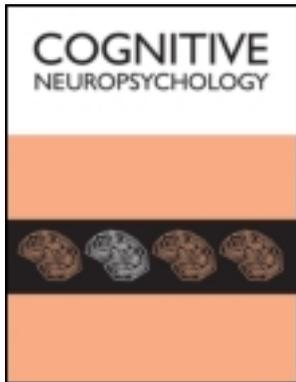


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Publisher: Routledge

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Cognitive Neuropsychology

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/pcgn20>

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Published online: 12 Nov 2013.

To cite this article: Gilles Vannuscorps, Michael Andres & Agnesa Pillon (2013) When does action comprehension need motor involvement? Evidence from upper limb aplasia, *Cognitive Neuropsychology*, 30:4, 253-283

To link to this article: <http://dx.doi.org/10.1080/02643294.2013.853655>

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When does action comprehension need motor involvement? Evidence from upper limb apraxia

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Motor theories of action comprehension claim that comprehending the meaning of an action performed by a conspecific relies on the perceiver's own motor representation of the same action. According to this view, whether an action belongs to the motor repertoire of the perceiver should impact the ease by which this action is comprehended. We tested this prediction by assessing the ability of an individual (D.C.) born without upper limbs to comprehend actions involving hands (e.g., throwing) or other body parts (e.g., jumping). The tests used a range of different visual stimuli differing in the kind of information provided. The results showed that D.C. was as accurate and fast as control participants in comprehending natural video and photographic presentations of both manual and nonmanual actions, as well as pantomimes. However, he was selectively impaired at identifying point-light animations of manual actions. This impairment was not due to a difficulty in processing kinematic information per se. D.C. was indeed as accurate as control participants in two additional tests requiring a fine-grained analysis of an actor's arm or whole-body movements. These results challenge motor theories of action comprehension by showing that the visual analysis of body shape and motion provides sufficient input for comprehending observed actions. However, when body shape information is sparsely available, motor involvement becomes critical to interpret observed actions. We suggest that, with natural human movement stimuli, motor representations contribute to action comprehension each time visual information is incomplete or ambiguous.

Keywords: Action comprehension; Neural simulation; Mirror neurons; Embodied cognition; Point-light animations; Upper limb apraxia.

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We are very grateful to Simone Bosbach who kindly provided us with the material of Experiments 5 and 6. We thank Marcel Brass, Martin G. Edwards, and Richard Ramsey for their helpful comments on a previous draft of this paper. We obtained the motion capture database from mocap.cs.cmu.edu. (database created with funding from NSF EIA-0196217) and Christian van Brussel built the application used to generate point-light animations from this database.

This research was supported by a Fonds National de la Recherche Scientifique (FNRS) grant [grant number 1.5.192.10F] to Agnesa Pillon.

How do we comprehend other people's actions? What kind of representations and processes allow us to interpret what conspecifics are doing when they move their hands or whole body as they do? One specific issue, which currently is being hotly debated, concerns the role of motor representations and processes in comprehending actions. The traditional view on this issue is that motor representations play no significant role in action comprehension. Within this view, a visuoperceptual analysis of the actor's body shape and motion (e.g., Giese & Poggio, 2003; Johansson, 1973; Marr & Vaina, 1982), integrated with the visual analysis of the objects possibly involved in the action (Kourtzi & Connor, 2011), provides inputs to a semantic system (Rothi, Ochipa, & Heilman, 1991) representing the conceptual features of the action, like its typical cause, purpose, and results, the typical agent and instrument involved, the needed energy, approximate duration, and so on (Tranel, Kemmerer, Adolphs, Damasio, & Damasio, 2003), thereby giving meaning to the perceived action.

This view has been recently challenged by "motor theories" of action comprehension, which claim that comprehending an observed action relies on the observer's own motor representations of the same action—that is, those that she uses when performing that action herself (e.g., Blakemore & Decety, 2001; Jeannerod, 2001; Rizzolatti, Fogassi, & Gallese, 2001). By accessing internal motor representations corresponding to the observed action, the observer automatically grasps the meaning of that action as if performing the action. The functional and neural mechanisms that are assumed to associate the observed action with the observer's own motor representations of the same action, thereby leading to action understanding, vary across the different motor theories. In the most influential theories, the association operates by direct visual-to-motor matching realized by "mirror neurons" located in the motor system (Rizzolatti et al., 2001; see Hommel, Musseler, Aschersleben, & Prinz, 2001, for the related common coding theory of perception and action) or by "neural simulation"—that is, activation of the same internal model and neural

network as those used to plan and execute the action oneself. In Jeannerod's (2001) words, this internal model includes "the goal of the action, the means to reach it, and its consequences on the organism and the external world" (p. S103). As for Blakemore and Decety (2001), they stressed the importance within the internal model of the stored predictions of the sensory consequences of previously self-generated movements and actions. When one is observing an action, the observed sensory consequences of that action would be mapped onto stored sensory predictions of one's own actions, which "could then be used to estimate the motor commands and intentions that would normally precede such an action" (Blakemore & Decety, 2001, p. 564).

An important point, however, is that these variants of motor theories of action comprehension all make the prediction that an individual's motor capabilities and experience—that is, whether the actions belong to her motor repertoire—should impact the ease by which the actions performed by others are comprehended. In particular, if an individual is incapable of performing an observed action, and thus to map this action onto her own motor repertoire, comprehending this action should be somewhat hindered. In this study, we provided a stringent test of this prediction by assessing the ability of an individual born without upper limbs (D.C.)—and who therefore has no motor repertoire of hand actions—to comprehend manual (e.g., throwing) as opposed to nonmanual (e.g., jumbling) actions.

By "action comprehension", we mean here categorizing various human movements or sequences of movements as instances of the same action—"throwing" or "jumping", for example—which entails discriminating this action from other actions having common features and, thereby, retrieving its meaning, including its typical cause, purpose, and results. This study did not concern, however, aspects of action comprehension related to the understanding of the mental states (i.e., intentions, needs, and desires) that lie behind the action.

Evidence cited in support of the motor theories of action comprehension mainly comes from

functional neuroimaging and transcranial magnetic stimulation (TMS) studies. It has been consistently found that observing actions performed by a conspecific elicited activation in frontal and parietal areas (among others) that are also activated during action execution (e.g., Decety et al., 1997; Gazzola & Keysers, 2009; Grèzes & Decety, 2001). A number of studies further showed that motor activation during action observation was specific to the observed movements. Thus, in a functional magnetic resonance imaging (fMRI) study, Buccino and colleagues (2001) found that observing actions made by mouth, hand, or foot elicits the somatotopic activation of the premotor cortex in the observer's brain. Even higher movement specificity was found in studies using TMS (for review, see Fadiga, Craighero, & Olivier, 2005). When the left motor cortex of subjects is stimulated while they observe hand actions, motor evoked potentials recorded from right-hand muscles show a selective increase in the very same muscles as those implied in the execution of the observed action (Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995; Maeda, Kleiner-Fisman, & Pascual-Leone, 2002; Sartori, Buccioni, & Castiello, 2012). Finally, converging evidence indicates that motor activation during action observation is modulated by the observer's motor repertoire (e.g., Calvo-Merino, Glaser, Grèzes, Passingham, & Haggard, 2005; Calvo-Merino, Grèzes, Glaser, Passingham, & Haggard, 2006; Haslinger et al., 2005; Stevens, Fonlupt, Shiffrar, & Decety, 2000). Stevens and colleagues (2000), for instance, found that the perception of biologically possible, but not impossible, movements elicits an increase of activation in the observer's premotor and parietal cortices. Calvo-Merino and colleagues (2006) found significantly greater changes of activation in the premotor and parietal brain areas of male and female ballet dancers when they observed dance movements that pertained to their own motor repertoire (gender-congruent movements) than movements that did not (gender-incongruent movements).

All these findings are consistent with motor theories of action comprehension. They do

support the hypothesis that observed actions are somewhat mapped onto the observer's own motor representations. However, as pointed out by several authors (e.g., Csibra, 2007; Hickok, 2009; Mahon & Caramazza, 2008), they do not demonstrate that such mapping is *constitutive* of the action comprehension processes. Automatic activation of the motor system during action observation could indeed result from other mechanisms, serving distinct purposes from that of action comprehension. For instance, motor activation could result from automatic visuomotor transformations involved in imitation and motor learning (e.g., Buccino et al., 2004; Jeannerod, 2005; Rizzolatti & Craighero, 2004) or action anticipation (e.g., Aglioti, Cesari, Romani, & Urgesi, 2008; Elsner, Falck-Ytter, & Gredebäck, 2012; Kilner, Vargas, Duval, Blakemore, & Sirigu, 2004; Urgesi et al., 2010). It could also reflect activation that automatically spreads to the motor system once the action has been recognized or comprehended (Mahon & Caramazza, 2008).

Compelling evidence for the necessary involvement of the observer's own motor representations and processes in action comprehension would consist in finding that damage to those representations/processes affects the individual's ability to understand other people's actions. Previous studies with individuals presenting with such a condition in the context of various aetiologies provided inconclusive evidence though.

A first group of studies have examined whether the action production deficit observed in brain-damaged patients with apraxia was associated with an impairment in action recognition or comprehension. Apraxia is typically caused by unilateral damage to frontal and/or parietal cortex and results in a deficit in action production that cannot be explained by aphasia or elementary sensory or motor deficit (De Renzi & Lucchelli, 1988). Buxbaum, Kyle, and Menon (2005) found that a group of 21 patients with limb apraxia were indeed impaired in both a production task in which they were asked to imitate transitive pantomimes (e.g., hammering) and a forced-choice gesture recognition task in which they had to

match a spoken word (a verb) to transitive pantomimes presented with semantically or spatially similar foils. Moreover, across the group, the correlation of transitive pantomime imitation and recognition was positive and reliable ($r = .75$, $p < .001$). Similar results were found by Pazzaglia and colleagues (Pazzaglia, Smania, Corato, & Aglioti, 2008) in a group of 21 patients with limb apraxia. Here, action recognition was assessed by asking patients to tell whether transitive and intransitive actions presented in video clips were correctly executed. Incorrect actions were performed with an inappropriate object, or an incorrect spatial position or hand/finger configuration. The results showed that the apraxic patients were significantly impaired in the action recognition task and, moreover, that there was a positive and significant correlation between their action execution and recognition scores ($r = .83$, $p < .00001$). In another study, the same research group (Pazzaglia, Pizzamiglio, Pes, & Aglioti, 2008) showed that the association between action execution and action recognition impairments was specific to the body part involved in the action. In this study, action recognition was assessed with an auditory action recognition task where patients had to listen to a sound corresponding to a hand action (e.g., using scissors), a mouth action (e.g., inflating a balloon), or a nonhuman action (e.g., the noise of an helicopter) and then to choose, among four pictures, the one corresponding to the heard sound. The results showed that apraxic patients who were specifically impaired in imitating actions involving the mouth were also more impaired with mouth-related than hand-related actions in the action recognition task. In contrast, patients who were specifically impaired in imitating upper limb actions were more impaired with hand than mouth actions in the recognition task.

These consistent findings of a positive correlation between the ability to perform actions and the ability to recognize/identify actions in apraxic patients is consistent with motor theories of action comprehension. (But see Tessari, Canessa, Ukmar, & Rumiati, 2007, for a weak and non-significant correlation between production and

comprehension across a group of 32 brain-damaged patients.) However, there are also reports of individual apraxic patients who are not impaired in action recognition. Two further studies (Negri et al., 2007; Papeo, Negri, Zadini, & Rumiati, 2010) have examined, in groups of unilateral brain-damaged patients, the correlation between the performance in action production (i.e., imitation of pantomimes) and action comprehension (i.e., naming pantomimes, or matching an action verb to an action picture, or matching a pantomime to an action picture). Although they again found positive and reliable correlations between the patients' performance in action production and action comprehension at the group level ($r = .35$, $p < .001$, and $r = .59$, $p < .05$, in Negri et al.'s, 2007, and Papeo et al.'s, 2010, study, respectively), they nevertheless showed a number of patients performing within the normal range in action comprehension despite being impaired in action production. In Negri et al. (2007), for instance, patients P.T. and S.V. performed at a normal level in action comprehension (they scored 93% and 90%, respectively, in the pantomime recognition task) in spite of their severe impairment in action production (in the pantomime imitation task, P.T. scored 27.5% and 35.6%, and S.V. scored 30% and 40%, respectively, for transitive and intransitive actions). In Papeo et al.'s (2010) study, 3 out of the 5 patients who were impaired in action production were not impaired in action comprehension: N.P. was impaired in action production (60% correct in pantomime imitation) while scoring within the normal range in pantomime naming (86.67%) and verb-to-picture matching (100%); patients I.N. and S.N. were impaired in action production (40% and 73.33%, respectively) but unimpaired in verb-to-picture matching (93.33% and 86.67%). Actually, the single-case data in Pazzaglia, Smania, et al.'s (2008) study revealed such dissociations as well: Within the group of 21 apraxics, 7 had no action comprehension deficit. Likewise, in Pazzaglia, Pizzamiglio, et al.'s (2008) study, 3 patients (nos. 17, 19, 21; cf. Table S2 in Pazzaglia et al.'s paper) out of the 7 patients with impaired imitation of limb-related actions

performed within the normal range for limb-related actions in the auditory action recognition test. These observations made at the individual level of analysis in fact corroborate the pattern observed in single-case studies of apraxic patients who did not show any action recognition/identification deficit despite their action production deficit (Bartolo, Cubelli, Della Sala, Drei, & Marchetti, 2001; Cubelli, Marchetti, Boscolo, & Della Sala, 2000; Rapcsak, Ochipa, Anderson, & Poizner, 1995; Rumiati, Zanini, Vorano, & Shallice, 2001).

Thus patients who are not able to accurately perform actions due to apraxia do not necessarily show a concomitant deficit in action comprehension. Such evidence could be viewed as a falsification of the motor theories of action comprehension. However, one may object that the patients with a production without comprehension deficit in fact had damage to components of the action production system that are not involved in action comprehension and are specific to action execution. Rizzolatti and Sinigaglia (2010), for instance, object to the supposition that any damage to the motor system should lead to a deficit in action comprehension. Actually, they argue, only parts of the motor system are endowed with the ability to match visual onto motor representations (i.e., with mirror properties) and are thus involved in action comprehension. On the other hand, they continue, that associations between action production and recognition deficits were found in a number of cases does provide critical evidence for the motor theory of action comprehension. We agree that, given their prevalence, associations need to be accounted for by a theory of action processing. However, alternative explanations for such associations should be considered. Within Rothi et al.'s (1991) model, for instance, an association of deficits in action imitation and action recognition or comprehension is expected in the condition of functional damage to the perceptual analysis of gestures and/or objects, to the input system storing a description of familiar gestures ("action input lexicon"), or to the action semantic system.

A second group of studies have examined action processing in patients showing lower level motor deficits. Serino and colleagues (2010) assessed action comprehension in 10 brain-damaged patients with hemiplegia consecutive to lesions in the motor system involving frontoparietal motor circuits, basal ganglia, or corticospinal fibres of the internal capsule. The patients were asked to name transitive and intransitive unimanual actions presented as point-light animations. (In these animations, only the joints of a moving actor are visible; cf. Johansson, 1973.) In the point-light movies, the actor performed each action with the arm corresponding either to the affected or to the unaffected side of the patient's body. The results showed that hemiplegic patients were more impaired at naming actions performed with the arm corresponding to their affected side than with the arm corresponding to the unaffected one. Converging results were found in a study by Arrighi, Cartocci, and Burr (2011) who found that patients with paraplegia due to severe spinal injury showed a greatly reduced sensitivity, compared with healthy controls, for detecting the presence of a point-light walker embedded into random noise. Such association between a locomotion deficit and a deficit in detecting a point-light walking figure in noise was not found, however, in adolescents showing early walking disabilities due to early periventricular brain lesions (Pavlova, Staudt, Sokolov, Birbaumer, & Krägeloh-Mann, 2003). The results of this study showed that, although visual sensitivity to a point-light walker embedded in a moving mask was lower in these adolescents than in a control group, it did not significantly correlate with either the severity of walking disability or the extent of damage along the pyramidal tract. On the other hand, the sensitivity was found to correlate negatively with the extent of periventricular lesions in the parieto-occipital region. This points to the need of considering the neural and functional damage that could be associated with motor damage and in fact account for the impaired perception of actions.

In sum, the available evidence as to whether action comprehension needs motor involvement

is confusing and contradictory. Some—but not all—individuals with a motor impairment are unable to recognize or comprehend actions they cannot perform. It is unclear whether discrepancies in ability are due to differences in the locus of damage to the motor system (e.g., distinct regions within the parietofrontal circuit, primary motor cortex, subcortical structures, spinal cord) and the nature of the concomitant impairment (e.g., apraxia vs. paralysis, various types of apraxia), the residual motor capabilities of the participants (or degree of severity of the motor disorder), the level of processing tapped in the action “recognition” task (ranging from just detecting a moving figure, to discriminating correctly from incorrectly performed actions, and identifying/naming a specific action), the sensitivity of the task, or the kind of visual action stimuli used (e.g., videos/photographs of actions, pantomimes, or point-light animations). Furthermore, current motor theories of action comprehension are not specified enough to allow definite predictions to be drawn about the kind of action production deficit (i.e., locus and severity of neural and functional damage) that should or should not be associated with an action comprehension deficit. In such a context, it is hard to determine in which conditions a given pattern of association or dissociation between action production and action comprehension constitutes appropriate evidence for or against the theory.

The empirical approach taken in this study constitutes an attempt to overcome these ambiguities. We investigated the issue of the influence of motor abilities on action comprehension by assessing

action comprehension in a neurologically intact individual, D.C., who has no hand motor representation, due to bilateral upper limb apraxia. The lack of hand function prevents him from acquiring a motor repertoire of hand-related actions but not of actions requiring primarily lower limbs (e.g., jumping) or mouth (e.g., whispering), which he performs normally. In other words, D.C. did not acquire the motor repertoire onto which the hand movements he observes in other people could be mapped. Therefore, according to motor theories of action comprehension, D.C.’s comprehension of actions should be less efficient than that of control subjects but only for those actions that are performed with movements he cannot map onto its own motor repertoire—that is, hand actions.¹

Examining action comprehension in the condition of bilateral upper limb apraxia first allows us to avoid ambiguities as to the nature of the functional impairment and the patient’s residual motor abilities: D.C. just never developed any motor representations for hand actions. Second, we assessed action comprehension in picture-naming tasks. There is a wide agreement that naming a visual stimulus entails its prior categorization and identification, which seems to be the level of “comprehension” that is assumed to rely on motor representations in motor theories of action comprehension. Third, to ensure sensitivity in detecting comprehension difficulties, we measured not only naming accuracy but also naming speed. Fourth, we tested action naming in various experiments that differed in the quantity or type of information provided in the visual stimuli. Actions were presented in video clips,

¹ The prediction tested in this study applies to theories of action comprehension based on a mechanism that maps directly the perceived movements onto the perceiver’s own motor representation of the same or similar movements (Blakemore & Decety, 2001; Jeannerod, 2001; Rizzolatti et al., 2001). Recent formulations of the “mirror neurons” theory (e.g., Rizzolatti & Sinigaglia, 2010) moved away from this view by emphasizing the importance of a class of mirror neurons (so-called “broadly congruent mirror neurons”) that would directly map the *goal* of a perceived action onto the goal of an action in the perceiver’s repertoire, regardless of whether the effector and movements are similar or different. We did not consider this hypothesis in the present study. It is unclear how a mechanism of *direct* execution–observation matching can operate when there are no motor characteristics in common between the motor plans involved in execution and the perceived motor act, and we are not aware of any attempt at describing how such a mechanism might work. One possibility that comes to mind is to suppose that “broadly congruent mirror neurons” in fact *indirectly* activate after the goal of the perceived action has been understood (by some other mechanism), in which case the mirror activity would be the consequence and not the means of action comprehension (for a similar view, see Csibra, 2007).

photographs, pantomimes, and point-light animations.

EXPERIMENTAL STUDY

General method: Participants

D.C. is a 51-year-old man with a Master's degree in Psychology. He presents a congenital bilateral upper limb aplasia due to in utero thalidomide exposure (Lenz, Pfeiffer, Kosenow, & Hayman, 1962). The left extremity is completely aplasic; on the right side, the radius is aplasic, and a partial (≈ 12 cm) humerus or ulna and two fingers (the small and the ring finger) had developed. The shoulder and elbow/wrist joints are absent or not functional. Therefore, D.C. can only move his right upper extremity as a whole and by a couple of centimetres in every direction, which nevertheless enables him to hold some objects by squeezing them between his chest and foreshortened limb. Finger mobility is too limited to allow him a precision or palm grip. Thus, he cannot grasp or manipulate any object. Because of the missing hand function, D.C. developed fine motor skills of the feet from early childhood, which allow him to use his feet for many typically hand-related actions of daily life (e.g., writing with a pen, typewriting, eating with a fork, washing himself, etc.).

D.C. never wore a prosthesis, and, importantly, he never experienced phantom limb sensations or movements. A few individuals (i.e., between 8%, Melzack, Israel, Lacroix, & Schultz, 1997, and 18%, Wilkins, McGrath, Finley, & Katz, 1998) born with congenital absence of a limb report to be able to "move" the phantom of their absent limb voluntarily. Actually, with one upper limb aplasic individual experiencing phantom limb sensations, evidence was found that TMS over her motor cortex evoked phantom limb movements (Brugger et al., 2000). This phenomenon is still poorly understood (see for discussion, Price, 2006; Reilly & Sirigu, 2011). It is important to note, however, that in individuals who never experienced phantom limb sensations, like D.C.,

even intense external stimulation (by TMS) of the motor cortex does not evoke any phantom movement sensations, which suggests that their motor cortex does not contain any representation of the missing limb (Reilly & Sirigu, 2011).

The experiments were also presented to 6 typically developed control participants matched with D.C. for gender, age (controls' range: 48–56 years), and number of years of education (D.C.: 17; controls' range: 16–19). All participants had normal or corrected vision, and no participant had a history of psychiatric or neurological disorder. The study was approved by the biomedical ethic committee of the Cliniques universitaires Saint-Luc, Brussels, and all participants gave their written informed consent prior to the study.

Naming actions in different viewing conditions

A first series of four experiments assessed D.C.'s efficiency in naming manual and nonmanual actions. Across these experiments, actions were presented in conditions varying in the kind of information provided by the visual stimulus, namely: (a) video clips depicting the movements of an actor with, if any, the target object and instrument typically involved in the action; (b) photographs consisting of a snapshot taken from the previous video clips; (c) videos of pantomimes of object-related actions, showing the movements of an actor toward a nonpresent object; (d) point-light animations of actions, displaying only the joints of an actor's body in motion.

Experiments 1 and 2: Naming manual and nonmanual actions presented in video clips and photographs

Method. Participants were presented with 40 manual and 20 nonmanual actions illustrated by video clips (Experiment 1) or photographs (Experiment 2) and were asked to name them as fast and as accurately as possible.

The material was prepared from a preliminary set of 82 actions selected among the items

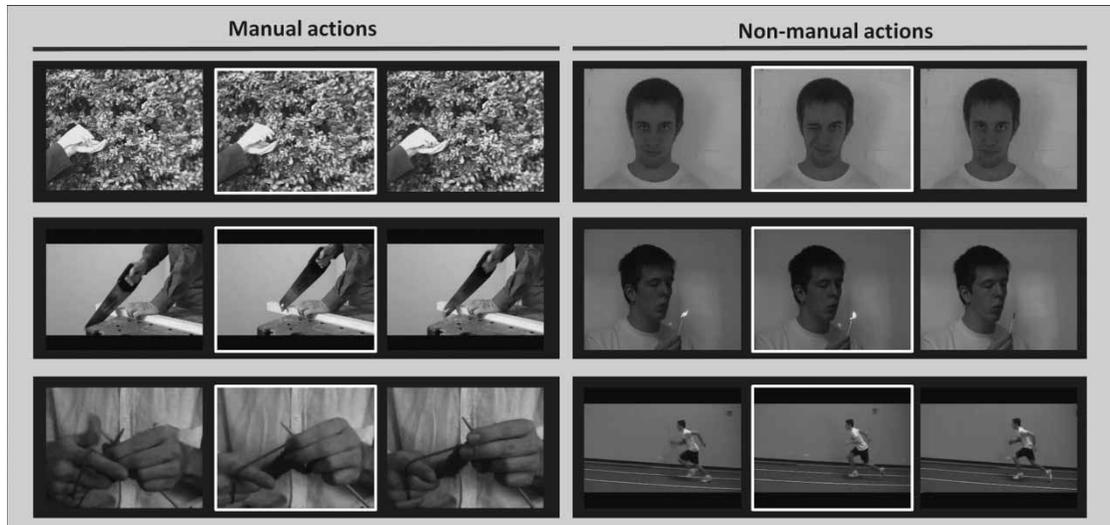


Figure 1. Examples of manual actions (from top to bottom, picking, sawing, knitting) and nonmanual actions (winking, blowing, running) used as stimuli in Experiment 1 (naming video clips) and Experiment 2 (naming photographs). Sample still frames are shown for video clips used in Experiment 1. The frames indicated here by a white border were used as photograph stimuli in Experiment 2.

present in a French psycholinguistic database (Bonin, Boyer, Méot, Fayol, & Droit, 2004). Then, 18 subjects not participating in the experiments were asked to rate on a 5-point scale whether making hand movements was important in performing each action (1 = not important and 5 = very important). On this basis, 40 “manual” (mean rating = 4.71; $SD = 0.19$) and 20 “nonmanual” (mean rating = 1.25; $SD = 0.27$) actions were selected (see Appendix A). The mean rating of “manuality” was significantly higher for manual than nonmanual actions, $t(58) = 56.87$, $p < .001$. Both sets of actions were matched in concept familiarity, $t(58) = 0.04$, $p = .97$, and imageability, $t(58) = 1.45$, $p = .15$. However, manual actions had significantly lower log name frequency, $t(29.8) = 2.11$, $p = .04$, and were acquired significantly later, $t(58) = 2.63$, $p = .01$, than nonmanual actions. Obviously, most manual actions involved a target object and/or an instrument whereas most nonmanual actions did not. None of the manual actions was within D.C.’s upper limb motor abilities, as he indicated in a questionnaire after the completion of the video naming task.

The selected actions were then filmed or, for a few of them, obtained from the web, and a photograph of the action was extracted from each movie clip (see examples in Figure 1). These stimuli were presented in the centre of a computer screen, using E-prime software (Psychological Software Tools, 2002, Pittsburgh, PA). The video clips and photographs had a size of 512×384 pixels, and they were displayed with a visual angle of 9° . The video clips had a frame rate of 25 frames a second and lasted 5 s.

The video clip and the photograph naming tasks were presented in separate sessions; the naming of photographs was presented before the naming of video clips. Each trial began with the presentation of a central fixation cross for 200 ms, followed by the stimulus, which was presented until the participants named the action. Five practice trials were provided to familiarize each participant with the experiment and the response mode. Accuracy was monitored by the experimenter, and response latencies were recorded online using a voice key device controlled by the E-prime software. The participants were equipped with a sensitive microphone

connected to a response-latency-measuring PST (Psychology Software Tool) serial response box. The response latency corresponded to the post-stimulus onset latency of the subject's vocalization. Malfunctioning of the voice key was checked by the experimenter.

Results and discussion. In the accuracy analysis, both target responses and acceptable alternatives (synonyms and near-synonyms of the expected verb, e.g., *dactylographier*/typewriting → *taper*/typing; *laver*/washing → *rincer*/rinsing; *cligner*/winking → *faire un clin d'oeil*/giving a wink) were considered as correct. However, only trials corresponding to the expected verb were considered in the response latency (RL) analysis (for a similar approach, see Druks et al., 2006). In the RL analysis, for each participant, we then excluded trials where the RL exceeded the participant's mean by 2 standard deviations (Experiment 1: 5.7% and 5.3% of the data from D.C. and controls, respectively; Experiment 2: 4.3% and 4.2% of the data from D.C. and controls, respectively). In addition to accuracy and RL measures, naming performance was characterized with an efficiency score (ES; e.g., Kennett, Eimer, Spence, & Driver, 2001). The ES (expressed in ms) was computed for each participant by dividing the mean RL by the proportion of correct responses in a given condition (thus, the higher the score the poorer the performance). This score allows us to combine accuracy and speed into a single measure of processing efficiency; also, it allows between-group comparisons unbiased by potential speed-accuracy trade-offs (Townsend & Ashby, 1978, 1983). The results are displayed in Figure 2.

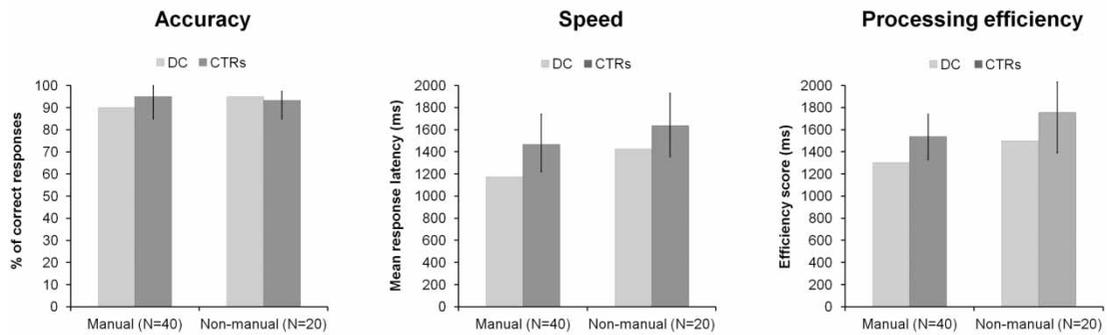
Planned comparisons were performed using Crawford and Howell's (1998) modified *t*-test to assess whether D.C.'s performance was significantly different from the performance of the control group. The results indicated that D.C.'s performance in naming videos (Experiment 1) was not significantly different from controls' performance whether for manual [accuracy: $t(5) = -0.84$, $p = .44$; RL: $t(5) = -1.28$, $p = .26$; ES: $t(5) = -1.41$, $p = .22$] or nonmanual [accuracy: $t(5) = 0.31$, $p = .77$; RL: $t(5) = -0.79$,

$p = .46$; ES: $t(5) = -0.90$, $p = .41$] actions. Likewise, in naming photographs (Experiment 2), D.C.'s performance was not significantly different from controls' performance whether for manual [accuracy: $t(5) = 0.44$, $p = .68$; RL: $t(5) = -0.72$, $p = .51$; ES: $t(5) = -0.74$, $p = .49$] or nonmanual [accuracy: $t(5) = -1.66$, $p = .16$; RL: $t(5) = -0.38$, $p = .72$; ES: $t(5) = 1.12$, $p = .31$] actions.

Some proponents of motor theories of action comprehension have claimed that the absence of an internal motor representation of an action should not prevent the comprehension of that action because other mechanisms, based on inferential processes, may fulfil this function (Rizzolatti & Craighero, 2004; Rizzolatti & Sinigaglia, 2008, 2010). Nevertheless, they argued, having an internal motor representation of an action onto which the observed action could be mapped should provide an "immediate" comprehension of the action. Hence, we evaluated the possibility that, although not being impaired in identifying manual actions, D.C. nevertheless was more efficient in identifying nonmanual than manual actions because of the involvement of internal motor representations in the identification of nonmanual but not in the identification of manual actions. To this end, we computed Crawford and Garthwaite's (2005) Revised Standardized Difference Test (RSDT) to assess whether D.C.'s discrepancy in performance between nonmanual and manual actions was different from the discrepancy between both kinds of action in the control group. The results indicated that D.C.'s difference in performance between nonmanual and manual actions was far from being significantly different from the difference between both kinds of action in the control group, either in the video naming task [accuracy: $t(5) = 0.71$, $p = .51$; RL: $t(5) = 0.81$, $p = .46$; ES: $t(5) = 0.53$, $p = .62$] or in the photograph naming task [accuracy: $t(5) = 1.47$, $p = .20$; RL: $t(5) = 0.35$, $p = .74$; ES: $t(5) = 1.6$, $p = .17$].

Moreover, we asked whether the kind of visual stimulus (video clips vs. photographs) influenced D.C.'s performance for manual and nonmanual

Naming video clips



Naming photographs

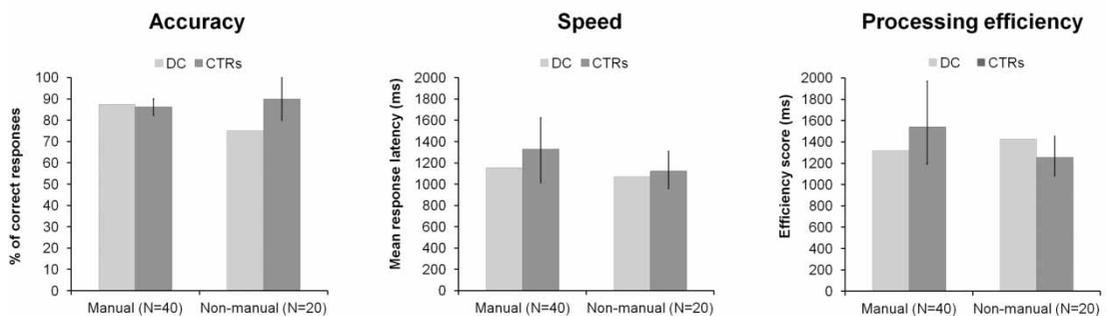


Figure 2. D.C.'s and control participants' percentage of correct responses, mean response latency, and efficiency score for the manual and nonmanual actions in the video clip (top) and photograph (bottom) naming task (Experiments 1 and 2). CTRs = control participants. Error bar = range.

actions in the same way as in control participants. The results (RSDT, Crawford & Garthwaite, 2005) indicated that D.C.'s difference in performance between video clips and photographs did not significantly differ from that found in control participants, for either manual [accuracy: $t(5) = 0.88$, $p = .42$; RL: $t(5) = 0.46$, $p = .66$; ES: $t(5) = 0.53$, $p = .62$] or nonmanual [accuracy: $t(5) = 1.17$, $p = .29$; RL: $t(5) = 0.29$, $p = .78$; ES: $t(5) = 1.65$, $p = .16$] actions.

Finally, because no significant effect of motor experience was detected in the video and the photograph naming tasks, we checked whether these tasks were sensitive enough to detect significant effects of variables that are known to influence action naming times for these kinds of stimuli in

healthy individuals. Bonin and colleagues (Bonin et al., 2004; Bonin, Roux, Méot, Ferrand, & Fayol, 2009) collected psycholinguistic norms (e.g., name agreement, image agreement, concept familiarity, age of acquisition, duration of the action rated from its verbal description) and naming latencies for video clips and photographs of actions with French-speaking participants. They reported that name agreement, image agreement, and age of acquisition were the main determinants of naming latencies for both video clips (Bonin et al., 2009) and photographs (Bonin et al., 2004). In addition, naming latencies for video clips were influenced by the estimated duration of the action. (Note that naming latencies and estimated action duration were *negatively*

correlated.) We performed stepwise regression analyses on the data of our video and photograph naming tasks by considering, as the dependent variable, the mean naming latency (computed over all participants, including D.C.) for each item and, as predictors of participants' naming latencies, name agreement, concept familiarity, estimated duration of the action, imageability, age of acquisition, log frequency, and number of phonemes of the target word. All the actions selected in our experiments were also included in Bonin and colleagues' norming studies although we did not use the same picture stimuli. Thus, the predictor values were extracted from Bonin et al. (2004) when they corresponded to ratings that had to be attributed on the basis of the modal name of the action (i.e., estimated duration of the action, imageability, and age of acquisition) or to the action itself, independently of the way it was pictured (i.e., concept familiarity). Name agreement, however, was computed on the basis of the participants' responses collected in our video and photograph naming task. Following Bonin et al. (2004, 2009), we computed the H statistic (Snodgrass & Vanderwart, 1980), which takes into consideration both the number of different names given for each picture and the proportion of participants giving each name. (H is higher when name agreement is low.) Lexical frequency (number of lemma occurrences per million in a corpus of subtitles of films) was extracted from New, Brysbaert, Veronis, and Pallier (2007). The results showed that, in the video naming task, name agreement and action duration were both significant predictors of participants' naming latencies [model: $F(2, 55) = 5.94, p < .01$, adjusted $R^2 = .15$; H : $\beta = .30, t = 2.46, p = .01$; action duration: $\beta = -.29, t = -2.34, p = .02$]. In the photograph naming task, the significant predictors of the naming latencies were name agreement and age of acquisition [model: $F(2, 55) = 18.91, p < .001$, adjusted $R^2 = .39$; H : $\beta = .49, t = 4.49, p < .001$; age of acquisition: $\beta = .27, t = 2.49, p = .01$]. Thus, it turned out that both the video and the photograph naming tasks used in our study were sensitive enough to replicate the main effects found in previous

action naming studies (Bonin et al., 2004, 2009) with a much larger group of participants and a much larger set of items.

Experiment 3: Naming pantomimes of actions

In manual actions, one may assume that when the picture stimulus displays an instrument that is strongly associated with a specific action (e.g., a grater, a screwdriver, a saw, or a hammer), there is no need to process body shape and motion in order to identify the performed action, since the action could be guessed from the instrument used. (Let us note, however, that only 21/40 manual action pictures in the previous experiments included an instrument at all.) In this experiment, participants had to name video clips showing *pantomimes* of object-related actions—that is, action depictions where only information about body shape and motion was present.

Method. Sixty pantomimes of manual, object-related actions (see Appendix B) were presented in video clips to participants who were asked to name them as fast and as accurately as possible (see examples in Figure 3). None of the actions performed in the pantomimes was within D.C.'s upper limb motor abilities, as he indicated in a questionnaire completed after the task. All video clips were sized 512×384 pixels, displayed at 9° of visual angle, with 25 frames/s, and lasted 5 s. The procedure was the same as that used in Experiments 1 and 2. Five trials were provided to familiarize each participant with the experiment and the response mode. Accuracy was monitored by the experimenter, and response latencies were recorded online using a voice key device controlled by the E-prime software.

Results. Any description of the pantomimes that reflects an accurate identification of the action performed was considered as a correct response, whatever the words used in the description (e.g., "raking" or "using a rake"). Trials with participants' errors were discarded in the RL analysis. For each participant, we then excluded trials where the RL exceeded the individual mean by 2 standard deviations (4.6% and 4.8% of the data



Figure 3. Sample still frames from two video clips used as stimuli in Experiment 3 (naming pantomimes). Top: sawing. Bottom: knitting.

in D.C. and controls, respectively). An efficiency score (ES) was computed from the accuracy and RL data of each participant. The results are displayed in Figure 4. Planned comparisons performed with Crawford and Howell's (1998) modified t -test indicated that D.C.'s performance in naming pantomimes of actions did not significantly differ from controls' performance as regards accuracy, $t(5) = 0.6$, $p = .57$. However, D.C. was faster than controls [RL: $t(5) = -2.04$, $p = .09$], and his efficiency score was significantly better than the scores of controls, $t(5) = -2.73$, $p = .04$.

Actually, D.C. did not show more difficulty in identifying manual actions from pantomimes than from more natural depictions of these actions—that is, video clips or photographs, which included the instrument and the target object, if any. Thus, results from the RSDT analyses (Crawford & Garthwaite, 2005) indicated that, when naming manual actions, D.C.'s difference in performance between pantomime and video clips did not significantly differ from the difference of performance found in control participants [accuracy: $t(5) = 0.84$, $p = .44$; RL: $t(5) = 0.43$, $p = .68$; ES: $t(5) = 0.95$, $p = .39$]. When D.C.'s performance

for manual actions was compared between pantomimes and photographs, a similar pattern emerged [accuracy: $t(5) = 0.09$, $p = .92$; RL: $t(5) = 0.87$, $p = .42$; ES: $t(5) = 1.30$, $p = .25$].

Finally, we could not perform a regression analysis similar to those performed for the video and the photograph naming tasks because no psycholinguistic norms (e.g., concept familiarity, age of acquisition, imageability) were available for most of the actions selected in the pantomime task, and, furthermore, we are not aware of any study reporting significant predictors of action naming speed with this kind of stimuli. Nonetheless, we checked whether the RLs were subjected to meaningful variance by performing a correlation analysis with name agreement (H , computed from the responses provided by the participants). The results showed that mean naming latencies significantly correlated with name agreement in this task as well, $r(56) = .59$, $p < .001$.

Experiment 4. Naming point-light animations of actions presented with gradual unmasking

Method. Participants were asked to name as accurately as possible 20 manual and 20 nonmanual

Naming pantomimes

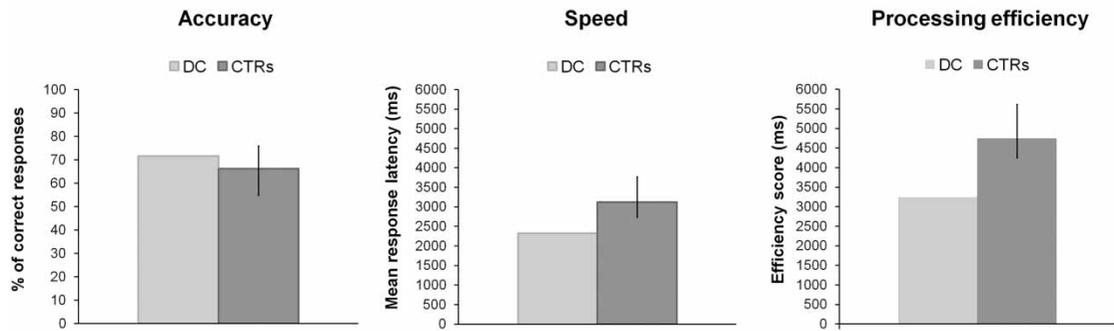


Figure 4. D.C.'s and control participants' percentage of correct responses, mean response latency, and efficiency score in the pantomime naming task (Experiment 3). CTRs = control participants. Error bar = range.

actions displayed as point-light animations (see illustrations in Figure 5) with a gradual unmasking paradigm. Most manual actions corresponded to object-directed actions, and most nonmanual actions did not (see Appendix C). The objects were obviously not present in the point-light animations, like in pantomimes. None of the manual actions was within D.C.'s upper limb motor abilities.

This material was constituted from a set of 83 point-light animations of actions created from a motion capture database (asf/amc format obtained from the Carnegie Mellon University Motion Capture Database, n.d.) with a software developed locally. Each point-light animation consisted of 12 red dots on a grey background, located at the major joints of the actor's body (centre of the head, shoulders, elbows, wrists, centre of pelvis, knees, and ankles). The dots were approximately 5 mm in diameter. The point-light actor was about 9 cm in height. In a preliminary experiment, two groups of 20 subjects not participating in this experiment were asked to name the actions presented in the point-light animation stimuli in two distinct conditions. Participants in Group 1 (mean age = 24.8 years; 10 males) were presented with the complete point-light animations. Participants in Group 2 (mean age = 23 years; 5 males) were presented with the same point-light animations, but with the dots representing elbows and wrist removed

from the animation. This was done in order to determine the importance of upper limb movements in the identification of each action. From this preliminary study, we selected 20 manual actions (>85% of correct naming in Group 1 and 0% correct naming in Group 2) and 20 nonmanual actions (>85% of correct naming in Group 1 and > 80% of correct naming in Group 2). We then inserted randomly moving dots to create dynamic noise (Perlin Noise) in order to camouflage the point-light animations. Each animation was embedded in 10 levels of noise (from 120 dots to 0 dots). Participants named 10 series of 40 randomized video clips of the same actions but embedded in decreasing levels of noise (from 120 dots to 0 dots).

Results. An item was scored correct at a given level of noise if it was also identified correctly at all the subsequent levels. This scoring procedure was used to avoid giving credit to guessing responses. The results are displayed in Figure 6. The area under the curve of individual performance across the different levels of noise was used as an index of overall performance and the maximum score of each individual as an index of maximal efficiency. Modified *t*-tests (Crawford & Howell, 1998) indicated that, for manual actions, D.C.'s overall performance, $t(5) = -3.77$, $p < .01$, and maximum score, $t(5) = -5.74$, $p < .01$, were significantly impaired in comparison with the overall

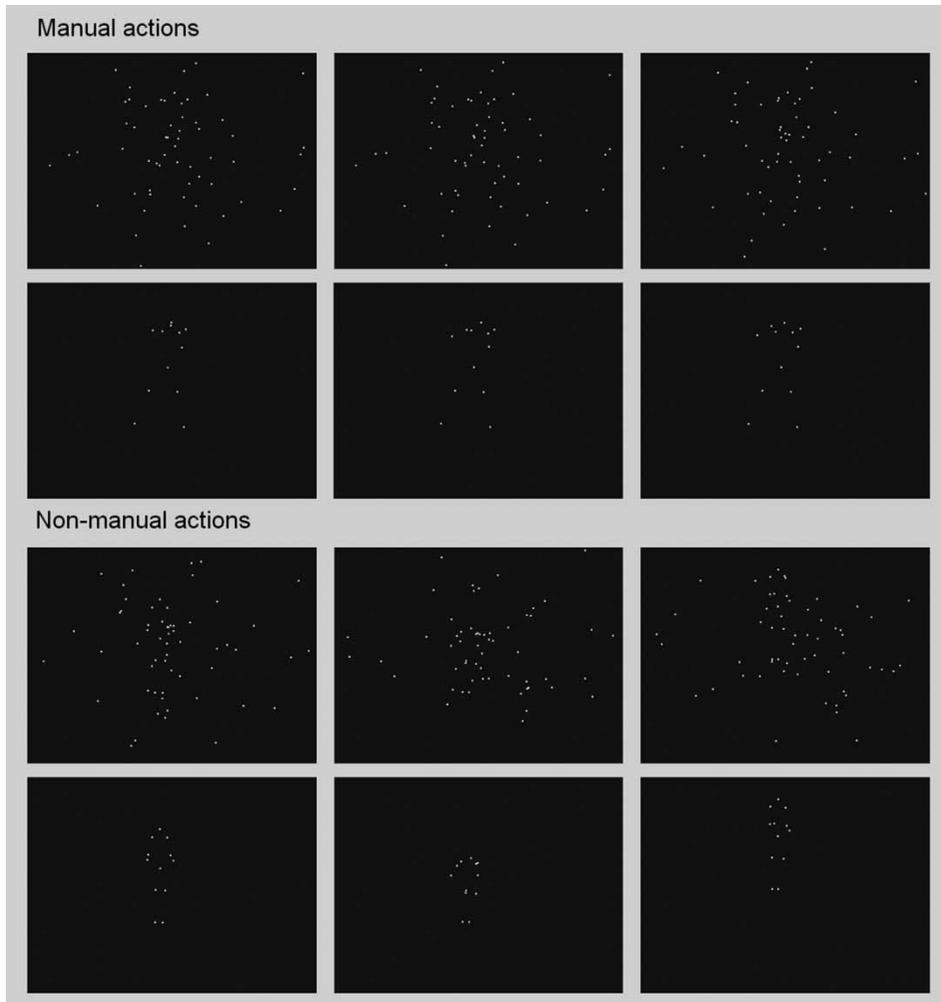


Figure 5. Sample still frames from video clips used as stimuli in Experiment 4. The examples displayed here show a manual action (playing a violin) and a nonmanual action (jumping in place) in a point-light animation with noise (48 random dots) and no noise.

performance and maximum score of control participants. However, for nonmanual actions, both D.C.'s overall performance, $t(5) = -1.42$, $p = .2$, and maximum score, $t(5) = -1.55$, $p = .17$, were within the range of the controls' performance. The results of RSDT (Crawford & Garthwaite, 2005) analyses revealed that the difference in overall performance between manual and nonmanual actions was nearly significantly greater in D.C. than in controls, $t(5) = 2.38$, $p = .06$, and that the difference in maximum score between both kinds of action

was significantly greater in D.C. than in controls, $t(5) = 3.11$, $p = .03$. On the whole, the results thus indicated that D.C.'s performance in identifying point-light animations of actions was *selectively* impaired for manual actions when compared to that of control participants.

Because of our scoring criteria, D.C.'s impaired performance for manual actions could be due to his responses not being consistently correct from one level to the subsequent one rather than to a consistent inability to identify manual actions. To

Naming point-light animations

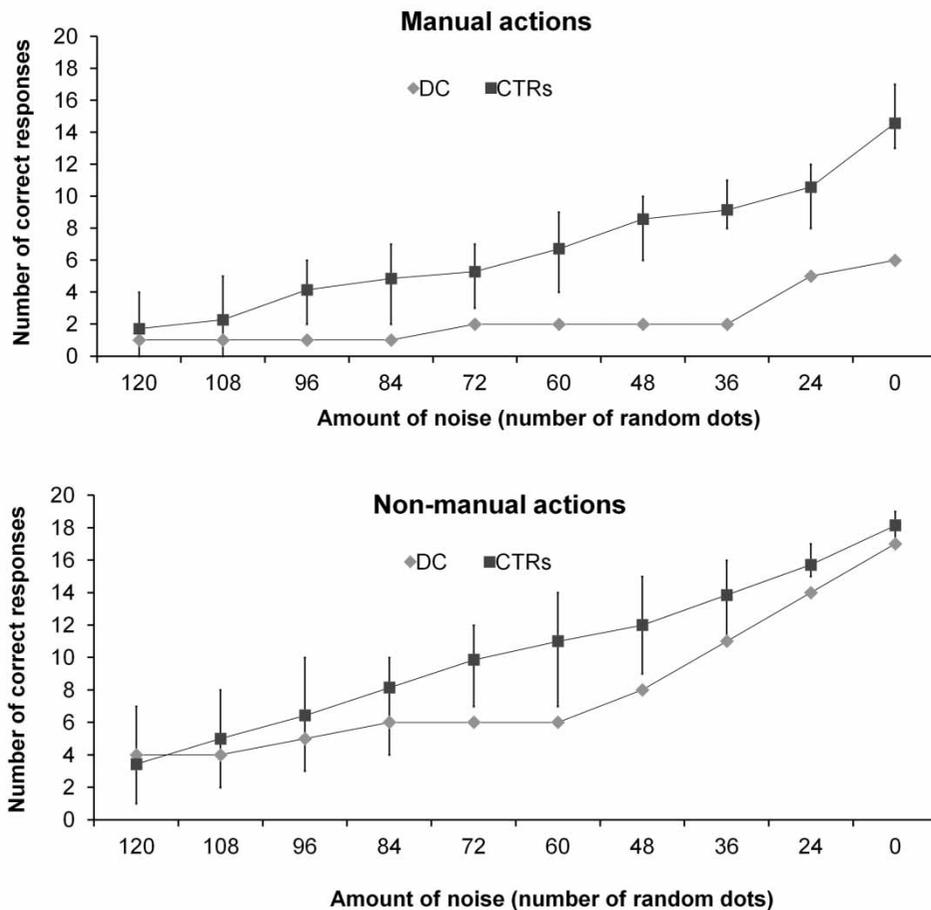


Figure 6. D.C.'s and control participants' number of correct naming responses for manual and nonmanual actions displayed as point-light animations and as a function of the amount of noise (Experiment 4). CTRs = control participants. Error bar = range.

address this issue, an additional analysis was performed with an item being scored correct or incorrect at a given noise level according to the accuracy of the response at that noise level whatever the response (correct or incorrect) to that item at subsequent noise levels. The same pattern of results was found with this scoring procedure (see Appendix D, Figure D1). Data analyses revealed that D.C.'s performance was significantly impaired in identifying manual [overall performance: $t(5) = -5.19, p < .01$; maximum score: $t(5) = -5.74, p < .01$] but not nonmanual [overall performance:

$t(5) = -1.16, p = .15$; maximum score: $t(5) = -1.55, p = .17$] actions and that the difference in performance between both kinds of actions (RSDT) was significantly greater in D.C. than in controls [overall performance: $t(5) = 3.41, p = .02$; maximum score: $t(5) = 3.11, p = .03$].

Interim discussion

The results of this first set of experiments showed that D.C. was as accurate and fast as control participants in naming natural video (Experiment 1)

and photographic (Experiment 2) presentations of both manual and nonmanual actions, as well as pantomimes (Experiment 3), but was selectively impaired at identifying manual actions in point-light animations (Experiment 4). These findings first suggest that motor involvement is not mandatory in order to rapidly and accurately identify actions in natural viewing conditions and, second, that motor involvement may become critical to interpret actions when visual information is incomplete. Whereas body shape, texture, and motion (albeit implied in photographs) are all present in video clips, photographs, and pantomimes, only motion information is present in point-light animations of actions. To account for this pattern of results, we propose that, because of the paucity of visual information, the percept derived from point-light actions is ambiguous and consistent with several actions. Motor representations automatically activated from biological motion stimuli could then help selecting the action that fits the best to the visual display. If motion stimuli do not activate any motor representation, however, identification of point-light actions would be compromised.

Two alternative accounts need to be addressed, however. First, D.C. might be impaired at identifying manual actions in point-light animations not because he had selective difficulties with this kind of (incomplete) stimuli, but rather because he was selectively impaired in processing visual (biological) motion. Although there is no apparent reason why apraxia could result in perceptual difficulties selective to motion, this is a logical possibility that is worth considering. Within this account, the processing of actions presented in videos, photographs, or pantomimes would not suffer from a visual motion processing impairment because body shape information present in these stimuli could suffice to derive coarse body postures or sequences of body postures from which actions could be identified. In contrast, a motion processing impairment would prevent action identification from point-light stimuli since motion is the only piece of information provided in these stimuli. This account is inconsistent with D.C.'s preserved ability to identify

nonmanual actions in point-light animations, unless visual motion processing was less demanding for nonmanual than manual actions. Although we are not aware of any evidence supporting this speculation, it is reasonable to propose, for example, that nonmanual actions typically imply effector movements that are wider and visually more dissimilar from one to another than those typically implied in manual actions.

The second alternative account for D.C.'s difficulty in identifying point-light actions would be that he was selectively impaired in processing visual motion in manual actions because visual motion processing in fact *depends on* motor representations. D.C.'s preserved ability to identify nonmanual actions in point-light animations would be due to his having internal motor representations of these actions. Within this account, like in the previous one, the processing of actions presented in videos, photographs, or pantomimes would not suffer from this impairment because motion information would not be required to identify natural actions. The next series of experiments addressed these alternative accounts.

Processing arm and whole-body kinematics

If D.C. was selectively impaired in identifying actions in point-light animations because of an underlying perceptual motion processing deficit rather than a deficit in processing these stimuli per se, then he should also be impaired in processing *natural* stimuli of both manual and nonmanual actions when a fine-grained analysis of motion information is required. Alternatively, if D.C. was impaired in identifying manual actions in point-light animations because of a deficit in motion processing due to the absence of corresponding motor representations, then he should also be impaired in processing natural stimuli of manual actions but not of nonmanual actions, when a fine-grained analysis of motion information is required. The two experiments reported in this section allowed us to assess D.C.'s ability to process fine-grained kinematics of an actor's hand and whole-body movements.

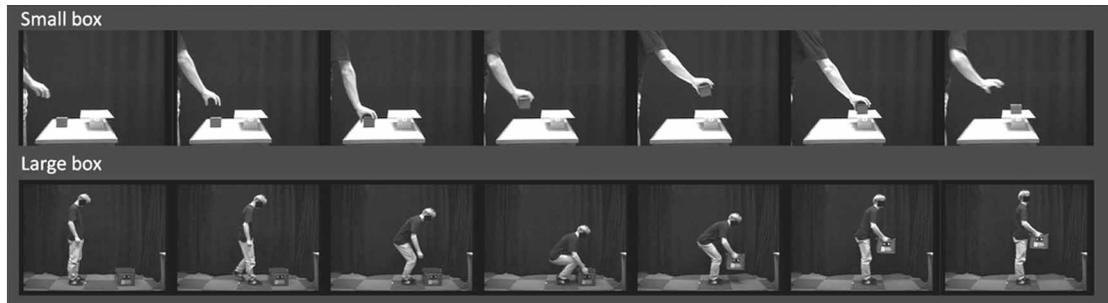


Figure 7. Illustration of the stimuli used in Experiments 5–6. Sample still frames from a video clip of an actor lifting a small box or a large box. The extracts of video clips are published with the kind permission of Simone Bosbach.

Experiment 5: Weight estimation

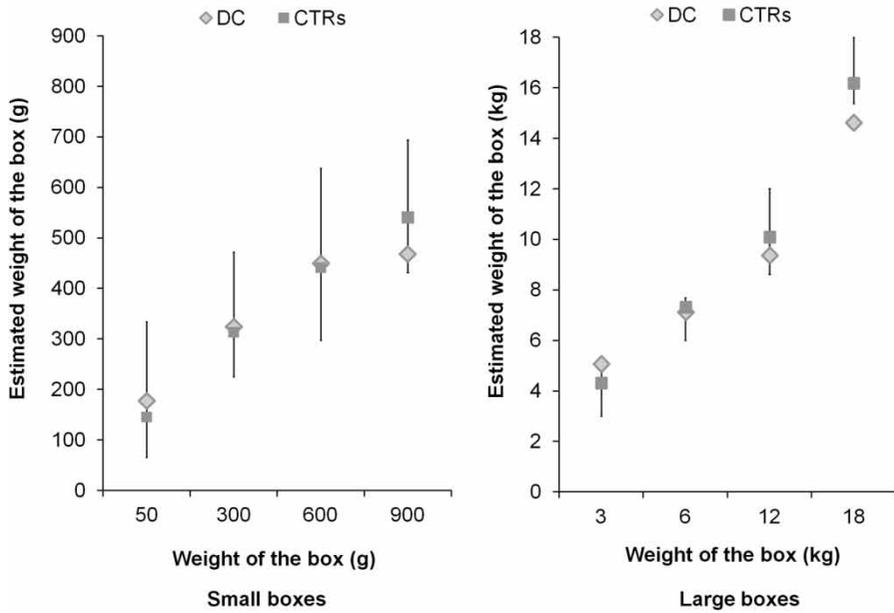
Method. Participants were presented with movie clips showing an actor lifting a box and were asked to estimate the box's weight. Such estimation required a fine-grained analysis of the actor's arm (when he lifted a small box) or whole-body movements (when he lifted a large box).

The material, provided by Simone Bosbach (Bosbach, Cole, Prinz, & Knoblich, 2005), involved 128 video clips showing two actors (a male and a female) lifting a small ($N = 64$) or a large ($N = 64$) box (see illustration in Figure 7). The small box was filled in with 0.05, 0.3, 0.6, or 0.9 kg, and the large box was filled in with 3, 6, 12, or 18 kg. In that way, all boxes in one condition (small or large) have exactly the same size and appearance. During the filming of the video clips, the actors were told the correct weight of the box before lifting it. In the small box condition, the video clip presented the actor's arm lifting a box from on a table and placing it onto a shelf. In the large box condition, the video clip showed the actor going up to a box that was placed on the ground and lifting it. Their faces were blacked out. The conditions were blocked (the large box condition being presented first), and the video clips within a condition were randomized. In order to make participants familiar with the various possible weights presented in the stimuli, each condition was preceded by a randomized presentation of one of the four video clips showing another actor lifting the four possible

weights. All of the video stimuli were displayed each in turn, in the centre of a computer screen, using E-prime software. Each trial began with the presentation of a central fixation cross for 200 ms, followed by a video clip lasting between 2850 ms and 5980 ms. Following the video clip, the question "What is the weight of the box?" was displayed with the four possible weights given as choice responses. Participants responded orally to the question, and the experimenter wrote down their responses. Participants were asked not to respond before the end of each video clip.

Results. Mean weight estimation was calculated for each actual weight. Small and large boxes were analysed separately. The results are displayed in Figure 8 (top). As can be seen in this figure, the weight estimations given by both D.C. and control participants were positively related to the actual weights of the boxes, whether small or large. Moreover, both D.C. and control participants tended to overestimate the actual weight of the smaller boxes (50 g and 300 g; 3 kg and 6 kg) and underestimate the actual weight of the larger boxes (600 g and 900 g; 12 kg and 18 kg). Crawford and Howell's (1998) modified t -tests indicated that D.C.'s weight estimations did not significantly differ from the estimations provided by the control participants whatever the weight of the small ($-0.68 \leq ts \leq 0.32$; all $ps > .52$) or of the large ($-1.99 \leq ts \leq 1.09$; $ps > .09$) boxes. Thus, D.C. was not

Weight estimation



Judging weight's expectation

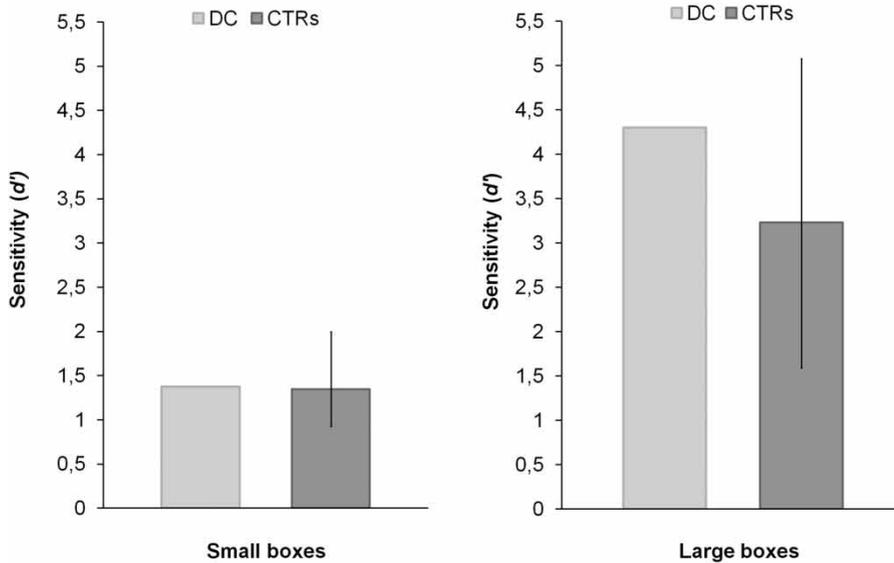


Figure 8. Top: D.C.'s and control participants' estimated weight of the small and large boxes as a function of the actual weight of the boxes (Experiment 5). Bottom: D.C.'s and control participants' sensitivity (d') to violations of the actor's expectation for the small and the large boxes (Experiment 6). CTRs = control participants. Error bar = range.

impaired in estimating the weight of the boxes on the basis of the movements of the actor's arm or whole body.

Experiment 6: Judging expectation about weight

Method. Participants were again presented with movies showing an actor lifting a box but, here, they were asked to estimate the actor's expectation about the box's weight. The stimuli (also provided by Simone Bosbach) were similar to those used in Experiment 5, except that during the filming of each video, the actors had been told either the correct or the incorrect weight of the box before lifting it. Hence, in half of the trials, the actor was deceived about box's weight. When viewing the videos, the participants had to judge in each trial whether the actor was deceived about the given weight. To make such judgements, the participants need to detect subtle mismatches between the prepared and the resulting movement (Bosbach et al., 2005).

The small and large box conditions were presented in blocks (the large condition being presented first), and the video clips within a condition were randomized. Each blocked condition was preceded by the random presentation of the eight video clips showing another actor lifting the four possible weights in both correct and deceived weight expectation conditions. The procedure was the same as that in Experiment 5, except that, in each trial, after the presentation of a central fixation cross for 200 ms and the video clip (lasting between 2320 ms and 5360 ms), the question "Was the actor correctly informed about the weight of the box?" was presented. Participants responded orally to the question, and the experimenter wrote down their responses. Participants were asked not to respond before the end of each video clip.

Results. Following the signal detection theory (Macmillan & Creelman, 2005), we calculated for each participant the number of hits (i.e., correct identifications of a violation of expectation) and of false alarms (i.e., false identifications of a violation of expectation) and then computed the d' sensitivity index. Small and large boxes were analysed

separately. The results are displayed in Figure 8 (bottom). As can be seen in this figure, both D.C. and control participants showed sensitivity to kinematic adjustments induced by the violations of expectation, although sensitivity was higher for large than for small boxes, in both D.C. and control participants. The results of the modified t -tests (Crawford & Howell, 1998) indicated that D.C.'s sensitivity to violations of expectations was not significantly different from the control participants' sensitivity, for either the small, $t(5) = 0.08$, $p = .93$, or the large, $t(5) = 0.78$, $p = .46$, boxes. Thus, here again, the results showed that D.C. was not impaired in perceiving the fine kinematics of an actor's arm or whole body. Moreover, as indicated by the RDST (Crawford & Garthwaite, 2005) analysis, D.C. was not significantly worse in detecting violations in small (involving arm kinematics) than in large (involving whole body kinematics) boxes when compared to control participants' estimations of small and large boxes, $t(5) = 0.38$, $p = .72$.

GENERAL DISCUSSION

In this study, we tested a prediction drawn from motor theories of action comprehension—namely, that an individual who has no motor representations of hand actions due to congenital absence of upper limbs should be less efficient than typically developed individuals in comprehending hand actions (e.g., throwing) whereas he should show no difficulty for actions performed with other body parts (e.g., jumping). We assessed action comprehension in an individual with such a condition, D.C., in a series of picture naming tasks that included different kinds of visual depictions of actions—that is, video clips, photographs, pantomimes, or point-light animations. Distinct patterns of results were found depending on the kind of visual depictions. D.C. was as efficient as control participants in naming natural video (Experiment 1) and photographic (Experiment 2) presentations of both manual and nonmanual actions, as well as pantomimes of object-related actions (Experiment 3). Moreover, he was as

efficient in identifying pantomimes, in which only information about body shape and motion was present, than natural depictions of manual actions performed with the target objects. However, D.C. was selectively impaired at recognizing point-light animations of manual actions (Experiment 4). This impairment was not due to a difficulty in processing kinematic information per se. D.C. showed no difficulty in identifying point-light animations of nonmanual actions. Furthermore, he was as accurate as control participants in two experiments that required extracting fine-grained information about an actor's arm or whole-body motion, like estimating the weight of a box lifted by an actor (Experiment 5) or judging an actor's expectation about a box's weight (Experiment 6). On the whole, these results indicated that action comprehension needs motor involvement when important visual features of the observed action—that is, the body parts involved—are missing.

These findings first suggest that one possible source of previous conflicting results obtained with motor-impaired individuals lies in the kind of stimuli used to test action comprehension. On the one hand, our results replicated those obtained with a number of patients with apraxia who, despite their action production deficit, performed within the normal range in identifying actions from pantomimes (e.g., Bartolo et al., 2001; Negri et al., 2007; Papeo et al., 2010; Rapcsak et al., 1995) or pictures (e.g., Rumiati et al., 2001). On the other hand, they are consistent

with those having reported that patients with hemiplegia (Serino et al., 2010) or paraplegia (Arrighi et al., 2011) had difficulties in naming or detecting point-light animations of actions.² Hence, both the results of this study and previous ones are consistent with the hypothesis that motor involvement in action comprehension is a function of the completeness of visual information.

Our findings have two major implications for theories of action comprehension. First, they challenge motor theories of action comprehension by showing that the visual analysis of body shape and motion provides sufficient input for comprehending observed actions. No corresponding internal motor representation is required in order to identify efficiently actions performed by somebody else. Second, they indicated that when body shape information is sparsely available, the motor repertoire of the observer becomes critical to interpret the observed action. We comment on each of these points in turn.

The outcome from the video, photograph, and pantomime naming tasks provides evidence against motor theories of action comprehension that is not liable to two important objections raised by evidence obtained with apraxic patients. First, we assessed action comprehension in an individual who had no motor repertoire of manual actions *at all*,³ a condition that is difficult to ascertain in apraxic patients. Not only may these patients have *residual* motor representations of actions that may suffice to support action identification, which probably requires less fine

² Unfortunately, it is unknown whether apraxic patients who were not impaired in identifying pantomimes would show difficulties in identifying point-light animations of actions and, as a corollary, whether plegic patients would show no difficulty in identifying pantomimes—this should be examined in future studies.

³ A reviewer asked whether D.C. may not have acquired upper limb motor representations on the basis of visual experience alone. Although studies with aplasic individuals provide some evidence against this conjecture (e.g., Gazzola et al., 2007; Reilly & Sirigu, 2011; Stoessel, Seitz, & Buetschli, 2009), one cannot formally rule out that the mere observation of upper limb movements performed by others could lead to the formation of memory traces in the premotor/motor cortex of an individual unable to perform these movements due to a congenital absence of upper limbs. In any event, such memory traces cannot be considered as parts of a *motor repertoire* of upper limb actions—that is, a repertoire of means allowing the generation of motor programmes in order to achieve specific goals with the upper limbs. Let us give a reminder here that, according to motor theories of action comprehension (Blakemore & Decety, 2001; Jeannerod, 2001; Rizzolatti et al., 2001), the comprehension of an observed action is not driven by the activation of motor representations per se but by the activation of these representations as parts of a motor plan previously generated by the observer to achieve a specific goal. The observer understands the action by retrieving the goal he achieved when he previously performed similar movements. Thus, D.C. cannot be regarded as having a motor repertoire of manual actions, since he has never been able to achieve the goals of typically manual actions with his upper limbs.

specification than action production, they may also have *intact* motor representations that are not expressed in action production because of an impairment of processes specifically involved in action execution (Rizzolatti & Sinigaglia, 2010). Second, some proponents of motor theories of action comprehension claimed that action comprehension by direct visuomotor matching was not the only mechanism available to comprehend actions, but indeed the mechanism “by which the meaning of the acts that are being observed are understood *immediately*” (Rizzolatti & Sinigaglia, 2008, p. 136; emphasis added). Hence, according to these authors, if motor representations of specific actions were lacking, these actions could be understood by alternative (e.g., inferential) means. Nevertheless, having motor representations onto which a perceived action can be mapped should allow faster and more efficient recognition. Here, we provided the first evidence that, in an individual lacking motor representations of specific actions (i.e., manual actions), these actions were comprehended both as fast and as efficiently as in individuals who normally developed motor representations for these actions. Moreover, and importantly, D.C.’s pattern of performance provides no evidence of a processing advantage in comprehending nonmanual actions, of which he had internal motor representations, over manual actions, of which he had no motor representations. Hence, evidence from these tasks is undoubtedly at odds with the hypothesis that fast and efficient comprehension of an action depends on accessing an internal motor representation of that action. Instead, it provides strong support to theories of action comprehension that assume that the core representations and processes on which action comprehension relies is constituted by the visual analysis of the actor’s body shape and motion (Giese & Poggio, 2003) and a conceptual action system (Rothi et al., 1991; Tranel et al., 2003) giving meaning to this percept.

However, our findings also suggested that this visual-to-conceptual processing is not able to handle action stimuli that lack information about body shape and texture, like point-light

animations of actions. In this case, motor involvement becomes critical to interpret the observed action. In addition to the above-mentioned evidence coming from studies with plegic patients, there is converging evidence from studies with healthy subjects pointing to the influence of the observer’s own motor repertoire in the processing of point-light animations of actions. For instance, Casile and Giese (2006) found that participants showed more perceptual sensitivity to point-light animations of actions they had previously learned to execute than to similar but not previously learned actions. Other studies (Jokisch, Daum, & Troje, 2006; Loula, Prasad, Harber, & Shiffrar, 2005; Prasad & Shiffrar, 2009) found that identifying the actor of actions presented as point-light animations was facilitated by the participants’ motor experience with that action. For instance, participants were more efficient at identifying the actor when the actions were performed by themselves (i.e., when they had motor experience with the actions) than when the actions were performed by friends (i.e., when they had visual experience with the actions) or unknown actors (Loula et al., 2005). Finally, TMS applied on the premotor cortex of participants selectively reduces their sensitivity to point-light animations of actions in comparison to point-light animations of a translating polygon embedded in similarly moving dots (van Kemenade, Muggleton, Walsh, & Saygin, 2012).

One may ask what is the real import of these observations made with point-light animations of actions, given that there are no stimuli resembling point-light animations in ecological settings. Were the cognitive and neural processes involved in processing point-light animations only triggered by these specific stimuli, these observations would have little implication. We suggest that point-light animations of actions in fact constitute a special case of degraded or ambiguous visual presentations of human actions. Motor involvement would be automatically triggered by any kind of visual action stimulus but would actually contribute to action processing only and each time visual information critical for performing the task is incomplete or ambiguous.

We see at least two possible, nonmutually exclusive, mechanisms by which motor processes may contribute to action comprehension. Both are based on the assumption that any human motion stimuli automatically activate motor representations in the observer's own motor repertoire. Then, a first possibility is that these motor representations generate top-down expectations that serve to fill in missing or ambiguous visual information so that a better defined visual percept can be formed (Wilson & Knoblich, 2005). The second possibility is that motor representations automatically derived from motion stimuli provide an additional source of information that is "read" by the conceptual system or combined with the outcome of conceptual processing in order to select between the various competing interpretations derived from ambiguous action percepts.

More research is required to understand how the motor system assists the visual or/and the conceptual system in order to achieve action comprehension under various visual conditions. Available evidence from neuroimaging studies (for reviews, see Blake & Shiffrar, 2007; Caspers, Zilles, Laird, & Eickhoff, 2010; Grèzes & Decety, 2001) suggests that, despite the many different methods, contrasts, and tasks (passive viewing, "one-back" task, silent naming, conceptual matching, etc.) employed, action processing most often elicited responses in both brain areas presumably related to motor planning (e.g., inferior frontal gyrus, premotor cortex, or/and inferior parietal lobe) and areas presumably related to visual and conceptual processing (e.g., lateral occipital area, fusiform gyrus, posterior superior temporal sulcus, or/and middle temporal gyrus). This general pattern of brain responses has been found with visual action stimuli as different as natural videos (e.g., Calvo-Merino et al., 2005; Gazzola & Keysers, 2009), pantomimes (e.g., Decety et al., 1997; Emmorey, McCullough, Mehta, & Grabowski, 2011), static images (e.g., Liljeström et al., 2008), pictograms (Assmus, Giessing, Weiss, & Fink, 2007), and point-light animations (e.g., Lingnau & Petris, 2013; Saygin, Wilson, Hagler, Bates, & Sereno, 2004). However, to

date, only two studies have directly contrasted brain responses to different kinds of visual stimuli within the same design. Beauchamp and colleagues (Beauchamp, Lee, Haxby, & Martin, 2003) compared the brain responses to natural videos and point-light animations of actions and found that, although both kinds of action stimuli preferentially activate the posterior superior temporal sulcus and the lateral fusiform gyrus when contrasted to tool stimuli, natural action videos elicited significantly stronger activation than point-light actions in these regions. In contrast, Grossman and Blake (2002) found that brain responses were as strong to point-light animations as to videos of whole bodies in motion within the superior temporal sulcus. None of these studies have reported different responses for natural videos than for point-light animations in frontal or parietal regions. However, the tasks used in these studies—namely, deciding whether the stimulus contained a human or a tool (Beauchamp et al., 2003) or a one-back task (Grossman & Blake, 2002)—could be performed without having to identify or comprehend the actions.

More relevant in the context of our hypothesis is a recent study by Lingnau and Petris (2013), who investigated the brain areas involved in understanding the goal of actions in comparison to identifying the effector of actions. Actions were presented as point-light displays in three viewing conditions defined by different levels (low, medium, high) of spatial noise. The results showed that, in the low noise condition—that is, when the actions are easy to comprehend—higher responses to the goal than to the effector task were observed in the left and right inferior frontal gyrus, left premotor cortex, and bilateral middle temporal gyrus. However, when the stimuli are more ambiguous (medium noise level), the difference between the goal and effector task is restricted to the left inferior frontal regions. These findings are consistent with the view that the middle temporal gyrus supports the retrieval of the meaning of the observed action but that motor representations stored in frontal areas can be recruited as additional information to select

between several competing alternatives when the visual display is ambiguous. Moreover, the view that the middle temporal gyrus—but not inferior frontal and premotor regions—is crucial for retrieving action meaning is in line with the findings of lesion studies reporting deficits in action understanding after damage to the posterior middle temporal gyrus (e.g., Kalénine, Buxbaum, & Coslett, 2010; Pillon & d'Honincthun, 2011; Vannuscorps & Pillon, 2011).

Our proposal on how motor processes may contribute to action comprehension is analogous to a proposal made in the related framework of the motor theory of speech perception. Actually, it is based on similar kind of evidence. The motor theory of speech perception holds that heard phonemes are recognized when they are matched onto the motor representation that would generate them in the perceiver (Liberman & Mattingly, 1985). Although this theory was supported by evidence showing that the motor areas involved in speech production were also activated when individuals perceived speech sounds (Wilson, Saygin, Sereno, & Iacoboni, 2004), numerous patients were reported with a preserved ability to recognize speech sounds despite an acquired (see for review, Hickok, 2010) or congenital inability to produce them (Lenneberg, 1962). Nevertheless, Moineau, Dronkers, and Bates (2005), for instance, found that Broca's aphasics whose lesion affects the motor speech system have selective difficulties in recognizing *degraded* (low-pass filtered and compressed) speech sounds (see also, Meister, Wilson, Deblieck, Wu, & Iacoboni, 2007). This suggested that, in normal conditions, the auditory system is sufficient to recognize speech sounds but that motor involvement may support perception under adverse conditions.

A last implication of our findings is that they raise doubts on whether point-light animations are the most appropriate kind of stimulus to study the cognitive and neural processes involved in action perception and comprehension. The use of point-light animations is pervasive and is becoming exclusive in the field of human motion perception (see, for example, the review by Blake

& Shiffrar, 2007). However, the findings of this study suggest that this particular kind of stimuli may engage processes that are not typical of action perception and comprehension in natural viewing conditions. Hence, studies on human motion perception and action comprehension should broaden the kinds of stimuli used, including the kinds and degrees of degradation of action displays, to get a better insight into the nature of the processes involved.

To conclude, the findings of this study challenged motor theories of action comprehension by showing that actions performed by others may be efficiently comprehended even if the observer lacks internal motor representations of these actions. However, they also showed that, under degraded visual conditions, comprehending what others are doing does need the observer's own motor representations. Empirical studies should now attempt at understanding how the motor system works in concert with the visual or/and the conceptual system in order to achieve action comprehension under various viewing conditions.

Manuscript received 19 July 2012

Revised manuscript received 20 September 2013

Revised manuscript accepted 24 September 2013

First published online 11 November 2013

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APPENDIX A

List of manual and nonmanual actions presented in Experiment 1 (naming video clips of actions) and Experiment 2 (naming photographs of actions)

<i>Actions</i>	<i>Modal name in French</i>	<i>Modal name in English</i>	<i>Modal name in French</i>	<i>Modal name in English</i>	
Manual actions	<i>Presser</i>	Squeezing	<i>Couper</i>	Cutting	
	<i>Nager</i>	Swimming	<i>Pincer</i>	Pinching	
	<i>Poster</i>	Posting	<i>Ramer</i>	Rowing	
	<i>Brancher</i>	Plugging in	<i>Dessiner</i>	Drawing	
	<i>Coller</i>	Pasting	<i>Percer</i>	Piercing	
	<i>Laver</i>	Washing	<i>Nettoyer</i>	Cleaning	
	<i>Vaporiser</i>	Spraying	<i>Tricoter</i>	Knitting	
	<i>Gratter</i>	Scratching	<i>Caresser</i>	Petting	
	<i>Chatouiller</i>	Tickling	<i>Peindre</i>	Painting	
	<i>Mesurer</i>	Measuring	<i>Clouer</i>	Nailing	
	<i>Cueillir</i>	Picking	<i>Dactylographier</i>	Typing	
	<i>Effacer</i>	Erasing	<i>Lancer</i>	Throwing	
	<i>Arroser</i>	Watering	<i>Gifler</i>	Slapping	
	<i>Verser</i>	Pouring	<i>Saupoudrer</i>	Sprinkling	
	<i>Planter</i>	Planting	<i>Se coiffer</i>	Coiffing	
	<i>Plier</i>	Folding	<i>Coudre</i>	Sewing	
	<i>Etrangler</i>	Strangling	<i>Tailler</i>	Trimming	
	<i>Râper</i>	Grating	<i>Se moucher</i>	Blowing one's nose	
	<i>Tordre</i>	Wringing out	<i>Scier</i>	Sawing	
	<i>Visser</i>	Screwing in	<i>Signer</i>	Signing	
	Nonmanual actions	<i>Sourire</i>	Smiling	<i>Lécher</i>	Licking
		<i>Se peser</i>	Weighing	<i>Dormir</i>	Sleeping
		<i>Cligner</i>	Winking	<i>Méditer</i>	Meditating
<i>Cracher</i>		Spitting	<i>Chuchoter</i>	Whispering	
<i>Souffler</i>		Blowing	<i>Têter</i>	Suckling	
<i>Chanter</i>		Singing	<i>Sauter</i>	Jumping	
<i>Marcher</i>		Walking	<i>Sentir</i>	Sniffing	
<i>Mordre</i>		Biting	<i>Courir</i>	Running	
<i>Ecouter</i>		Listening to	<i>S'agenouiller</i>	Kneeling	
<i>Crier</i>		Screaming	<i>Bailler</i>	Yawning	

APPENDIX B

List of actions presented as pantomimes in Experiment 3

<i>Actions</i> <i>French description</i>	<i>English description</i>
<i>Regarder avec des jumelles</i>	Looking through binoculars
<i>Allumer un briquet</i>	Lighting a lighter
<i>Jouer de la contrebasse</i>	Playing a double bass
<i>Utiliser une torche électrique</i>	Shining a flashlight
<i>Visser un bouchon</i>	Screwing on a cap
<i>Taper à la machine</i>	Typing
<i>Lancer un frisbee</i>	Throwing a frisbee
<i>Gratter une allumette</i>	Lighting a match
<i>Tirer à l'arbalète</i>	Firing a crossbow
<i>Se mettre du vernis à ongles</i>	Putting on nail polish
<i>Utiliser un râteau</i>	Raking
<i>Jouer du piano</i>	Playing piano
<i>Utiliser une calculatrice</i>	Using a calculator
<i>Jouer du saxophone</i>	Playing the saxophone
<i>Jouer au tennis</i>	Playing tennis
<i>Utiliser des ciseaux</i>	Using scissors
<i>Peindre</i>	Painting
<i>Tricoter</i>	Knitting
<i>Visser avec un tournevis</i>	Screwing with a screwdriver
<i>Utiliser une pelle</i>	Digging with a shovel
<i>Verser avec une cruche</i>	Pouring from a jug
<i>Tirer à la carabine</i>	Shooting with a rifle
<i>Lancer un boomerang</i>	Throwing a boomerang
<i>Jouer de la flûte</i>	Playing a flute
<i>Tirer au revolver</i>	Shooting with a revolver
<i>Jouer de la trompette</i>	Playing a trumpet
<i>Utiliser un éventail</i>	Using a fan
<i>Fumer une cigarette</i>	Smoking a cigarette
<i>Creuser un trou</i>	Digging a hole
<i>Faire un cercle avec un compas</i>	Tracing out a circle with a compass
<i>Faire de l'escrime</i>	Fencing
<i>Jouer de la harpe</i>	Playing a harp
<i>Tirer à l'arc</i>	Shooting with a bow and arrow
<i>Ouvrir la porte avec une clé</i>	Unlock a door with a key
<i>Coudre un bouton</i>	Sewing on a button
<i>Jouer au lance-pierre</i>	Shooting a slingshot
<i>Jouer des maracas</i>	Shaking maracas
<i>Jouer de la guitare</i>	Playing a guitar
<i>Clouer</i>	Nailing
<i>Se mettre du rouge à lèvres</i>	Putting on lipstick
<i>Jouer du violon</i>	Playing a violin
<i>Téléphoner</i>	Telephoning
<i>Arroser avec un arrosoir</i>	Watering with a watering can
<i>Fumer la pipe</i>	Smoking a pipe
<i>Utiliser une loupe</i>	Using a magnifying glass
<i>Gommer</i>	Erasing
<i>Utiliser un chronomètre</i>	Timing with a stopwatch
<i>Scier</i>	Sawing

(Continued overleaf)

APPENDIX B (Continued)

<i>Actions</i> <i>French description</i>	<i>English description</i>
<i>Jouer au yoyo</i>	Playing yoyo
<i>Fumer le cigare</i>	Smoking a cigar
<i>Donner des coups de hache</i>	Splitting wood with an axe
<i>Jouer de l'accordéon</i>	Playing an accordion
<i>Se brosser les dents</i>	Brushing one's teeth
<i>Jouer de l'harmonica</i>	Playing a harmonica
<i>Se limer les ongles</i>	Filing one's nails
<i>Jouer au pingpong</i>	Playing ping pong
<i>Donner des coups de fouet</i>	Whipping
<i>Passer le balai</i>	Sweeping
<i>Se peigner</i>	Combing
<i>Jouer à la toupie</i>	Spinning a top

APPENDIX C

List of manual and nonmanual actions presented in Experiment 4 (naming actions presented as point-light animations)

<i>Manual actions</i>		<i>Nonmanual actions</i>	
<i>French description</i>	<i>English description</i>	<i>French description</i>	<i>English description</i>
<i>Scier</i>	Sawing	<i>Sauter à cloche-pied</i>	Hopping
<i>Coudre</i>	Sewing	<i>Sauter à pieds-joints</i>	Jumping in place
<i>Porter une caisse</i>	Lifting a box	<i>Faire la roue</i>	Doing cartwheels
<i>Boire</i>	Drinking	<i>Faire le moonwalk</i>	Moonwalking
<i>Conduire</i>	Driving	<i>Marcher à reculons</i>	To walk backwards
<i>Se raser</i>	Shaving	<i>Grimper à l'échelle</i>	Climbing the ladder
<i>Applaudir</i>	Clapping	<i>Ramasser un objet par terre</i>	Picking up an object on the floor
<i>Pêcher</i>	Fishing	<i>Pousser quelque chose</i>	Pushing something
<i>Écrire au tableau</i>	Writing on the board	<i>S'agenouiller</i>	Kneeling
<i>Nager le papillon</i>	Swimming the butterfly stroke	<i>Faire du skateboard</i>	Skateboarding
<i>Balayer</i>	Sweeping	<i>Marcher</i>	Walking
<i>Creuser</i>	Digging	<i>Faire un shoot au football</i>	Kicking a football
<i>Jouer du violon</i>	Playing a violin	<i>S'asseoir</i>	Sitting
<i>Mettre du déodorant</i>	Putting on deodorant	<i>Courir</i>	Running
<i>Se peigner</i>	Combing	<i>Faire un demi-tour en sautant</i>	Doing a half-turn by jumping
<i>Tirer à l'arc</i>	Shooting with a bow and arrow	<i>Monter un escalier</i>	Climbing stairs
<i>Ratisser</i>	Raking	<i>Donner un coup de pied</i>	Kicking
<i>Tirer au fusil</i>	Shooting with a gun	<i>Faire un salto</i>	Doing a somersault
<i>Faire un shoot au basket-ball</i>	Shooting a basketball	<i>Faire un tour complet en sautant</i>	Doing a full turn by jumping
<i>Fendre des bûches</i>	Splitting logs with an axe	<i>S'accroupir</i>	Squatting

APPENDIX D

Experiment 4 (naming point-light animations), additional results.

The results displayed here were obtained by scoring an item as correct/incorrect at a given noise level whatever the response (correct or incorrect) to that item at subsequent noise levels (Figure D1).

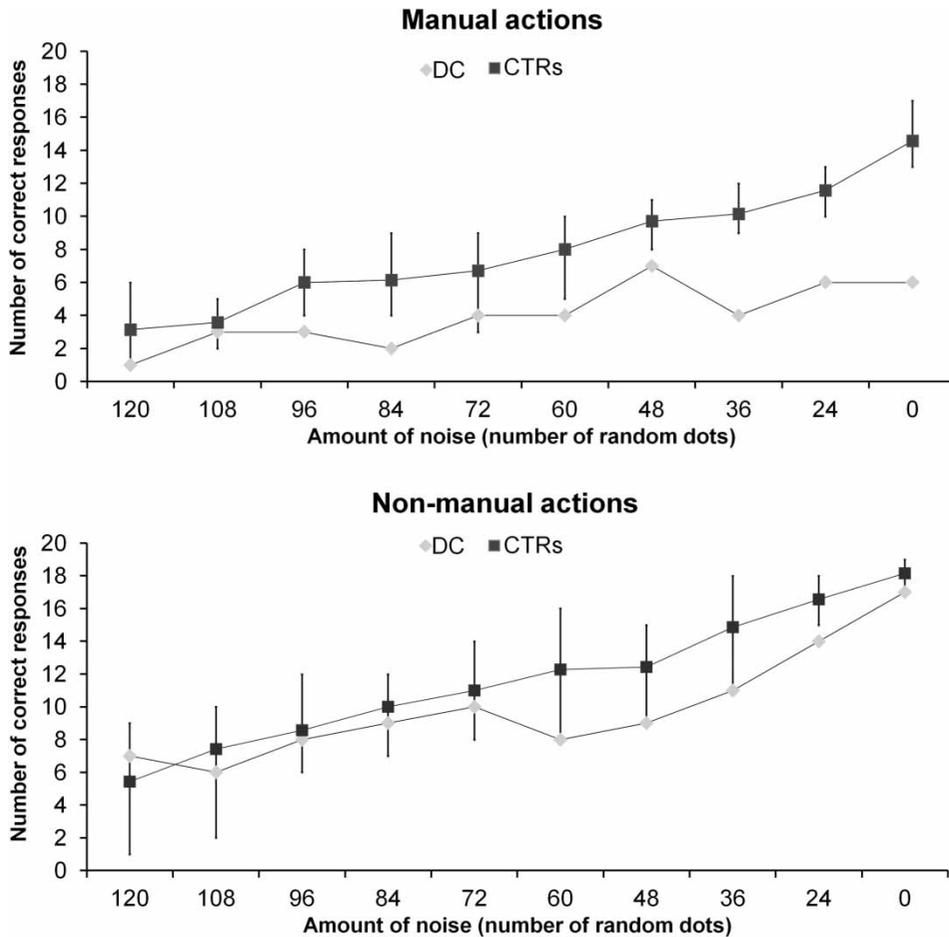


Figure D1 D.C.'s and control participants' number of correct naming responses for manual and nonmanual actions displayed as point-light animations and as a function of the amount of noise (Experiment 4). CTRs = Control participants. Error bar = range.