosthetic with myoelectric elbows and cosmetic hands from 11 to 15 years old. ID3 used switch-based right and left arms prosthetics as child and still uses occasionally a switch-based right arm prosthetic as an adult. Importantly, none of the prosthetics used by ID2 and 3 included elbow or wrist joints with natural degrees of freedom.

This study was approved by the Committee on the Use of Human Subjects from Harvard University (Protocol: IRB14-2556) and the Ethic Committee for Experiments involving Human Subjects of

the University of Trento (Protocol: 2014-032). All participants gave written informed consent prior to the study.

### 2.2. Materials

Stimuli consisted of 4 different pairs of photographs of an actor who remained stationary except for the position of his right (four photographs) or left (four photographs) upper limb (see Fig. 1, a–d). The four pairs of stimuli satisfied two requirements. First, the shortest path between the two hand positions, i.e., an external rotation of the hand by  $90^\circ$  with the palm oriented toward the body for the pairs of stimuli a and b and internal rotation of the hand by  $90^\circ$  with the palm away from the body for the pairs of stimuli c and d, was biomechanically impossible. The maximum external and internal rotation of the hand with these hand postures is of only  $0$ – $10^\circ$  (Nordin and Frankel, 2001). Second, the longer and biomechanically possible path between the two hand positions, i.e., an internal rotation of the hand by  $270^\circ$  with the palm oriented toward the body for the pairs of stimuli a and b and external rotation of the hand by  $270^\circ$  with the palm away from the body for the pairs of stimuli c and d, corresponded to a movement impossible to execute with the lower limbs. The maximum external and internal rotation of the foot is of only  $45^\circ$  and  $40^\circ$ , respectively (Nordin et al., 2001).

### 2.3. Procedure

The experiment can be visualized at <http://www.testable.org/experiment/7/919310/start>. During the experiment, participants remained seated at about 60 cm from a computer screen. They were first exposed to the rabbit-duck picture (Brugger and Brugger, 1993) and told "this stimulus can be perceived as a duck or as a rabbit. If a person was shown 100 times this same picture, it is likely that s/he would sometimes perceive the rabbit and sometimes the duck. Obviously, none of these responses would be correct or incorrect. This phenomenon demonstrates that the perception of the same stimulus can differ from time to time and from person to person. In the experiment that will follow, we are interested in the kind of movements that people perceive when they see rapidly presented pictures of a human body in different positions. This is also an example of perceptual ambiguity. Sometimes you may see a movement going in one direction, sometimes in another direction. There is no correct or incorrect

response. We simply ask you to relax and tell us what you see.” This phase was added after pre-tests to avoid biasing participants from thinking about the plausibility of the perceived movements presented in the experiment.

Subjects then performed a block of 8 familiarization trials followed by a block of 80 trials (2 sides x 2 movements x 5 ISIs x 4 iterations) in which stimuli were pseudo-randomly mixed. Each trial started with the presentation of a blank screen for 500 ms followed by four cycles of two different hand positions separated by one blank screen. These cycles were presented at 5 different presentation speeds. Following Shiffrar and Freyd (1990), the fastest speed involved presenting the photographs for 100 ms separated by a 50 ms interstimulus blank screen and the second, third, fourth and fifth presentation rate involved presenting the photographs for 150, 200, 250, and 300 ms and the blank screen for 100, 150, 200 and 250 ms, respectively. After the last photograph of each trial, the participants viewed a blank screen for one second and then a response figure showing two possible paths of apparent motion between the actor's hand positions (e.g., see Fig. 1, e-f). This figure was displayed until a response was provided. There were two versions of each response figure. In one version, the shortest path was labelled “A” and the longest “B”. In the other version, the assignment of letters was reversed. When the response figure appeared, participants were asked verbally whether or not they had perceived a movement, and if they had, whether the perceived movement corresponded to one of the two movements displayed on the figure, and indicate which one by naming the corresponding letter, or whether they had perceived some other movement, and to describe it.

The experiments were controlled with the E-Prime software (Psychological Software, 2002, Pittsburgh, PA) and presented on a 15.6 in. anti-glare screen set at 1366 × 768 pixels and 60 Hz. Participants' responses were recorded online by the experimenter.

### 3. Results

For each participant we tallied the number of times a particular response (“short path”, “long path”, “no movement perceived” or “another movement”) was chosen at each ISI. “No movement” and “Another movement” responses represented 1.4% and 0.7% of the responses in the controls and the individuals with dysplasia (IDs), respectively. The data of one control participant (C7, see Fig. S1) were excluded because his response profile deviated more than 2 standard deviations from that of the other controls.

We then looked for the presence of the typical bias toward a long and biomechanically plausible path modulated by the ISI in both groups of participants. As shown in Fig. 3, participants from both groups were more likely to perceive longer and

biomechanically possible movements than short and biomechanically impossible movements at the longest ISIs (Controls: ISIs > 150 ms, both paired sample *t*-tests,  $t_s(14) > 1.89$ ,  $ps(\text{uni}) < 0.05$ ; IDs: ISIs > 50 ms, all Wilcoxon Signed Rank tests,  $Z_s > 2$ ,  $ps(\text{uni}) < 0.05$ ) and, in both groups, this bias was strongly positively correlated with the ISI (Controls:  $r(5) = 0.98$ ; IDs:  $r(5) = 0.98$ ). Thus, like the typically developed participants, the IDs showed the two behavioral features typically reported as evidence for an effect of the biomechanical constraints in this task (Hep-tulla-Chatterjee et al., 1996; Funk et al., 2005; Shiffrar and Freyd, 1990, 1993).

We further investigated the presence of differences between the IDs and the controls on these two indexes. A stronger bias toward the “long” path or a different influence of the ISIs on this effect in the controls' performance would indicate a minor contribution of motor simulation. In contrast to this possibility, we found that the modulation of the bias toward perceiving the longer and biomechanically possible movement by the ISIs was virtually indistinguishable for the two groups (both  $r = 0.98$ ) and that, if anything, the IDs had a general, although not statistically significant (Mann-Whitney *U* tests for all ISIs: all  $15.5 \leq U_s \leq 22$ , all  $0.05 < ps < 0.2$ ), trend to show a larger bias toward biomechanically possible movements than the controls (Fig. 3).

How can we explain, then, that one of the subjects tested by Funk et al. (2005), C. L., almost always perceived the short but biomechanically impossible path? A possible explanation is that C. L.'s profile reflects a normal variability of performance in this task rather than a direct consequence of his congenital absence of upper limbs. To explore this possibility, we looked at the individual data of the 16 control participants and of the 5 IDs tested in this study (see Fig. S1 and S2). In support of this hypothesis, we found that C. L.'s profile was, in fact, virtually identical to that of two of the 16 typically developed participants (C7 and C14, see Fig. S1). In contrast, as shown in Fig. S2, the 5 dysplastic participants tested in this study all perceived significantly more often the longer and biomechanically possible movement (all  $\chi^2(1) > 3.8$ , all  $ps \leq 0.05$ ) and this bias was strongly correlated with the ISI in 4 of them (ID1, 2, 3 and 5: all  $r(5) > 0.7$ , all  $p < 0.1$ ).

### 4. Discussion

The IDs' response profiles were characterized by the two typical indexes of an influence of the biomechanical bias in apparent movement perception: they perceived a significantly larger number of “long” than “short” paths and the frequency of choosing the longest and anatomically plausible path was modulated by stimulus exposure duration and ISI. This finding suggests that the computations underlying the biomechanical bias in apparent body

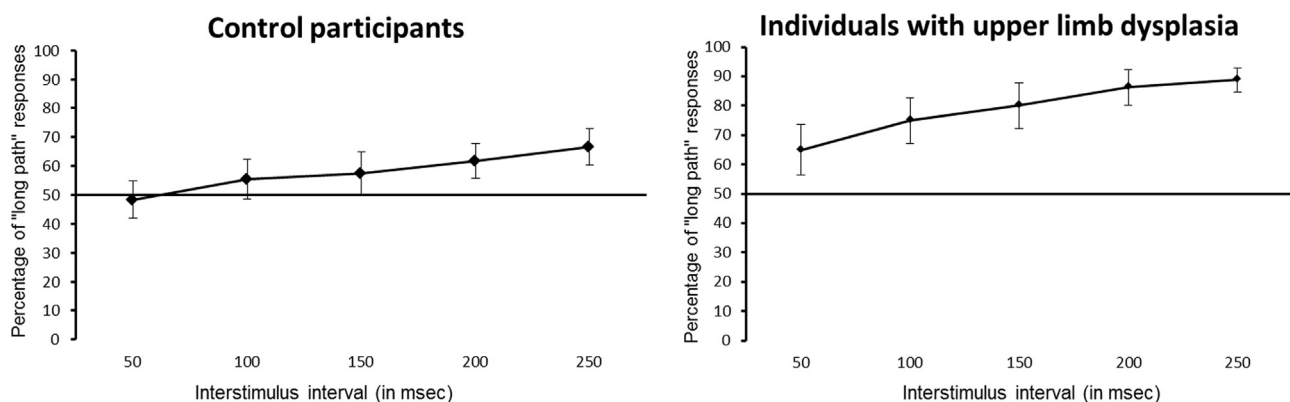


Fig. 3. Mean percentage and standard error of the mean (vertical bars) of “long paths” chosen by the control participants and the IDs at each level of interstimulus interval.

movement perception may be intrinsic to the visual system.

This finding corroborates previously published results showing that individuals with upper limb dysplasia's speed and accuracy at judging the laterality of hand drawings is influenced by the biomechanical complexity of the different hand postures and orientations (Brugger et al., 2000; Funk and Brugger, 2008; Vannuscorps et al., 2012; Vannuscorps and Caramazza, 2015). It also corroborates the observation of a typical biomechanical bias in the apparent movement task in an individual, A. Z., born without fully developed upper limbs (Funk et al., 2005). The present study goes beyond the previous evidence, however, by demonstrating the presence of a typical biomechanical bias in apparent movement perception in individuals totally deprived of upper limbs and who have never experience phantom limb sensations.

An alternative interpretation of our results could be that the IDs' perception of the longest path of hand movement reflects their recruitment of the corresponding lower limb motor representations. It is known that the dysplasics' motor system used to execute lower limb actions is activated when they observe hand actions (Aziz-Zadeh et al., 2011; Gazzola et al., 2007). This account can be dismissed, however, on the ground that our stimuli were selected specifically to ensure that the longer and biomechanically possible path between the two hand positions corresponded to a movement that is impossible to execute with the lower limbs due to their very different skeletal and muscular features and degrees of freedom (Nordin and Frankel, 2001).

Admittedly, the effect of the biomechanical constraints in the IDs may be supported by different computations from those supporting this effect in typically developed participants. A finding of this study, namely, that the IDs had a (statistically non-significant) tendency to perceive more often the biomechanically possible path than the controls may even seem to encourage this hypothesis. However, several arguments speak against this possibility. First, the tendency for the 5 IDs tested in this study to perceive more biomechanically possible paths than the controls seems unlikely to stem from a true difference between the populations. The smaller bias in the controls was driven by only a few individuals (3 out of 16) who almost always perceived the short but biomechanically impossible path (C7, C12 and C14, see Fig. S1) and, although none of the 5 IDs tested in our study showed this rare profile, it has been reported previously in a similar individual (Funk et al., 2005, see above). Second, 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 on body perception can be observed even after transient lesions to the motor system (Ganis et al., 2000; Pelgrims et al., 2010; Sauner et al., 2006) and in patients suffering from diverse conditions preventing the normal execution of body movements (e.g., Helmich et al., 2007; Fiorio et al., 2006).

Seemingly at odds with our conclusion, the results of a recent study have been interpreted as evidence that the perception of apparent movement of the body requires a contribution of motor areas (Orgs et al., 2016). In this study, the authors found that observing a sequence of three pictures displaying an actor's body in different postures recruits significantly more the primary motor system and the supplementary motor area when the body postures are ordered and create the perception of a fluent body movement than when they are disordered and do not create an apparent movement of the body. However, the reported activation of the motor system could result from, rather than constitute the source of, the perception of apparent body movement. In any case, our finding constitutes existence proof that the typical effect of the biomechanical bias on the perceived path of apparent body movement previously used to support theories claiming that our perception of others' bodies and movements is supported by

somatosensory and motor representations of our own body can rely exclusively on visual processes unaided by motor simulation.

In sum, our finding has two major implications for current theories of action perception. First, our finding demonstrates that there is no need to appeal to motor simulation to account for the influence of body constraints on body movement perception and that it can be a natural consequence of how the *visuo-perceptual system* processes and represents human bodies (Marr and Vaina, 1982; Tessari et al., 2010; Vannuscorps et al., 2012; Vannuscorps and Caramazza, 2015, 2016). Second, this finding serves as a cautionary note against the argument that the influence of biomechanical or other motor constraints on action perception can be taken as evidence of the crucial role of observers' body motor representations in action perception. This conclusion, of course, does not preclude that somatosensory and motor representations may nevertheless influence the processing of body movements in some (other) tasks or under some conditions such as, for instance, in tasks benefitting from the ability to perform motor imagery (e.g., Ionta et al., 2016), short term memory for body postures (e.g., Pernigo et al., 2012) or the recognition of actions perceived in adverse conditions (Vannuscorps et al., 2013). Future research will have to address the fundamental questions of how the visual system encodes information about the biomechanical constraints of body part movements, how this implicit knowledge constrains action perception, and how and when motor representations acquired through motor experience can contribute to the processing of observed actions.

## Acknowledgements

We are very grateful to all the participants in this study and to Moritz Wurm for his comment on an earlier version of the paper. 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. This research was supported by the Fondazione Cassa di Risparmio di Trento e Rovereto (Societa' Mente Cervello) and the Provincia Autonoma di Trento.

## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.neuropsychologia.2016.05.029](https://doi.org/10.1016/j.neuropsychologia.2016.05.029).

## References

- Aziz-Zadeh, L., Sheng, T., Liew, S.-L., Damasio, H., 2011. Understanding otherness: The neural basis of action understanding and empathy in a congenital amputee. *Cereb. Cortex* 22, 811–819.
- Blakemore, S.J., Decety, J., 2001. From the perception of action to the understanding of intention. *Nat. Rev. Neurosci.* 2, 561–567.
- Brugger, P., Brugger, S., 1993. The easter bunny in october: is it disguised as a duck? *Percept. Mot. Skills* 76, 577–578.
- 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. *Proc. Natl. Acad. Sci. USA* 97, 6167–6172.
- Burt, P., Sperling, G., 1981. Time distance and feature trade-off in visual apparent motion. *Psychol. Rev.* 88, 171–195.
- Decety, J., Grèzes, J., 1999. Neural mechanisms subserving the perception of human actions. *Trends Cognit. Sci.* 3, 172–178.
- 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. *J. Int. Neuropsychol. Soc.* 14, 81–89.
- Funk, M., Shiffar, M., Brugger, P., 2005. Hand movement observation by individuals born without hands: phantom limb experience constrains visual limb perception. *Exp. Brain Res.* 164, 341–346.
- Funk, M., Lutz, K., Hotz-Boendermaker, S., Roos, M., Summers, P., Brugger, P., Hepp-Reymond, S.S., Kollis, S.S., 2008. Sensorimotor tongue representation in

- individuals with unilateral upper limb amelia. *NeuroImage* 43, 121–127.
- Galantucci, B., Fowler, C.A., Turvey, M.T., 2006. The motor theory of speech perception reviewed. *Psychon. Bull. Rev.* 13, 361–377.
- Ganis, G., Keenan, J.P., Kosslyn, S.M., Pascual-Leone, A., 2000. Transcranial magnetic stimulation of primary motor cortex affects mental rotation. *Cereb. Cortex* 10, 175–180.
- Gazzola, V., Keysers, C., 2009. The observation and execution of actions share motor and somatosensory voxels in all tested subjects: single-subject analyses of unsmoothed fMRI data. *Cereb. Cortex* 19, 1239–1255.
- Gazzola, V., van der Worp, H., Mulder, T., Wicker, B., Rizzolatti, G., Keysers, C., 2007. Aphasics born without hands mirror the goal of hand actions with their feet. *Curr. Biol.* 17, 1235–1240.
- Glenberg, A.M., Witt, J.K., Metcalfe, J., 2013. From the revolution to embodiment: 25 years of cognitive psychology. *Perspect. Psychol. Sci.* 8, 573–585.
- Grosjean, M., Shiffrar, M., Knoblich, G., 2007. Fitts' law holds in action perception. *Psychol. Sci.* 18, 95–99.
- Grossman, E., 2006. Evidence for a network of brain areas involved in perception of biological motion. In: Knoblich, G., Thornton, I.M., Grosjean, M., Shiffrar, M. (Eds.), *The Human Body: Perception from the Inside Out*. Oxford University Press, New York, pp. 361–386.
- 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.
- Heptulla-Chatterjee, S., Freyd, J., Shiffrar, M., 1996. Configural processing in the perception of apparent biological motion. *J. Exp. Psychol.: Hum. Percept. Perform.* 22, 916–929.
- Ionta, S., Villiger, M., Jutzeler, C.R., Freund, P., Curt, A., Gassert, R., 2016. Spinal cord injury affects the interplay between visual and sensorimotor representations of the body. *Sci. Rep.* 6, 20144.
- Knoblich, G., 2008. Bodily and motor contributions to action perception. In: Klatzky, R., MacWhinney, B., Behrmann, M. (Eds.), *Embodiment, Ego-Space, and Action*. Psychology Press., New York, pp. 43–76.
- Mahon, B.Z., Caramazza, A., 2008. A critical look at the embodied cognition hypothesis and a new proposal for grounding conceptual content. *J. Physiol. – Paris* 102, 59–70.
- Marr, D., Vaina, L., 1982. Representation and recognition of the movements of shapes. *Proc. R. Soc. Lond.* 214, 501–524.
- Nordin, M., Frankel, V.H., 2001. *Basic Biomechanics of the Musculoskeletal System*, 3rd ed. Lippincott Williams And Wilkins., Philadelphia.
- Orgs, G., Dovern, A., Hagura, N., Haggard, P., Fink, G.R., Weiss, P.H., 2016. Constructing visual perception of body movement with the motor cortex. *Cereb. Cortex* 26, 440–449.
- Parsons, L.M., 1987. Imagined spatial transformations of one's hands and feet. *Cognit. Psychol.* 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. *Hum. Brain Mapp.* 32, 1802–1810.
- Pernigo, S., Moro, V., Avesani, R., Miatello, C., Urgesi, C., Aglioti, S.M., 2012. Massive somatic deafferentation and motor deafferentation of the lower part of the body impair its visual recognition: a psychophysical study of patients with spinal cord injury. *Eur. J. Neurosci.* 36, 3509–3518.
- 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 judgments: a transcranial magnetic stimulation study. *Eur. J. Neurosci.* 23, 2215–2224.
- Shiffrar, M., Freyd, J.J., 1990. Apparent motion of the human body. *Psychol. Sci.* 1, 257–264.
- Shiffrar, M., Freyd, J.J., 1993. Timing and apparent motion path choice with human body photographs. *Psychol. Sci.* 4, 379–384.
- Stevens, J.A., Fonlupt, P., Shiffrar, M., Decety, J., 2000. New aspects of motion perception: selective neural encoding of apparent human movements. *Neuroreport* 11, 109–115.
- Stoekel, M.C., Seitz, R.J., Buettel, C.M., 2009. Congenitally altered motor experience alters somatotopic organization of human primary motor cortex. *Proc. Natl. Acad. Sci. USA* 106, 2395–2400.
- Stoekel, 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. *J. Neurophysiol.* 93, 813–818.
- 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.
- Thornton, I., Pinto, J., Shiffrar, M., 1998. The visual perception of human locomotion. *Cognit. Neuropsychol.* 15, 535–552.
- Vannuscorps, G., Caramazza, A., 2015. Typical biomechanical bias in the perception of congenitally absent hands. *Cortex* 67, 147–150.
- Vannuscorps, G., Caramazza, A., 2016. Typical action perception and interpretation without motor simulation. *Proc. Natl. Acad. Sci. U. S. A* 113, 86–91.
- Vannuscorps, G., Pillon, A., Andres, M., 2012. The effect of biomechanical constraints in the hand laterality judgment task: where does it come from? *Front. Hum. Neurosci.* 6, 299.
- Vannuscorps, G., Andres, M., Pillon, A., 2013. When does action comprehension need motor involvement? Evidence from upper limb apraxia. *Cogn. Neuropsychol.* 30, 253–283.
- Wilson, M., 2001. Perceiving imitable stimuli: consequences of isomorphism between input and output. *Psychol. Bull.* 127, 543–553.
- Wilson, M., 2006. Covert imitation: how the body schema acts as a prediction device. In: Knoblich, G., Thornton, I.M., Grossjean, M., Shiffrar, M. (Eds.), *The Human Body: Perception from the Inside Out*. Oxford University Press, New York, pp. 211–228.