

# Typical action perception and interpretation without motor simulation

Gilles Vannuscorps<sup>a,b,c,1</sup> and Alfonso Caramazza<sup>a,b</sup>

<sup>a</sup>Center for Mind/Brain Sciences, Università degli Studi di Trento, Mattarello, 38122, Italy; <sup>b</sup>Department of Psychology, Harvard University, Cambridge, MA 02138; and <sup>c</sup>Institute of Psychological Sciences, Université catholique de Louvain, Louvain-la-Neuve, 1348, Belgium

Edited by Randolph Blake, Vanderbilt University, Nashville, TN, and approved November 17, 2015 (received for review August 25, 2015)

Every day, we interact with people synchronously, immediately understand what they are doing, and easily infer their mental state and the likely outcome of their actions from their kinematics. According to various motor simulation theories of perception, such efficient perceptual processing of others' actions cannot be achieved by visual analysis of the movements alone but requires a process of motor simulation—an unconscious, covert imitation of the observed movements. According to this hypothesis, individuals incapable of simulating observed movements in their motor system should have difficulty perceiving and interpreting observed actions. Contrary to this prediction, we found across eight sensitive experiments that individuals born with absent or severely shortened upper limbs (upper limb dysplasia), despite some variability, could perceive, anticipate, predict, comprehend, and memorize upper limb actions, which they cannot simulate, as efficiently as typically developed participants. We also found that, like the typically developed participants, the dysplastic participants systematically perceived the position of moving upper limbs slightly ahead of their real position but only when the anticipated position was not biomechanically awkward. Such anticipatory bias and its modulation by implicit knowledge of the body biomechanical constraints were previously considered as indexes of the crucial role of motor simulation in action perception. Our findings undermine this assumption and the theories that place the locus of action perception and comprehension in the motor system and invite a shift in the focus of future research to the question of how the visuo-perceptual system represents and processes observed body movements and actions.

action perception | motor simulation | mirror neurons

Our social life rests in large part on our capacity to perceive and interpret others' behavior accurately to anticipate their upcoming actions and adjust our own behavior appropriately. The impairment of this ability in the context of autism, schizophrenia, various types of dementia, or following stroke or head injury has tragic consequences for both patients and society. However, how the human mind and brain supports these abilities remains a major challenge. In this study, we addressed a specific issue regarding the relationship between visual and motor processes in action perception and recognition: Does efficient perception and interpretation of action rely on unconscious, covert motor simulation of the observed movements?

The traditional view on this issue is that efficient perception and interpretation of human movement does not rely on motor simulation but rather on computations occurring in the visuo-perceptual system supported by basic perceptual processes and information extrapolated from perceptual learning (1–5). This view has been challenged by a series of motor simulation theories of perception which, despite their differences, all assume that efficient perceptual processing of others' actions cannot be achieved by visual analysis of the movements alone but requires unconscious covert imitation—motor simulation—of the observed movements (6–13). In this view, motor simulation of an observed action allows the observer to retrieve knowledge about that action automatically, as if the observer were performing the action herself.

Over the past 20 y, this paradigm-shifting idea—that motor simulation is a core feature of movement perception—has become the dominant neurobiological account of the perception and interpretation of action and has had a great impact in the scientific and medical community (e.g., refs. 14–16). However, to date, the interpretation of the results from neuroimaging, behavioral, neuropsychological, and transcranial magnetic stimulation (TMS) studies that have been cited in support of motor simulation theories of perception remains unsettled (*SI Discussion, 1*) (17–19).

Here, we investigated the role of motor simulation on the perception and interpretation of action in five individuals who were cognitively and neurologically intact but were born with an extremely rare condition: bilateral upper limb dysplasia, characterized by a congenital absence of upper limbs. The rationale is straightforward. The individuals with dysplasia (IDs) never developed any upper limb motor representations or processes that could be mobilized to execute observed upper limb movements covertly (*SI Discussion, 2*) (20–22). Thus, the expectation from the motor simulation theories of perception is that the performance of the IDs should differ from that of the control participants in tasks that assess aspects of movement processing requiring motor simulation.

In contrast with that prediction, across eight sensitive tasks (no ceiling or floor effect) assessing different aspects of the perceptual processing of action, we found that individuals born without upper limbs can perceive, anticipate, predict, comprehend, and memorize observed actions with the same accuracy and speed as the controls. Furthermore, in all the tasks, some IDs performed well above the mean of the controls. In addition, and crucially, we also found that the IDs' perception of upper limb movements was characterized by the same perceptual biases (anticipatory and biomechanical biases) as found in the response profile of control participants—perceptual biases that have been taken as evidence for a role of motor simulation in perception.

## Significance

How do we perceive and interpret others' actions? In recent years, the dominant view on this issue is that efficient perceptual processing of others' actions cannot be achieved by visual analysis of the movements alone but requires unconscious, covert motor simulation of the observed movements. This idea has developed a large following in many disciplines such as psychology, neuroscience, neurology, psychiatry, and philosophy of mind and has started to influence the study and treatment protocols of patients suffering from conditions affecting the perception and interpretation of action (such as autism, schizophrenia, and various dementias). In this paper, however, we report evidence that efficient perception and interpretation of actions can be achieved without motor simulation.

Author contributions: G.V. designed research; G.V. performed research; G.V. analyzed data; and G.V. and A.C. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

<sup>1</sup>To whom correspondence should be addressed. Email: gvannuscorps@fas.harvard.edu.

This article contains supporting information online at [www.pnas.org/lookup/suppl/doi:10.1073/pnas.1516978112/-DCSupplemental](http://www.pnas.org/lookup/suppl/doi:10.1073/pnas.1516978112/-DCSupplemental).

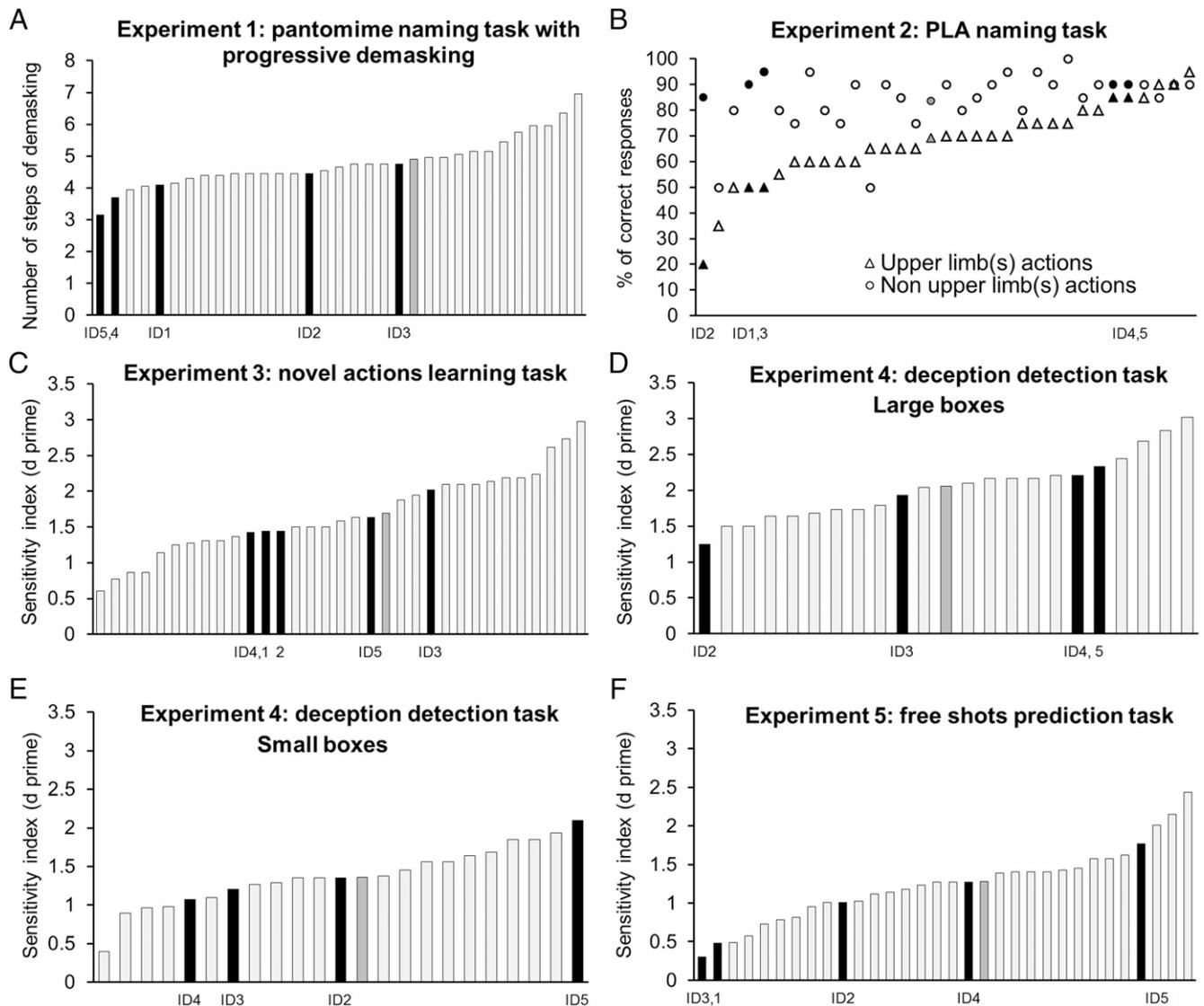
This set of findings challenges the central premise of the models of action perception and interpretation centered on motor simulation: They show that the visuo-perceptual system can support efficient perception and interpretation of action unaided by motor simulation.

## Results

The most frequent functional role attributed to motor simulation is that it underlies efficient (i.e., fast and accurate) comprehension of actions (6–12). Experiment 1 tested this hypothesis. Participants viewed video clips of an actress pantomiming 20 different instrumental actions (e.g., playing a guitar, typing). Only body

movements were shown, without any object or context. Participants were asked to name each action at 14 165-ms steps in a gradual unmasking paradigm from 330 ms to 2,640 ms. An item was scored correct at a given level of demasking (from 1 to 14) if it also was identified correctly at all subsequent levels and was scored 15 if not recognized. Contrary to expectations from the motor simulation hypothesis, the IDs were as (or more) accurate and fast as the controls in recognizing pantomimes of action (Fig. 1A and Fig. S14).

Another proposed role of motor simulation is that it provides critical complementary information to enhance stimulus identification



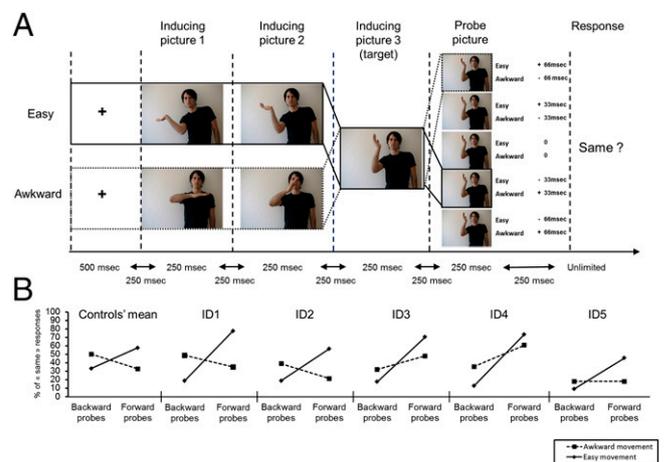
**Fig. 1.** Results of experiments 1–5 by individual participant (see also Figs. S1 and S2). IDs are shown in black; control participants are shown in light gray; the mean of the controls is shown in darker gray. We applied two-tailed modified  $t$  tests (48) to test whether the performance of each ID was different from the performance of the controls. (A) The IDs were either as efficient [IDs 1–4: all modified  $t$  tests,  $t_s(26) < -0.21$ , all  $P_s > 0.12$ ] or more efficient [ID5: modified  $t$  test,  $t(26) = -2.36$ ,  $P < 0.05$ ] than the controls in pantomimes recognition. (B) All the IDs were as accurate as the controls at naming the non-upper limb actions [all modified  $t$  tests,  $t_s(26) > 0.11$ , all  $P_s > 0.18$ ]. All the IDs [all modified  $t$  tests,  $t_s(26) > -1.45$ , all  $P_s > 0.08$ ] except ID2 [modified  $t$  test,  $t = -3.72$ ,  $P < 0.001$ ] were as accurate as the controls in naming upper limb actions. We applied the Bayesian standardized difference test (BSDT) (49) to test whether the discrepancy in the ID's performance between the two categories of stimuli was significantly different from the discrepancy between the two categories in the control group. The discrepancy in performance between the upper limb and the lower limb actions was larger in IDs 1, 2, and 3 than in the controls (all BSDT  $P < 0.05$ ) but not in ID 4 and 5 (both BSDT  $P > 0.5$ ). In comparison with the controls both ID 4 and 5 performed relatively better for upper limb actions (both modified  $t$  tests,  $t_s = 1.19$ ) than for lower limb actions (both modified  $t$  tests,  $t_s = 0.52$ ). (C) All the IDs were as efficient as the controls in discriminating learned from novel actions [all modified  $t$  tests,  $t_s(26) > -0.19$ , all  $P_s > 0.45$ ]. (D and E) The IDs were as sensitive as the controls to violation of the actors' expectations for the large boxes (D) [all modified  $t$  tests,  $t_s(17) > -1.74$ , all  $P_s > 0.05$ ] and the small boxes (E) (all modified  $t$  tests,  $t_s(17) > -0.71$ , all  $P_s > 0.05$ ]. (F) IDs 1, 2, 4, and 5 were as sensitive as the controls to the outcome of the shots [all modified  $t$  tests,  $t_s(25) > -1.76$ , all  $P_s > 0.05$ ], but ID 3 was less sensitive [modified  $t$  test,  $t(25) = -2.15$ ,  $P = 0.04$ ].

under adverse perceptual conditions (13, 19, 23, 24). Experiment 2 used point-light animations to test this hypothesis. Participants viewed video clips of an actor reduced to 12 light dots placed on his main joints (center of the head, shoulders, elbows, wrists, center of pelvis, knees, and ankles) performing 20 upper limb actions (e.g., fishing) and 20 non-upper limb actions (e.g., walking backward) and were asked to name the actions. IDs 1, 2, and 3 were significantly less accurate in recognizing upper limb actions than non-upper limb (normal range) actions. However, in contrast to the motor simulation hypothesis, IDs 4 and 5 performed well above the mean of the controls for both upper limb and non-upper limb actions (Fig. 1*B* and Fig. S1*B*).

Another possibility is that motor simulation is particularly important in learning to recognize new actions (25, 26). Experiment 3 tested this hypothesis. Participants were asked to memorize 21 video clips (lasting between 2.1 and 2.4 s) of an actress performing meaningless gestures with the upper limb(s). Videos did not include any context or objects, and the actress's body and face were kept neutral (27). Participants had to recognize the memorized clips from among 21 similar video clips. We calculated the number of correct (hits) and incorrect (false alarms) recognitions of previously learned actions and computed the  $d'$  sensitivity index of each participant. The performance of the IDs was indistinguishable from that of control participants (Fig. 1*C* and Figs. S1*C* and S2*C*).

Motor simulation has been assumed to support the ability to make inferences based on a fine-grained analysis of others' kinematics (28, 29). Experiments 4 and 5 examined this hypothesis. In experiment 4, participants viewed video clips of an actor's arm lifting a small box or of an actor's whole body lifting a large box containing one of four different weights (small box: 0.05, 0.3, 0.6, or 0.9 kg; large box: 3, 6, 12, or 18 kg) and had to decide after each trial whether the actor knew the correct weight of the box before lifting it (28). We calculated the number of correct (hits) and incorrect (false alarms) identifications of a violation of the actor's expectation and then computed the  $d'$  sensitivity index for each participant. In experiment 5 participants viewed video clips showing a player shooting a basketball; the clip was interrupted at the instant the ball left the player's hands, and the participant had to predict the outcome of the shot (29). We calculated the number of correct (hits) and incorrect (false alarms) identifications of the successful free shots and computed the  $d'$  sensitivity index for each participant. The performance of the IDs in these tasks was indistinguishable from that of control participants (Fig. 1*D-F* and Figs. S1*D-F* and S2*D-F*). Thus, the ability to infer the outcome of others' actions from their kinematics does not require motor simulation.

Still, motor simulation may support more basic perceptual processes underlying our perception of others' movements. For instance, to process others' movements in real time despite the informational lag imposed by neural transmission, our perceptual system typically anticipates the outcome of their movements by shifting the perceived position of the effectors forward along their plausible trajectories (30). According to the motor simulation theories of perception, perceptual anticipation (PA) of others' movements and its tuning to biomechanically plausible movements depends on motor simulation of the observed movements (13, 30). To test this hypothesis, in experiment 6, participants watched series of three sequentially presented pictures inducing the perception of a hand movement that would be either awkward or easy to continue along the same trajectory, and they were asked to decide whether a subsequent probe picture matched the last picture in the series (Fig. 2*A*). Foils showed the arm shifted slightly backward or forward along its initial trajectory. We compared the number of "same" responses across probe type (forward and backward) and movement condition (easy and awkward). Both IDs and controls showed a significant bias toward forward probes in the easy condition, but this bias was absent or was significantly smaller in the awkward condition (Fig. 2*B*). Thus, like the controls, the IDs perceive the position of moving hands as shifted slightly forward along their trajectory (action anticipation) but did so only when the anticipated position was not biomechanically awkward. The finding that perceptual anticipation in the IDs is shaped by implicit knowledge of biomechanics

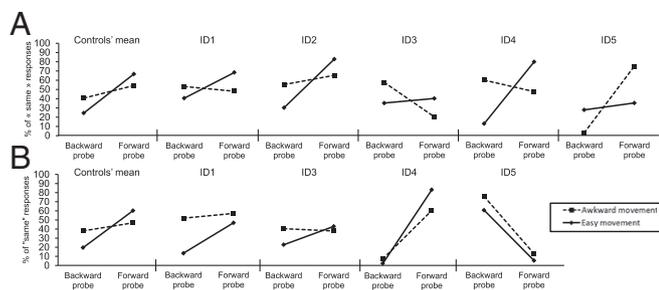


**Fig. 2.** Methods and results of experiment 6. (*A*) Materials and methods. One probe picture is the same as the target, and the others (the foils) show the actor's hand shifted 33 ms or 66 ms forward (+) or backward (−) relative to its position on the target (depending on the condition). Shown within solid lines is an example of a trial from the easy condition ending with a one-frame-backward foil. In dotted lines is an example of a trial from the awkward condition ending with a two-frames-backward foil. (*B*) Results. All tests were two tailed. Control participants [paired  $t$  test,  $t(19) = 6.49$ ,  $P < 0.001$ ] and the five IDs [all  $\chi^2(1) > 24$ , all  $P_s < 0.001$ ] made more "same" responses for forward than for backward probes in the easy movement condition, but this forward bias was absent (in controls and in IDs 1, 2, and 5) or was significantly smaller [in IDs 3 and 4, both  $\chi^2(1) > 20$ , both  $P_s < 0.01$ ] in the awkward movement condition. The size of the forward bias in the easy movement condition did not differ significantly between the IDs and the controls [all modified  $t$  tests,  $0.75 < t(19) < 1.98$ , all  $P_s > 0.05$ ].

shows that the computations underlying this effect are intrinsic to the visual system.

A critical issue, however, is whether the PA effect observed in experiment 6 also holds for the perception of continuous movement (31). Therefore in experiment 7 we asked participants to watch a series of video clips showing a computerized 3D actor performing a rotation of the arm away from or arriving at an awkward position and to decide whether a subsequent probe picture matched the position of the hand at the end of the video (Fig. S3*A*). Again, foils showed the arm shifted slightly backward or forward along its initial trajectory, and we compared the number of "same" responses across probe type (forward and backward) and movement condition (easy and awkward). IDs 1, 2, and 4, like the controls, showed the typical bias toward forward rather than backward foils when the hand moved out of, but not into, an awkward position (Fig. 3*A*). IDs 3 and 5 did not show the same profile. However, their performance was similar to that of some individual control participants (Fig. S3*C*), suggesting that their performance reflects variability intrinsic to the task.

Finally, experiment 8 was carried out to ensure that the results reported in experiments 6 and 7 could be replicated with another body movement. Participants were presented video clips showing a computer-generated actor performing an extension/flexion of the right shoulder and were asked to decide whether a subsequent probe picture matched the position of the hand at the end of the video (Fig. S3*B*). ID2 was not tested in this experiment because she was able to perform movements of the stumps similar to the presented extension/flexion of the arm. Results from this experiment were analyzed similarly to the results of experiments 6 and 7. IDs 1, 2, and 4, like the controls, showed the typical bias toward forward rather than backward foils when the hand moved out of an awkward position but did not show that bias (controls and IDs 1 and 3) or showed less bias (ID4) when it moved into an awkward condition (Fig. 3*B*). ID5 did not show the same profile, but his performance did not differ significantly from that of the control participants (see the profiles of control participants 26 and 30 in Fig. S3*D*).



**Fig. 3.** Results of experiments 7 and 8 (see also Fig. S3). All tests were two tailed. (A) Results of experiment 7. Control participants produced a significantly larger number of “same” responses for forward than for backward probes in the easy condition [paired  $t$  test,  $t(14) = 4.93$ ,  $P < 0.001$ ], but this bias was not significant [paired  $t$  test,  $t(14) = 1.59$ ,  $P = 0.13$ ] and was significantly smaller in the awkward movement condition [repeated measures ANOVA,  $F(1, 14) = 5.41$ ,  $P = 0.04$ ]. IDs 1, 2, and 4 showed the same profile, with a significant forward bias in the easy condition [all  $\chi^2(1) > 4$ , all  $P_s < 0.05$ ] of the same size as that of the controls [all modified  $t$  tests,  $0.61 < t_s(14) < 1.10$ , all  $P_s > 0.05$ ], but showed either no bias (IDs 1 and 4) or a significantly smaller bias [ID2:  $\chi^2(1) > 16$ ,  $P < 0.01$ ] in the awkward condition. IDs 3 and 5 did not show any significant bias in the easy condition [both  $\chi^2(1) < 1$ , both  $P_s > 0.5$ ] but showed either a significant backward bias [ID3,  $\chi^2(1) = 9.77$ ,  $P < 0.01$ ] or forward bias [ID5,  $\chi^2(1) > 30$ ,  $P < 0.05$ ] in the awkward condition. (B) Results of experiment 8. Control participants produced a significantly larger number of “same” responses for forward than for backward probes in the easy movement condition [paired  $t$  test,  $t(14) = 4.64$ ,  $P < 0.001$ ], but this bias was not significant [paired  $t$  test,  $t(14) = 0.89$ ,  $P = 0.38$ ] and was significantly smaller in the awkward movement condition [repeated measures ANOVA,  $F(1, 14) = 5.43$ ,  $P = 0.03$ ]. IDs 1 and 4 showed the same profile of a significant forward bias in the easy movement condition [both  $\chi^2(1) > 6.64$ , both  $P_s < 0.01$ ] that was significantly larger than in the awkward movement condition [both  $\chi^2(1) > 6$ ,  $P < 0.01$ ] and was the same size as that of the controls [both modified  $t$  tests,  $-0.3 < t_s(14) < 0.93$ , both  $P_s > 0.05$ ]. ID3 showed the same trend, although it was not significant [ $\chi^2(1) = 1.83$ ,  $P = 0.1$ ]. ID5 showed a significant backward bias in both conditions [both  $\chi^2(1) > 20$ ,  $P_s < 0.01$ ].

## Discussion

In this study, we tested predictions derived from motor simulation theories of perception (6–13), which assume that efficient perceptual processing of others’ actions cannot be achieved by visual analysis of the movements alone but requires unconscious covert imitation—motor simulation—of the observed movements. The results we report here challenge this view. In the eight experiments, we found that most of the IDs, although they were incapable of simulating observed upper limb movements in their motor system, could perceive, anticipate, predict, comprehend, and memorize upper limb actions as accurately, as rapidly, and with the same sensitivity and biases as typically developed participants.

This evidence cannot be dismissed on the ground that we simply failed to find evidence for a difference of performance between IDs and the control participants because of a lack of statistical power. All the experiments were sensitive, with no ceiling or floor effects and, despite some performance variability (SI Discussion, 3), in all the tasks some of the dysplastic participants performed well above the mean of the controls, including younger controls with a high level of education. In addition, and crucially, we found positive evidence that the IDs’ perception of upper limb movements was characterized by the same perceptual biases (anticipatory and biomechanical biases) found in the response profile of control participants—perceptual biases that have been taken as evidence for a role of motor simulation in perception (7, 13, 30).

Our findings thus considerably extend previous results obtained with IDs or congenital paralysis (19, 32–35). It has been shown that individuals with congenital paralysis of facial muscles recognize facial expressions despite their inability to perform facial movements (32). It also has been found that individuals with upper limb

dysplasia are influenced by body biomechanical constraints when asked to judge the laterality of hand drawings (33–35). The present study goes well beyond the scope of this previous evidence by demonstrating that motor simulation contributes neither to the ease (speed) of action recognition nor to its robustness and does not contribute to the ability to anticipate others’ movements perceptually, to predict the outcome of their actions, to read their mental states from their kinematics, or to memorize their body postures and movements. Another distinctive feature of the experimental results reported in this study is that they demonstrate the ability of the visuo-perceptual system, in the absence of motor simulation, to detect, process, and use information about body shape and movement to perceive and interpret observed actions efficiently even when they are presented in extreme, impoverished conditions. IDs performed comparably with controls when actions were to be recognized from only the very first movements and from configurations of the upper limbs (experiment 1) or from the displacement of only four dots representing the actor’s wrists and elbows (experiment 2), when very similar actions had to be discriminated after only a short exposure (experiment 3), when very subtle cues in the kinematics of the actors’ upper limb movements had to be used to make perceptual decisions (experiments 4 and 5), or when subtle perceptual biases were investigated (experiments 6–8).

An alternative interpretation of these findings might be that the IDs’ efficiency in perceiving and interpreting action arises from their “simulation” of the observed upper limb movements and actions with their lower limbs. It is known that in dysplasics the motor system used to execute lower limb actions is activated when they observe hand actions (36, 37). However, this alternative interpretation of the results produces two seemingly insurmountable challenges for current versions of the motor simulation theories (SI Discussion, 4). First, although the effectiveness of simulation in aiding action perception depends on the degree of similarity between the observed action and the observer’s own motor representation of that action (38, 39), the very different skeletal and muscular features and degrees of freedom of the arms and legs and of the hands and feet (40) make it virtually impossible to imitate the observed upper limb actions with the lower limbs. For example, the different mechanical limits of external rotation and of extension/flexion of the shoulder and the hip (40) make it very difficult to attribute the performance of the dysplasics in experiments 6, 7, and 8 as reflecting the effects of simulation of the observed arm movements by the feet. Second, and more importantly, the hypothesis that motor simulation contributes to the perception of action is of interest because the hypothesis assumes that motor simulation operates through a non-cognitively-mediated direct matching process between an observed, uninterpreted movement and the observer’s own motor representation of that movement (18). It is unclear, however, how a mechanism of direct execution–observation matching could operate when there are no motor characteristics in common between the motor plans involved in execution and the observed motor act. Effector-independent motor simulation thus requires the prior categorization of the observed action as an act of a particular type that, once interpreted, can be associated with the motor program of the same action executed with a different effector from the observed one (36, 41, 42).

Our findings thus clearly challenge the central premise of the motor simulation theories of perception: They demonstrate that it is possible to account for efficient action perception and interpretation and, crucially, to explain the kind of performance profiles that have been used so far to support the motor theory of perception (e.g., the anticipatory and biomechanical biases in perception of body movements) without appealing to the concept of motor simulation. The findings reported in this study thus support models of action perception and comprehension that distinguish perceptual, conceptual, and motor stages of processing (e.g., ref. 2). According to these models, when a movement is perceived, a visuo-perceptual analysis of the actor’s body shape and motion provides a visual description of the action, which serves as input to a conceptual system containing conceptual features or attributes of the action (e.g., its typical duration, function, goal, and so forth). As our

findings show, these two stages of processing are necessary and sufficient to support the rapid, sensitive, and robust perception and interpretation of actions and to compensate for neural transmission delay through biomechanically tuned perceptual anticipation. According to these models, motor simulation occurs by both a non-cognitively-mediated direct route, supporting effector-specific covert imitation of observed movements occurring in parallel to the conceptual processing, and by a cognitively-mediated indirect route following the conceptual processing (2). However, motor simulation is not required for efficient perception and interpretation of action.

Admittedly, it is possible that the sensitivity to movement kinematics, perceptual anticipation, perceptual tuning toward biomechanically easy movements, and the efficient memory of novel upper limb movements and action recognition found in the IDs are all based on processes and representations different from those supporting the same abilities in the typically developed individuals; that is, the IDs use only visuo-perceptual computations, but the typically developed participants rely on motor simulation as well. Future studies are needed to elucidate this question with the help of neuropsychological studies of patients suffering from brain damage that affects their ability to imitate observed actions covertly, among others. However, several arguments speak against this possibility.

First, we found that the perception and interpretation of action was not only in efficiency but also qualitatively similar in the two groups. An analysis of the qualitative performance of the IDs in experiments 1–5 showed that they made errors on the same stimuli as the typically developed participants (Fig. S2), suggesting that their performance is affected by the same variables. Even more importantly, in experiments 6–8 we observed that the IDs' perception of upper limb movements is influenced by the same anticipatory and biomechanical biases that affect control participants' performance. This result demonstrates that the IDs' and the controls' perception of body movements cannot be distinguished from each other even at the level of the finest-grained characteristics; thus it is difficult to assume that they are using different strategies in all these tasks.

Second, this conclusion is consistent with computational modeling results showing that action perception and identification can be explained by exclusively visual processes and representations (1). It also is in line with the results from neuropsychological studies showing that damage to various parts of the motor system such as the basal ganglia (43, 44), the inferior parietal lobe (43–45), the inferior frontal gyrus (43, 45, 46), the left premotor cortex (43, 45), the primary motor cortex (43, 45), and the bilateral superior parietal lobule (46) cause motor or praxis disorders (a disorder affecting the capacity to perform actions despite preserved basic motor and somatosensory functions) but do not necessarily hamper action identification.

Third, and crucially, there seems to be no evidence incompatible with this conclusion. Indeed, the interpretation of the results from neuroimaging, behavioral, neuropsychological, and TMS studies, which have been cited in support of motor simulation theories of perception, remains unsettled (*SI Discussion, 1*). Moreover, one important aspect of our results is that they are based on experiments that used the same materials and procedures used in studies (28–30) that have been interpreted as providing conclusive evidence in favor of motor simulation theories of perception. We showed, for instance, with the same material and procedure as in the seminal paper by Wilson et al. (30) that, in contrast to the initial interpretation, the tuning of action anticipation toward biomechanically easy movements does not require motor simulation. Using the material and procedure from Bosbach et al. (28), we showed that, contrary to the initial interpretation of the results of that study, the ability to detect mismatches between prepared and executed actions and to use such detection to infer the mental state of an actor does not require motor simulation of the observed movements. Finally, using the materials from Aglioti et al. (29), we showed that the ability to predict the outcome of an action efficiently does not require motor simulation. Our results demonstrate that motor simulation is not needed to obtain the performance profiles that have been used to support the motor simulation theory of perception. In fact, within models that do not attribute a causal role to motor simulation in action perception, these results are taken to indicate

that motor experience contributes not only to the acquisition of motor representations but also to the acquisition of spatiotemporal knowledge about actions and that the latter, not motor simulation, shapes action perception (47). The observation reported here that IDs 1, 2, and 3 were better at recognizing non-upper limb actions than upper limb actions in experiment 2 (see also ref. 19) and that ID3 was impaired in predicting the outcome of the basketball free shot in experiment 5 also point to this possibility (although this difficulty also could be explained by the IDs having different visual experiences of these actions). Collectively, these results call for the development of fresh hypotheses about how knowledge acquired through motor experience helps shape visually and conceptually based computations of body actions.

In conclusion, several motor simulation theories of perception have proposed that efficient perceptual processing of others' actions cannot be achieved by the visual analysis of the movement alone but requires a process of motor simulation, that is, a covert execution of the observed movements. Our findings challenge this view and, although the extent to which these results generalize to typically developed participants remains an open question, they underscore the need for a shift in the burden of proof concerning the role of motor simulation in perception. **Future research must address the fundamental questions of how the visuo-perceptual and cognitive systems support efficient and effector-constrained perception and interpretation of actions.** In this latter framework, fundamental questions remain concerning how the visual system encodes information about the biomechanical constraints of body part movements, how this implicit knowledge constrains action perception, and how knowledge acquired through motor experience helps shape the processing of observed actions (*SI Discussion, 1*). In addition to its theoretical significance, this set of findings serves as a cautionary note in the application of principles derived from motor simulation theories of perception to the understanding or treatment of neurological and psychiatric conditions (e.g., refs. 14–16).

## Materials and Methods

The experimental investigations were carried out from October 2013 to June 2014 in sessions lasting between 60 and 120 min. The study was approved by the biomedical ethics committee of the Cliniques Universitaires Saint-Luc, Brussels, Belgium, and all participants gave written informed consent before the study. During the experiment, participants were seated in front of a computer screen located at a distance of about 60 cm. The experiments were controlled with the E-Prime software (Psychological Software, 2002) and presented on a 15.6-inch Dell Latitude E5530 anti-glare laptop screen set at 1,366 × 768 pixels and 60 Hz.

**Participants.** Five individuals born with severely shortened or completely absent upper limbs (see *SI Materials and Methods* for details) and five groups of control participants were tested (Table S1). No participant had a history of psychiatric or neurological disorder. None of the IDs had history of phantom limb sensations or movements (*SI Materials and Methods*). Most of the tasks were presented to more than one group of control participants (Table S2) so that we were able to compare each ID with a sample of control participants matched in age, gender, and education. Because no difference in performance was observed across the different control groups for any of the tasks, and because the results obtained when the each of the IDs was compared with the matched control group led to the same conclusions, we decided not to report the results of the different groups in the main text. Results of the different groups and the comparison of each ID with the respective control group are presented in Fig. S1.

**Materials and Procedures.** A detailed description of the materials and procedures of the eight experiments is provided in *SI Materials and Methods*. The actions pantomimed in experiment 1 are listed in Table S3; the upper limb and non-upper limb actions presented in experiment 2 are listed in Table S4; and supplemental results are given in Tables S5 and S6.

**ACKNOWLEDGMENTS.** We thank Beatrice Agostini and Angelika Lingnau, Seana Coulson, Simone Bosbach, Salvatore Aglioti and Cosimo Urgesi, and Margaret Wilson, for providing the material used in experiments 1, 3, 4, 5, and 6, respectively, and Pr. Didier Lacombe for help in recruiting ID3. Christian van Brussel built the application used to generate the point-light animations used in experiment 3 from a motion-capture database created with funding from National Science Foundation Grant EIA-0196217 and obtained

from [www.mocap.cs.cmu.edu](http://www.mocap.cs.cmu.edu). This research was supported by the Fondazione Cassa di Risparmio di Trento e Rovereto, the Provincia Autonoma di

Trento, and by an additional Postdoctoral Grant by Fonds Spécial de Recherche, Université catholique de Louvain (to G.V.).

- Giese MA, Poggio T (2003) Neural mechanisms for the recognition of biological movements. *Nat Rev Neurosci* 4(3):179–192.
- Rothi LJ, Ochipa C, Heilman KM (1991) A cognitive neuropsychological model of limb praxis. *Cogn Neuropsychol* 8:443–458.
- Johansson G (1973) Visual perception of biological motion and a model for its analysis. *Percept Psychophys* 14:201–211.
- Marr D, Vaina L (1982) Representation and recognition of the movements of shapes. *Proc R Soc Lond B Biol Sci* 214(1197):501–524.
- Jellema T, Perrett DI (2005) Neural basis for the perception of goal-directed actions. *The Cognitive Neuroscience of Social Behaviour*, eds Easton A, Emery EJ (Psychology, New York), pp 81–112.
- Blakemore SJ, Decety J (2001) From the perception of action to the understanding of intention. *Nat Rev Neurosci* 2(8):561–567.
- Hommel B, Müsseler J, Aschersleben G, Prinz W (2001) The Theory of Event Coding (TEC): A framework for perception and action planning. *Behav Brain Sci* 24(5):849–878, discussion 878–937.
- Jeannerod M (2001) Neural simulation of action: A unifying mechanism for motor cognition. *Neuroimage* 14(1 Pt 2):S103–S109.
- Jeannerod M (2005) Is motor cortex only an executive area? Its role in motor cognition. *Motor Cortex in Voluntary Movements. A Distributed System for Distributed Functions*, eds Riehle A, Vaadia E (CRC, Boca Raton, FL), pp 241–256.
- Rizzolatti G, Craighero L (2004) The mirror-neuron system. *Annu Rev Neurosci* 27:169–192.
- Rizzolatti G, Sinigaglia C (2010) The functional role of the parieto-frontal mirror circuit: Interpretations and misinterpretations. *Nat Rev Neurosci* 11(4):264–274.
- Wolpert DM, Doya K, Kawato M (2003) A unifying computational framework for motor control and social interaction. *Philos Trans R Soc Lond B Biol Sci* 358(1431):593–602.
- Wilson M, Knoblich G (2005) The case for motor involvement in perceiving conspecifics. *Psychol Bull* 131(3):460–473.
- Rizzolatti G, Fabbri-Destro M, Cattaneo L (2009) Mirror neurons and their clinical relevance. *Nat Clin Pract Neurol* 5(1):24–34.
- Dapretto M, et al. (2006) Understanding emotions in others: Mirror neuron dysfunction in children with autism spectrum disorders. *Nat Neurosci* 9(1):28–30.
- McCormick LM, et al. (2012) Mirror neuron function, psychosis, and empathy in schizophrenia. *Psychiatry Res* 201(3):233–239.
- Hickok G (2009) Eight problems for the mirror neuron theory of action understanding in monkeys and humans. *J Cogn Neurosci* 21(7):1229–1243.
- Caramazza A, Anzellotti S, Strnad L, Lingnau A (2014) Embodied cognition and mirror neurons: A critical assessment. *Annu Rev Neurosci* 37:1–15.
- Vannuscorps G, Andres M, Pillon A (2013) When does action comprehension need motor involvement? Evidence from upper limb apraxia. *Cogn Neuropsychol* 30(4):253–283.
- Reilly KT, Sirigu A (2011) Motor cortex representation of the upper-limb in individuals born without a hand. *PLoS One* 6(4):e18100.
- Stoeckel MC, Seitz RJ, Buetefisch CM (2009) Congenitally altered motor experience alters somatotopic organization of human primary motor cortex. *Proc Natl Acad Sci USA* 106(7):2395–2400.
- Funk M, et al. (2008) Sensorimotor tongue representation in individuals with unilateral upper limb amelia. *Neuroimage* 43(1):121–127.
- Avenanti A, Anella L, Candidi M, Urgesi C, Aglioti SM (2013) Compensatory plasticity in the action observation network: Virtual lesions of STS enhance anticipatory simulation of seen actions. *Cereb Cortex* 23(3):570–580.
- Lingnau A, Petris S (2013) Action understanding within and outside the motor system: The role of task difficulty. *Cereb Cortex* 23(6):1342–1350.
- Meltzoff AN (2005) Imitation and others minds: The “like me” hypothesis. *Perspectives on Imitation: From Neuroscience to Social Science*, eds Hurley S, Chater N (MIT Press, Cambridge, MA), pp 55–77.
- Gallese V, Rochat M, Cossu G, Sinigaglia C (2009) Motor cognition and its role in the phylogeny and ontogeny of action understanding. *Dev Psychol* 45(1):103–113.
- Wu YC, Coulson S (2014) A psychometric measure of working memory capacity for configured body movement. *PLoS One* 9(1):e84834.
- Bosbach S, Cole J, Prinz W, Knoblich G (2005) Inferring another's expectation from action: The role of peripheral sensation. *Nat Neurosci* 8(10):1295–1297.
- Aglioti SM, Cesari P, Romani M, Urgesi C (2008) Action anticipation and motor resonance in elite basketball players. *Nat Neurosci* 11(9):1109–1116.
- Wilson M, Lancaster J, Emmorey K (2010) Representational momentum for the human body: Awkwardness matters, experience does not. *Cognition* 116(2):242–250.
- Kerzel D (2006) Why eye movements and perceptual factors have to be controlled in studies on “representational momentum”. *Psychon Bull Rev* 13(1):166–173, discussion 174–177.
- Calder AJ, Keane J, Cole J, Campbell R, Young AW (2000) Facial expression recognition by people with mobius syndrome. *Cogn Neuropsychol* 17(1):73–87.
- Vannuscorps G, Caramazza A (2015) Typical biomechanical bias in the perception of congenitally absent hands. *Cortex* 67:147–150.
- Funk M, Brugger P (2008) Mental rotation of congenitally absent hands. *J Int Neuropsychol Soc* 14(1):81–89.
- 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.
- Gazzola V, et al. (2007) Aplasias born without hands mirror the goal of hand actions with their feet. *Curr Biol* 17(14):1235–1240.
- Aziz-Zadeh L, Sheng T, Liew S-L, Damasio H (2012) Understanding otherness: The neural bases of action comprehension and pain empathy in a congenital amputee. *Cereb Cortex* 22(4):811–819.
- Casile A, Giese MA (2006) Nonvisual motor training influences biological motion perception. *Curr Biol* 16(1):69–74.
- Calvo-Merino B, Grèzes J, Glaser DE, Passingham RE, Haggard P (2006) Seeing or doing? Influence of visual and motor familiarity in action observation. *Curr Biol* 16(19):1905–1910.
- Nordin M, Frankel VH (2001) *Basic Biomechanics of the Musculoskeletal System* (Lippincott Williams and Wilkins, Philadelphia), 3rd Ed.
- Csibra G (2007) Action mirroring and action interpretation: An alternative account. *Sensorimotor Foundations of Higher Cognition. Attention and Performance XXII*, eds Haggard P, Rosetti Y, Kawato M (Oxford Univ Press, Oxford, UK), pp 435–459.
- Cook R, Bird G, Catmur C, Press C, Heyes C (2014) Mirror neurons: From origin to function. *Behav Brain Sci* 37(2):177–192.
- Negri GAL, et al. (2007) What is the role of motor simulation in action and object recognition? Evidence from apraxia. *Cogn Neuropsychol* 24(8):795–816.
- Papeo L, Negri GA, Zadini A, Rumiati RI (2010) Action performance and action-word understanding: Evidence of double dissociations in left-damaged patients. *Cogn Neuropsychol* 27(5):428–461.
- Buxbaum LJ, Kyle KM, Menon R (2005) On beyond mirror neurons: Internal representations subserving imitation and recognition of skilled object-related actions in humans. *Brain Res Cogn Brain Res* 25(1):226–239.
- Rumiati RI, Zanini S, Vorano L, Shallice T (2001) A form of ideational apraxia as a defective deficit of contention scheduling. *Cogn Neuropsychol* 18(7):617–642.
- Southgate V (2013) Do infants provide evidence that the mirror system is involved in action understanding? *Conscious Cogn* 22(3):1114–1121.
- Crawford JR, Howell DC (1998) Comparing an individual's test score against norms derived from small samples. *Clin Neuropsychol* 12:482–486.
- Crawford JR, Garthwaite PH (2007) Comparison of a single case to a control or normative sample in neuropsychology: Development of a Bayesian approach. *Cogn Neuropsychol* 24(4):343–372.
- Vannuscorps G, Andres M, Pillon A (2014) Is motor knowledge part and parcel of the concepts of manipulable artifacts? Clues from a case of upper limb apraxia. *Brain Cogn* 84(1):132–140.
- Lenz W, Pfeiffer R, Kosenow W, Hayman D (1962) Thalidomide and congenital abnormalities. *Lancet* 279:45–46.
- Delrue MA, Lacombe D (2002) Association of ectrodactyly and distal phocomelia. *Genet Couns* 13(3):319–325.
- Gallese V, Gernsbacher MA, Heyes C, Hickok G, Iacoboni M (2011) Mirror neuron forum. *Perspect Psychol Sci* 6(4):369–407.
- 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(6):1239–1255.
- Fadiga L, Fogassi L, Pavesi G, Rizzolatti G (1995) Motor facilitation during action observation: A magnetic stimulation study. *J Neurophysiol* 73(6):2608–2611.
- Kilner JM, Paulignan Y, Blakemore SJ (2003) An interference effect of observed biological movement on action. *Curr Biol* 13(6):522–525.
- Urgesi C, Candidi M, Ionta S, Aglioti SM (2007) Representation of body identity and body actions in extrastriate body area and ventral premotor cortex. *Nat Neurosci* 10(1):30–31.
- van Kemenade BM, Muggleton N, Walsh V, Saygin AP (2012) Effects of TMS over premotor and superior temporal cortices on biological motion perception. *J Cogn Neurosci* 24(4):896–904.
- Pobric G, Hamilton AF (2006) Action understanding requires the left inferior frontal cortex. *Curr Biol* 16(5):524–529.
- Wilson M (2001) Perceiving imitable stimuli: Consequences of isomorphism between input and output. *Psychol Bull* 127(4):543–553.
- Cotelli M, et al. (2006) Action and object naming in frontotemporal dementia, progressive supranuclear palsy, and corticobasal degeneration. *Neuropsychology* 20(5):558–565.
- Daniele A, et al. (2013) Selective impairment of action-verb naming and comprehension in progressive supranuclear palsy. *Cortex* 49(4):948–960.
- Silveri MC, Ciccarelli N (2007) The deficit for the word-class “verb” in corticobasal degeneration: Linguistic expression of the movement disorder? *Neuropsychologia* 45(11):2570–2579.
- Grossman M, et al. (2008) Impaired action knowledge in amyotrophic lateral sclerosis. *Neurology* 71(18):1396–1401.
- Stoeckel MC, Pollok B, Witte OW, Seitz RJ, Schnitzler A (2005) Shrinkage of somatosensory hand area in subjects with upper extremity dysmelia revealed by magnetoencephalography. *J Neurophysiol* 93(2):813–818.
- Vetter RJ, Weinstein S (1967) The history of the phantom in congenitally absent limbs. *Neuropsychologia* 5:335–338.
- Brugger P, et al. (2000) Beyond re-membering: Phantom sensations of congenitally absent limbs. *Proc Natl Acad Sci USA* 97(11):6167–6172.
- Melzack R (1990) Phantom limbs and the concept of a neuromatrix. *Trends Neurosci* 13(3):88–92.
- Mercier C, Reilly KT, Vargas CD, Aballea A, Sirigu A (2006) Mapping phantom movement representations in the motor cortex of amputees. *Brain* 129(Pt 8):2202–2210.
- Gallagher S, Meltzoff AN (1996) The earliest sense of self and others: Merleau-Ponty and recent developmental studies. *Philos Psychol* 9(2):213–236.
- Pavlova M, Staudt M, Sokolov A, Birbaumer N, Krägeloh-Mann I (2003) Perception and production of biological movement in patients with early periventricular brain lesions. *Brain* 126(Pt 3):692–701.