UNIVERSITE CATHOLIQUE DE LOUVAIN
Faculté de psychologie et des sciences de l'éducation

ON THE ROLE OF MOTOR REPRESENTATIONS AND PROCESSES IN THE COMPREHENSION OF ACTIONS AND OBJECTS

Promotrice:
Professeure **Agnesa Pillon**

Thèse présentée en vue de l'obtention
du grade de Docteur en sciences psychologiques
et de l'éducation par
Gilles Vannuscorps

Louvain-la-Neuve, Belgique
Avril 2013

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Promotrice:
Pr. **Agnesa Pillon**, Université catholique de Louvain

Membres du jury:

Pr. **Pierre Feyereisen**, Université catholique de Louvain
Pr. **Mariane Frenay**, Université catholique de Louvain, Présidente du jury
Pr. **Philippe Peigneux**, Université libre de Bruxelles
Pr. **Raffaella Rumiati**, Scualo Internationale Superiore di Studi Avanzati
Pr. **Dana Samson**, Université catholique de Louvain

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List of abbreviations

M1	Primary motor cortex
dPM	Dorsal premotor cortex
EBA	Extrastriate body area
ERP	Evoked response potential
F5	Ventral premotor cortex (monkey's brain)
fMRI	Functional magnetic resonance imaging
HLJ	Hand laterality judment
IPL	Inferior parietal lobe
IPS	Intraparietal sulcus
IT	Inferior temporal cortex
MEG	Magnetoencephalography
MEP	Motor evoked potential
PET	Positron emission tomography
PF	Rostral inferior parietal lobule (monkey's brain)
PLA	Point-light action
PLD	Point-light display
PM	Premotor cortex
pMTG	Posterior middle temporal gyrus
pSTS	Posterior superior temporal sulcus
rTMS	Repetitive transcranial magnetic stimulation
SMA	Supplementary motor area
SPL	Superior parietal lobe
STS	Superior temporal sulcus
TMS	Transcranial magnetic stimulation
vPM	Ventral premotor cortex

INTRODUCTION

Every day, we see dozens of objects having a particular shape, color, motion and so forth as well as people moving their legs, raising their arms, turning their wrists, opening their mouths and grasping objects. Immediately, and without conscious effort, we identify these objects and these body movements as instances of "a car", "a pen", "a dog", "drinking", or "running" and retrieve *conceptual knowledge* about these categories (i.e., concepts) such as what is the usual function of a car, the living habits of a dog, or the probable purpose and results of the observed movements. How the human mind and brain achieves this process of *comprehension* is the question that we addressed in this thesis. We focused on two particularly controversial issues. The first issue concerns the nature of conceptual knowledge involved in the process of comprehension: Is conceptual knowledge or, in other words, concepts, composed of traces of previous sensory-motor experience directly stored as motor and sensory representations in sensory and motor representational systems? Or is such knowledge stored in an "abstract" or "amodal" format, within a distinct representational system, remote from sensory-motor systems, which represents in a common format all types of knowledge whatever the modality of experience (visual, auditory, motor) that has supported their acquisition?

In philosophy, this debate may be traced back to more than 2000 years ago when it set the rationalist view of Plato, according to which concepts are mental entities distinct from "sensory impressions", against the empiricism of Aristotle assuming that ideas are copies of sensory experience. In contemporary cognitive psychology and neuroscience, this debate is held mainly between proponents of "embodied" theories of concepts and proponents of "amodal" theories of concepts. Embodied theories of concepts assume that a concept is represented in a sensory-motor format in the sensory-motor brain systems

that were active when the different types of information about that concept were acquired. Knowledge about what "hammers" look like and how they must be held and manipulated is represented in, respectively, a visual format in a vision-specific representational system in or nearby the visual system involved in viewing hammers and in a motor format in a motor-specific representational system in or nearby the motor system implied in using hammers. According to "amodal" theories of concepts, however, knowledge involved in the process of comprehension is represented in a unique "abstract" or "amodal" format, common to all kinds of information, within heteromodal cortex remote from the sensory and motor systems. The second issue addressed in this work concerns more specifically the role of motor representations and processes in the *comprehension of observed actions performed by others*. This debate sets a "traditional view" in cognitive psychology assuming that the comprehension of observed actions relies on a visuo-perceptual analysis of the actor's body shape and motion which provides inputs to a "amodal" semantic system, against "motor simulation" theories of action comprehension, claiming that comprehending an observed action relies on the observer's own motor representations of the same action, i.e., those that she uses when performing that action herself. In this view, by accessing internal motor representations corresponding to the observed action, the observer automatically grasps the meaning of that action *as if* performing the action.

One way to inform these two theoretical debates is to examine the role of motor representations and processes in comprehension of actions and, within objects, of manipulable artifacts. Motor representations, indeed, are part of the concepts of actions and of manipulable artifacts within the "embodied" theories but not within the "amodal" theories of concepts. In addition, motor representations play a role in action comprehension according to motor simulation theories of action comprehension, but not

within the traditional view in cognitive psychology. The research carried out in this thesis aimed at gathering evidence pertaining to this question.

To date, this question has been mainly addressed with functional brain imaging studies. As a whole, these studies have provided robust evidence that different parts of the motor system are activated when we view actions and manipulable objects or merely read words denoting them. This has been claimed to support the embodied theories of concepts and/or the motor simulation theories of action comprehension. However, functional brain imaging can reveal activity in regions that are not *causally* involved in a task. Therefore, these studies lend *plausibility* to the hypothesis that motor representations support comprehension but are not direct evidence for that hypothesis. In this thesis, we used the empirical paradigm of the single case study in cognitive neuropsychology in an attempt to overcome this limitation of functional brain imaging. In particular, we examined the performance of brain-damaged patients presenting with conceptual, praxic, or motor disorders and of an individual presenting with atypical motor development due to upper limb aplasia, in various tasks involving the identification and comprehension of actions and manipulable artifacts. Under the hypothesis that motor representations play a role in comprehension of actions and/or manipulable artifacts, loss or absence of motor representations should prevent or at least hamper their comprehension.

1. PRELIMINARY DEFINITIONS

At the outset of this thesis, it is important to explain what we mean by "the role of motor representations and processes in the comprehension of actions and objects".

The term "object" will refer hereafter to "concrete entities", with the exception of humans, which include man-made objects, or artifacts. Unless otherwise indicated, by "manipulable artifacts" we refer to artifacts which (1) can be picked up and moved with

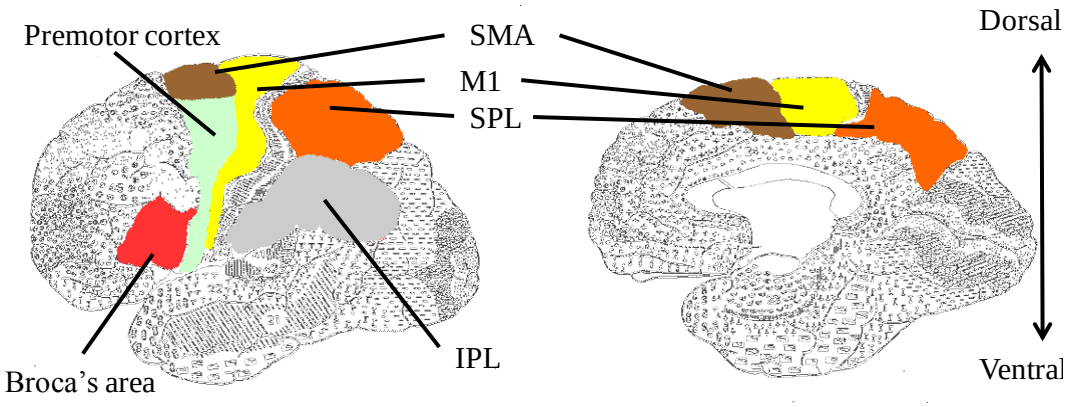
one or both hands and (2) are associated with a specific hand action involving either grasping the artifact to use it as a tool or manipulating it in order to achieve a result (Saccuman et al., 2006). The term "action", however, is more polysemous and has so far been used in different frameworks and perspectives in which it has referred to different levels of description of human activities, ranging from elementary motor acts such as "reaching", "turning the forearm", and "opening the hand" to large sequences of human activities composing events such as "going to the restaurant" or "writing a dissertation". In this thesis, the term "action" will refer to a purposeful human behavior corresponding, in Cooper and Shallice's (2000) framework, to an "intermediate" level of description. This intermediate level, which we will refer to hereafter as "actions", includes a series of activities such as "drinking", "brushing one's teeth", or "imagining". Actions are thus more abstract and flexible than the motor acts that can compose them in the sense that they can be interrupted, and that their kinematic and timing properties are defined only coarsely. In contrast, actions are more concrete and defined in time and local physics than are the scripts that they compose (Schank & Abelson, 1977).

By "comprehension", we refer to the ability to recognize a sensory input as being an instance of a known category of object or action, and to access conceptual knowledge about it so that we are able, for instance, to name it. Thus, "comprehending" a viewed hammer means being able to categorize this stimulus as an instance of "hammer" and thereby retrieve information pertaining to that category of objects, that is not present in the stimulus, such as its typical weight, location in a house, or what it is used for, its purpose or function. When observing someone who, a hammer at the hand, drives a nail in a wall, "comprehending" this stimulus refers to the ability to recognize this action as an instance of the action "hammering" and retrieve hidden features about that category of action such as its approximate duration, energy, noise and so on, so that we are able to

name it. Throughout this thesis, this ability was tested with naming tasks, word/picture verification tasks, word/picture matching tasks, and tasks that require the explicit retrieval of knowledge about objects and actions such as their function or what they look like. Thus, to be clear, by "comprehending an action", we do not refer to the ability to infer the desires or mental states that lie behind the action of an agent (e.g.,"she wants to embellish his flat" or "she is nervous"; Baker, Saxe, & Tenenbaum, 2009; Dennett, 1987). "Comprehending an action" is also different from being able to judge the "correctness" of an action, that is, to judge whether an observed action is realized with a correct speed of movement, movement amplitude, finger and hand disposition and so forth (e.g., Buxbaum, Kyle, & Menon, 2005).

By "motor representations and processes" we mean representations and processes that are involved in representing, planning, executing, and controlling movements. Motor representations and processes are rooted in the cortical brain system implied in action production, including object manipulation (see Box 1), although the precise role of these different brains areas in representing and processing movements is not clear (e.g., Halsband & Lange, 2006; Johnson-Frey, 2004; Lewis, 2006). "Motor knowledge" will refer, more specifically, to knowledge of motor patterns acquired through motor experience and which give a processing advantage for the execution of actions that the agent has performed before. Hence, as an early child tries to use a hammer, she slowly learns how to grasp the hammer properly and how to coordinate muscles to perform the most efficient movement. This learning includes learning how to coordinate the different limbs, what strength must be applied, how fast the movement must be, how the hammer must be grasped and so on. Motor knowledge refers to all these different kinds of motor information that the child can subsequently quickly access to use the hammer without having to compute it de novo. Such motor knowledge is to be distinguished from

declarative knowledge about how objects must be manipulated or action executed, that does not require motor experience, and is not formulated in a motor format.



Box 1| Main components of the action production system.

Frontal part. M1: Primary motor cortex. It has a somatotopic organization, i.e., muscles of the leg, arm and face are controlled by partially distinct cortical regions (Grafton, Woods, Mazziotta, & Phelps, 1991). It is implied in the final stage of movement execution. **Premotor cortex**. It is generally divided in a dorsal and a ventral part. The dorsal premotor cortex would be mainly involved in the planning and control of sensory-guided movements. The ventral premotor cortex has a rough somatotopic organization (Rizzolatti, Luppino, & Matelli, 1998). It would be involved in planning and making complex, multiple-joint movements. **Broca's area**. Traditionally though as an area devoted to language production, it also activates during grasping and manipulation of tools (e.g., Binkofski et al., 1999; Fadiga & Craighero, 2006). **SMA**: Supplementary motor area. It is implied in the control of internally generated movements, the control of movement sequences and in bimanual coordination. **Parietal part. SPL: S**uperior parietal lobule. It is involved in representing the current position of the limbs relative to one's body. **IPL**: Inferior parietal lobe. It may be involved in the selection of the limb to use for a task at hand, for preparing motor execution (Chaminade, Meltzoff, & Decety, 2005; Goldenberg & Hagmann, 1998), or it could store representations of hand movement gestures associated with object use (Buxbaum et al., 2005).

2. THEORETICAL FRAMEWORK

In this section, we introduce the general theoretical frameworks that have guided our empirical research with a focus on their various assumptions about the role of motor representations and processes in the comprehension of actions and/or manipulable artifacts. *A priori*, motor representations could have three types of roles, which we will

attempt to distinguish in each theoretical construct. First, they could be *necessary* for successful comprehension. Second, they could be *functional without being necessary*. Third, they could be *ancillary*, either because they are parts of the concepts of actions and of manipulable artifacts without being important in their representations, or because they are not part of these concepts at all.

2.1. The amodal view of concepts

Within the amodal view of concepts, motor representations are not parts of concepts and do not support comprehension of manipulable artifacts or actions. When an action, an object, or a word is perceived, comprehension requires two stages of processing/representations. First, the sensory input is processed and matched to an internal modality-specific representation. By modality-specific, it is meant that the representation is built in the same format as that of the sensory input (e.g., a visual representation for a visual input). Numerous models have been proposed to explain how our mind and brain achieves this process of "recognition" (e.g., Giese & Poggio, 2003; Humphreys, Price, & Riddoch, 1999; Marr & Vaina, 1982; Poggio & Edelman, 1990; see for reviews, Giese, 2004; Kourtzi & Connor, 2011; Riesenhuber & Poggio, 2000). One proposal based on neuropsychological evidence assumes that when an object is perceived, visual recognition comprises a number of distinct steps including edge and color extraction, grouping of local image features, segmentation of objects from the background and from other objects that may be present, and building of a view-point independent representation that can be matched onto a "structural description" of previously seen objects–stored in long term memory (Humphreys et al., 1999). In the action domain, a possibility is that an observed action is processed both in terms of a series of displacements in space (via "optic-flow detectors") and in terms of a sequence of

body postures (via a kind of "snapshot" detector) that we can compare with previously seen patterns of body postures and movements stored in the visual system (Giese & Poggio, 2003).

Second, once a modality-specific representation is activated, it provides input to a conceptual system in which it is given meaning. In this conceptual system, concepts are represented as a set of conceptual features or attributes of the object or action (Caramazza, Hillis, Rapp, & Romani, 1990; but see Collins & Loftus, 1975; Collins & Quillian, 1969) stored in an "abstract" or "amodal" format (Caramazza et al., 1990; Caramazza & Shelton, 1998; Quillian, 1969; Pylyshyn, 1984) in heteromodal association cortex (e.g., Rogers et al., 2004). By "amodal", it is meant that the information about the different features or attributes that jointly constitute a concept is represented in a different format and in a different neural network from the representations and neural network that have been involved during perception or action. Thus, the conceptual feature about what a hammer looks like is represented distinctly from the modality-specific representation that is involved in viewing. Modality-specific representations that support perception and action are transformed ("transducted") into another, "abstract", format of information to feed the conceptual system (Pylyshyn, 1984). Different theories may be distinguished as regards to the constraint(s) that determine(s) the *organization* of conceptual knowledge According to the "Organized Unitary Content Hypothesis" (OUCH) conceptual knowledge is represented in a unitary conceptual system whose organization is determined by the strength of association between the various semantic features that compose a concept (Caramazza et al., 1990; Tyler & Moss, 2001). The more often features that compose a concept occur together in the environment, the more they are "associated", and the more they are represented in close proximity in the "semantic space". According to the "Domain-Specific Knowledge Hypothesis" (DSK), distinct

conceptual systems are specialized in representing and processing knowledge about specific categories of objects, those that had a fitness value in human evolution, like animals, plant, conspecifics, and may be tools (Caramazza & Shelton, 1998; Mahon & Caramazza, 2009). In the "Sensory-Functional" hypothesis, the organization of conceptual knowledge is driven by the organization of the sensory systems and is composed of two main semantic sub-systems, one storing "functional" or non-sensory knowledge (e.g., the function and typical location of an object, the habits of an animal, the purpose of an action, associative and encyclopedic knowledge and so on) and the other "visual" or "sensory" knowledge, e.g., knowledge about the visual properties of objects (their shape, parts, color) but also other features such as the taste of fruits and the feel of a plant (Bird, Howard, & Franklin, 2000; Warrington & McCarthy, 1983; Warrington & Shallice, 1984). However, what is important to note is that all these "amodal theories" of concepts share the hypothesis that the format of representation of conceptual knowledge is amodal, *independent* from sensory-motor representations. Thus, in this view, motor representations are not part of concepts.

These two stages of processing and representations are necessary and *sufficient* for achieving comprehension. However, in everyday life, comprehension is often achieved to allow us to communicate and interact with others and our environment. For that purpose, the conceptual system is connected to output modality-specific representations such as phonological representations (for oral naming), orthographical representations (for written naming) and, for manipulable artifacts and actions, the motor representations associated with their use and execution (e.g., Rothi, Heilman, & Ochipa, 1991). It should be noted that in most of amodal views, these stages are not conceived of as discrete and their activation strictly sequential (e.g., Caramazza, 1997; Dell, Schwartz, Martin, Saffran, & Gagnon, 1997; Humphreys et al., 1999; McClelland, 1979; Rumelhart &

McClelland, 1981; but, see Levelt, 1989). Actually, it is generally assumed that information spreads between the different representational levels in a continuous way, so that partial information from one stage begins to feed the next stages before its computation is complete (for review of evidence, see Humphreys et al., 1999; Spivey, Grosjean, & Knoblich, 2005).

2.2. Embodied theories of concepts.

Embodied theories of concepts, in contrast to amodal theories, assume that concepts *are* input and output modality-specific (e.g., auditory, visual, motor) representations anchored in or nearby the sensory-motor systems that were involved in their acquisition (e.g., Allport,1985; Barsalou, 1999, 2008; Martin, 2007; Martin, Ungerleider, & Haxby, 2000; Pulvermüller, 1999, 2005). There is no "transformation" or "transduction" of modality-specific representations to form abstract representations. Therefore, comprehending *is* retrieving (called also "simulating" or "re-enacting") the sensory-motor information associated with an object, an action, or a word. When we perceive a hammer, for instance, retrieving conceptual knowledge about what a hammer is consists in re-activating or "simulating" using it, touching it, seeing it used by others, hearing the sound it makes when it is used and so forth.

Hence, under this theoretical construct, motor representations activated during object use and action production *are parts* of the concepts of manipulable artifacts and actions. Different variants of this general theory may be distinguished, among which we will discuss here only the most popular ones (see for other variants Gallese & Lakoff, 2005; Kiefer & Spitzer, 2001; Patterson, Nestor, & Rogers, 2007). It will be important to note that, in the context of slightly different theoretical articulations, the theories that we will discuss below vary in the role they ascribe to motor representations in

comprehension, on whether actions or only manipulable artifacts are considered, and on which parts of the motor system are thought to store motor representations involved in comprehension.

The modern theoretical articulation of the embodied theories of concepts may be traced back to Allen Allport's (1985) book chapter called "distributed memory, modular subsystems and dysphasia". In this chapter, he proposes a model of the organization of conceptual knowledge called "matrix memory" (see Figure 1) based on three assumptions. First, concepts are represented by activity patterns in "cell assemblies" distributed across a range of what he called "sensory-motor attribute domains" (p. 52). These sensory-motor attribute domains encompass every class of sensory-motor interaction that we can have with our environment, and store knowledge in the "same neural elements" (p. 53) as those that support these sensory-motor interactions. Thus there is a visual domain, an auditory domain, a tactile domain, and so on. There are also motor domains, namely (a) a *kinaesthetic domain*, which stores representations related to object manipulation, and (b) an *action orientated domain* which stores higher-order motor representations, for instance, the sequence of acts involved in the execution of an action. As a consequence, objects and actions which depend differently on the different sensory-motor modalities are represented differently in brain. Thus, to take the same example as Allport (1985), the object *telephone* would be represented by a cell assembly distributed over the different modality-specific cortices involved in the different kinds of interactions that we have with telephones and would include auditory representations, stored in the same neural elements that support the perception of sound, visual representations, stored in the same neural elements as those that are used to perceive the different visual (e.g., shape, color) features of objects and so on (see "telephone" and "clouds" on Figure 1). Second, comprehension of a word, an object, or an action requires a "re-activation" of the

cell assembly which represents the concept. Third, the different "attribute domains" may be selectively impaired by brain damage, thereby preventing access to the knowledge stored in that attribute domain.

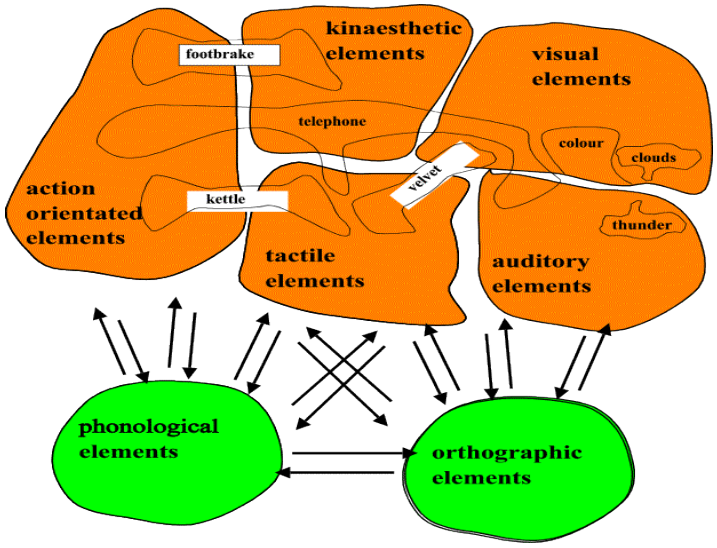


Figure 1| Allport's (1985) "matrix memory"

In green, the stores of orthographic and phonological elements providing input to the attribute domains. In orange, the attribute domains which store knowledge acquired though the corresponding sensory-motor modality. The central idea is that the same neural elements that are involved in coding a sensory-motor attribute constitute the cell assemblies that represent familiar concepts. This figure displays a simplified version of the model. Some attribute domains are not represented (e.g., gustatory or smell elements) and each attribute domain contains several other attribute domains (e.g., for vision: color, shape, movement and so on.). Note the distribution of the concept "telephone" across all domains. Figure adapted from Allport (1985).

A direct consequence of this theoretical construct is that motor representations *are part* of the concepts of actions and artifacts. However, Allport (1985) assumes that damage to a particular attribute domain should not impair object concepts that are "distributed over many different attribute domains and, hence, over widely dispersed regions so that they are not very vulnerable to focal brain injury" (p. 54). Thus, one could

say that, in this view, motor representations are parts of the concepts of actions and manipulable artifacts but *ancillary* to efficient comprehension.

Alex Martin (Martin, 1998, 2007; Martin & Chao, 2001; Martin et al., 2000) proposed a closely similar framework, that he labeled the "sensory-motor theory" (Martin, 1998), of how *object* concepts are organized and represented in mind and brain. The core of this theory is the same as that of Allport's "matrix memory" hypothesis. First, conceptual knowledge is represented in different modality-specific subsystems. Thus, Martin et al. (2000, p. 1023) wrote "the semantic representation of an object is composed of stored information about the features and attributes defining that object, including its typical form, color, motion, and the motor movements associated with its use [..]. Within this network the features that define an object are stored close to the primary sensory and motor areas that were active when information about that object was acquired". Second, these modality-specific subsystems are dissociable from one another. A main difference from Allport's view, however, emerged from Martin's attempt to account for how focal brain damage may cause conceptual category-specific deficits, i.e., selective or disproportionate impairments of conceptual knowledge related to one category of objects (see for review, Capitani, Laiacona, Mahon, & Caramazza, 2003). To this aim, he added to Allport's (1985) theory the "differential weighting hypothesis" (borrowed from Warrington & McCarthy, 1987). According to this hypothesis, some types of modality-specific information have a particularly high discriminatory value for identifying certain categories of objects, like visual information for animals or motor information for tools (for a critique of this assumption see Caramazza & Shelton, 1998). Thus, Martin et al. (2000) proposed:

> The central idea is that we need to utilize information about relatively subtle differences in visual form to distinguish one four-legged animal from another.

> We know animals, and we distinguish among them by their physical features-primarily shape and, to a lesser extent, color and pattern (consider, for example, the difference between a leopard, a tiger, and a jaguar, or between a horse, a donkey, and a zebra). But tools are different. […] identifying individual tools is dependent on accessing information about object-associated patterns of visual motion, stored in the posterior region of the left middle temporal gyrus, and accessing information about object-associated patterns of motor movements stored in left premotor cortex. (p. 1027 – 1028).

A direct consequence of this modification is that motor representations are not only part of the concepts of manipulable artifacts, but they are also important for their identification/comprehension. In Martin et al. (2000), for instance, identifying tools is claimed to be *dependent* on the ability to retrieve object-associated patterns of motor movements stored in the left premotor cortex. What *dependent* means is not very clear, but Martin et al. (2000) illustrate this claim by referring to patients who are unable (high error rate) to name and comprehend artifacts after premotor lesions, which suggests that by "dependent" they mean "*necessary*". Note that in subsequent formulations of that theory, the brain areas storing "use-associated motor skills of man-made manipulable objects such as common tools" also comprised the left intra-parietal sulcus (Martin, 2007).

Another theory of "embodied" object and action concepts has been put forward by Pulvermüller (1999, 2005; see Figure 2). His theory is based on the principle of Hebbian learning and the idea that "the entire cortex is associative and that neurons that are often activated simultaneously will make up cell assemblies representing concepts" (Pulvermüller, 1999, p. 253). Thus, if an object is frequently perceived, a set of neurons

in the *primary and higher order* visual cortices will become active at the same time and form a cell assembly that represents the shape of the object. If the word corresponding to the object is heard at the same time, the cell assembly representing that object will also include neurons in the auditory cortex. If a motor behavior co-occurs because the object is used or an action executed, the cell assembly will include neurons in both motor and sensory cortices and so on. Hence, the localization of the conceptual representation of an object or action is a function of where in the cortex activity occurred simultaneously during past sensory and/or motor experience with that object or action. To this point, there is no main difference from Allport's (1985) view. The main difference is that according to Pulvermüller (1999, 2005), a cell assembly requires, to be functional, the integrity of all its parts. Hence, there is a shift from a view of the conceptual system in term of a set of dissociable modality-specific subsystems (Allport, 1985; Martin, 2007; Martin et al., 2000) to a view of a distributed but unitary functional system of modality-specific representations.

In Pulvermüller's (1999, 2005) view, motor representations are thus *necessary* for the comprehension of actions and manipulable man-made objects. Pulvermüller (2005, p. 581), for instance, wrote "grounding of language in action is essential, as comprehension of action-related language and concepts is impaired after lesions of the motor system. […]Tool words, for example, relate to actions for which the tools are made, [and] can be understood only because both speaker and listener can relate them to similar motor programs". According to Hebbian learning principle, the parts of the brain assumed to store motor representations required for comprehension are those involved in the actual execution or use of each particular action and manipulable artifact and includes neurons in the motor, premotor, prefrontal, and parietal cortex. It is predicted, for instance, that disruption of the hand area of the primary motor or premotor cortex will affect

specifically hand-related concepts while the disruption of the leg areas should affect specifically leg related concepts (Cf. Figure 2).

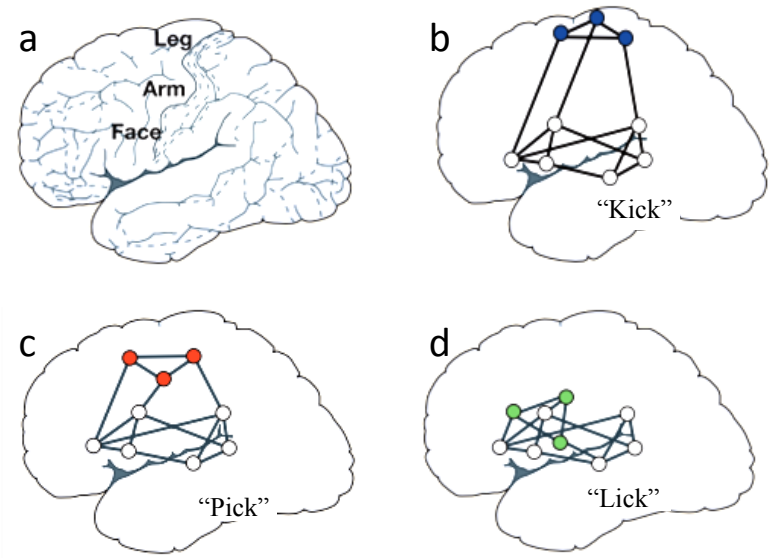


Figure 2| The organisation of conceptual knowledge in the brain according to Pulvermüller (1999; 2005). Illustration.

a : Approximate location of the face/articulators, arm/hand and foot/leg motor representations in the motor and premotor cortex. **b**, **c**, **d :** Distributed cells assemblies of the words « Kick », « Pick », « Lick » and their meaning. Note that, for illustration purpose, only the brain areas implied in auditory word processing, action execution and word production are displayed. The network is also assumed to spread in visual areas involved in action perception, emotional areas involved in processing the emotional content of the actions and so on. Figure adapted from Pulvermüller (1999).

A last popular theory of embodied concepts has been put forward by Barsalou (1999, 2008). His proposal, which is by far the most elaborate model of embodied theories of concepts, relies on three main components: Perceptual Symbols, Simulators and Simulations. Barsalou assumes that patterns of activation induced by sensory-motor experience in sensory-motor areas are stored or "captured" within association brain areas following the principle of Hebbian learning. One stored pattern of activity, in one modality, for one given concept of object ("pen") or action ("hammering") corresponds to

one "Perceptual symbol". Thus, as Barsalou proposed (1999, p. 582) "Perceptual symbols are neural representations in sensory-motor areas of the brain" and (p. 585) "each type of symbol becomes established in its respective brain area. Visual symbols become established in visual areas, auditory symbols in auditory areas, proprioceptive symbols in motor areas, and so forth". During motor experience with a hammer, for instance, different parts of the motor system implied in muscle contraction and coordination, grasping and so on are activated. This pattern of activation across the motor system during motor experience is stored in a "motor" perceptual symbol. Another "visual" perceptual symbol stores the activity in the visual system elicited by the view of hammers. Thus, each object or action concept is composed of several perceptual symbols which role is to control the re-activation (simulation) of the sensory-motor elements that compose a concept during cognitive activities such as comprehension. The several "Perceptual Symbols" that compose a concept are organized into a "Simulator" that controls the re-activation of the perceptual symbols that compose it. This re-activation is a "Simulation".

As Pulvermüller (1999, 2005), Barsalou assumes that, once activated during motor experience, motor representations become necessary for achieving comprehension of actions and manipulable artifacts. As Barsalou (1999, p. 585) wrote, his theory assumes that "When a sensory-motor area is damaged, categories [of concepts] that rely on it during the processing of perceived instances exhibit deficits in conceptual processing. […] For example, damage to visual areas disrupts the conceptual processing of categories specified by visual features (e.g., birds). Analogously, damage to motor and somatosensory areas disrupts the conceptual processing of categories specified by motor and somatosensory features (e.g., tools)". Brain areas storing motor representations ("a representation of the actions that the agent performs") are assumed to be the premotor and

parietal areas, but Barsalou also cite evidence that TMS on the primary motor cortex interfere with the processing of action words, in support of his theory (Pulvermüller, Hauk, Nikulin, & Ilmoniemi, 2005).

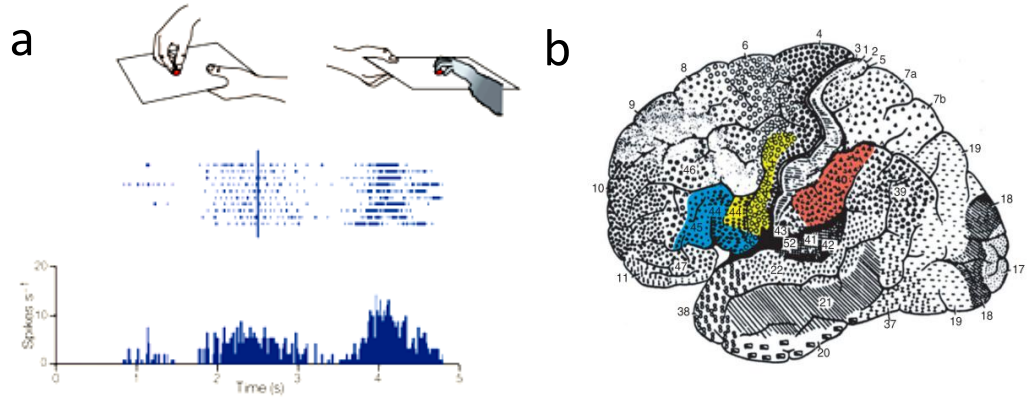
2.3. Motor simulation theories of action comprehension

In contrast to embodied theories of concepts, "motor simulation" theories of action comprehension (Blackemore & Decety, 2001; Jeannerod, 2001, 2005; Rizzolatti & Craighero, 2004; Rizzolatti, Fogassi & Gallese, 2001) are not theories about the organization and representation of conceptual knowledge. Rather these are theories about how the brain achieves action comprehension, based on the general idea of "knowing by simulated doing" (Schwartz & Black, 1999), which origin may be found in James's (1890) and Greenwald's (1970) ideomotor theory. In particular, it is assumed that comprehending an observed action relies on the observer's own motor representations of the same action, i.e., those that she uses when performing that action herself (e.g., Blakemore & Decety, 2001; Jeannerod, 2001, 2005; Rizzolatti et al., 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. Several variants of motor simulation theories may be distinguished.

The most popular theory is the "direct-matching" hypothesis, proposed by Rizzolatti and colleagues after the discovery of "mirror-neurons" in the macaque monkey's brain, i.e., neurons in the areas F5 and PF of the monkey's brain that discharge both when the monkey observes an action and when it performs the same action (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996; see for reviews, Rizzolatti et al., 2001; Rizzolatti & Craighero, 2004). In humans, similar neurons are assumed to

populate (among other purely visual and purely motor neurons) the inferior parietal lobule (corresponding to area PF in monkeys), the ventral premotor cortex and the posterior part of the inferior frontal gyrus (corresponding to area F5 in the monkey's brain), bilaterally (see Box 2). Based on the properties of these neurons, the authors proposed that they constitute a matching system that automatically translates the results of the visual analysis of an observed action into its corresponding motor command in the observer's brain. Thereby, mirror neurons allow action comprehension because the observer knows what she is doing when she performs the same action (Rizzolatti et al., 2001; Rizzolatti & Craighero, 2004).

Thus, in this view, motor representations play a role in the comprehension of observed actions and the brain areas that support the visuo-motor matching are the inferior parietal lobe, the ventral premotor cortex and Broca's area (Rizzolatti & Craighero, 2004; Rizzolatti & Sinigaglia, 2010). This role of motor representations may be defined as "functional", but not necessary. Indeed, action comprehension by direct visuo-motor matching is not the only mechanism available to comprehend actions. Hence, these authors assume that the direct-matching hypothesis "does not exclude the possibility that other, more cognitive processes based on object and movement descriptions could also participate to action comprehension" (Rizzolatti et al., 2001, p. 662). However, the direct visuo-motor matching is the only mechanism "by which the meaning of the acts that are being observed are understood *immediately*" (Rizzolatti & Sinigaglia, 2008, p. 136; emphasis added) or which "allows the observer to understand the actions of others without needing inferential processing" (Rizzolatti & Sinigaglia, 2010, p. 268). Thus, having motor representations onto which a perceived action can be mapped should allow faster and more efficient recognition.



Box 2| Mirror Neurons.

Mirror neurons were first described more than one decade ago in the anterior part of the ventral premotor cortex of the macaque monkey. These are visuo-motor neurons which are activated when a monkey performs a hand or mouth goal-directed motor act (e.g., grasping, tearing, biting or manipulating an object) and when the monkey merely sees a conspecific or a human experimenter performing a similar act. (a) Response of a neuron in area F5 of a monkey's brain during the observation of the experimenter's grasping movement, and when the monkey performs the same action. (b) Lateral view of a human cerebral cortex with classical cytoarchitectonic subdivision showing the areas that belong to the mirror system (colored areas). In yellow, the lower part of the precentral gyrus corresponding to the ventral premotor cortex and the posterior part of the pars opercularis (BA 44). In Blue, Anterior part of the pars opercularis (BA44) and pars triangularis (BA45). In red, the supramarginalis gyrus in the inferior parietal lobe (area 40). Figure (a) adapted from Rizzolatti et al. (2001) and (b) from Fogassi and Ferrari (2010).

In another motor simulation theory (Blakemore & Decety, 2001), action comprehension uses a mechanism labeled the "forward model" that we use to predict the sensory consequences of our own actions (Wolpert, Miall, & Kawato, 1998). When we perform actions, an intention to act (e.g., waving goodbye) is converted in a forward model that generates predictions about the expected sensory consequences of that action, which is then compared with the sensory consequence of the actual action and serves to control it. The hypothesis is that the same mechanism could be used to comprehend the

actions performed by others if used in the reverse direction. When we observe someone waving goodbye, the visual perception of her hand movements activates in the observer's brain the forward model associated with the same movements which can then be used in the reverse direction to estimate the motor command and, then, the intention that we have when we perform the same movement.

It is hypothesized that retrieving the motor representations of our own actions make it possible to estimate what the person's intention is (e.g., "waving goodbye"), which cannot be read directly from their motor movements. Therefore, motor representations are *necessary* to comprehend others' actions. The forward model is stored in the cerebellum but which exact part of the motor system store motor representations of one's own actions is unknown.

According to Jeannerod's (2001, 2005) view, action comprehension relies on a neural simulation of the action, that he calls an "S-state" (for "Simulation-state") and "which includes the goal of the action, the means to reach it, and its consequences on the organism and the external world" (Jeannerod, 2001, p. 103). The neural simulation of action activated by action observation engages the same regions as those activated by action execution and action imagination. It is assumed that "the motor cortex is part of this network, which also includes cortical areas located in the superior and inferior parietal lobules, the ventral premotor cortex, and the supplementary motor area (SMA)" (Jeannerod, 2005, p. 249). In this theoretical construct, neural simulation of an observed action allows comprehending others' actions by activating "in the observer's brain, the same mechanisms that would be activated, were that action intended or imagined by the observer". It is claimed that, when an action is observed "the simulation must provide a frame to the perception of the action: the observer understands the action she sees to the extant she can simulate it […] A mere observation without activation of the motor system

would only provide a description of the visible aspects of the movements of the agent, but it would not give precise information about the intrinsic components of the observed action which are critical for understanding what the action is about, what its goal is, and how to reproduce it" (Jeannerod, 2005, p. 250).

In this theory, it is hypothesized that neural simulation of action is *necessary* for action comprehension. The brain regions that support neural simulation during observation of actions correspond to the brain regions that are also involved in action production. However, the overlap between action production and observation is not complete and some brain areas are assumed to be specifically involved in action production, such as the cingular gyrus (BA 24) and the superior frontal gyrus (BA 10). Moreover, even within the shared brain regions, Jeannerod hypothesizes that some neuron populations may be specific to action production and constitute "cues for attributing the actions to the self or to another" (Jeannerod, 2005, p. 246).

2.4. Interim summary

The theoretical space to which we will refer in this thesis involves three main positions. According to the amodal view, motor representations are not part of the concepts of actions or manipulable artifacts and they do not support the comprehension of observed actions. In contrast, both "embodied theories" of concepts and "motor simulation" theories of action comprehension share the assumption that motor representations are involved in comprehension of actions (Rizzolatti & Craighero, 2004; Rizzolatti et al., 2001; Jeannerod, 2001; Blakemore & Decety, 2001), manipulable artifacts (Martin, 2007; Martin et al., 2000), or both (Barsalou, 1999, 2008; Pulvermüller, 1999, 2005).

3. EMPIRICAL EVIDENCE

In this section, we summarize the available evidence on the role of motor representations and processes in comprehension. Evidence was provided by means of functional brain imaging, behavioral experiments, transcranial magnetic stimulation, and neuropsychological group or single case studies. One way to organize this set of empirical evidence is to separate evidence from studies aiming at describing and characterizing the motor cortical activity elicited by the perception and processing of manipulable artifacts and actions (or by words that refer to them) from evidence from studies assessing the consequences of transient or permanent damage to different parts of the motor system. This brief review will allow us to delineate the hypothesis space that we addressed in this thesis.

3.1. Characterizing motor cortical activity during the processing of actions and manipulable artifacts

During the last 15 years, a considerable number of studies that have used a variety of methods such as fMRI, PET, single pulse TMS combined with electromyography, behavioral studies, MEG and ERPs studies (see Box 3) have gathered numerous data pertaining to the question whether, how, and when motor areas of the brain are activated when manipulable artifacts, actions or words that refer to them are perceived and processed in different tasks.

Although differences emerged across studies on the exact regions that were involved (e.g., Caspers, Zilles, Laird, & Eickoff, 2010), their lateralization (e.g., Hauk & Pulvermüller, 2011), or possible influence of the task (e.g., Kellenbach, Brett, & Patterson, 2003), seven main empirical generalizations can be drawn from available evidence:

Box 3| Methods.

Methods for studying brain activity.

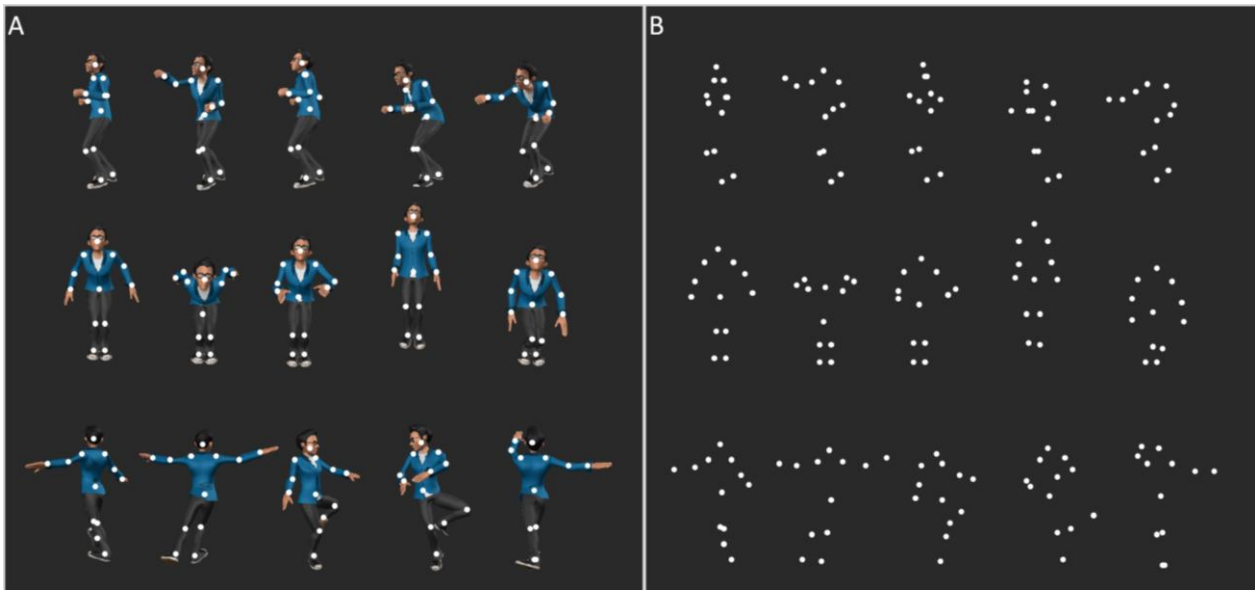
Functional magnetic resonance imaging (fMRI) and *Positron Emission Tomography* (PET) are methods for studying changes in blood flow. Increase and decrease of blood flow correlate with neuronal activity (Logothetis, Pauls, Augath, Trinath, & Oeltermann, 2001). Thus, these methods allow localizing brain regions in which neuronal activity change in reaction to a given task or type of item. They are characterized by a high spatial resolution (millimeters) but have a relatively poor timing resolution (several seconds). *Evoked Response Potentials* (ERPs) and *Magnetoencephalography* (MEG) are direct measures of brain activity and have a very precise temporal resolution (millisecond) but a poor spatial resolution (several centimeters). In *Transcranial Magnetic Stimulation* (TMS), a stimulating coil is held over the head of a participant and a pulse of current flowing through the coil generates a magnetic field that passes through the subject's scalp and causes neurons of the site of stimulation to depolarize. If used on the primary motor cortex, this produces muscle activity that is referred to as a Motor Evoked Potential (MEP) that can be recorded by electromyography. Changes in the MEP evoked by a given intensity of TMS disclose the activity level of the underlying neurons.

Methods for inducing transient lesion.

TMS is also used to transiently disrupt the function of a given cortical area, by creating a « virtual brain lesion ». It can be applied as single pulses delivered at a certain time (Single pulse TMS) or in trains or repetitive pulses at a given intentisy and frequency (repetitive TMS, rTMS). As compared to single pulse TMS, rTMS produces longer-lasting effect and can increase or decrease the neuronal activity depending on intensity and frequency of stimulation.

(1) Processing manipulable artifacts or words that refer to them activates the left premotor cortex and the left inferior parietal lobe. In an fMRI study Chao and Martin (2000) found that viewing and naming tools elicits more activation in the left ventral premotor cortex and inferior parietal cortex than viewing faces, animals, or vehicles. This pattern of tool-preferential activation is now corroborated by a large number of studies using different methods (fMRI or PET) or kinds of stimuli modality (e.g., sounds, pictures, or written words) (Devlin et al., 2002; Gerlach, Lau, Gade, & Paulson, 2000; Gerlach, Lau, & Paulson, 2002; Grabowski, Damasio, & Damasio, 1998; Grèzes &

Decety, 2002; Grèzes, Armony, Rowe, & Passingham, 2003; Grafton, Fadiga, Arbib, & Rizzolatti, 1997; Kraut, Moo, Segal, & Hart, 2002; Martin, Wiggs, Ungerleider, & Haxby, 1996; Mecklinger, Gruenewald, Besson, Magnié, & von Cramon, 2002; for reviews, see Martin, 2007, Lewis, 2006, Johnson-Frey, 2004, and Culham & Valyear, 2006).



Box 4| Point-Light Displays: Illustration

In PLAs, the actor is portrayed by 12 dots originally attached to his head and the main joints of his body during the recording session (A). Information contained in the stimulus is therefore reduced to the displacement of these dots during action execution (B).

(2) Processing actions or words that refer to them activates the premotor cortex and the inferior parietal lobe. Functional brain imaging studies consistently report activation in the premotor and inferior parietal cortex during the processing of actions concepts in a great variety of tasks (e.g, naming tasks, similarity judgment tasks, reading tasks) and with a series of different stimuli such as video clips of actions (Buccino et al., 2001), actions depicted by a few light dots originally placed on the actor's main joints, i.e., point-light displays (see Box 4; Saygin, 2007; Saygin, Wilson, Hagler, Bates, & Sereno,

2004), static pictures of actions (Urgesi, Moro, Candidi, & Aglioti, 2006), sounds of actions (Aziz-Zadeh, Iacoboni, Zaidel, Wilson, & Mazziotta, 2004; Lewis, Brefczynski, Phinney, Janik, & DeYoe, 2005; Gazzola, Aziz-Zadeh, & Keysers, 2006; Caetano, Jousmäki, & Hari, 2007) and action verbs or sentences (see for reviews, Willems & Haggort, 2007; Pulvermüller, 2005; Fischer & Zwaan, 2008).

(3) Action observation also activates Broca's area and the superior parietal lobe. In addition to the brain areas common to action observation and action word processing, the observation of actions also activates the posterior inferior frontal gyrus in the location of Broca's area (e.g., Buccino et al., 2001; Decety et al., 1997) and the superior parietal lobe (e.g., Montgomery, Isenberg, & Haxby, 2007). Figure 3 illustrates the results of Caspers et al.'s (2010) meta-analysis of the studies reporting on the coordinates of brain activation elicited by action observation.

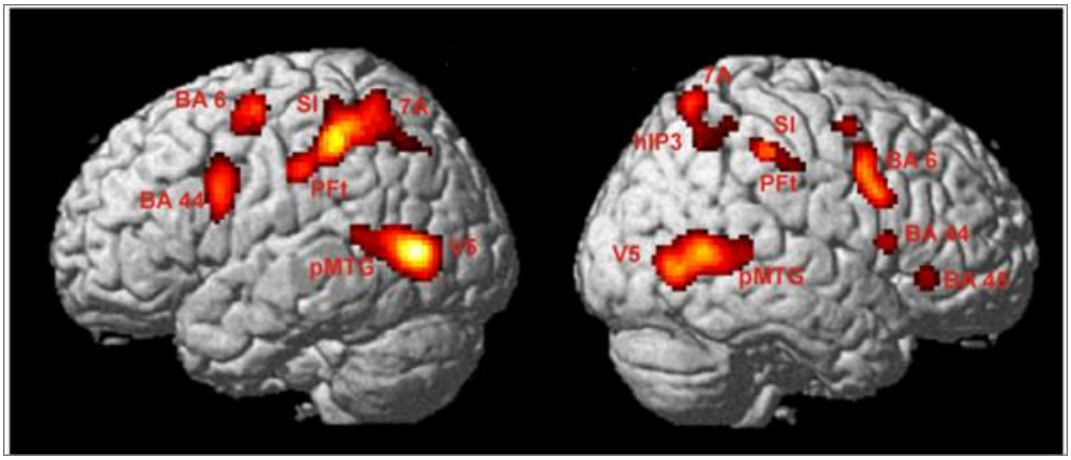


Figure 3| Cortical areas activated by the observation of hand actions.

Cortical areas activated by the observation of hand actions from a meta-analysis of 67 functional brain imaging studies (fMRI and PET) that have assessed the human brain network underlying action observation. The results show a bilateral network composed of the premotor cortex (BA6), Broca's area (BA 44 and 45), inferior parietal lobe (Area PF), superior parietal lobe (BA7), and the posterior middle temporal gyrus (pMTG). Figure adapted from Caspers et al. (2010).

(4) Motor activation during action observation is modulated by motor experience. It has been shown that manual preference in object manipulation influences the laterality of IPL and PM activation caused by the viewing of tools (Kan, Kable, Van Scoyoc, Chatterjee, & Thompson-Schill, 2006; Lewis, Phinney, Brefczynski, & DeYoe, 2006). Also, the brain activity in the same network increases for the view of the same object after manipulation training (Kiefer, Sim, Liebich, Hauk, & Tanaka, 2007; Weisberg, van Turennout, & Martin, 2007) and it is greater when objects associated with extensive motor experience (door knobs) are viewed in comparison to comparably manipulable artifacts with no self-reported motor experience (artificial rock climbing holds; Handy et al., 2006). As regards actions, it has been shown that viewing dance movements that the observer is used to performing activates more the intra-parietal sulcus and the premotor cortex than dance movements that she is not use to performing (Calvo-Merino, Glaser, Grèzes, Passingham, & Haggard, 2005) or that she is only used to seeing (Calvo-Merino, Grèzes, Glaser, Passingham, & Haggard, 2006).

(5) Motor activation during action observation is finely tuned to motor involvement during actual execution. Using fMRI, it has been found that viewing someone chewing, grasping a cup with the hand, or kicking a ball with the foot, activates in the observer's premotor cortex and parietal lobe the same specific neural circuits that plans or execute mouth, hand, or feet actions, respectively (Buccino et al., 2001; Figure 4). Similar somatotopic activation has been reported in other studies also using visually-presented actions (Wheaton, Thompson, Syngeniotis, Abbott, & Puce, 2004; Sakreida, Shubotz, Wolfensteller, & von Cramon, 2005; see the meta-analysis by Van Overwalle & Baetens, 2009) or stimuli like action sounds (Gazzola, Aziz-Zadeh, & Keysers, 2006) or written verbs (Hauk, Johnsrude, & Pulvermüller, 2004) or written sentences (Tettamanti et al.,

2005; see also Aziz-Zadeh, Wilson, Rizzolatti, & Iacoboni, 2006) that participants had to read. Even more specific coupling was found in studies using transcranial magnetic stimulation (TMS) and electromyography (EMG). In particular, it was found that when the left motor cortex of a participant was stimulated while she observed hand actions, motor evoked potentials recorded from right hand muscles showed 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, Bucchioni, & Castiello, 2012).

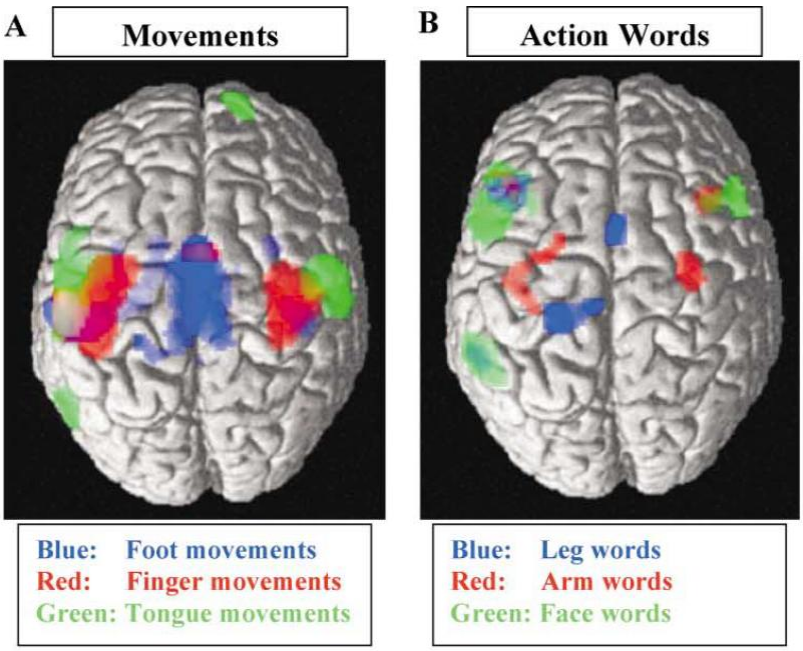


Figure 4| Somatotopic activation of the premotor cortex during action execution and action words processing.

A : Somatotopic activation of the premotor cortex during the execution of foot (blue), finger (red) and tongue (green) movements. During the scanning, the participants were asked to move each body part four times during 21 seconds. **B:** Somatotopic activation of the premotor cortex during the reading of leg (blue), arm (red) and face (green) words. During the scanning, the participants were presented to 50 words for each category and 150 other « neutral » words. The baseline were strings of meaningless hash marks matched in leght with the words. Brain areas activated by the words were directly adjacent to or overlapped with the brain areas activated by actual movement. Figure adapted from Hauk et al. (2004).

(6) Processing manipulable artifacts, actions, or words that refer to them influences action production. It has been found that passively viewing a manipulable artifact (Glover, Rosenbaum, Graham, & Dixon, 2004; Bub, Masson, & Cree, 2008; Bub, Masson, & Bukach, 2003; Tucker & Ellis, 1998, 2001), the movement of a body part (Brass, Bekkering, & Prinz, 2001; Kilner, Paulignan, & Blakemore, 2003; see for review Wilson & Knoblich, 2005), or a written word that refers to an action or a manipulable artifact (Boulenger et al., 2006; Bub et al., 2008) influences the participants' movement production abilities. Bub and colleagues (2008), for instance, asked participants to perform a specific grasping gesture as fast as possible after a visually-presented "go-signal". The go-signal could be a word or a picture and these could refer to a manipulable artifact that is usually grasped in a way that is congruent with the grasping gesture they had to perform, or to a manipulable artifact that is incongruent with it. While the identity of the artifact presented on the screen as go-signal was irrelevant for the task, participants were faster to perform the target grasping gesture when the go-signal was congruent with that gesture than when it was not.

*(7) The activation of the motor system is fast***.** There is now considerable evidence that reading or hearing an action word activates the premotor cortex about 200-250 msec after word onset time (see for review, Hauk, Shtyrov, & Pulvermüller, 2008). Hauk and Pulvermüller (2004), for instance, have recorded ERPs during silent reading of face-, arm-, and leg-related action words and showed effector specific differential activity in the premotor already at about 200 msec after word onset. Pulvermüller et al. (Pulvermüller, Shtyrov, & Ilmoniemi, 2005; Shtyrov, Hauk, & Pulvermüller, 2004) have also found similar results between 170 and 200 msec using MEG while participants listened to face and leg-related action words. Boulenger et al. (2006) observed that the reading of an

action verb influences the kinematic of the execution of an action as soon as 200 msec after the onset of the word. There is also evidence that viewing an action activates the motor cortex very rapidly (see for review, Hauk et al., 2008). In one of these studies (Gangitano, Mottaghy, & Pascual-Leone, 2001), TMS was used to stimulate the left primary motor cortex and recorded the MEPs in the contro-lateral hand muscle while participants were viewing a hand grasping a ball. TMS pulse was delivered at five different times, corresponding to different phases of finger aperture. They found that MEPs amplitudes in the observer hand muscle correlated positively with the finger aperture of the observed hand at the time of the pulse, thereby demonstrating that modification of activations in an observer's primary motor cortex is very fast during the observation of actions (Gangitano et al., 2001; see also Gangitano, Mottaghy, & Pascual-Leone, 2004).

Taken all together, these observations are compatible with the prediction of the embodied view of concepts: actions, manipulable artifacts, and the words that refer to them activate motor brain areas. Motor simulation theories of action comprehension are also supported by these data since action observation activates parts of the motor cortex that are similar to those implied in action production. Accordingly, these results have been widely interpreted as evidence in favor of these theories. However, if these observations support the view that the motor system could be implied in comprehension, they do not indicate whether motor activation supports comprehension or, in other words, whether motor representations are part of the concepts of manipulable artifacts and actions.

Several non-mutually exclusive alternative interpretations can be advanced. One possibility is that motor activation indeed reflects the retrieval of motor representations,

but this retrieval *follows* rather than precedes concept retrieval. Within the amodal view of the processes and representations involved in comprehension, motor representations do not support the comprehension process but their activation is nevertheless very likely to occur automatically from the spreading of activation from the conceptual system to the different output stores of representations that ensure response preparation (cfr. 1.2.1; see for a similar view Mahon & Caramazza, 2008; Hickok, 2010).

It has been objected that the activation of the motor system is so fast that it cannot follow comprehension (Pulvermüller, 2005). However, if this objection holds for theories assuming that the activation of the different stages of processing is strictly sequential (e.g., Levelt, 1989), it does not for theories assuming that partial information from one stage may feed the next before its computation is complete (e.g., Caramazza, 1997; Dell et al., 1997; Humphreys et al., 1999; McClelland, 1979; Rumelhart & McClelland, 1981). In these theories, indeed, during written and spoken word recognition, a word can activate several close coordinated concepts and, before selection is achieved, the partly-activated concepts already send information to the output systems, thereby activating phonological and orthographical representations implied in naming and motor representations involved in action production.

In addition, as far as visual stimuli are concerned, motor activation could reflect processes that operate in parallel to conceptual processing but are independent from it, such as automatic activation of motor representations from the structural description of visually-presented artifacts (e.g., Rumiati & Humphreys, 1998), visuo-motor 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).

The retrieval of motor representations can also reflect a conscious or unconscious process of 'motor imagery', which could be useful for performing some tasks, such as tasks requiring to retrieve explicitly knowledge about how actions and manipulable objects must be manipulated (Mahon & Caramazza, 2008; see for a more general discussion Machery, 2007). It is remarkable that the same areas found for manipulable artifacts and action (word) processing have also consistently been observed during voluntary and involuntary motor imagery (Jeannerod & Frack, 1999).

Finally, activation of motor representations may rely on a mere "Pavlovian" association (Mahon & Caramazza, 2008). Catmur, Walsh, and Heyes (2007) reported evidence that supports this hypothesis. In a first phase, they applied TMS on participants' primary motor cortex and recorded MEPs in their little finger and index while they viewed little finger and index movements. They found that watching index movements augmented the index MEPs and that watching little finger movements augmented little finger MEPs. In a second phase, they trained their participants to make movements with their index when they viewed movements made with the little finger, and to make movements with their little finger when they viewed movements performed with the index. The third phase was similar to the first one. However, the relationship between the observed finger movements and the MEPs observed in the first phase was reversed. Thus, after training, watching index movements augmented the MEPs recorded in the little finger and vice-versa.

In sum, while these studies have provided a great amount of evidence that is consistent with the notion that motor representations play a role in comprehension, they do not provide evidence for a causal relation between motor activation and concept retrieval. Therefore, they do not provide relevant evidence to decide between amodal and embodied views of concepts or motor simulation theories of action comprehension.

3.2. Lesion studies

A way to decide between these theories is to test the prediction, put forward by the different theories which attributes a role to motor representations in comprehension, that a lesion (virtual or real) to parts of the motor system should impair comprehension of actions and of manipulable artifacts.

3.2.1. Transient lesions evoked by TMS

A first way to test these predictions is to use TMS to create a transient "virtual brain lesion" (see Box 3; Pascual-Leone, Bartes-Faz, & Keenan, 1999; Walsh & Rushworth, 1999) in different parts of the motor system held to contribute to comprehension. To date, three main types of studies have been carried out: (1) studies testing the role of primary motor and premotor cortex in action word processing; (2) studies testing the role of the premotor cortex and Broca's area in the processing of observed actions; (3) studies testing the role of the inferior parietal lobe on retrieving manipulation knowledge about tools.

The studies assessing the role of the primary motor and premotor cortex in action word processing led to very mixed and ambiguous results. In a study by Gerfo et al. (2008), participants were asked to perform lexical morphological transformations. Stimulus material included state nouns (i.e., nouns referring to abstract concepts; e.g., the beauty), action nouns (i.e., nouns referring to manipulable objects; e.g., the pen), state verbs (e.g., to doubt) and action verbs (e.g., to clap). Participants were first presented with a noun in singular form or a verb in the first singular person and then with a cue indicating the morphological form in which the word was to be produced aloud. Nouns could be produced at the plural or singular form and verbs at the first singular or third singular form. Participants performed the task before (baseline) and after 10 minutes of rTMS trains applied on the left primary motor cortex. The authors found *slower* response

latencies for action nouns and verbs, but not for state nouns and verbs, after rTMS. However, in a lexical decision task with action-related words and pseudowords, Pulvermüller et al. (2005) found *faster* response latencies after TMS on the primary motor cortex. The stimuli were leg/feet-related action words, arm/hand-related action words, and pseudowords, presented for 100 msec. When participants performed the task, single pulse TMS was applied 150 msec after word onset to the left or right leg/feet or arm/hand area of the primary motor cortex. The authors found *faster* response latencies for leg/feet-related action words after left leg/feet stimulation than left arm/hand stimulation. However, no significant effect of the left stimulation site was observed for arm/hand-related action words and no interaction between stimulation site and type of word was found after right stimulation. In another study, Willems and colleagues (Willems, Labruna, D'Esposito, Ivry, & Casasanto, 2011) also found faster response latencies in a lexical decision task for action verbs, but not for abstract verbs, after rTMS on the left than on the right premotor cortex. Several other studies found no significant effect of TMS on the processing of action words. Papeo et al. (Papeo, Vallesi, Isaja, & Rumiati, 2009) found no evidence for an influence of TMS applied on the hand area of the primary motor cortex in tasks requiring to count the number of syllables of action verbs or to judge whether a verb refers to an action (e.g., to clap) or a mental state (e.g., to believe). Tomasino et al. (Tomasino, Fink, Sparing, Dafotakis, & Weiss, 2008) found that TMS applied to the hand area of the primary motor cortex facilitates (faster RLs) the processing of action verbs in a task requiring motor imagery (from the verb, imagine yourself performing the action. Does it require a hand rotation? Yes/no), but did not find any effect of TMS when participants had to judge the frequency of a word (Is this a word you would frequently read in newspapers? Yes/No), or to silently read a word (Silently read the verb and press the button when you are done).

In sum, the available evidence as to whether the primary motor and the premotor cortices play a role in the processing of action words is confusing and contradictory. Some — but not all — studies found an effect of the TMS on action word processing and, among the studies that reported an effect of the TMS, this effect went in opposite directions.

Another set of studies assessed the effect of TMS on the processing of visually-presented body movements (van Kemenade et al., 2012; Pobric & Hamilton, 2006) or the processing of pictures of body postures (Candidi, Urgesi, Ionta, & Aglioti, 2008; Urgesi, Calvo-Merino, Haggard, & Aglioti, 2007; Urgesi, Candidi, Ionta, & Aglioti, 2007). In Urgesi, Candidi et al.'s (2007) study, participants were presented the picture of a body posture (probe) followed by a mask (500 msec) and then the same picture (target) and a different one (foil). They had to decide as fast as possible which picture matched the probe. Foils could be either a different actor adopting the same body posture or the same actor adopting a slightly different posture. During the presentation of the mask, two TMS pulses were applied separated by a 150 msec interval. TMS was applied on the left or on the right ventral premotor cortex or extrastriate body area (EBA). The authors found that TMS on the bilateral premotor cortex, in comparison to EBA, specifically increased the response latency when the foil was the same actor adopting a different body posture. In vanKemenade et al. (2012), participants had to discriminate point-light displays of human actions from "scrambled" versions of the same stimulus, or geometrical forms (e.g., a diamond) from their scrambled versions. These stimuli were presented within a mask composed of a variable number of "noise" dots of the same size and color as the dots composing the stimuli. Before the task, participants received rTMS on the premotor cortex, the posterior part of the superior temporal sulcus, or a control site (vertex). The authors found that rTMS on the premotor cortex, but not on the other stimulation sites,

increased specifically the rate of false-alarms in the task requiring to discriminate point-light displays of human actions from their "scrambled" versions. Pobric and Hamilton (2006) presented their participants with video clips displaying either a hand lifting a box and placing it on a shelf, or a ball falling from the top of the screen and bouncing. Participants were asked to judge on a five-point scale either (1) the weight of the box, (2) the weight of the ball or (3) the amount of time the hand was visible on the screen in the box lifting video clips. During each video clip, participants received rTMS on the inferior frontal gyrus (Broca's area) or a control site. rTMS affected significantly and specifically participants' estimation of the weight of the boxes.

In sum, the available evidence suggests that a virtual lesion of the premotor cortex or of the inferior frontal gyrus (Broca's area) interferes with participants' performance in tasks involving the recognition of body postures (Urgesi, Candidi et al., 2007), the sensitivity to PL actions in a detection task (vanKemenade et al., 2012) and the fine-grained analysis of an actor's arm movements (Pobric & Hamilton, 2006). However, none of these tasks required to retrieve conceptual knowledge about the actions. It is thus not obvious whether they are relevant to the question of the role of motor representations in comprehension of actions. Furthermore, it is important to note that performance in these tasks may be altered due to TMS interfering with task-specific representations or processes, that is, representations and processes not involved in action comprehension. TMS on the vPM, for instance, could affect the maintenance of a body posture in working memory (Urgesi, Candidi et al., 2007; see also Wilson, 2001) or decision-making processes related to biological motion (vanKemenade et al., 2012). The IFG could also play a role in processing fine-grained kinematics of body movements that are not directly relevant to comprehend observed actions in everyday life.

Finally, three studies have shown that rTMS applied on the inferior parietal gyrus interferes with the performance of participants when they have to explicitly retrieve knowledge about how tools are manipulated, but not when they have to retrieve knowledge about their usual context of use or their function (Andres, Pelgrims, & Olivier, in press; Ishibashi, Lambon Ralph, Saito, & Pobric, 2011; Pelgrims, Olivier, & Andres, 2011). These results are at variance with the embodied view of concepts claiming that motor representations play a role in retrieving conceptual knowledge about manipulable artifacts (Barsalou, 1999, 2008; Martin, 2007; Martin et al., 2000; Pulvermüller, 1999, 2005).

3.2.2. Studies of patients suffering from motor and praxis disorders

Another way to test the same predictions is to investigate the consequences of damage to parts of the motor system that are assumed to support comprehension of actions and manipulable artifacts. Extant results pertaining are contradictory.

In favor of theories attributing a role to motor representations and processes in the comprehension of actions and manipulable artifacts, several studies have reported brain damaged patients who had action production difficulties *and* difficulties at comprehending and naming actions or manipulable artifacts. Such patients have been reported both in the context of apraxia (Buxbaum et al., 2005; Buxbaum & Saffran, 2002; Negri et al., 2007; Papeo, Negri, Zadini, & Rumiati, 2010; Pazzaglia, Pizzamiglio, Pes, & Aglioti, 2008; Pazzaglia, Smania, Corato, & Aglioti, 2008) and lesions including different parts of the fronto-parieto-subcortical motor system such as the left inferior parietal lobe (CG: Papeo et al., 2010; 6 patients in Pazzaglia, Smania et al., 2008), Broca's area (11 patients in Pazzaglia, Smania et al., 2008) and the left primary motor cortex (ST: Papeo et al., 2010; 14 patients in Pazzaglia, Smania et al., 2008). A similar association of deficit

has also been reported between a motor disorder and greater difficulties at naming or comprehending action verbs in comparison to object nouns in various diseases affecting predominantly the motor system such as Parkinson's Disease, Motor-Neuron Disease, Cortico-Basal Degeneration and Progressive Supra-nuclear Palsy (Albani, Pignatti, & Mauro, 2010; Bak, O'Donovan, Xuereb, Boniface, & Hodges, 2001; Bak & Hodges, 2004; Bak et al., 2006; Bertella et al., 2002; Cotelli et al., 2006; Cotelli et al., 2007; Daniele, Giustolisi, Silveri, Colosimo, & Gainotti, 1994; Daniele et al., 2012; Grossman et al., 2008; Herrera & Cuetos, 2012; Herrera, Rodriguez-Ferreiro, & Cuetos, 2012; Hillis, Oh, & Ken, 2004; Hillis et al., 2006; Hodges & Bak, 1997; Pignatti, Ceriani, Bertella, Mori, & Semenza, 2006; Péran et al., 2003; Rodríguez-Ferreiro, Menéndez, Ribacoba, & Cuetos, 2009; Silveri & Ciccarelli, 2007; Silveri et al., 2012; Spatt, Bak, Bozeat, Patterson, & Hodges, 2002). Nonetheless, there were also reports of patients who had no difficulty with actions and manipulable artifacts in naming or word/picture matching tasks despite damage to the motor system. For instance, several apraxic patients obtained results in the normal range when asked to identify (naming or word/picture matching tasks) manipulable artifacts in the context of lesions affecting many different parts of the motor system such as the left basal ganglia (FS: Negri et al., 2007; NP: Papeo et al., 2010), the left inferior parietal lobe (IN: Papeo et al., 2010; 6 patients in Pazzaglia, Smania et al., 2008), Broca's area (3 patients in Pazzaglia, Smania et al., 2008; DR: Rumiati, Zanini, Vorano & Shallice, 2001) and the left primary motor cortex (4 patients in Pazzaglia, Smania et al., 2008; DR: Rumiati et al., 2001) and the left (FG: Rumiati et al., 2001) or bilateral superior parietal lobule (Rapcsak, Ochipa, Anderson, & Poizner, 1995). Preserved action identification has also been observed in the context of apraxia and lesions to the basal ganglia (FS: Negri et al., 2007; NP: Papeo et al., 2010), the inferior parietal lobe (A9 in Buxbaum et al., 2005; DR: Negri et al., 2007; IN: Papeo et

al., 2010), Broca's area (A9: Buxbaum et al., 2005; ZA: Negri et al., 2007; DR: Rumiati et al., 2001), the left premotor cortex (A9: Buxbaum et al., 2005; ZA and DR: Negri et al., 2007) and the primary motor cortex (DR: Negri et al., 2007; DR: Rumiati et al., 2001) and the left (FG: Rumiati et al., 2001) or bilateral superior parietal lobule (Rapcsak et al., 1995) as well as in the context of lesions described as "left fronto-parietal lesions" (MF: Bartolo, Cubelli, Della Sala, Drei, & Marchetti, 2001).

In sum, some — but not all — individuals with damage to the motor system and impairments in action production are unable to comprehend actions and manipulable artifacts. Although the number of studies reporting on patients with brain damage including the motor system impaired in the comprehension of actions and manipulable artifacts is impressive, the comprehension deficit reported in these studies cannot be ascribed, without ambiguity, to the motor system being damaged. Actually, all these patients had brain damage that included, but was not limited to the motor system. Thus, that action or manipulable artifact comprehension was impaired in these studies does not constitute compelling evidence that the comprehension deficit is *caused* by damage to the motor system (see Shallice, 1988 for a more general discussion about the empirical value of associations of deficits). On the other hand, studies reporting on dissociations could be viewed as evidence against the view that motor representations support comprehension. However, such evidence from dissociation patterns could also be questioned, for the three following reasons.

First, dissociations allow the inference that the integrity of the whole motor system is not required to comprehend accurately actions and manipulable artifacts. However, they do not falsify the theories that propose that *only some parts* of the motor system are required for achieving comprehension of actions and manipulable artifacts (Jeannerod, 2001; Martin, 2007; Martin et al., 2000; Rizzolatti et al., 2001) nor, *a fortiori*, the theories

that do not explicitly specify which parts of the motor system are required (e.g., Allport, 1985; Blakemore & Decety, 2001). The pattern of brain-damaged patients with preserved comprehension in the context of impaired production of actions could be accounted for by brain damage affecting, in these cases, brain areas or parts of brain areas (e.g., a part of the inferior parietal lobe or a part of the premotor cortex) that are specifically involved in action production or object use while the parts of the motor system or the types of motor representations that support comprehension remained preserved. Rizzolatti and Sinigaglia (2010), for instance, wrote:

> The claim is that, if the human parieto-frontal mirror system were involved in action understanding, motor syndromes following its damage (for example, ideomotor apraxia) would be accompanied by a deficit in action recognition. The assumption is that there is a one-to-one correspondence between motor and mirror sectors in the parieto-frontal circuit. This assumption is wrong. As clearly shown by electrophysiological mapping, there are motor sectors in the monkey inferior parietal lobule (and even in area PFG) with and without mirror neurons. Thus, dissociations between motor deficits and action understanding deficits can and do occur. It is the opposite result — that specific action recognition deficits can occur following motor circuit damage — that is striking and that provides a compelling argument for the crucial role of mirror neurons in this function. (p. 270)

It could be argued, for instance, that at least some apraxic patients with preserved comprehension could have "sufficient" motor representations to achieve conceptual processing. Motor representations, indeed, are rarely completely disrupted in apraxia. The

errors of apraxic patients, for instance, often consist in executing the appropriate manipulation movements but with temporal and spatial inaccuracies. This suggests that some residual motor knowledge has been accessed, which may suffice to support identification. This objection is all the more difficult to address that the theories which attribute a role to motor representations in comprehension do not specify the kind of functional deficit in action production or the kind of error in action production that *should* be associated with a comprehension deficit.

Second, because activations in the motor system caused by the viewing of actions or manipulable artifacts were often bilateral (e.g., see for reviews, Caspers et al., 2010; Lewis, 2006), some authors argued that only *bilateral* damage to the motor system should impair the comprehension of actions (e.g., Rizzolatti et al., 2001). Actually, the vast majority of the apraxic patients who showed preserved comprehension of actions did have unilateral damage (Negri et al., 2007; Papeo et al., 2010; Pazzaglia, Smania, et al., 2008; Pazzaglia, Pizzamiglio, et al., 2008; Rumiati et al., 2001; but see Rapcsak et al., 1995).

Third, since only accuracy, not easiness (i.e., speed) or efficiency of processing, was recorded in these patients when comprehension was assessed, these studies do not allow us to rule out that motor representations are *functional* rather than *necessary* for comprehension (Rizzolatti et al., 2001; Rizzolatti & Sinigaglia, 2010). Under this hypothesis, indeed, lack or degradation of motor representations should not prevent but only hamper the identification of actions and/or manipulable artifacts in apraxic patients.

In sum, the only firm empirical generalization that can be drawn from these neuropsychological studies is that the integrity of the whole cortico-subcortical motor system is not required to comprehend actions and manipulable artifacts accurately. These results are thus at odd with variants of the embodied view of concepts claiming that

potentially all parts of the motor system involved in the production of actions are also involved in comprehension (Pulvermüller, 1999, 2005).

3.3. Conclusion

Available evidence allows us to draw the following conclusion: while there is much behavioral and functional brain imaging evidence for the existence of motor activation during the comprehension of actions, of manipulable artifacts and of the words that refer to them, none of these studies provides evidence that motor representations are part of the concepts of actions and manipulable artifacts or contribute to their comprehension. On the contrary, TMS studies have provided data that are problematic at least for the view that the inferior parietal lobe is necessary to retrieve concepts of manipulable artifacts. In addition, patient studies have reported compelling evidence against at least the strongest version of the embodied view of concepts, i.e., that claiming that potentially all parts of the motor system implied in action production and object use store motor representations required to comprehend actions and manipulable artifacts (Pulvermüller, 1999, 2005).

Thus, a large hypothesis space remains to be explored between the hypothesis that motor representations are not part of concepts and do not contribute to comprehension (still viable), and the (now falsified) hypothesis that all parts of the motor system store motor representations that support comprehension. This thesis aimed at gathering data to inform this issue.

4. OUTLINE OF THIS THESIS

The research carried out in this thesis and presented in the following chapters aimed at gathering empirical evidence pertaining to the role of motor representations and processes

in the comprehension of actions and manipulable artifacts. This issue was addressed through three different approaches.

First, three studies were conducted to test whether loss or absence of motor representations affects the comprehension of actions and manipulable artifacts. The first two studies were conducted with a neurologically intact individual, DC, presenting with atypical motor development due to upper limb aplasia. In the first study, presented in chapter 1, we used a timed naming task to assess DC's ability to identify manipulable artifacts for which he has motor knowledge (previously used with his feet) *versus* those for which he had no motor knowledge (never used). Under the assumption that the richer the conceptual representation of an object is, the easier that object is identified, if motor representations are part of the concepts of manipulable artifacts, he should identify (name) artifacts for which he has motor knowledge more rapidly than those for which he has no motor knowledge. In the second study, presented in chapter 2, we assessed his ability to name actions involving hands (e.g., throwing) or other body parts (e.g., jumping). If motor representations play a role in the comprehension of observed actions, DC should name hand actions less efficiently than actions performed with other body parts. These studies allowed us to avoid ambiguities as to the nature of the functional impairment and the residual motor abilities of apraxic patients: DC has never developed any motor representations for hand actions and numerous manipulable artifacts. The third study was conducted during a three year period with a patient presenting with progressive bilateral damage to the motor system in the context of corticobasal degeneration (CBD). His ability to name actions and manipulable artifacts was tested in various tasks, including timed naming tasks. Studying a patient with bilateral brain damage to the motor system and using timed naming tasks allowed us to overcome the problems related to the

location of the lesion and the sensitivity of the tasks identified in previous studies with apraxic patients.

Second, we carried out the single-case study of a brain-damaged patient presenting with a conceptual deficit for actions and artifacts while other categories of concepts, like animals or plants, were preserved. We examined the patient's knowledge about different categories of actions and artifacts (e.g., manipulable and non-manipulable artifacts) and different types of attributes about them (e.g., what they look like, what is their function, how to manipulate or execute them). The aim was to evaluate which of the extant theories of conceptual knowledge organization, including the domain-specific knowledge hypothesis (Caramazza & Shelton, 1998), the sensory/functional hypothesis (Bird et al., 2000; Warrington & McCarthy, 1983), the motor simulation theory (Rizzolatti & Craighero, 2004; Rizzolatti et al., 2001) and the embodied theories of concepts (Barsalou, 1999, 2008; Martin, 2007; Martin et al., 2000; Pulvermüller, 1999, 2005), could account for the his profile of performance. This study is reported in chapter 4.

Third, one study was conducted to addressed directly an evidence that is often cited in favor of motor simulation theories - the observation that intrinsic properties of the motor system are reflected in the responses of healthy participants in the hand laterality judgment (HLJ) task (Parsons, 1987). In this task, participants are presented with left and right hand drawings displayed in different orientations and postures and are asked to say as fast as possible whether the observed hand is a left or a right one. Their judgments are slower when a hand is displayed on the screen in a position that would be difficult to reach with their own hand. This observation is often interpreted in favor of the motor simulation theories, which postulates that the motor system influence the visual perception of other's actions and bodies (e.g., Jeannerod, 2001; Grush, 2004; Munzert, Lorey & Zentgraf, 2009). However, a plausible alternative hypothesis is that the visual

system may be able, through visual experience, to derive implicit knowledge of how a body part moves and, then, to use this knowledge to constrain visual processing of body parts. Since DC has no hands but a normal visual experience with others' bodies, we assessed his performance in the HLJ task to test disentangle these two hypotheses. This study is reported in chapter 5.

CHAPTER 1

IS MOTOR KNOWLEDGE PART AND PARCEL OF THE CONCEPTS OF MANIPULABLE ARTIFACTS? CLUES FROM A CASE OF UPPER LIMB APLASIA[1]

Abstract

The sensory-motor theory of conceptual representations assumes that motor knowledge of how an artifact is manipulated is constitutive of its conceptual representation. Accordingly, if we assume that the richer the conceptual representation of an object is, the easier that object is identified, manipulable artifacts that are associated with motor knowledge should be identified more accurately and/or faster than manipulable artifacts that are not (everything else being equal). In this study, we tested this prediction by investigating the identification of manipulable artifacts in an individual, DC, who was totally deprived of hand motor experience due to upper limb aplasia. This condition prevents him from interacting with most manipulable artifacts, for which he thus has no motor knowledge at all. However, he had motor knowledge for a subset of them, which he learned to use with his feet. We contrasted DC's performance in a timed picture naming task for manipulable artifacts for which he had motor knowledge *versus* those for which he had no motor knowledge. No detectable advantage on DC's naming performance was found for artifacts for which he had motor knowledge compared to those for which he did not. This finding suggests that motor knowledge is not part of the concepts of manipulable artifacts.

[1] This section is a modified version of an article with identical title by Vannuscorps and Pillon, currently in revision in *Brain and Cognition*

1. INTRODUCTION

What are the constituents of the conceptual representation of manipulable artifacts? What is there in the concept of a hammer? According to an influential theory developed within the framework of cognitive neuropsychology (Rothi, Ochipa, & Heilman, 1991), the conceptual representation of a manipulable artifact includes knowledge of its typical physical features (shape, texture, weight) and knowledge of what it is used for, its purpose or function. Such conceptual representation is conceived of as amodal or "symbolic" and is connected to input and output modality-specific representations. Input modality-specific representations provide the perceptual description of the visual object or of the visual motion of the body parts interacting with it. Once the conceptual representation of the artifact is accessed from this perceptual description, it activates output modality-specific representations that encode the phonological form associated with the artifact (for naming) or the learned motor programs associated with its use. What is important for the purpose of this study is that, within this view, motor knowledge of how an artifact is used is *not* constitutive of its conceptual representation.

In contrast, the sensory-motor theory of conceptual representations assumes that conceptual knowledge of a manipulable artifact is distributed over modality-specific sensory and motor representations that are encoded during one's body sensorimotor interactions with the artifact. In this view, conceptual knowledge of an artifact thus *includes* motor knowledge of how it is used (e.g., Allport, 1985; Damasio, 1990; Martin, Ungerleider, & Haxby, 2000). Evidence cited in support of this theory refers to functional neuroimaging (e.g., Chao & Martin, 2000; Gerlach, Lau, & Paulson, 2002; Saccuman et al., 2006) and behavioral (e.g., Bub, Masson, & Cree, 2008; Myung, Blumstein, & Sedivy, 2006) studies that showed that motor representations are automatically activated when manipulable artifacts are viewed, named, or identified, even when there is no

intention to act upon them. However, that motor knowledge is automatically activated when manipulable artifacts are viewed or identified is not evidence that motor knowledge is *part of* their conceptual representation (Mahon & Caramazza, 2008).

In favor of the functional independence of conceptual and motor knowledge, there are reports of brain-damaged patients with apraxia who can recognize and name artifacts while they cannot demonstrate how to use them (e.g., Negri et al. 2007; Rapcsak, Ochipa, Anderson, & Poizner, 1995; Rumiati, Zanini, Vorano, & Shallice, 2001; for review, see Mahon & Caramazza, 2005). However, such evidence is not compelling either. Difficulties in manipulating artifacts might arise from damage to motor implementation processes that operate *after* spared motor knowledge has been retrieved. Moreover, even if access to motor knowledge was indeed degraded in these cases, the patients seldom made omission errors when asked to manipulate artifacts, or content errors, like using a toothbrush like a comb. Their errors mostly consisted in executing the appropriate manipulation movements but with temporal and spatial inaccuracies, which suggests that some residual motor knowledge has been accessed, which may suffice to support identification.

Be it as it may, evidence that patients can identify artifacts without being able to correctly use them is problematic only for variants of the sensory-motor theory that feature motor knowledge as indispensable (e.g., Gallese & Lakoff, 2005) or most diagnostic for identifying a manipulable artifact (e.g., Warrington & McCarthy, 1987). Under these theoretical variants, lack or degradation of motor knowledge indeed should prevent the identification of manipulable artifacts. However, the sensory-motor theory in itself is not committed to that strong prediction. If motor knowledge is part of manipulable artifact concepts, without being the central piece of these concepts, lack or degradation of such knowledge should somewhat hamper or delay the identification of

manipulable artifacts — not necessarily *prevent* it. To our knowledge, this somewhat weaker prediction has never been tested in patients unable to manipulate artifacts, since only accuracy, not easiness (i.e., speed) or efficiency of processing, was recorded when identification was assessed.

In this study, we tested this prediction by investigating the identification of manipulable artifacts in an individual, DC, who was totally deprived of hand motor experience due to upper limb aplasia. This condition prevents him from interacting with most manipulable artifacts, for which he thus has no motor knowledge at all. However, DC learned to use a subset of artifacts with his feet and, thereby, had motor knowledge for a subset of them. This allowed us to assess the status of motor knowledge vis-a-vis the conceptual representation of manipulable artifacts in a within-subject design. Thus, we contrasted DC's performance in a timed picture naming task, for two sets of manipulable artifacts — those with which he had motor experience (Set 1) *versus* those with which he had no motor experience *at all* (Set 2). Given that both sets of items may differ in terms of potentially confounding variables, we also recorded the performance of typically developed control participants for both sets of manipulable artifacts and used it as a baseline for the analysis of DC's difference in performance between both item sets (Cf. Case-controls design in neuropsychology; Crawford & Garthwaite, 2005).

Before going farther, and in order to avoid misunderstandings, it may be useful to clarify what we mean by DC having « no motor knowledge at all » for a series of manipulable artifacts. Actually, both the term « motor » and the term « knowledge » are important in this phrase. By « motor knowledge », we mean motor programs and skills that an individual acquires through his actual and repeated use of an object in its conventional function. These acquired motor programs related to object use have to be distinguished from two other kinds of manipulation-related information that can be

accessed when viewing an object. First, an individual may access some knowledge of how an object is usually used even if he never used it himself and, hence, does not have any learned motor patterns associated with it. For example, he may *know* how a saw is to be used and how hands and arms moved when people use it, just because he already saw someone else using it or because he already read instructions describing how to use it. Such visual or declarative knowledge is to be distinguished from *motor* knowledge acquired through the actual use of the object. Second, viewing any object with its specific shape, structure and volume, even if it was never encountered before, may cue specific motor interactions with it (« affordances »). Such on-line, form-derived motor programs are also distinct from *acquired* motor programs, which represent conventional manipulation patterns linked to the conventional function of familiar objects. Thus, due to upper limb aplasia, DC could not acquire any *motor knowledge* of how using most manipulable artifacts although he is presumably able to access the two other kinds of manipulation-related information when viewing them, just like normally-developed individuals.

We reasoned that, within the sensory-motor theory, the inclusion of motor knowledge in the content of the conceptual representation of manipulable artifacts should make this representation richer than that of manipulable artifacts that were not associated with motor experience and, thereby, lacks motor features. Semantically rich stimuli, that is, stimuli with high numbers of semantic features, are processed faster in tasks involving object identification (e.g., semantic categorization) than stimuli with low numbers of features (Pexman, Holyk, & Monfils, 2003) and such higher processing efficiency can also be observed in hemodynamic responses (Pexman, Hargreaves, Edwards, Henry, & Goodyear, 2007). Therefore, we predicted that if motor knowledge was constitutive of the conceptual representation of manipulable artifacts, DC should identify (name) more

rapidly artifacts for which he has motor knowledge compared to those for which he has no motor knowledge at all. On the contrary, if motor knowledge was not constitutive of the conceptual representation of manipulable artifacts, having motor knowledge associated with them should not make the concepts richer and, therefore, should not facilitate the identification of these manipulable artifacts.

2. METHOD

2.1. Participants

DC is a 51 year-old man with a Master's Degree in Psychology, with a congenital absence of both arms and hands due to thalidomide-related embryopathy. He had never experienced any phantom limb sensation and never had any prosthesis similar to biological hands or arms. He developed an unmatched ability to use some objects with his feet (e.g., writing with a pen) but he reported being unable to use a large range of other familiar objects (e.g., a hammer or a saw). Five right-handed normally developed control subjects, matched with DC for gender, age (mean = 53.8; range = 48-56), and number of years of education (mean = 17.2; range = 16-19), also participated in the study. All participants gave written informed consent prior to the study. 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.

2.2. Material and procedure

The stimuli consisted in 110 color photographs of manipulable artifacts. These items were selected among items for which information regarding spoken name frequency (New, Brysbaert, Paller, & Veronis, 2007), concept familiarity, imageability, and age of acquisition (Alario & Ferrand, 1999; Bonin, Meot et al., 2003; Bonin, Peereman,

Malardier, Meot, & Chalard, 2003) were available in French lexical databases. An artifact was deemed manipulable (1) when it can be picked up and moved with one or both hands and (2) if it is associated with a specific hand action involving either grasping the artifact to use it as a tool or manipulating it in order to achieve a result (Saccuman et al., 2006). Authors (e.g., Mahon et al., 2007) have proposed to make a further distinction, within the class of manipulable objects, between those that are associated with motor movements that unambiguously allow their identification (e.g., hammer, scissors, toothbrush) and those that are associated with motor movements that are less predictive of their identity (e.g., frying pan, suitcase, candle). Involvement of motor knowledge in object identification, if any, could mainly concern the first kind of manipulable artifacts, hereafter, the "strongly manipulable" (SM) artifacts. In order to select a subset of SM artifacts within our set of 110 items, we followed the procedure of Magnié and colleagues (Magnié, Besson, Poncet, & Dolisi, 2003). We presented the name of the 110 artifacts to 20 subjects (mean age: 26; 6 males) who did not participate in the main experiment and we asked them to judge on a five-point scale how easily (1=very difficult; 3= easy; 5=very easy) they could pantomime the action usually associated with each artifact so that any person watching this action could identify the artifact. The artifacts with a manipulability rating equal or larger than 3 (N = 69) were considered as SM artifacts. All data analyses were performed on the whole set of artifacts and on the subset of SM artifacts.

The 110 photograph stimuli were displayed on a computer screen with a size of 400 x 400 pixels, on a white background. The participants were asked to name each photograph as fast and as accurately as possible. In each trial, a fixation point was presented in the centre of the screen for 200 msec; then the screen was cleared for 500 msec and the stimulus was displayed until the voice key was triggered. The next trial began after an

interval of 1000 msec. The experiment was controlled by the E-Prime software (Psychological Software, 2002, Pittsburgh, PA). The participants were equipped with a sensitive built-in microphone connected with an RT-measuring PST (Psychology Software Tool) serial response box. Malfunctioning of the voice key and participants' responses were registered on-line by the experimenter.

Table 1.1. Distribution of the stimuli in the various sets of items used the picture naming task (SET 1=Already used by DC; SET 2=Never used by DC) and mean (and standard deviation) values of lexical and conceptual variables in each set.

ALL MANIPULABLE ARTIFACTS (N=92)	**SET 1** (N=64)	**SET 2** (N=28)	***t***	***p***
Spoken word frequency[1]	19.31 (34.14)	14.49 (32.58)	0.63	0.53
Age of acquisition[2]	2.57 (0.66)	2.95 (0.65)	2.53	< 0.01
Concept familiarity[2]	3.47 (1.06)	2.50 (2.90)	4.19	< 0.01
Imageability[3]	4.35 (0.45)	4.18 (0.70)	1.34	0.18
Manipulability[4]	3.61 (0.82)	3.75 (0.91)	0.72	0.47
STRONGLY MANIPULABLE ARTIFACTS (N=69)	**SET 1** (N=48)	**SET 2** (N=21)	***t***	***p***
Spoken word frequency[1]	21 (37.62)	10.19 (10.06)	1.29	0.20
Age of acquisition[2]	2.47 (0.60)	2.84 (0.57)	2.37	< 0.05
Concept familiarity[2]	3.5 (1.11)	2.47 (0.86)	3.72	< 0.01
Imageability[3]	4.41 (0.38)	4.46 (0.37)	0.46	0.65
Manipulability[4]	3.97 (0.56)	4.17 (0.58)	1.34	0.18

[1] Number of lemma occurrences per million in a corpus of subtitles of films (New et al., 2007); [2] From Alario and Ferrand (1999) and Bonin, Peereman, et al. (2003); [3] From Bonin, Meot, et al. (2003); [4] See Method section.

Once the naming task was completed, the artifact photographs were presented again to each participant, who was asked to tell whether he had already used the artifact. From the 110 artifacts, only those that all control participants had already used (N = 92) were included in the analyses. These stimuli were then divided into two sets according to their having been used (Set 1) or never used (Set 2) by DC. The number and characteristics of items in each set is provided in Table 1.1. Stimuli in Set 1 and Set 2 did not significantly differ in terms of spoken word frequency, imageability, and

manipulability. However, concept familiarity was significantly higher and age of acquisition significantly lower in Set 1 in comparison to Set 2.

3. RESULTS

Trials with voice key failures (0.4% of control participants' trials, no trial in DC) and with exceptionally long naming latencies (i.e., trials with latencies of 6,048 msec in Control 1, 6,057 msec in Control 2, and 16,559 ms in Control 4, no trial in DC) were excluded from the analyses. No other trimming of the data was applied. Response latency analyses were carried out over correct responses only. Distinct analyses were performed with the whole set of manipulable artifacts and with the set of SM (strongly manipulable) artifacts only. Figure 1.1 displays error rate, mean response latency, and mean efficiency score in DC and each control participant for both sets of items, separately for the whole set of artifacts and for SM artifacts only. The efficiency score (expressed in ms) was computed for each participant by dividing the mean response latency by the proportion of correct responses in a given condition (thus, the higher the score the poorer the performance). This score allows combining the measures of accuracy and speed into a single measure of processing efficiency; also, it allows between-group comparisons unbiased by potential speed-accuracy tradeoffs (Townsend & Ashby, 1978, 1983).

We computed Crawford and Garthwaite's (2005) Revised Standardized Difference Test (RSDT) over each dependent variable (error rate, response latency, and efficiency score) in order to test whether the discrepancy in DC's naming performance between Set 1 and Set 2 of manipulable artifacts significantly differed from the discrepancy between both sets in control participants. Considering the whole set of manipulable artifacts, the analyses revealed that the discrepancy in DC's performance between Set 1 and Set 2 did not significantly differ from that found in control participants, whether error rate [$t(4) = .83$, $p = .45$], response latency [$t(4) = .03$, $p = .98$], or efficiency score [$t(4) = .70$, $p =$

.52] was considered as the dependent variable. When only SM artifacts were analyzed, similar results emerged. The discrepancy in DC's naming performance between Set 1 and Set 2 did not significantly differ from that found in control participants, whether in terms of error rate [t (4) = .89, p = .42], response latency [t (4) = .09, p = .94], or efficiency score [t (4) = .38, p = .72].

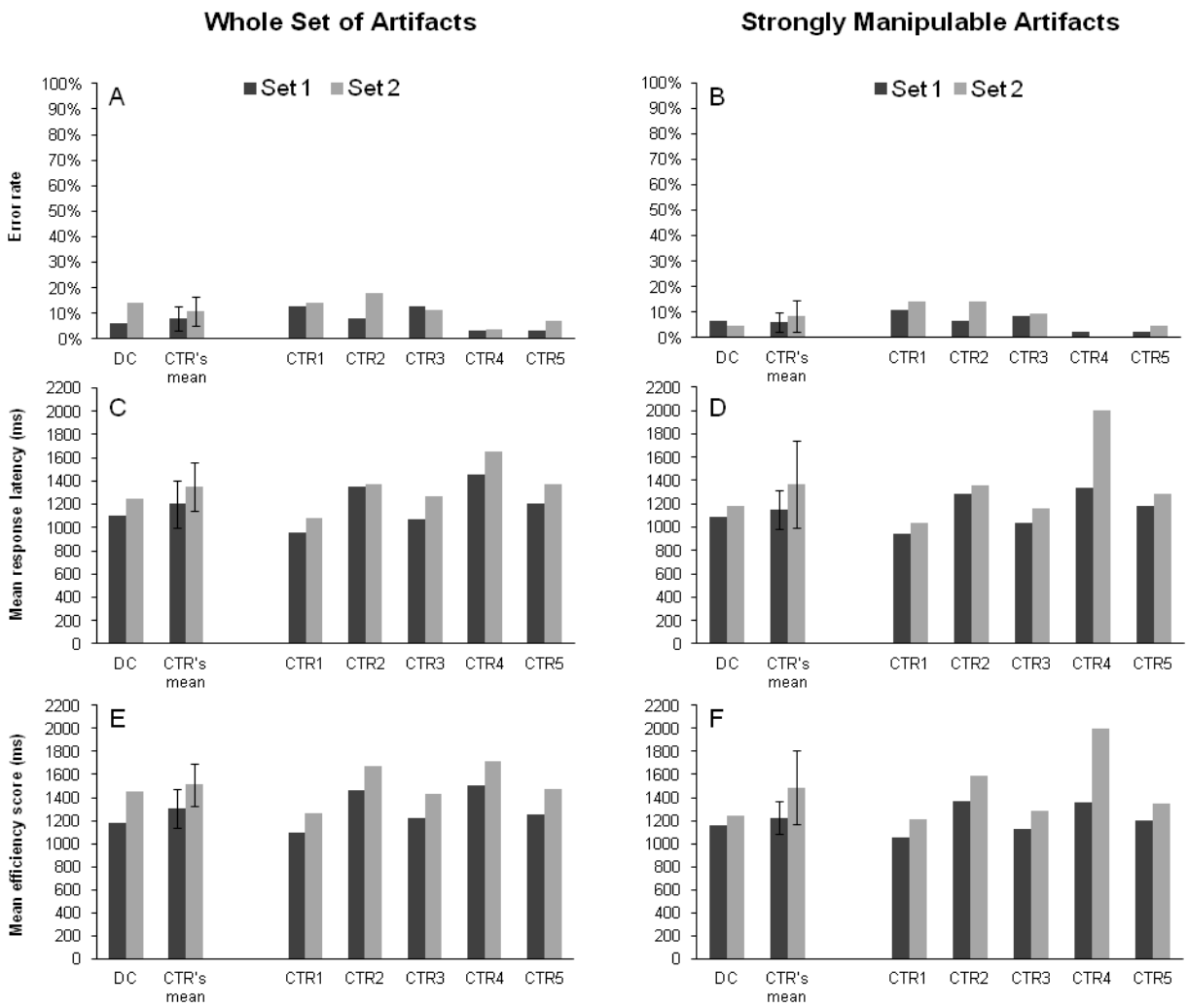


Figure 1.1| DC's and control participants' error rate (A-B), mean response latency (C-D), and inverse efficiency score (E-F) in the picture naming task, for manipulable artifacts that were used (Set 1) or never used (Set 2) by DC, when considering the whole set (*left*) or only strongly manipulable (*right*) artifacts. Error bars represent 1 S.D. from the mean.

We then carried out a by-item analysis of variance with covariates (ANCOVA) over the response latencies of DC and control participants for each item. The aim of this analysis was threefold: (1) increasing statistical power for testing the interaction between Group (DC vs. controls) and Set of items (Set 1 vs. Set 2), by considering items (N=84 or N=64) as the random factor; (2) controlling for the potential effect of the variables of concept familiarity and age of acquisition, which were not matched between Set 1 and Set 2 (see 2.2. Material and Procedure); and (3) testing whether concept familiarity and age of acquisition, which are known to be important determinants of picture naming times in healthy participants (e.g., Alario et al., 2004), significantly interacted with Group; a significant interaction between Group and conceptual-lexical variables might suggest the existence of qualitatively different conceptual-lexical representations in DC and control participants. The ANCOVA was thus carried out with response latency as the dependent variable, items as the random factor, Group (DC vs. Controls) as within-item factor, Set of items (Set 1 vs. Set 2) as between-item factor, and concept familiarity and age of acquisition as covariates. For each item, we entered into the analysis the response latency of DC and the median of the response latencies of control participants. These data were then inverse transformed for satisfying ANCOVA's normality assumptions. When the whole set of artifacts were considered, the analysis disclosed no significant effect of Group [F (1, 80) < 1], Set of items [F (1, 90 < 1], or Group x Set interaction [F (1, 80) < 1]. As for the continuous variables, the analysis yielded a significant effect of age of acquisition [F (1, 80) = 12.10, p < .001] and no significant effect of concept familiarity [F (1, 80) < 1]. Importantly, neither age of acquisition [F (1, 80) = 1.16, p = .29] nor concept familiarity [F (1, 80) < 1] significantly interacted with Group. The ANCOVA performed with SM artifacts yielded similar results, namely, no significant effect of Group [F (1, 60) = 1.55, p = .22], Set of items [F (1, 60) < 1], or Group x Set interaction

[F (1, 60) < 1]. The analysis also revealed a significant effect of age of acquisition [F (1, 60) = 5.11, p < .05] and no significant effect of concept familiarity [F (1, 60) < 1]. Age of acquisition [F (1, 60) = 1.77, p = .19] or concept familiarity [F (1, 60) < 1] did not significantly interact with Group.

These results of by-item analyses confirmed those obtained with RSDT analyses, which are in essence by-subject analyses, by showing that the discrepancy in the naming performance between the artifacts of Set 1 and Set 2 was not significantly different in DC and control participants, and this was true also for SM artifacts. To obtain positive evidence that the effect of Set of items was equivalent in DC and control participants, we conducted a Bayesian analysis (Wagenmakers, 2007) to estimate the likelihood of the null hypothesis being true for the Group x Set of items interaction. We applied the method recently described by Masson (2011) to compute the posterior probabilities for H_0 (interaction absent) and H_1 (interaction present) using the sum of squares for the interaction effect from the by-item ANCOVA. For the whole set of artifacts, this analysis indicated that the posterior probabilities were .90 for H_0 (i.e., the null hypothesis has a 90% chance of being true) and .10 for H_1; with SM artifacts, the probabilities were .86 for H_0 and .14 for H_1. According to Raftery's (1995) classification of evidence into « weak » (.50–.75), « positive » (.75–.95), « strong » (.95–.99), and « very strong » (> .99), the probability values obtained for the whole set and for the subset of SM artifacts both provide positive support for H_0 (interaction absent) hypothesis.

Finally, we sought positive evidence that DC's naming performance, that is, both his naming accuracy and speed, was influenced by variables that also influenced naming accuracy and speed in control participants. With this aim, we performed stepwise regression analyses with imageability, concept familiarity, and age of acquisition as predictors of DC' naming accuracy (correct/incorrect) or response latency and, in separate

analyses, of control participants' naming accuracy (percentage of correct responses per item) or response latency. The results showed that imageability was the only significant predictor of both DC's accuracy [Model: chi-square = 3.85, $p < .05$; Imageability: Wald = 4.19, $p < .05$, Exp(B) = 2.97] and response latency [Model: F (1, 82) = 17.26, $p < .001$, Adjusted R square = .16; Imageability: Beta = -0.42, t = -4.16, $p < .001$] when the whole set of artifacts was considered, and the only significant predictor of DC's accuracy when SM artifacts were considered [Model: chi-square = 3.81, $p = .05$; Imageability: Wald = 4.02, $p < .05$, Exp(B) = 8.36]. The same variable emerged from the regression analyses performed over the data of control participants. Imageability was the only significant predictor of both controls' accuracy [Model: F (1, 90) = 13.15, $p < .001$, Adjusted R square = .12; Imageability: Beta = .36, t = 3.63, $p < .001$] and response latency [Model: F (1, 90) = 34.38, $p < .001$, Adjusted R square = .27; Imageability: Beta = -0.53, t = -5.86, $p < .001$] when the whole set of artifacts was considered, and the only significant predictor of both controls' accuracy [Model: F (1, 66) = 22.61, $p < .001$, Adjusted R square = .24; Imageability: Beta = .51, t = 4.75, $p < .001$] and response latency [Model: F (1, 66) = 19.75, $p < .001$, Adjusted R square = .22; Imageability: Beta = -0.48, t = -4.44, $p < .001$] when SM artifacts were considered.

In light of the outcomes of these regression analyses, it appears that the significant effect of age of acquisition found in the ANCOVA analyses, in which imageability was not introduced, was likely due to age of acquisition being correlated with imageability. The important point, however, is that both types of analyses showed that the naming performance of DC and control participants was predicted by the same variables. This finding gives no support to the view that DC's conceptual representations of manipulable artifacts presented some qualitative difference with those of control participants.

4. DISCUSSION

Manipulable artifacts that, in DC, benefited from being associated with motor experience and, thereby, motor knowledge of how using and manipulating them, were not identified more accurately or rapidly than manipulable artifacts that were not associated with motor experience. If motor knowledge indeed enriched the conceptual representation of manipulable artifacts, then their identification should have been facilitated compared to manipulable artifacts whose conceptual representation lacks motor features. Thus, the present findings are at odds with the view that the concepts of manipulable artifacts include motor knowledge of how they are used.

An objection that can be raised against this conclusion is that it is based on a negative result. In this context, it is foremost important to note that Bayesian analyses of the data provided positive support for the hypothesis that DC's performance was not different for the artifacts he already used compared to those he never used. Still, one may ask whether the picture naming task used in this study was appropriate and sensitive enough to disclose a significant effect of the presence of motor features in the conceptual representation of artifacts on DC's naming accuracy or speed. We have reasons to believe that the picture naming task was indeed appropriate for that purpose. First, there is ample evidence that naming a visually-presented object entails retrieving its core and distinctive conceptual features (for recent review, see Taylor, Devereux, Acres, Randall, & Tyler, 2012) and that performance in this task is sensitive to even subtle, real (e.g., Woollams, Cooper-Pye, Hodges, & Patterson, 2008) or temporary virtual (e.g., Pobric, Jefferies, & Lambon Ralph, 2007), damage to conceptual representations. Second, we found positive evidence that the naming performance of both DC and control participants was significantly affected by the degree of imageability of the items. To our knowledge, the imageability effect is unanimously assumed to reflect conceptual processing. According

to Plaut and Shallice (1993), imageability in fact indexes the richness of a conceptual representation, i.e., the number of conceptual features it is composed of. The higher processing efficiency for concepts with richer representations would be due to the system being able to settle faster into a stable pattern of activation when more semantic features are activated. In this view, the imageability effect found in both DC's and control participants' naming performance indicates that the picture naming task was indeed able to disclose an effect of conceptual richness — and hence, a facilitation effect of the presence of motor features in the concepts of manipulable artifacts, if any. That DC's naming accuracy and speed was sensitive to imageability — and not to the presence of motor features — therefore provides positive support to the view that motor features are *not* constitutive of the concepts of manipulable artifacts.

This finding corroborates the conclusion previously drawn from the pattern of performance of brain-damaged patients who were able to name artifacts for which they were unable to demonstrate the use (e.g., Negri et al., 2007; Rapcsak et al., 1995; Rumiati et al., 2001). However, in these studies, the amount of patients' residual motor knowledge about the artifacts they were able to name was unknown and only naming accuracy, not speed, was measured. The empirical approach taken in this study allowed us to show further that having no motor knowledge *at all* for manipulable artifacts does not yield any detectable processing disadvantage in comparison with manipulable artifacts associated with motor knowledge.

The finding of this study is also in line with evidence obtained in studies using a variety of paradigms with healthy participants. For instance, Bub and colleagues (Bub, Masson, & Bukach, 2003) asked participants to learn associations between colors and gestures (i.e., pinch, poke, closed grasp, and open grasp). The participants were then presented with colored photographs of artifacts and asked to produce the gesture

previously associated with the color in which the artifact is displayed (Experiment 2) or to name the artifact (Experiment 3). The color in which each artifact was displayed corresponded to gestures that were either congruent or incongruent with the gesture naturally associated with the artifact. A strong congruency effect was found in response latency when the task of the participants was to produce the gesture associated with the color but not when their task was to name the artifact. This suggested that motor knowledge of how an artifact is manipulated is indeed activated upon the visual presentation of the artifact but this activation has no detectable impact on object naming. In a recent rTMS study (Pelgrims, Olivier, & Andres, 2011), it was found that virtual lesions of the anterior part of the left supramarginalis gyrus interfere with the performance of participants in a task in which they had to decide whether two objects are used by adopting the same hand posture, but not with their performance in determining whether two objects are normally used in the same context or have a similar function. Thus, interfering with the functioning of a brain region critically involved in processing motor knowledge associated with artifacts did not hamper conceptual processing of those artifacts. Finally, in a developmental study (Zinchenko & Snedeker, in press), the issue was investigated by assessing how children and adults categorize unknown objects. A novel tool (a « dax ») was presented to adults and 5-year-old and 3-year-old children together with its function and how to manipulate it. Then, two other, unlabelled, tools were presented to them, one having the same function and one having the same manipulation pattern as the tool initially labeled as a « dax ». When asked to indicate which one was a « dax », the three groups of participants preferentially showed the tool with the same function rather than the tool with the same manipulation pattern. Assuming that the content of concepts is what drives the categorization of objects, this finding suggests that motor information plays no part in the content of tool concepts.

Moreover, it is important to note that the finding of this study should not be viewed as conflicting with previous evidence showing that motor representations are automatically activated when participants simply observe manipulable artifacts or listen to their name. Evidence for such motor activation is compelling; it was consistently found in both functional neuroimaging (for review, see Martin, 2007) and behavioral studies (e.g., Bub, Masson, & Cree, 2008). For instance, Chao and Martin (2000) found that viewing or naming pictures of tools selectively activated the left posterior parietal and left ventral premotor cortices, two regions that are assumed to store information about hand movements associated with the use of manipulable artifacts. Findings from behavioral studies confirmed that motor activation is related to the retrieval of motor knowledge of how an artifact is used. Bub and colleagues (Bub et al., 2008), for instance, found that, upon the visual presentation of the picture of a manipulable artifact or of its name, the response latencies for performing a given gesture were longer when the gesture was not compatible with the gesture typically associated with the artifact. This result indicated that artifacts or names of artifacts automatically evoke motor knowledge of how they are used (see also Bub & Masson, 2012). Within a theory of artifact concepts that ascribes conceptual and motor knowledge to two distinct representational levels (e.g., Humphreys, Riddoch, & Quinlan, 1988; Rothi et al., 1991), automatic motor activation is viewed as the consequence of activation spreading and cascading from the pre-conceptual (object or word recognition processes) to the conceptual and then to the motor level of representation. Because of the cascading flow of information between the conceptual and motor levels, motor representations are activated while conceptual processing is not completed.[2] In that way, even if information derived from the motor level of

[2] In dual route models of object identification (e.g., Rumiati & Humphreys, 1998), motor features associated with a manipulable artifact are, in addition, directly activated from the structural properties of the

representation is not relevant for the task in hand, it is nevertheless available and can affect, under some circumstances or experimental manipulations, the accuracy or speed of the participants' responses in that task.

Given these assumptions, the results of an eye-tracking experiment (Myung et al., 2006; Experiment 2), which were presented as compelling evidence that motor knowledge is part of the concept of an artifact, are in fact consistent with an alternative explanation. In this experiment, participants were presented with an array of four object pictures and asked to point to the one matching a simultaneously presented spoken word. When the object picture shared manipulation features with the target word (i.e., the picture of a typewriter and the word "piano"), it was fixated more often by participants than unrelated or visually-matched object pictures. Within a theory positing two distinct representational levels for conceptual and motor knowledge, this effect would result from both conceptual and motor features being automatically activated from the target word and the object picture while participants perform the word-to-picture matching task. Thus, during the matching process, both kinds of information are available, which caused interference (i.e., more eye fixations) for rejecting the object sharing motor features with the named object.

In conclusion, this study adds new evidence to the view that motor knowledge is not part and parcel of the concepts of manipulable artifacts. This view does not preclude automatic activation of motor knowledge when manipulable artifacts are identified. However, it urges greater effort in developing and testing fresh hypotheses on why motor knowledge of artifacts is automatically activated if it is not for the purpose of identification.

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visually-presented artifact. This direct source of activation may also produce activation of motor features before conceptual processing is completed.

CHAPTER 2

WHEN DOES ACTION COMPREHENSION NEED MOTOR INVOLVEMENT? EVIDENCE FROM UPPER LIMB APLASIA[3]

Abstract

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 (DC) 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 DC was as accurate and fast as control participants in comprehending natural video and photographic presentations of both manual and non-manual actions, as well as pantomimes. However, he was selectively impaired at recognizing point-light animations of manual actions. This impairment was not due to a difficulty in processing kinematic information *per se*. DC 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

[3] This section is a modified version of an article with identical title by Vannuscorps, Andres and Pillon, currently under review in *Cognitive Neuropsychology*.

representations contribute to action comprehension each time visual information is incomplete or ambiguous.

1. INTRODUCTION

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 the way they move them? 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 visuo-perceptual 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, i.e., 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 that used to plan and execute the action oneself. In Jeannerod' s (2001: S103) 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". 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 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" (Blackemore & Decety, 2001: 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 (DC) — and who therefore has no motor repertoire at all for hand actions — to comprehend manual (e.g., throwing) as opposed to non-manual (e.g., jumping) 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 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 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 transcranial magnetic stimulation (TMS). 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, Bucchioni, & 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 visuo-motor 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 etiologies provided inconclusive evidence, however.

A first group of studies have examined whether the action production disorder presented 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, elementary sensory or motor deficit (De Renzi & Lucchelli, 1988). Buxbaum and colleagues (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 = 0.83, 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 with both transitive and intransitive actions performed with the mouth or hand. The patients were asked to listen to a sound corresponding to either a hand action (e.g., using scissors), a mouth action (e.g., inflating

a balloon), or a non-human 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 are 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 ($r = 0.35$, $p < .001$ and $r = 0.59$, $p < .05$, in Negri et al.'s and Papeo et al.'s 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 PT and SV 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, PT scored 27.5% and 35.6% and SV 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: NP 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 IN and SN 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 (no. 17, 19, 21; Cf. Table S2) 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 present with 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 be associated with 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 do constitute critical evidence supporting the motor theory. Given their prevalence, associations indeed 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 ("input action lexicon"), or to the action semantic system.

A second group of studies have examined action processing in patients presenting with 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 fronto-parietal motor circuits, basal ganglia, or corticospinal fibers of the internal capsule. The patients were asked to name transitive and intransitive actions presented as point-light animations. (In these animations, only the joints of a moving actor are visible; Cf. Johansson, 1973.) Each point-light movie was displayed as performed with the arm of the patient's affected or unaffected side of the body. The results showed that hemiplegic patients were more impaired at naming actions performed with the arm corresponding to their affected side than unaffected one. Converging results were found in a study by Arrighi and colleagues (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 presenting with 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 in comparison to a control group, it correlate neither to the severity of walking disability nor to 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 parieto-frontal 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, the contribution of available evidence is all the more hard to assess that current motor theories of action comprehension do not specify the kind of neural and functional damage to the motor system, including the behavioral features of the action production deficit,

that *should* be associated with an action comprehension deficit. In other words, what we would need to know, to evaluate previous evidence, is what kind of damage to the motor system should be expected to significantly impair the functioning of the mirror-neuron system (Rizzolatti et al., 2001) or the neural simulation network (Jeannerod, 2001) or, in other words, what kind of damage should impair access and/or use of internal motor representations corresponding to perceived actions.

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, DC, who has no motor representations *at all* for hand actions, due to bilateral upper limb aplasia. This condition prevents him from acquiring a motor repertoire of hand actions but not of actions requiring primarily lower limbs (e.g., jumping) or mouth (e.g., whispering), which he performs normally. According to motor theories of action comprehension, DC's comprehension of actions should be less efficient compared to control subjects' but only for those actions he cannot map onto its own motor repertoire, i.e., hand actions.

Examining action comprehension in the condition of bilateral upper limb aplasia first allows us to avoid ambiguities as to the nature of the functional impairment and the patient's residual motor abilities: DC 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, from which we calculated a processing efficiency index.

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, photographs, pantomimes, and point-light animations.

2. EXPERIMENTAL STUDY

2.1. Participants

DC is a 51 year-old man with a Master's Degree in Psychology. He presents a congenital bilateral upper limb aplasia (right side: two fingers attached to a foreshortened humerus; left side: aplasic) due to in-utero thalidomide exposure (Lenz, Pfeiffer, Kosenow, & Hayman, 1962). He 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 DC, 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 was also presented to 6 typically developed control participants matched with DC for gender, age (DC: 50; controls' range: 48-56), and number of years of education (DC: 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.

2.2. Naming actions in different viewing conditions

A first series of four experiments assessed DC's efficiency in naming manual and non-manual actions. Across these experiments, actions were presented in conditions varying in the kind of information provided by the visual stimulus, namely: (1) video clips depicting the movements of an actor with, if any, the target object and instrument typically involved in the action; (2) photographs consisting of a snapshot taken from the previous video clips; (3) videos of pantomimes of object-related actions, showing the movements of an actor toward a non-present object; (4) point-light animations of actions, displaying only the joints of an actor's body in motion.

2.2.1. Experiments 1 and 2: Naming manual and non-manual actions presented in video clips and photographs

Materials and Method

Participants were presented with 40 manual and 20 non-manual actions illustrated by video clips (Experiment 1) or photographs (Experiment 2) and 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 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 "non-manual" (mean rating = 1.25; SD = 0.27) actions were selected

(see Appendix A). The mean rating of "manuality" was significantly higher for manual than non-manual actions [t (58) = 56.87; $p < 0.001$]. Both sets of actions were matched in conceptual familiarity [t (58) = 0.04; $p = 0.97$] and imageability [t (58) = 1.45; $p = 0.15$]. However, manual actions had significantly lower log name frequency [t (29.8) = 2.11; $p = 0.04$] and were acquired significantly later [t (58) = 2.63; $p = 0.01$] than non-manual actions. Obviously, most manual actions involved a target object and/or an instrument whereas most non-manual actions did not.

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. These stimuli were presented in the center of a computer screen, using E-prime software (Psychological Software Tools, 2002, Pittsburgh, PA). The video clips and photographs had a size of 512 x 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 seconds.

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.

Results and Discussion

In the accuracy analysis, both target responses and acceptable alternatives (synonyms of the expected verb, including compound verbs, and more specific verbs) were considered as correct. However, only trials corresponding to the expected name

were considered in the response latency (RL) analysis (for a similar approach, see Druks et al., 2006). Moreover, trials with RL outside the range (> 2 SD) of the individual's mean in each condition were excluded (Experiment 1: 5.7% and 5.3% of the data from DC and controls, respectively; Experiment 2: 4.3% and 5.6% of the data from DC and controls, respectively). Accuracy and RL measures were combined into an efficiency score (ES) (Kennett, Eimer, Spence, & Driver, 2001; Townsend & Ashby, 1978, 1983) expressed in milliseconds and 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, like for response latencies). The results are displayed in Figure 2.1.

We applied Crawford and Howell's (1998) modified *t*-test to assess whether DC performance was significantly different from the performance of the control group. The results indicated that DC's performance in naming videos (Experiment 1) was not significantly different from controls' performance whether for manual [accuracy: t (5) = -0.84, p = 0.44; RL: t (5) = -1.23, p = 0.27; ES: t (5) = -1.32, p = 0.24] or non-manual [accuracy: t (5) = 0.31, p = 0.77; RL: t (5) = -0.59, p = 0.58; ES: t (5) = -0.71, p = 0.51] actions. Likewise, in naming photographs (Experiment 2), DC's performance was not significantly different from controls' performance whether for manual [accuracy: t (5) = 0.44, p = 0.68; RL: t (5) = -0.62, p = 0.56; ES: t (5) = -0.66, p = 0.54] or non-manual [accuracy: t (5) = -1.66, p = 0.16; RL: t (5) = -0.37, p = 0.73; ES: t (5) = 1.23, p = 0.27] actions.

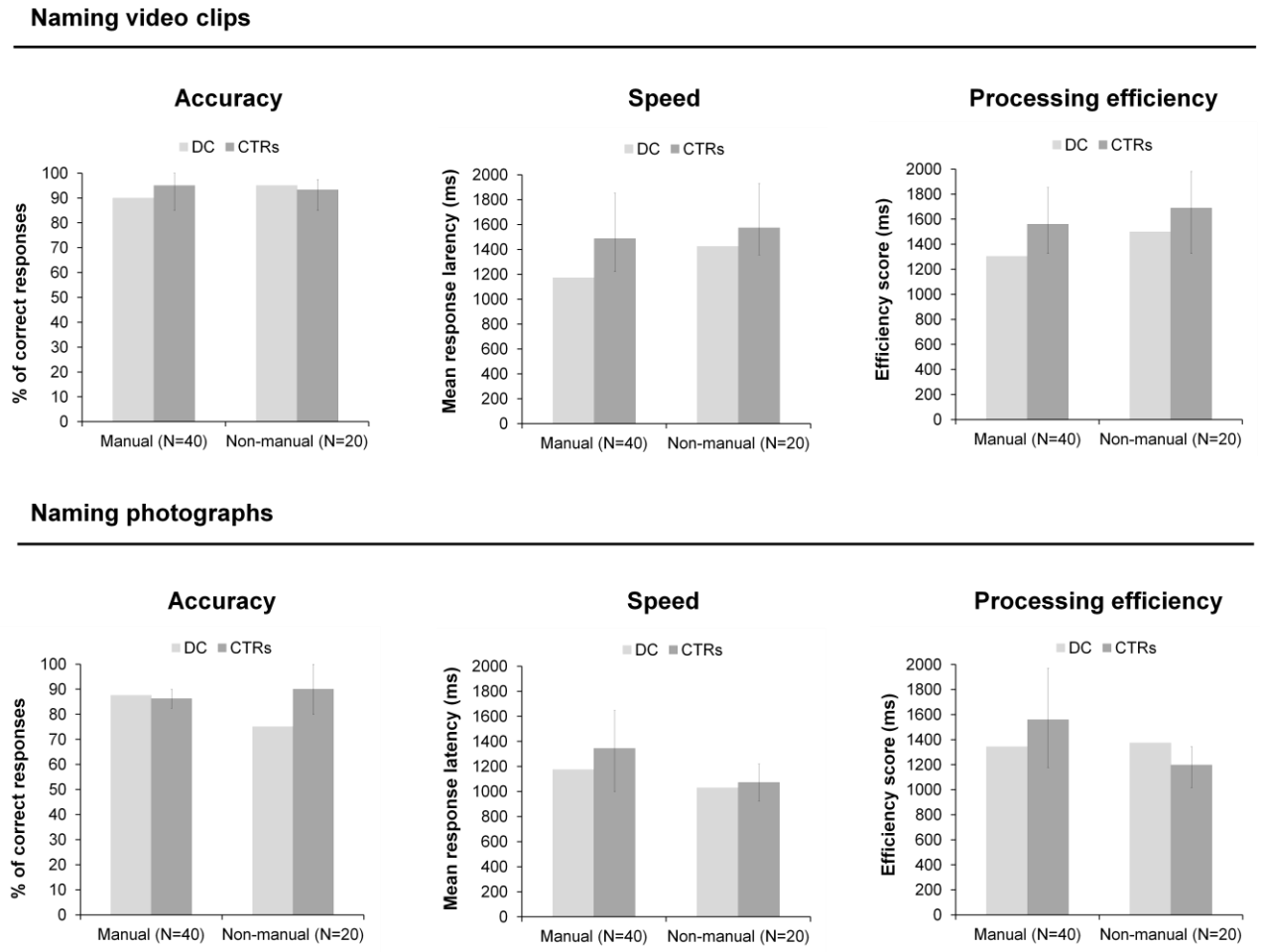

Figure 2.1| DC's and control participants' percentage of correct responses, mean response latency, and efficiency score for the manual and non-manual actions in the video clip (**top)** and photograph (**bottom**) naming task (Experiments 1 and 2). CTRs = Control participants. Error bar = range.

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 fulfill 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, DC nevertheless was more efficient in identifying

non-manual than manual actions because of the involvement of internal motor representations in the identification of non-manual 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 DC's discrepancy in performance between non-manual and manual actions was different from the discrepancy between both kinds of action in the control group. The results indicated that DC's difference in performance between non-manual 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 = 0.51; RL: t (5) = 0.80, p = 0.46; ES: t (5) = 0.56, p = 0.59] or in the photograph naming task [accuracy: t (5) = 1.47, p = 0.20; RL: t (5) = 0.17, p = 0.87; ES: t (5) = 1.2, p = 0.28].

Finally, we asked whether the kind of visual stimulus (video clips vs. photographs) influenced DC's performance for manual and non-manual actions in the same way as in control participants. The results (RSDT, Crawford & Garthwaite, 2005) indicated that DC' difference in performance between video clips and photographs did not significantly differ from that found in control participants, either for manual [accuracy: t (5) = 0.88, p = 0.42; RL: t (5) = 0.56, p = 0.60; ES: t (5) = 0.54, p = 0.61] or non-manual [accuracy: t (5) = 1.17, p = 0.29; RL: t (5) = 0.13, p = 0.90; ES: t (5) = 1.46, p = 0.20] actions.

2.2.2. Experiment 3: Naming pantomimes of actions

In object-related manual actions, one may assume that when the instrument involved in the action is highly specific (e.g., "typing" or "grating"), there is no need to process body shape and motion in order to identify the performed action. (Let us note, however, that only 19/40 manual actions in the previous experiments could be of this type.) 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.

Materials and Methods

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. All video clips were sized 512 x 384 pixels, displayed at 9° of visual angle, with 25 frames/second, and lasted 5 seconds. The procedure was the same as 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. Moreover, trials with RL outside the range (> 2 SD) of the individual's mean in each condition were excluded (4.6% and 4.8% of the data in DC and controls, respectively). An efficiency score (ES) was computed from the accuracy and RL data of each participant. The results are displayed in Figure 2.2. Crawford and Howell's (1998) modified *t*-test indicated that DC's performance in naming pantomimes of actions did not significantly differ from controls' performance as regards accuracy [t (5) = 0.6, p = 0.57]. However, DC was faster than controls [RL: t (5) = -2.04; p = 0.09] and his efficiency score was significantly better than the scores of controls [t (5) = -2.73; p = 0.04].

Actually, DC did not encounter any difficulty in identifying pantomimes in comparison with the most natural depictions of manual actions, i.e., video clips, which included, if any, the instrument and the target object. Thus, results from the RSDT analyses (Crawford & Garthwaite, 2005) indicated that, when naming manual actions, DC'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 = 0.44; RL: t (5) = 0.43, p = 0.68; ES: t (5) = 0.95, p = 0.39]. When DC's performance for manual actions was compared between pantomimes and photographs, a similar pattern emerged [accuracy: t (5) = 0.09, p = 0.92; RL: t (5) = 0.87, p = 0.42; ES: t (5) = 1.30, p = 0.25].

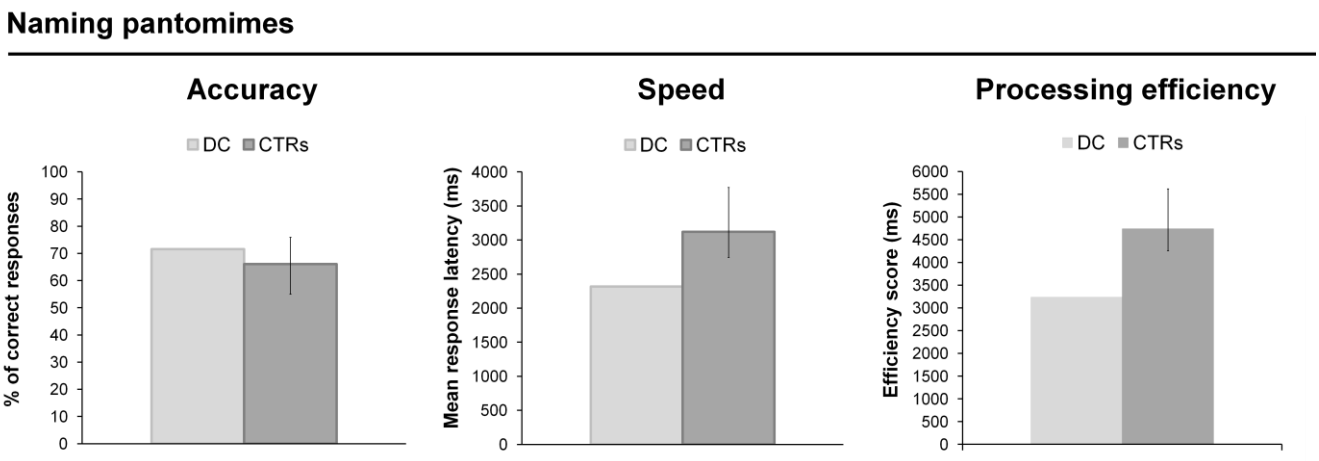

Figure 2.2| DC's and control participants' percentage of correct responses, mean response latency, and efficiency score in the pantomime naming task (Experiment 3). CTRs = Control participants. Error bar = range.

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

Materials and Method

Participants were asked to name as accurately as possible 20 manual and 20 non-manual actions displayed as point-light animations with a gradual unmasking paradigm.

Most manual actions corresponded to object-directed actions and most non-manual actions did not (see Appendix C). The objects were obviously not present in the point-light animations, like in pantomimes.

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 mocap.cs.cmu.edu) with the PointLightSystem 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; 10 males) were presented with the complete point-light animations. Participants in Group 2 (Mean age= 23; 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 non-manual 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 dot). 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 dot). 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.

Results

The results are displayed in Figure 2.3. 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, DC's overall performance [t (5) = -3.77, $p < 0.01$] and maximum score [t (5) = -5.74, $p < 0.01$] were significantly impaired in comparison with the overall performance and maximum score of control participants. However, for non-manual actions, both DC's overall performance [t (5) = -1.42, $p = 0.2$] and maximum score [t (5) = -1.55, $p = 0.17$] 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 non-manual actions was nearly significantly greater in DC compared to controls [t (5) = 2.38, $p = 0.06$] and that the difference in maximum score between both kinds of action was significantly greater in DC compared to controls [t (5) = 3.11, $p = 0.03$]. On the whole, the results thus indicated that DC's identification of point-light animations of actions was *selectively* impaired for manual actions when compared to control participants'.

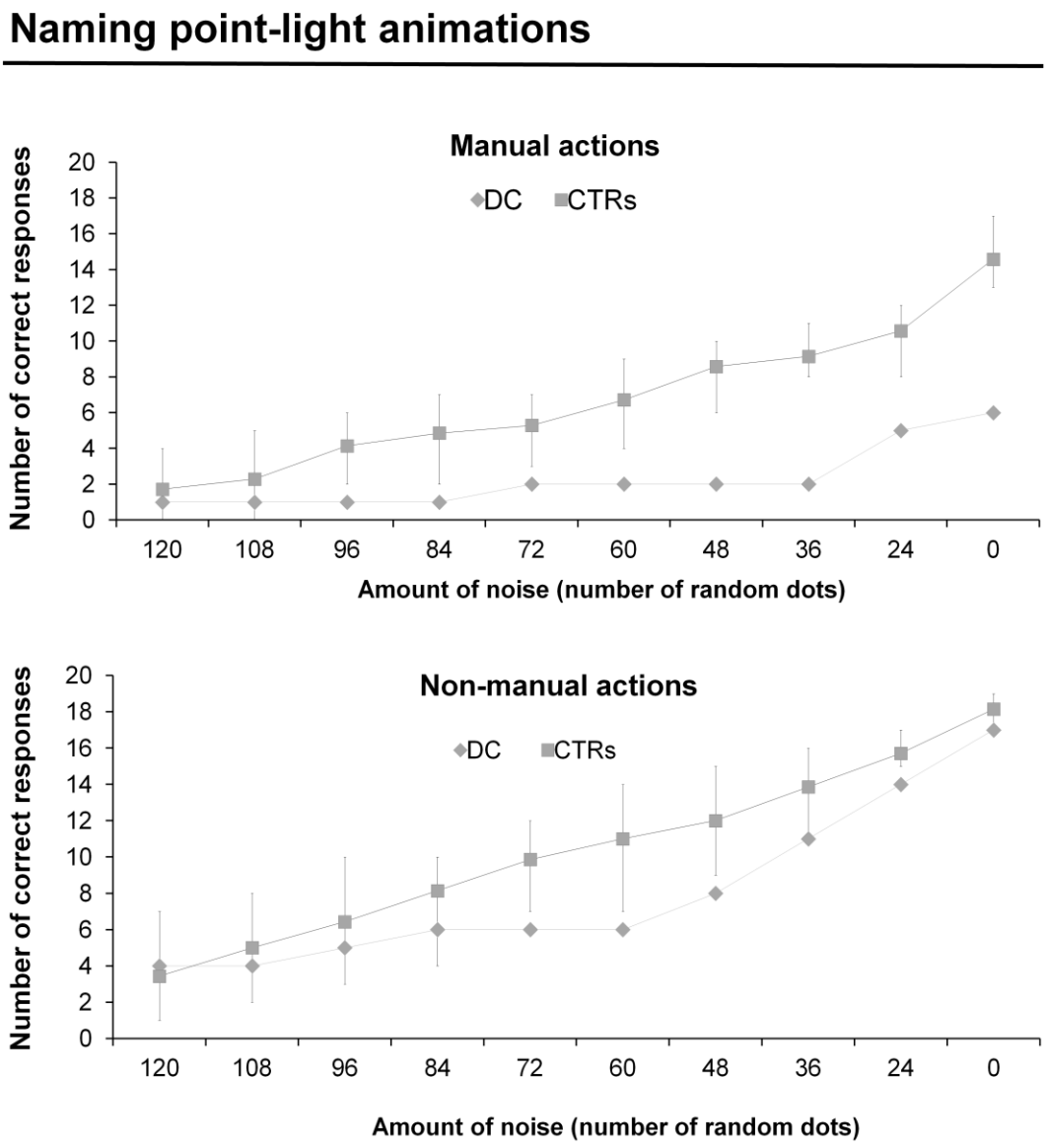

Figure 2.3| DC's and control participants' number of correct naming responses for manual and non-manual actions displayed as point-light animations and as a function of the amount of noise (Experiment 4). CTRs = Control participants. Error bar = range.

2.3. Interim Discussion

The results of this first set of experiments showed that DC was as accurate and fast as control participants in naming natural video (Experiment 1) and photographic (Experiment 2) presentations of both manual and non-manual 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. A possible account for this pattern of results is 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 needs to be addressed, however. First, DC 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 motion. Although there is no apparent reason why aplasia 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 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 perception impairment would prevent action identification from point-light stimuli since motion is the only piece of information provided in these stimuli. Within this account, DC's preserved ability to identify non-

manual actions in point-light animations could be ascribed to these actions requiring coarser visual motion processing than manual actions.

The second alternative account for DC'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. DC's preserved ability to identify non-manual 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 familiar actions. The next series of experiments addressed these alternative accounts.

2.4. Processing arm and whole-body kinematics

If DC 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 non-manual actions when a fine-grained analysis of motion information is required. Alternatively, if DC 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 non-manual actions, when a fine-grained analysis of motion information is required. The two experiments reported in this section allowed us to assess DC's ability to process fine-grained kinematics of an actor's hand and whole-body movements.

2.4.1. Experiment 5: Weight estimation

Materials and 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 or whole-body movements when he lifted small or large boxes, respectively.

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; 0.05, 0.3, 0.6, or 0.9 kg) or a large (N = 64; 3, 6, 12, or 18 kg) box. 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 center 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 analyzed separately. The results are displayed in Figure 2.4 (top). As can be seen in this figure, the weight estimations given by both DC and control participants were positively related to the actual weights of the boxes, whether small or large. Moreover, both DC 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 DC's weight estimations did not significantly differ from the estimations provided by the control participants whatever the weight of the small ($-0.68 \leq t\text{s} \leq 0.32$; all $p\text{s} > 0.52$) or of the large ($-1.99 \leq t\text{s} \leq 1.09$; $p\text{s} > 0.09$) boxes. Thus, DC was not impaired in estimating the weight of the boxes on the basis of the movements of the actor's arm or whole-body.

2.4.2. Experiment 6: Judging weight's expectation

Materials and 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 judgments, 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 analyzed separately. The results are displayed in Figure 2.4 (bottom). As can be seen in this figure, both DC and control participants showed sensitivity to kinematic adjustments induced by the violations of expectation, although sensitivity was higher for large than small boxes, in both DC and control participants. The results of the modified *t*-tests (Crawford & Howell, 1998) indicated that DC's sensitivity to violations of expectations was not significantly different from the control participants' sensitivity, either for the small [t (5) = 0.08; p = 0.93] or the large [t (5) = 0.78; p = 0.46] boxes. Thus, here again, the results showed that DC was not impaired in perceiving the fine kinematics of an actor's arm or whole body. Moreover, as indicated by RDST (Crawford & Garthwaite, 2005) analyses,

DC 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 = 0.72].

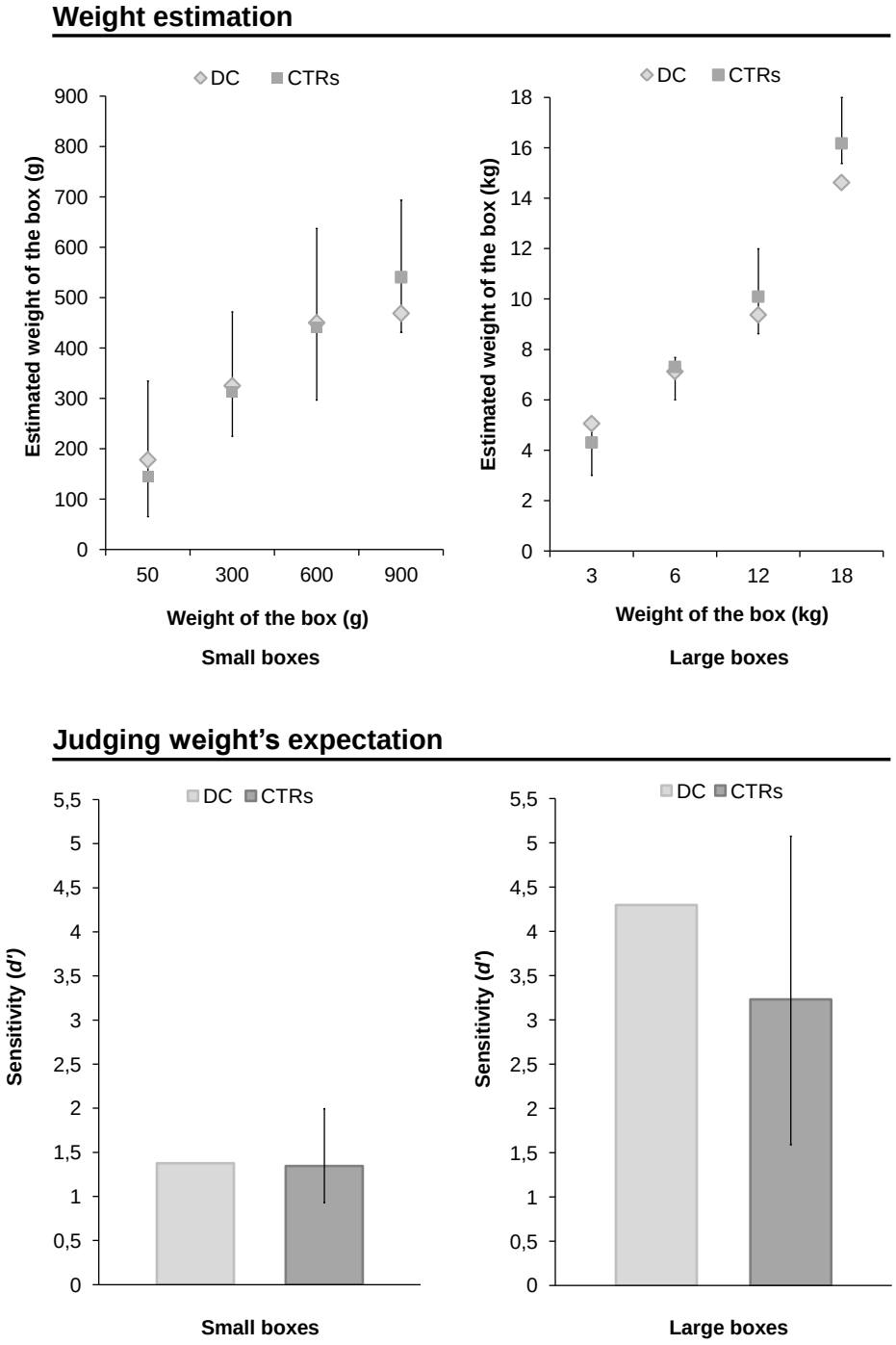

Figure 2.4| Top. DC's and control participants' estimated weight of the small and large boxes as a function of the actual weight of the boxes (Experiment 5). **Bottom**. DC's and control participants' sensitivity (*d'*) to violations of the actor's expectation for the small and the large boxes (Experiment 6). CTRs = Control participants. Error bar = range.

3. 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, DC, in a series of picture naming tasks that included different kinds of visual depictions of actions, i.e., video clips, photographs, pantomimes, or point-light animations. Distinct patterns of results were found depending on the kind of visual depictions. DC was as efficient as control participants in naming natural video (Experiment 1) and photographic (Experiment 2) presentations of both manual and non-manual 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, DC 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*. DC showed no difficulty in identifying point-light animations of non-manual 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 only when important visual features of the observed action, i.e., 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.[4] 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 will 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*, a condition that is difficult to ascertain in apraxic patients. Not only these patients

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

may have *residual* motor representations of actions that may suffice to support action identification, which likely requires less fine 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 visuo-motor 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: 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 in individuals who normally developed motor representations for these actions. Moreover, and importantly, DC's pattern of performance provides no evidence of a processing advantage in comprehending non-manual 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 is 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 would 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 action processing only and each time visual information critical for performing the task is incomplete or ambiguous.

We see at least two possible, non mutually exclusive, mechanisms by which motor processes may contribute action comprehension. The first possibility is that the observer's own motor repertoire is automatically activated by human motion stimuli and generates top-down expectations that serve to fill in missing or ambiguous visual information (Wilson & Knoblich, 2005). Within this hypothesis, the observer's motor knowledge directly impacts or even is part of the visual perceptual processing of human motion. The second possibility is that motor representations automatically derived from motion stimuli constitutes an additional source of information that is "read" by the conceptual system in order to constrain the identification of ambiguous action displays.

Our proposal on how motor processes may contribute 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 and colleagues (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.

APPENDIX A. List of manual and non-manual actions presented in Experiment 1 (naming video clips of actions) and Experiment 2 (naming photographs of actions).

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

APPENDIX B. List of actions presented as pantomimes in Experiment 3.

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

French description	**English description**
Gommer	Erasing
Utiliser un chronomètre	Timing with a stopwatch
Scier	Sawing
Jouer au yoyo	Playing yoyo
Fumer le cigare	Smoking a cigar
Donner des coups de hache	Splitting wood with an ax
Jouer de l'accordéon	Playing an accordion
Se brosser les dents	Brushing one's teeth
Jouer de l'harmonica	Playing a harmonica
Se limer les ongles	Filing one's nails
Jouer au pingpong	Playing ping pong
Donner des coups de fouet	Whipping
Passer le balai	Sweeping
Se peigner	Combing
Jouer à la toupie	Spinning a top

APPENDIX C. List of manual and non-manual actions presented in Experiment 4 (naming actions presented as point-light animations).

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

CHAPTER 3

ON THE ROLE OF THE MOTOR SYSTEM IN COMPREHENDING ACTIONS AND MANIPULABLE ARTIFACTS. A LONGITUDINAL STUDY OF A PATIENT WITH CORTICOBASAL DEGENERATION[5]

Abstract

According to motor theories of comprehension (MTC), the comprehension of human actions and manipulable artifacts is supported, in part or entirely, by the motor system. In this study, we tested MTC by investigating the ability of a patient presenting with extensive damage to the motor system (due to corticobasal degeneration) to comprehend such "motor-related" stimuli. The patient was presented with several motor, praxis, and picture naming tasks (with motor- and non-motor-related stimuli) at different times during a three-year period. The results showed that, throughout this period, JR presented increasingly severe motor and praxic disorders that paralleled increasing brain atrophy within bilateral motor brain areas. On the other hand, throughout the same period, the patient's performance in naming actions and manipulable artifacts remained unimpaired in comparison with that of control participants. An additional assessment carried out at the end of the three-year period corroborated this finding with larger sets of items and a measure of naming speed. These results are difficult to reconcile with MTC and suggest that the neural and functional system representing knowledge that is involved in comprehending actions and manipulable artifacts is largely independent from the system allowing the selection, planning, and execution of the motor patterns associated with actions and manipulable artifacts.

[5] This section is a modified version of an article with identical title by Vannuscorps, Dricot and Pillon, which is currently in preparation.

1. INTRODUCTION

Every day, we view multiple actions and objects that we are effortlessly able to recognize as "hitchhiking" or "washing", "pens" or "computers". Actually, we immediately "comprehend" these actions or objects, in the sense that we immediately know what is the probable purpose of the observed movements or the usual function of the seen objects. The issue addressed in this study is whether the motor system is involved in the comprehension process of human actions and manipulable artifacts. Here, "motor system" is used in the broad sense of the representations and processes that support the production of movements in humans (from selection to planning and execution) and which includes, at the neural level, the motor system proper (primary motor cortex, premotor cortex, supplementary motor area, basal ganglia, and cerebellum) as well as cortical associative areas to which it is connected and that are known to be involved in movement production like the inferior and superior parietal lobe and the inferior frontal lobe.

Within the tradition of cognitive psychology, the motor system is not assumed to play any role in the comprehension of actions or objects. When an action or an object is perceived, it is given meaning when its perceptual representation gains access to stored conceptual knowledge representing, in an amodal or "symbolic" format (Caramazza, Hillis, Rapp, & Romani, 1990; Caramazza & Shelton, 1998; Fodor, 1983; Landauer & Dumais, 1997; McClelland & Rogers, 2003), the features of that category of actions (like its typical cause, purpose, or consequence; Cf. Tranel, Kemmerer, Adolphs, Damasio, & Damasio, 2003) or of that category of objects (like its function or typical location). Within this perspective, the motor system is considered as a mere output device involved in the representation, planning, control, and execution of movements. Moreover, the representation of conceptual knowledge would be sustained by brain areas located in

heteromodal cortex that are remote from brain areas sustaining the representation and processing of movements. Different variants of this view can be identified depending on whether conceptual knowledge is organized in an unitary space whose organization reflects the way in which the features of objects are statistically related to one another in the world (Caramazza et al., 1990; Tyler & Moss, 2001), in multiple stores each containing knowledge about a specific kind of conceptual feature, like visual (what the object look like) or functional (what it is used for) features (Warrington & McCarthy, 1984), or in multiple stores each containing knowledge pertaining to one specific category of objects, like animals, plant, or artifacts (Caramazza & Shelton, 1998). However, they all share a common thread: the motor system is not involved in representing conceptual knowledge drawn in comprehension.

This traditional view has been recently challenged by a range of new proposals, all assuming that the motor system plays a critical role in the representation of knowledge implicated in the comprehension of human actions and manipulable artifacts. We will refer to this theoretical framework as the "Motor Theories of Comprehension" (MTC).

Two main theoretical proposals can be distinguished within this framework, namely, the sensory-motor theory and the simulation theory. According to the sensory-motor theory, the motor system partly *stores* conceptual knowledge about human actions and manipulable artifacts (Allport, 1985; Barsalou, 1999, 2008; Damasio, 1989; Patterson, Nestor, & Rogers, 2007; Pulvermüller, 1999, 2005). This follows from the assumption that knowledge about an action or an object is stored in the sensory and motor systems that were active during experience with that action or that object. Comprehending an action or a manipulable artifact thus consists in "re-activating", among others, their motor features stored within the motor system. In some views, knowledge is just distributed across a network of functional and neural systems each

representing a kind of modality-specific feature (Allport, 1985; Pulvermüller, 1999) while, in others, modality-specific stores of knowledge are bound together by one multi- or supra-modal system, a "hub" (Patterson et al., 2007). However, they all implies that the motor system plays a critical role in comprehending actions and manipulable artifacts, but not other objects such as animals, plants, or non-manipulable artifacts.

Within the motor simulation theory, it is assumed that comprehending an action performed by another individual requires that the observer internally simulates that action, that is, covertly executes the movements implicated in that action. Likewise, identifying a manipulable artifact requires that the observer covertly performs the movements that are involved in their actual use (e.g., Gallese & Lakoff, 2005; Rizzolatti & Craighero, 2004; Rizzolatti, Fogassi, & Gallese, 2001; Witt, Kemmerer, Linkenauger, & Culham, 2010). Motor simulation of actions is achieved by "mirror neurons" that automatically transform an observed action onto the motor commands that the observer would activate herself to perform the same action. In that way, the observer immediately comprehends the action *as if* she performed it herself (Rizzolatti et al., 2001). In a related proposal, it is assumed that "seeing a tool automatically evokes a motor simulation of acting on the tool" and that this motor simulation plays a functional role in the ability to name a tool (Witt et al., 2010, p. 1217). Thus, within this approach, comprehending actions and manipulable artifacts depends on the motor production system that is recruited in order to covertly perform actions or use manipulable artifacts.

MTC have been supported by evidence from functional neuroimaging studies that consistently found that the motor system was activated when actions and manipulable artifacts were simply viewed or named (see for reviews, Hauk, Shtyrov, & Pulvermüller, 2008; Johnson-Frey, 2004; Lewis, 2006; Mahon & Caramazza, 2008; Noppeney, 2008; Pulvermüller & Fadiga, 2010). Chao and Martin (2000), for instance, found with fMRI

that viewing tools compared with animals, faces, and houses, preferentially activates the left posterior parietal and the left ventral premotor cortex, two brain areas that are involved in the use of tools. Buccino and colleagues (2001) found that observing actions made by mouth, hand, or foot elicits in the observer a somatotopic activation in the premotor cortex. Additional evidence that viewing actions and artifacts activates the motor representations involved in executing or using them was provided by behavioral studies, which found that viewing an action (Boulenger et al., 2006; Brass, Bekkering, & Prinz, 2001; Kilner, Paulignan, & Blakemore, 2003; see for review Wilson & Knoblich, 2005) or a manipulable artifact (Bub, Masson, & Bukach, 2003; Bub, Masson, & Cree, 2008; Glover, Rosenbaum, Graham, & Dixon, 2004) influences the observer's own execution of movements. Bub et al. (2008), for instance, asked their participants to perform a specific grasping gesture as fast as possible after a visually-presented "go-signal". The go-signal was sometimes the picture of a manipulable artifact which should normally be grasped in a way that is congruent with the grasping gesture they had to perform and sometimes incongruent with it. While the identity of the artifact presented on the screen as go-signal was irrelevant for the task, the participants were faster to perform the target grasping gesture when the go-signal was congruent with that gesture than when it was not.

However, as pointed out by several authors (e.g., Csibra, 2007; Hickok, 2009; Mahon & Caramazza, 2008), that the perception of an action or an object activates the motor system *as if* the perceiver executed that action or used that object does not demonstrate that the motor system plays a causal role in comprehending that action or that object. One alternative hypothesis is that motor activation does not precede but *follows* the comprehension of the action or the object, i.e., that motor activation follows access to conceptual knowledge (Mahon & Caramazza, 2008).

Compelling evidence in favor of MTC would consist in finding that damage to the motor system causes an impairment in comprehending actions and manipulable artifacts. Several studies have examined the ability of patients suffering from apraxia in processing visually-presented actions and/or manipulable artifacts in naming and/or word/picture matching tasks. Apraxia is typically caused by unilateral damage to frontal and/or parietal cortex and results in disorders of movement production that cannot be explained by language or elementary sensory or motor impairments (De Renzi & Lucchelli, 1988). In favor of MTC, individual patients or groups of patients with apraxia also showed impaired performance in a naming or a word/picture matching task with visually-presented actions (Buxbaum, Kyle, & Menon, 2005; Negri et al., 2007; Papeo, Negri, Zadini, & Rumiati, 2010; Pazzaglia, Smania, Corato, & Aglioti, 2008; Pazzaglia, Pizzamiglio, Pes, & Aglioti, 2008) or manipulable artifacts (Buxbaum & Saffran, 2002; Negri et al., 2007; Papeo et al., 2010). Nonetheless, there were also reports of apraxic patients who performed in the normal range with actions and manipulable artifacts in naming or word/picture matching tasks (Bartolo, Cubelli, Della Sala, Drei, & Marchetti, 2001; Cubelli, Marchetti, Boscolo, & Della Sala, 2000; Negri et al., 2007; Papeo et al., 2010; Pazzaglia, Smania, et al., 2008; Pazzaglia, Pizzamiglio, et al., 2008; Rapcsak, Ochipa, Anderson, & Poizner, 1995; Rumiati, Zanini, Vorano, & Shallice, 2001).

Such dissociations between praxic and comprehension abilities could be viewed as a falsification of MTC. However, three kinds of objections have been raised to such evidence. First, it has been objected that the patterns of performance observed in apraxic patients do not provide relevant evidence because these patients do not suffer from a sufficiently "low level" motor disorder (Meteyard, Cuadrado, Bahrami, & Vigliocco, 2012). Only the patterns of performance of patients suffering from "direct damage to the motor system" (Meteyard et al., 2012, p. 797), like in the conditions of motor neuron

disease, progressive supra-nuclear palsy, or cortico-basal degeneration, would constitute a relevant source of evidence. Second, because activations in the motor system caused by the viewing of actions or manipulable artifacts were often bilateral (e.g., see for meta-analyses, Caspers, Zilles, Laird, & Eickhoff, 2010; Lewis, 2006), some authors argued that only *bilateral* damage to the motor system should impair the comprehension of actions (e.g., Rizzolatti et al., 2001). Actually, the vast majority of the apraxic patients who showed preserved comprehension of actions did have unilateral damage (Bartolo et al., 2001; Negri et al., 2007; Papeo et al., 2010; Pazzaglia, Smania, et al., 2008; Pazzaglia, Pizzamiglio, et al., 2008; Rumiati et al., 2001; but see Rapcsak et al., 1995). Third, it has been suggested that apraxic patients with normal comprehension of actions may have damage to parts of the action production system that are not involved in comprehension (e.g., Rizzolatti & Sinigaglia, 2010).

The study reported in this paper constituted an attempt to address these objections. We investigated the comprehension of actions and manipulable artifacts in a patient, JR, suffering from *extensive* and *bilateral* damage to the motor system in the context of corticobasal degeneration (CBD). Actually, CBD is an interesting condition to address these objections. First, CBD patients suffer from progressive praxic *and* motor disorders (Leiguarda et al., 2003; Leiguarda, Lees, Merello, Starkstein, & Marsden, 1994; Peigneux et al., 2001; Spatt, Bak, Bozeat, Patterson, & Hodges, 2002; Stamenova, Roy, & Black, 2009). Second, they present with a *bilateral* brain atrophy (Borroni et al., 2008; Dickson et al., 2002; Kouri et al., 2011) and decreased metabolism (Peigneux et al., 2001) affecting the posterior parietal, posterior frontal, and basal ganglia structures that underlie movement production.

A few previous studies had gathered data pertaining to our issue with CBD patients (see for review, Stamenova et al., 2009). However, the results were mixed and

ambiguous. Thus, Silveri and Ciccarelli (2007) asked 5 CBD patients to name 50 pictures of actions and 50 pictures of objects (25 "artificial objects" and 25 "natural objects") (task 1), 16 tools and 16 actions from the picture of a tool (task 2), and 16 actions from a pantomime (task 3). The results showed that the patients performed significantly below the control group in all tasks and sets of items and that they performed significantly worse for actions than objects in the two first tasks. Spatt et al., (2002) tested 5 CBD patients with a set of 20 manipulable artifacts in a naming and a variety of other comprehension tasks. They found that all patients performed below the controls' range of performance at most of the tasks. However, Cotelli and colleagues (Cotelli et al., 2006) reported ambiguous results. They found that a group of 10 CBD patients was significantly and disproportionately impaired in naming 60 pictures of actions in comparison to 60 pictures of objects and was worse in naming actions that involved hand movements (e.g., to squeeze) than actions that did not (e.g., to fly). However, the patients performed at ceiling in a word/picture matching task in which they were asked to point to the picture (among two) that corresponded to a spoken verb. Finally, two other studies found that CBD patients showed normal performance in a picture naming and a word/picture matching task with action and tool stimuli (Chainay & Humphreys, 2003; Graham, Zeman, Young, Patterson, & Hodges, 1999).

These discrepant results could arise from differences in the localization of brain damage, which, in some cases, may extend outside the motor system. It is remarkable that all the patients who had impaired performance with actions and manipulable artifacts in Spatt et al.'s (2002) and Silveri and Ciccarelli's (2007) studies also presented with other cognitive disorders, like dysexecutive, language, attentional, and/or visuospatial and perceptual disorders, which suggests that, in these cases, brain damage extended beyond the motor system. In such a context, the impairment with actions and manipulable

artifacts in naming and/or matching tasks cannot be ascribed without ambiguity to the motor system being damaged. The possibility that the deficit may be due to damage outside the motor system is all the more difficult to rule out that these studies did not report the performance of CBD patients with other categories of stimuli like animals, plants, and non-manipulable artifacts. Hence, one cannot rule out that these patients in fact suffered from a deficit that would impair any category of visually-presented stimuli (e.g., a visuo-perceptual or name retrieval deficit). As for studies that have reported CBD patients with preserved performance with actions and tools in naming and matching tasks, they also have limitations. Their material included too small sets of (often very familiar) actions and objects to provide compelling evidence for preserved comprehension. In Graham et al.'s study (1999), for instance, the naming task involved only 15 action pantomimes and 6 pictures of tools. In Chainay and Humphreys' study (2003), the patient was tested with only 16 pictures of tools. Similarly, in Cotelli et al. (2006), the patients' discrepant performance in the naming and the word/picture matching task with actions may be due to the word/picture matching task being not sensitive enough to detect a comprehension impairment (Cf. Breese & Hillis, 2004).

In this study, we carried out a three-year longitudinal investigation of a patient, JR, who presented with progressive movement production disorders in the context of otherwise preserved cognitive abilities. Furthermore, we assessed his comprehension of a large number of "motor-related" stimuli, i.e., actions (total number of 274 items) and manipulable artifacts (192 items in total), and also of matched sets of non-motor-related stimuli, i.e., animals, plants, and non-manipulable artifacts.

Comprehension of visually-presented action and object stimuli was primarily assessed in picture naming tasks. There is broad agreement that naming a visual stimulus entails not only that it has been accurately perceived but also comprehended, in the sense

that core conceptual features of the category of actions or objects (i.e., the concept) to which it belongs have been successfully (albeit mostly implicitly) accessed in memory. Also, the picture naming task is widely if not unanimously considered as the most sensitive task to detect impaired access to core and distinctive features of object concepts (e.g., Pobric, Jefferies, & Ralph, 2007; Woollams, Cooper-Pye, Hodges, & Patterson, 2008).[6]

The study was designed to test the two following predictions derived from MTC. First, damage to the motor system should selectively or disproportionately impair the comprehension of motor-related stimuli (actions and manipulable artifacts) in comparison to non-motor-related stimuli (animals, plants, and non-manipulable artifacts). Furthermore, among motor-related stimuli, those that are associated with more complex movements should be more impaired than those associated with less complex movements. Second, the progressive atrophy of the brain areas sustaining the motor system should cause not only a progressive decline of movement production abilities but also a progressive decrease of JR's ability to comprehend motor-related stimuli.

2. EXPERIMENTAL STUDY

2.1. Participants

JR is a right handed man with a Master's Degree in engineering (17 years of formal education) who worked as international consultant in a bank. He was 81 years-old when

[6] We had also included word-picture verification tasks in our protocol of investigation. We did so in order to be able to determine whether a naming deficit, if present, was due to an impairment at the word retrieval level or at the conceptual level of processing entailed in the naming task. Because no naming deficit was observed in JR whatever the set of stimuli or the period of assessment, and since the word-picture verification task is known to be less sensitive to detect a mild/moderate conceptual impairment than the naming task, we decided not to report here the results of the word/picture verification tasks, for the sake of brevity. Of course, the results obtained in the word-picture verification tasks led to the same conclusions as those drawn from the naming tasks and are available on request.

the study began in July 2009 and 84 when the study ended in 2012. JR first presented at the hospital in November 2008. At this time, he complained of walking difficulties and of difficulties to execute fine movements with the left hand (e.g., buttoning his shirt), which he reported to have increased since January 2008. The neurological examination noted the presence of a slight left limb dystonia. A brain Magnetic Resonance Imaging (MRI) performed in January 2009 showed a frank diffuse cortico-subcortical atrophy with clear parietal and slight right hemisphere predominance (see Figure 3.1). A neuropsychological examination in May 2009 concluded that JR had bilateral but left hand predominant ideomotor apraxia but no other sign of cognitive dysfunction. On the basis of the insidious unilateral onset, asymmetric course, and gradual progression of JR's limb apraxia and limb dystonia, JR's condition has been diagnosed as probable CBD by an experimented neurologist and according to international descriptions (Rinne, Lee, Thompson, & Marsden, 1994). One month after this diagnosis, JR was included in this study. In June 2010, in face of his increasing walking difficulties, JR was prescribed PROLOPA 3x125 mg/day. In September 2010, the treatment was inefficient and thus augmented (PROLOPA 3x250mg/day). In December 2010, the treatment was still inefficient and was stopped. The resistance of JR's movement disorder to dopaminergic medication is a further argument for the diagnosis of CBD.

Most of the tasks presented to JR were also presented to a group of healthy, control participants that differed across the tasks. The characteristics of each control group of participants will be presented with the tasks in which they participated. All participants had a normal or corrected to normal vision and no 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 written informed consent prior to the study.

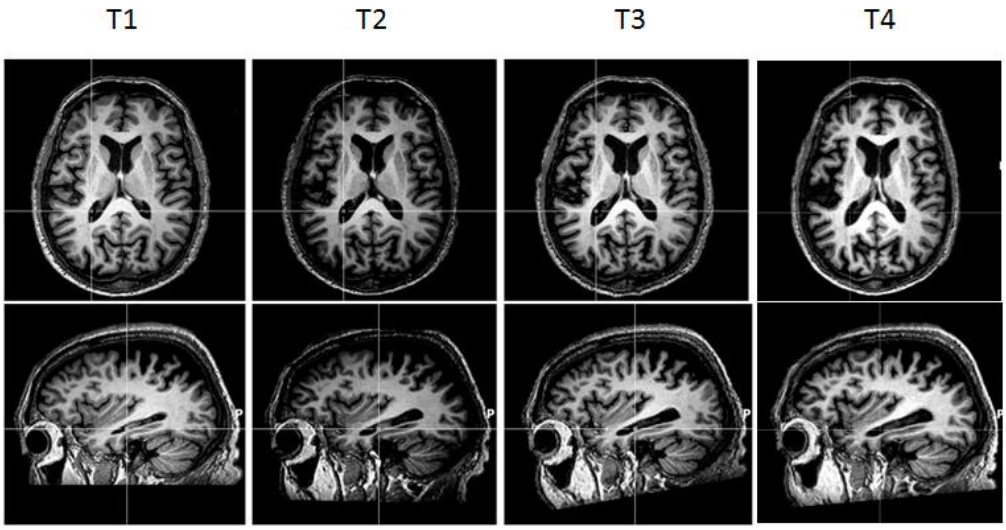

Figure 3.1| Transversal (top) and sagittal (bottom) sections of JR's brain at T1, T2, T3, and T4.

2.2. Longitudinal study of motor, praxic, and comprehension abilities in JR

The investigations of the longitudinal study took place in summer 2009, summer 2010, summer 2011, and spring 2012, at the patient's home, in sessions lasting between 60 and 90 minutes. These four periods of investigation will be labeled T1, T2, T3, and T4, respectively. At each period, four sets of examination were carried out: (1) Neuropsychological tests; (2) Voxel-based morphometry of the brain; (3) Tests assessing motor and praxic abilities; (4) Picture naming tasks evaluating the comprehension of motor-related and non-motor-related stimuli; (5) Tasks assessing praxis and comprehension with the same set of motor-related items.

We used Crawford and Howell's (1998) modified *t*-test to establish whether JR's performance differed significantly from that of the control group and we used Crawford and Garthwaite's (2007) Bayesian Standardized Difference Test (BSDT) to test whether the discrepancy in JR's performance between two sets of items was significantly different from the discrepancy between them in the control group. We also used the McNemar test (McNemar, 1947) to test whether JR's performance at different tests or sets of items significantly decreased over time.

2.2.1. Neuropsychological examination

Method

The battery of neuropsychological tests included a general measure of JR's cognitive functioning, as well as of his memory (auditory-verbal and visuo-spatial short-term, long-term, and working memory), executive functions, spatial abilities, visuo-perceptual skills, and access to the structural representation of objects (see the list of tests in Table 3.1). We also included a short language examination (see the language tasks in Table 3.2).

Results

As shown in Table 1, JR's performance remained in the normal range over the three-year period in most of the neuropsychological tests. Nonetheless, his performance was impaired in the Stroop task, his responses being significantly slower than controls' in the reading condition, already from T1, and in all the other conditions from T3. Moreover, interference indexes (interference condition minus naming condition) showed impaired processing either in accuracy or speed at T1, T2, and T3. The indexes were in the normal range at T4, but this could be due to JR being very slow in responding at that moment. In the Trail Making Test, JR also made significantly more errors than controls at T3 and could not terminate the task at T3 and T4. However, this impaired performance was likely due to impaired retrieval of the sequence of the alphabet itself. When asked to recite the alphabet after the Trail Making Test at T3 and T4, JR forgot many letters and was unable to reach the end of the alphabet. JR's ability to access the structural description system (Humphreys, Riddoch, & Quinlan, 1988) was slightly impaired at T3, and almost impaired at T4 when the global performance is considered. Finally, as shown in Table 3.2, JR became unable to write at T3.

Table 3.1. Neuropsychological exams in patient JR from T1 to T4.

TESTS	T1 JR's score	T1 JR vs. controls	T2 JR's score	T2 JR vs. controls	T3 JR's score	T3 JR vs. controls	T4 JR's score	T4 JR vs. controls
GLOBAL FUNCTIONING								
Minimal Mental State Examination [1]	30	n.a	29	n.a	30	n.a	28	n.a
SHORT TERM MEMORY								
Number span forward	5	*z* = -0.91	6	*z* = 0	5	*z* = -0.91	5	*z* = -0.91
Spatial Span forward [2]	5	*z* = -1	6	*z* = -0.33	n.a	n.a	6	*z* = -0.33
WORKING MEMORY								
Number span backward	5	*z* = 0.82	5	*z* = 0.82	5	*z* = 0.82	5	*z* = 0.82
Spatial Span backward [2]	5	*z* = 0	3	*z* = -1	n.a	n.a	5	*z* = 0
LONG TERM MEMORY								
RL/RI [3]								
Free recall 1	11	*z* = 1.58	7	*z* = -0.26	8	*z* = 0.20	11	*z* = 1.58
Free recall 2	11	*z* = 0.88	12	*z* = 1.32	7	*z* = -0.89	10	*z* = 0.44
Free recall 3	13	*z* = 1.16	8	*z* = -1.08	12	*z* = 0.71	13	*z* = 1.16
Delayed recall	11	*z* = 0.30	5	*z* = -2.42	9	*z* = -0.60	13	*z* = 1.18
Doors Test [4]								
Part A	12	P99	10	P75	9	P50	11	P90 - 95
Part B	6	P75	9	P95-P99	5	P50	5	P50
Total	18	P90	19	P95	14	P50	16	P75
EXECUTIVE FUNCTIONS								
Trail Making Test [5]								
Duration A	62	*z* = 0.72	52	*z* = 0.17	65	*z* = 0.89	n.a	n.a
Duration B	133	*z* = 0.29	97	*z* = - 0.41		Impossible	n.a	n.a
Duration B - A	71	*z* = 0.05	45	*z* = -0.6		n.a	n.a	n.a
Errors A	0	*z* = 0.13	0	*z* = 0.13	0	*z* = 0.13	n.a	n.a
Errors B	0	*z* = 0.33	4	*z* = -4.73		Impossible	n.a	n.a
Errors B - A	0	*z* = 0.41	4	*z* = -7.13		n.a	n.a	n.a
Fluency								
Letter fluency (P)	22	*z* = 0.01	19	*z* = -0.27	24	*z* = 0.2	14	*z* = -0.75
Category fluency (Animals)	27	*z* = -0.07	31	*z* = 0.41	34	*z* = 0.78	33	*z* = 0.67
Stroop Test [5]								
Duration								
Naming	81	*z* = -1.33	82	*z* = -1.41	90	*z* = -2.08	121	*z* = -4.67
Reading	59	*z* = -2.5	58	*z* = -2.33	65	*z* = -3.5	81	*z* = -6.17
Interference	171	*z* = -1.5	166	*z* = -1.34	200	*z* = -2.41	201	*z* = -2.44
Errors								
Naming	1	*z* = -3.14	0	*z* = 0.31	0	*z* = 0.31	0	*z* = 0.31
Reading	1	*z* = -7.54	0	*z* = 0.15	0	*z* = 0.15	0	*z* = 0.15
Interference	5	*z* = -7.05	3	*z* = -3.97	1	*z* = -0.89	0	*z* = -0.64
Interference index								
Duration	90	*z* = -1.28	84	*z* = -1.04	110	*z* = -2.08	80	*z* = -0.88
Errors	4	*z* = -5.10	3	*z* = -3.71	1	*z* = -0.93	0	*z* = 0.46
SPATIAL ABILITIES								
Line bisection [6]								
20 cm	-4 mm	*z* = - 0.74	-4 mm	*z* = - 0.74	+5 mm	*z* = - 0.96	+5mm	*z* = - 0.96
5 cm	+0.5 mm	*z* = - 0.2	0 mm	*z* = 0.06	0 mm	*z* = 0.06	+1mm	*z* = - 0.56
Bell test [6]								
Duration	183	*z* = -0.82	126	*z* = 0.15	200	*z* = -1.11	163	*z* = -0.47
Miss	2	*z* = 0.24	1	*z* = 0.69	1	*z* = 0.69	2	*z* = 0.24
VISUAL PROCESSING								
B.O.R.B [7]								
Minimal feature view	25	*z* = 0.85	23	*z* = -0.15	25	*z* = 0.85	25	*z* = 0.85
Object/Non-Object decision								
A: Hard	26	*z* = -0.45	24	*z* = -1.36	24	*z* = -1.36	25	*z* = -0.91
B: Hard					22	*z* = -0.72	22	*z* = -0.72
B: easy					28	*z* = -1.79	28	*z* = -1.79
A: Easy					27	*z* = -0.79	29	*z* = 0
Global performance					101	*z* = -2.4	104	*z* = -1.9

[1] Folstein, Folstein, and McHugh (1975); French norms from Derouesné et al. (1999); [2] Smirni, Villardita, and Zappala (1983); [3] Van der Linden et al. (2004); [4] Baddeley, Emslie, and Nimmo-Smith (1994); [5] Reitan (1955); French norms from Meulemans (2008); [6] Gauthier, Dehaut, and Joanette (1989); French norms from Rousseaux et al. (2001); [7] Riddoch and Humphreys (1993)

Table 3.2. Language examinations in patient JR from T1 to T4.

TESTS	T1	T2	T3	T4
REPETITION				
Regular nouns	20	20	20	19
Regular verbs	20	20	20	20
Pseudo-words	16	20	20	19
READING				
Regular nouns	20	20	20	20
Regular verbs	20	20	20	20
Irregular nouns	20	18	18	20
Pseudo-words	19	17	19	19
WRITING				
Regular nouns	20	20	n.a	n.a
Regular verbs	20	20	n.a	n.a
Irregular nouns	17	19	n.a	n.a
Pseudo-words	20	20	n.a	n.a
AUDITORY LEXICAL DECISION TASK				
Nouns	36/36	36/36	n.a	36/36
Pseudo-nouns	34/36	34/36	n.a	34/36
Verbs	36/36	36/36	n.a	36/36
Pseudo-verbs	33/36	36/36	n.a	36/36
PICTURE NAMING TASK				
Lexis[1]	54/64 (z = 0.6)			51/64 (z = 0)

[1]de Partz, Bilocq, De Wilde, Seron, and Pillon (2001).

2.2.2. Voxel-based morphometry of the brain

This technique of brain analysis was used to measure JR's grey matter volume loss in several regions within the motor system from T1 to T4 in comparison with volume loss reported in healthy subjects of the same age (Fjell et al., 2009).

Method

Magnetic resonance imaging scanning was performed on a 3T Philips Achieva scanner provided with a eight channels head coil at the *Université catholique de Louvain* and *Cliniques universitaires Saint-Luc*, Brussels. Fast gradient echo (MP-RAGE) scans were obtained according to the following protocol: one axial acquisition, FOV = 230, Matrix = 284 x217, Resolution = 0.81x0.95x1 mm, TR = 9.3 ms, TE = 4.6 ms, Flip angle = 8. After image processing procedures (Fennema-Notestine et al., 2009), we gathered data about the volume of subcortical and the thickness of cortical parts of the

motor system. The scans were segmented as described by Fischl et al. (2002, 2004) to yield volumetric data for basal ganglia (caudate, pallidum, putamen). The cortical surface was reconstructed using a semi-automatic method (Fischl & Dale, 2000; Salat et al., 2004) and parcellated following Fischl et al. (2004) in 34 cortical ROIs, which anatomical borders may be found in Desikan et al. (2006). Among the available ROIs, 8 cortical regions within the motor system were selected, i.e., the caudal middle frontal gyrus, the pars opercularis and triangularis, the precentral gyrus, the superior frontal gyrus, the inferior parietal lobe, the supramarginal gyrus, and superior parietal gyrus.

Results

As shown in Figure 3.2, grey matter volume loss in JR largely exceeded that of the healthy elderly control participants reported by Fjell et al. (2009) in most of the ROIs. Volume loss was the largest in the basal ganglia (mean = -6.06%) followed by the posterior frontal ROIs (mean = -4.88%) and the parietal ROIs (mean = -2.73%). In the basal ganglia, the volume loss exceeded largely the normal rate in all the ROIs except in the left putamen and there was a right hemisphere predominance. In the posterior frontal ROIs, the largest volume loss was observed in the left caudal middle frontal gyrus, the left precentral gyrus and the bilateral pars opercularis and triangularis (all > 5%). Volume loss was weaker in the right precentral gyrus and did not exceed the normal one in the right caudal middle frontal gyrus. Finally, volume loss in the parietal ROIs concerned mainly the bilateral supramarginal gyri and the left superior parietal lobe. In contrast, the inferior parietal and right superior parietal lobe showed less volume loss.

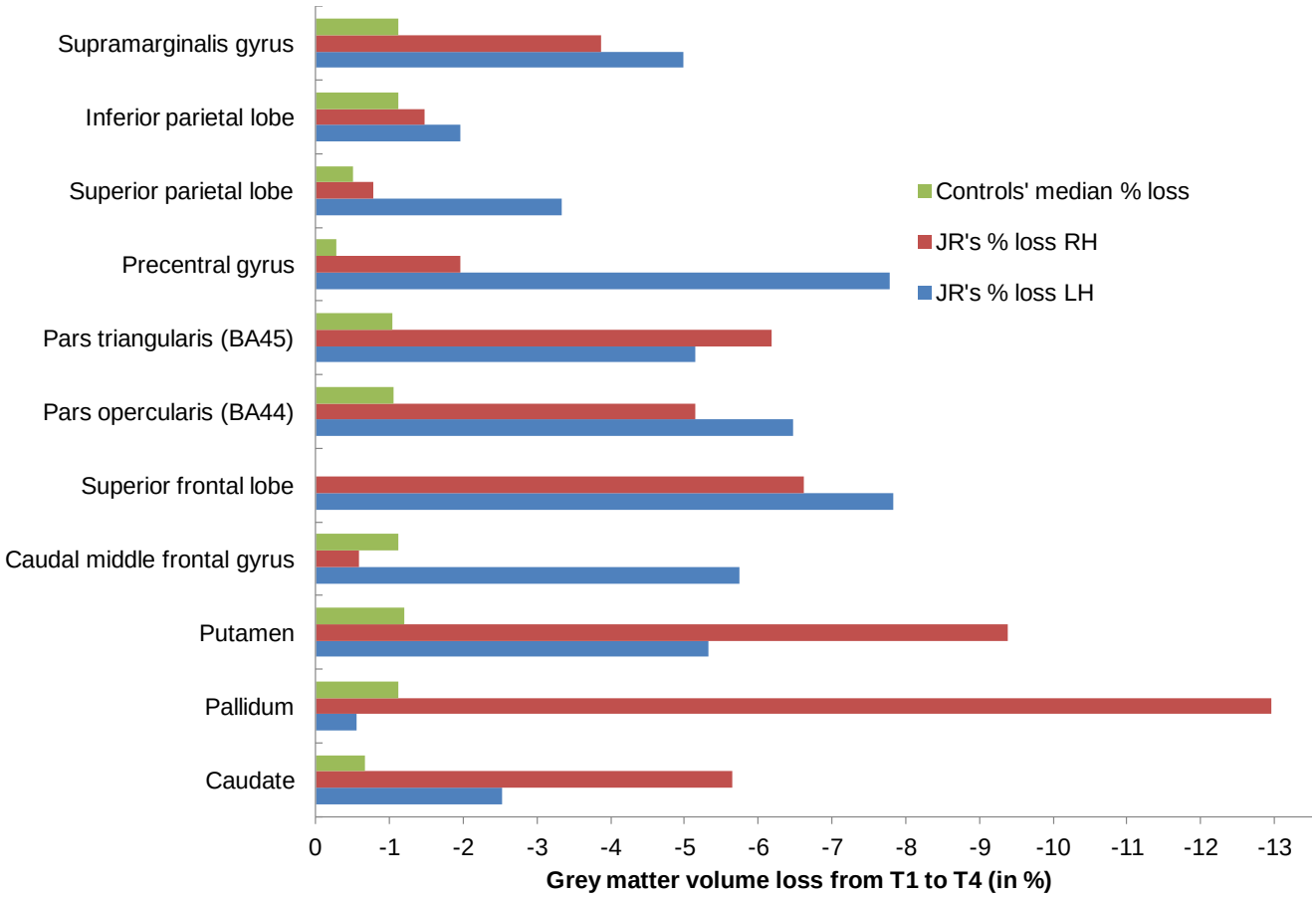

Figure 3.2| JR's percentage of volume loss between T1 and T4 in the motor system ROIs, for the left (red) and right (blue) hemisphere. Green bars represent the normal volume loss in the same ROIs in healthy elderly control participants (Mean age= 75.6) calculated from the annual rate reported by Fjell et al. (2009).

2.2.3. Motor and praxis examination

2.2.3.1. Questionnaires of everyday-life activities

Method

This part of the motor examination was presented to JR in 2009, 2011, and 2012 and was composed of two questionnaires in which JR was asked to report on his functional independence in daily activities. The index of independence in *Activities of Daily Life* (ADL, Katz, Ford, Moskowitz, Jackson & Jaffe, 1963) included six activities, namely, bathing, dressing, going to the toilet, transferring, continence, and feeding, scored from 1

to 4 (where 1 = independent and 4 = total dependence). The *Instrumental Activities of Daily Living Scale* (IADL, Lawton & Brody, 1969) was composed of eight activities, i.e., telephoning, shopping, food preparation, housekeeping, laundering, use of transportation, use of medicine, and financial behavior, rated from 1 to 3 (where 1 means no particular difficulty, 2 a need of help and 3 means a total inability).

Results

JR was independent for all everyday-life activities at T1 (ADL=6; IADL=11). At T3, he needed help for most activities such as to wash the lower part of his body, to dress, to stand up, to go to the toilet, to prepare food, to do housekeeping, and to use means of transportation (ADL=10; IADL=14). At T4, he needed help for all the activities and started to use a rolling-chair (ADL=16; IADL=20).

2.2.3.2. Upper limb motor tests

Method

This battery of tests was presented to JR at T1 and T4 by an occupational experienced clinician. JR's handgrip strength was assessed with a *Jamar Hydraulic Hand Dynamometer*. JR's gross hand dexterity was tested with the *Box and Block Test* (Mathiowetz, Volland, Kashman, & Weber, 1985) which scores the number of blocks of 1 cm (3/8 in.) that the patient is able to grasp with one hand in the ipsilateral compartment of a box, displace over a 15.2 cm (6 in.) partition, and release in the contralateral compartment of the box in 60 sec. Finally, his finger dexterity was examined with the *Purdue Pegboard Test* (Tiffin & Asher, 1948) which scores the maximal number of small pegs that the patient is able to insert into the small holes of a board in 30 seconds using only one hand.

Results

As shown in Table 3.3, JR's hand and finger dexterity was impaired at T1, decreased from T1 to T4 and was always worse for the left hand. In contrast, his grip strength was in the normal range and showed no sign of asymmetry at T1, although it subsequently decreased predominantly for the left hand, that was selectively impaired at T4.

Table 3.3. Standardized motor tests in patient JR in T1 and T4.

TESTS	T1		T4	
	JR's score	JR vs. controls	JR's score	JR vs. controls
Strength (Jamar hand dynamometer)[1]				
Right hand	35 kg	*z* = -1.46	30kg	*z* = -1.7
Left hand	30 kg	*z* = -1.47	1.5kg	*z* = -3.15
Hand dexterity (Box & Block Test)[2]				
Right hand	43	*z* = -2.82	23	*z* = -5.63
Left hand	30	*z* = -3.73	10	*z* = -6.11
Finger dexterity (Purdue Pegboard)[3]				
Right hand	9	*z* = -3.45	6	*z* = -5.05
Left hand	5	*z* = -5.69	1	*z* = -8.47

[1] Mathiowetz et al. (1985); [2] Mathiowetz, Volland, Kashman, and Weber (1985); [3] Tiffin and Asher (1948).

2.2.3.3. Battery of limb apraxia

Method

JR's performance in this battery of tasks was compared to that of 15 right-handed elderly control participants (eight men; Mean age = 68.4 years) whose performance was reported in Peigneux et al. (2001). The battery was presented to JR at each period of assessment. It was composed of a gesture recognition task, a gesture imitation task, and a pantomime execution on verbal command task. In the gesture recognition task, the patient was presented with the video clip of 60 gestures, 40 uni-manual and 20 bi-manual,

equally divided in meaningful [7] and meaningless gestures. Meaningful and meaningless gestures were matched in movement components (whole limb or hand/finger complex), kinematic (dynamic or static gestures), and global complexity. The patient was asked to decide, for each gesture, whether it referred to a known or an unknown gesture. In the gesture imitation task, JR was asked to imitate the 40 uni-manual gestures (20 meaningful, 20 meaningless). Each trial started with the video display of a gesture that JR was asked to watch carefully "in order to reproduce exactly the same arm, hand, and finger movements and positions". Imitation was allowed when the video clip ended. In the pantomime execution on verbal command task, which probed the 20 uni-manual, meaningful gestures, the examiner orally named the gesture to-be-mimed (e.g., "to comb") and JR was asked to mime it as well as possible. For transitive gestures, he was asked to mime the action "as if he really held the tool". The order of the tasks, hands, and sets of items is shown in Table 3.4 between brackets. JR's performance was videotaped and analyzed according to Peigneux and Van der Linden's (2000) scheme (adapted from Rothi, Ochipa, & Heilman, 1997) which distinguishes content, spatial, temporal, and "other" errors. A gesture was considered incorrect if it involved any of these types of errors.

Results

The results are displayed in Table 3.4. JR's performance in gesture recognition was within the normal range at every period. As regards the motor production tasks, JR was already impaired in imitating meaningful gestures with the left hand and in executing pantomimes on verbal command with both hands at T1. His performance in imitating

[7] Meaningful gestures included both transitive (N= 12) and intransitive (N= 8) actions but, here, we will not report separately the results for each type of gestures because normal controls' performance for each type was not available.

meaningless gestures appeared to be preserved in T1, as indicated by his z score. However, in this task, controls' performance is very poor (mean = 56% correct) and shows high variability (SD = 15.5%), which probably makes this task not sensitive enough to detect moderate impairments. From T1, JR's performance decreased sharply (and significantly in most tasks) throughout the subsequent periods of assessment. From T3, his performance became significantly impaired in all the production tasks, types of gestures, and hands. At T4, he was unable to perform any gesture with the left hand and he accurately executed only 35% of the pantomimes on verbal command and, respectively, 25% and 10% of the meaningful and meaningless gestures on imitation. Throughout the three-year period, he consistently showed worse performance with the left compared to the right hand in tasks involving meaningful gestures while this difference was not or less observed in the scores of the meaningless gesture imitation task. However, his imitation of meaningless gestures with the right hand was consistently closer from the model than his imitation with the left hand. Thus, when all errors were counted, he made a total of 23, 25, and 35 errors with the left hand and of 15, 18, and 24 errors with the right hand at T1, T2, and T3, respectively (see Table 3.5).

As shown in Table 3.5, the analysis of JR's gesture production errors revealed a predominance of spatial errors and some temporal errors. No content errors were observed, except a partial perseveration in the imitation of right hand gestures at T4. The spatial errors consisted mainly in difficulties to position and orient the hands correctly with respect to the body, in an apparent difficulty to coordinate the independent movement of different fingers, in wrong digital configurations, in reduced movement amplitude, and in producing movement with the wrong articulator (e.g., hammering movement done by shoulder rather than elbow and wrist movements). The temporal errors concerned mainly movement slowing and speed irregularities. On the whole, JR's

pattern of performance and errors in the gesture production tasks suggested that, by reference to Rothi et al. (1991) praxis model, he had an impairment at both the gesture representational level and the "innervatory patterns" level of the praxis system.

Table 3.4. Praxis examination in patient JR from T1 to T4. Percentage of correct responses by condition.

TESTS	T1	T2	T3	T4	T1/last session McNemar test χ^2
GESTURE RECOGNITION TASK					
Discrimination[1]	92% (z = 1.22)	95% (z = 1.91)	92% (z = 1.22)	82% (z = -0.87)	2.5
DELAYED IMITATION					
Meaningful gestures					
Right hand (3)	75% (z = -1.81)	60% (z = -3.74)	55% (z = -4.39)	25% (z = -8.13)	5.78*
Left hand (5)	60% (z = -3.74)	40% (z = -6.33)	10% (z = -10.20)	n.t.	8.1**
Meaningless gestures					
Right hand (4)	40% (z = -1.03)	30% (z = -1.68)	20% (z = -2.32)	10% (z = -2.97)	3.12$^{\bullet}$
Left hand (6)	45% (z = -0.71)	30% (z = -1.68)	10% (z = -2.97)	n.t.	5.14*
PRODUCTION ON VERBAL COMMAND					
Right hand (1)	70% (z = - 5.16)	70% (z = -5.16)	55% (z = -9.04)	35% (z = -14.20)	4*
Left hand (2)	55% (z = - 9.04)	35% (z = -14.20)	20% (z = -18.07)	n.t.	3.27$^{\bullet}$
GLOBAL PERFORMANCE IN EXECUTION					
Right hand	62% (z = -2.37)	53% (z = -3.44)	50% (z = -3.87)	24% (z = -7.26)	15.61**
Left hand	53% (z = -3.44)	35% (z = -5.81)	13% (z = -8.61)	n.t.	30.03**

Brackets = Order of passation. [1] In comparison to 10 control participants. n.t. = not tested. $^{\bullet}$ $p < 0.1$; * $p < 0.05$; ** $p < 0.01$

Table 3.5. Praxis examination in patient JR from T1 to T4. Distribution of errors by condition.

	T1				T2				T3				T4			
	CE	**TE**	**SE**	**Other**	**CE**	**TE**	**SE**	**Other**	**CE**	**TE**	**SE**	**Other**	**CE**	**TE**	**SE**	**Other**
DELAYED IMITATION																
Meaningful gestures																
Right hand	0%	20%	80%	0%	0%	40%	60%	0%	0%	18%	82%	0%	4%	22%	74%	6%
Left hand	0%	33%	58%	8%	0%	29%	65%	6%	0%	22%	74%	3%	0%	0%	0%	100%
Meaningless gestures																
Right hand	0%	22%	74%	4%	0%	17%	83%	0%	0%	33%	67%	0%	0%	6%	82%	12%
Left hand	0%	13%	67%	20%	0%	20%	76%	4%	0%	14%	77%	8.5%	0%	0%	0%	100%
PRODUCTION ON VERBAL COMMAND																
Right hand	0%	0%	83%	17%	0%	17%	83%	0%	0%	25%	62%	12.5%	0%	24%	71%	6%
Left hand	0%	0%	91%	9%	0%	27%	67%	7%	0%	32%	64%	4%	0%	0%	0%	100%

CE: Content error; TE: Temporal error; SE: Spatial error

2.2.4. Comprehension of motor-related vs. non-motor-related stimuli

JR's comprehension of motor-related and non-motor-related stimuli was assessed in two picture naming tasks presented at each period: (1) the "Animal, Manipulable Artifact, Plant, and Action" (AAPA) naming task, which included two categories of motor-related stimuli (human actions and manipulable artifacts) and two categories of non-motor-related stimuli (plants and animals); (2) the "Artifacts/Actions 1" (AA1) picture naming task, which included pictures of human actions, manipulable artifacts, and non-manipulable artifacts.

Table 3.6. Mean and standard deviation of the spoken word frequency, concept familiarity, imageability, and age of acquisition for the various subsets of items in the naming tasks used in the study.

Naming task	N	Spoken word frequency [1]	Familiarity [2]	Imageability [3]	Age of acquisition
AAPA					
Animals	24	10.36 (10.76)	2.67 (0.81)	4.44 (0.43)	2.44 (0.57)
Plants	24	6.82 (7.27)	2.87 (0.76)	4.51 (0.40)	2.52 (0.56)
Manipulable artifacts	22	5.59 (6.19)	2.79 (1.06)	4.41 (0.38)	2.69 (0.71)
Human actions	24	6.93 (8.54)	2.87 (0.81)	4.22 (0.34)	2.38 (0.57)
Artifacts/Actions 1 (AA1)					
Manipulable artifacts	16	5.63 (8.12)	2.79 (0.64)	4.56 (0.56)	n.a.
Non-manipulable artifacts	16	11.25 (16.80)	3.01 (1.33)	4.62 (0.32)	n.a.
Actions	32	40.61 (61.94)	3.20 (0.61)	3.75 (0.46)	n.a.
Production/comprehension					
Tools	50	11.39 (25.28)	2.86 (1.07)	4.29 (0.53)	2.77 (0.66)
Actions	20	39.22 (94.81)	n.a.	n.a.	n.a.
Artifacts/Actions 2 (AA2)					
Actions	150	14.68 (20.34)	2.45 (0.69)	n.a	n.a
Manipulable artifacts	54	4.58 (9.59)	2.53 (0.83)	n.a	n.a
Non-manipulable artifacts	51	23.28 (50.97)	2.65 (1.10)	n.a	n.a

[1] Number of lemma occurrences per million in a corpus of subtitles of films (New, Brysbaert, Pallier & Veronis, 2007); [2] From Alario and Ferrand (1999), Bonin, Peereman, Malardier, Meot, and Chalard (2003), and Bonin et al. (2004) for the items of the "Motor-related/non motor-related concepts" naming task; rated on a five point scale (1=low, 5=high familiarity) by 20 subjects (mean age=35.95) for the items of the Artifacts/Actions battery 1 and by 23 subjects (Mean age = 23) on a similar scale for the items of the Artifacts/Actions battery 2. [3] From Alario and Ferrand (1999), Bonin et al. (2003), and Bonin et al. (2004). n.a=non-available

All the picture stimuli were colour photographs with no context. The photographs of actions depicted all the persons, objects, or instruments typically involved in the action. The characteristics of nouns and verbs corresponding to these stimuli in terms of spoken word frequency, concept familiarity, imageability, and age of acquisition, when available, are displayed in Table 3.6. The photographs were presented in full-screen mode (15.4 inch screen) using PowerPoint software. Each task was preceded by a few examples designed to familiarize the patient with the task.

2.2.4.1. The "Animal, Manipulable Artifact, Plant, and Action" (AAPA) picture naming task

Method

This task was presented to JR and to 12 control participants matched with him in gender, age [mean = 70.33; modified t (11) = 1.23, p = 0.24], and years of education [mean = 14.42; modified t (11) = 1, p = 0.34]. All control participants achieved at least 21/22 on a shortened, twenty-two item version of the MMSE (mean = 21.5).

This naming task included 94 picture stimuli divided in 46 motor-related (24 actions and 22 manipulable artifacts) and 48 non-motor-related (24 animals and 24 plants) stimuli. The action set contained actions performed with different body parts (14 upper limb actions, 7 mouth actions, 3 whole-body actions). Among them, 16 actions were made by an actor with an artifact (e.g., sawing) and 8 were bodily actions (e.g., swimming). Manipulability of the artifacts was estimated by three independent judges who were asked to tell whether these artifacts, embedded in whole set of 120 other artifacts, entailed manipulation, that is, whether the utilization of the object entailed specific and fine hand movements (Saccuman et al., 2006). The 22 manipulable artifacts reached 100% agreement across the judges. The four categories of items were matched

for spoken name frequency [F (3, 90) = 1.39, p = 0.25], age of acquisition [F (3, 90) = 1.14, p = 0.34], concept familiarity [F (3, 90) < 1], and imageability [F (3, 90) = 2.40, p > 0.05].

Participants were presented with the 94 photographs in one session and asked to name them within 20 seconds. The naming of actions was elicited by the beginning of a sentence, i.e., "*il ou elle est en train de"* which requires being completed by the infinitive form of a verb ("*en train de* $Verb_{inf}$" is the French equivalent of English "$Verb_{ing}$").

Results

Both the target naming responses and acceptable alternatives were considered as correct. Acceptable alternatives were synonyms, nominal or verbal phrase (e.g., "small dog" for "dog"), more specific words and, for actions, a response referring to a subcomponent of the action and being consistent with the picture stimulus (e.g., "rincing" instead of "washing"). The results are displayed in Figure 3.3. JR's performance in naming actions and manipulable artifacts was within the normal range of performance at T1 [both modified *t*s (11) > -0.2; both *p*s > 0.85], remained within the normal range in all the following periods of assessment [all modified *t*s (11) > -1.23; all *p*s > 0.2], and did not significantly decrease over time (both McNemar tests, χ^2 < 1.33; both *p*s > 0.25). Unexpectedly, JR's performance was consistently and significantly below the control group's performance in naming animals [all modified *t*s (11) < -2.73; all *p*s < 0.05]. In naming plants, JR's performance was impaired at the second period [modified t (11) = -3.12, p < 0.01] but was within the normal range at the three other periods [all modified *t*s (11) > -1.8, all *p*s > 0.1]. Nevertheless, as for the motor-related stimuli, his performance for animals and plants did not significantly decrease from T1 to T4 (both McNemar tests, χ^2 < 1.33; both *p*s > 0.25).

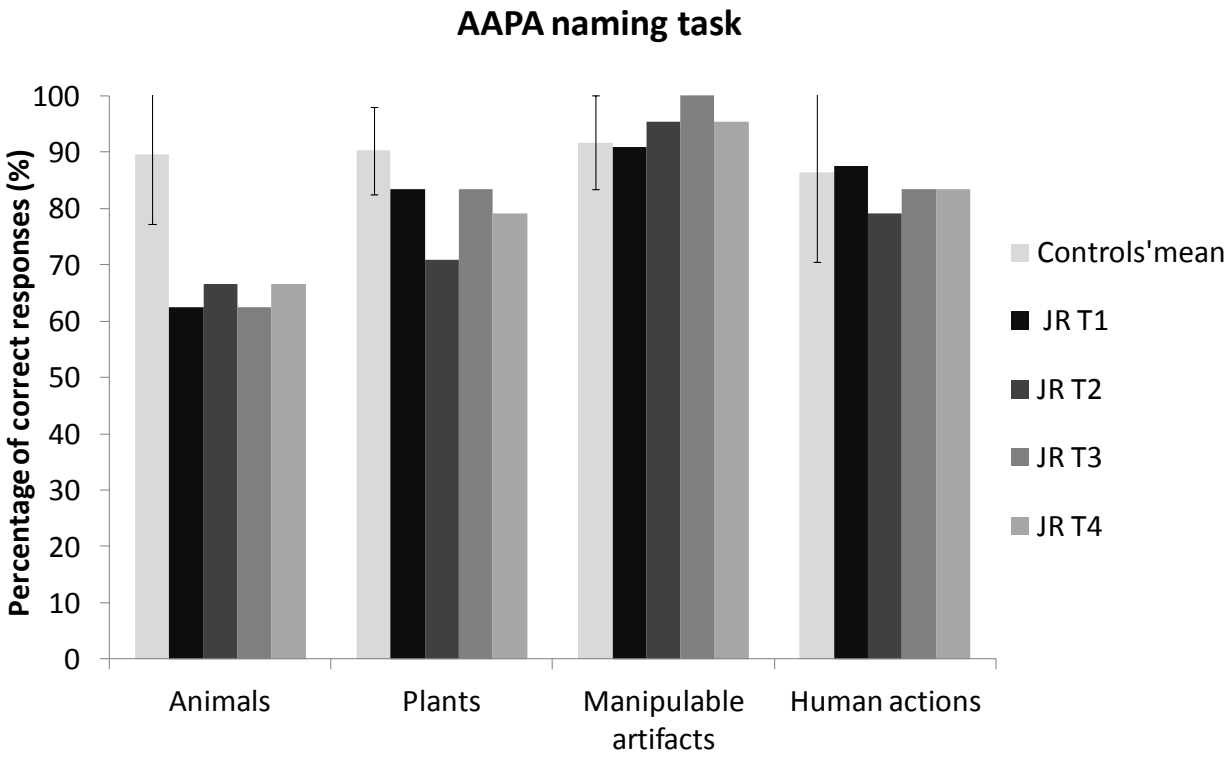

Figure 3.3| JR's and control participants' percentage of correct responses at the "AAPA naming task". Error bar = range.

2.2.4.2. The "Artifacts/Actions 1" (AA1) picture naming task

Method

This task was presented to JR and to a group of 8 younger control participants [mean = 62.62; modified t (7) = 10.87, $p < 0.01$] matched with him in gender and years of education [mean = 16.25; modified t (7) = 1, $p = 0.35$], taken from a previous study (Vannuscorps & Pillon, 2011).

The stimuli included 32 pictures of human actions, 16 pictures of manipulable artifacts, and 16 pictures of non-manipulable artifacts. The action set contained actions performed with different body parts (17 upper limb actions, 5 mouth actions, 10 whole body actions). Among them, 11 actions were made by an actor with an artifact (e.g., hammering) and 8 did not include any artifact (e.g., dancing). Manipulability of the

artifacts was estimated by three independent judges who were asked to tell whether a pre-selected set of 60 artifacts entailed manipulation, i.e., whether the utilization of the object entailed specific and fine hand motion (Saccuman et al., 2006). Only items unanimously judged as manipulable or non-manipulable were selected. The three sets of items were matched in concept familiarity [F (2, 61) = 1.28, p = 0.29]. However, actions had significantly lower imageability and higher spoken word frequency than both categories of artifacts [all ts (30) > 2.2; all ps < 0.01], which did not significantly differ with respect to these variables, however [both ts (30) < 1.2; both ps > 0.2]. The task was presented with the same procedure as that used in the "AAPA" naming task.

Results

The scoring criteria were the same as for the "AAPA" naming task. The main results are displayed in Figure 3.4. JR's performance was within the range of the controls'

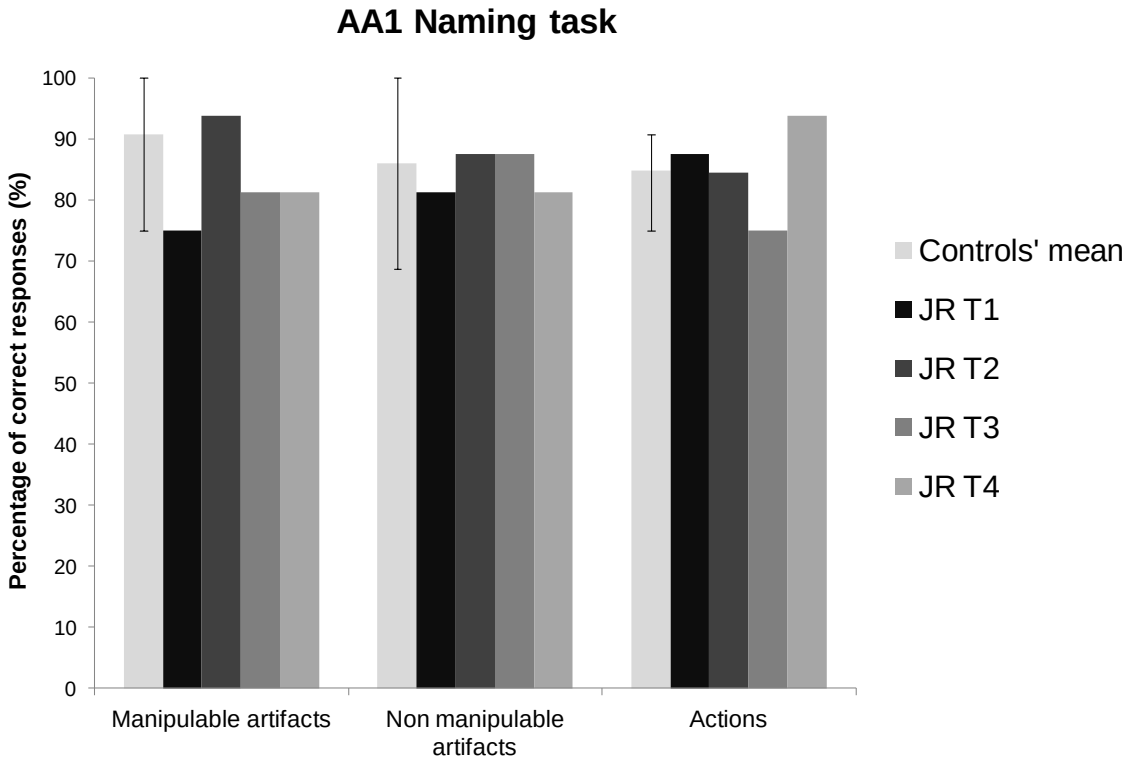

Figure 3.4| JR's and control participants' percentage of correct responses at the naming task of the "Artifacts/Actions 1" battery. JR's results are displayed for all periods of assessment from T1 to T4. Error bar = range.

performance for the three categories of stimuli and at the four periods of assessment [all modified *t*s (7) > -2; all *p*s > 0.05]. Furthermore, his performance did not significantly decrease from T1 to T4 (all McNemar tests, $\chi^2 < 0.25$; all *p*s > 0.6).

2.2.5. Praxis and comprehension of the same set of motor-related items

Method

The material consisted in a "Production/Comprehension" battery, which contained a picture naming task, a picture association task assessing function vs. manipulation knowledge, an object/manipulation matching task, and a pantomime on verbal command task, all probing the same set of 50 manipulable artifacts. In addition, there was a naming task and a pantomime on verbal command task probing the same set of 20 instrumental actions.

In the naming task, JR was presented in one session with the 50 manipulable artifacts and the 20 instrumental actions (manual actions all performed with a manipulable artifact) and asked to name them. This task has not been presented to a control group.

The picture association task was presented to JR and to a group of 8 younger control participants [mean = 62.62; modified t (7) = 10.87, $p < 0.01$] matched with him in gender and years of education [mean = 16.25; modified t (7) = 1, p = 0.35], taken from a previous study (Vannuscorps & Pillon, 2011). This task assessed JR's ability to explicitly retrieve knowledge about the function of the artifacts (function condition) and knowledge about the way they are conventionally manipulated (manipulation condition). Furthermore, the manipulation condition in this picture association task allows us to assess the representational component of the praxis system without requiring any movement execution. Participants were presented with a picture of a manipulable artifact (probe item) with, below it, an array of three pictures of manipulable artifacts. In the

function condition, they were asked to point to the artifact that, within the array, has a function similar to that of the probe; in the manipulation condition, they were asked to point to the artifact that is manipulated in a similar way as the probe. The same material was used in both conditions, that is, the same probe items and the same array of choices were displayed in the same order in both the function and the manipulation conditions. This allowed us to match perfectly the material used in both conditions. Thus, in both the function and the manipulation condition, the probe item (e.g., a cigarette lighter) was presented with, below it, a picture of an object having a similar function (e.g., a match), a picture of an object that is manipulated in a similar way (e.g., a chronometer), and a visually-related object (e.g., a salt shaker). However, in 28% of the trials, the same picture served as the target response for both the function and the manipulation conditions, the two other pictures in the array being two visually-related foils (e.g., the probe item was a tiller, the function and manipulation target response was a steering wheel and the two visually-related foils were a ring and a lifebuoy). These trials were designed in order to discourage the participants to discard the picture he chosen in the first presentation of the probe when presented with it the second time. The probe artifacts, the function and the manipulation targets, and the visually-related foils were matched in imageability [F (2, 47) < 1], age of acquisition [F (2, 47) < 1], and familiarity [F (2, 47) < 1]. The participants underwent the function and the manipulation conditions in an ABBA order: they performed the first half of the trials in the function condition and the second half of the trials in the manipulation condition in one session and, in another session, the order was reversed.

The object/manipulation matching task assessed JR's knowledge of how an artifact is conventionally manipulated, here again, without requiring any movement execution. Four video clips were created for each of the 50 manipulable artifacts. One video clip

corresponded to the pantomime of the correct use of the artifact, another corresponded to the use of a semantically related item (semantic foil, e.g., the foil for the hammer was the pantomime of a screwdriver), another to the use of the artifact with a wrong digital configuration (digital configuration foil, e.g., hammering with only two fingers holding the hammer), and another to the use of the artifact with a wrong movement (movement foil, e.g., hammering with faster up than down movements). Three lists were created, each containing a clip of the 50 correct pantomimes associated with a clip of one of their three foils. The different kinds of foils were similarly distributed in the three lists (in each list, 17 foils of one kind and 18 of the two other kinds). The three lists were proposed to JR in three different sessions. A trial comprised the following sequence of events: (1) The photograph of an artifact was displayed on a computer screen until the patient agreed to move to the next step; (2) Two video clips showing a man pantomiming the use of an object were subsequently presented on the left and right side of the screen. The left video clip was launched first by the experimenter and, when it was terminated, the right one was launched. JR was asked to decide which video clip depicted the correct manipulation of the artifact. He was also asked to wait the end of the second video clip before responding. There was no time limit and JR was allowed to watch again any video clip as many times as he wanted.

In the pantomime on verbal command task, JR was asked to pantomime the use of the 50 artifacts and to pantomime the 20 actions from their spoken names with his right (less affected) hand. His performance was videotaped and analyzed according to Peigneux and Van der Linden's (2000) scheme. This task has not been presented to a control group and not presented to JR at T4.

Results

The main results for actions are displayed in Figure 3.5a. For the naming task, the scoring criteria were the same as those used in the naming tasks described above. JR's naming performance was relatively high at T1 and was the same at T4. In contrast, in the pantomime on verbal command task, JR's performance was already poor at T1 and then decreased from T1 to T3 (McNemar test, $\chi^2 = 3.5$, $p = 0.06$).

The results for manipulable artifacts are displayed in Figure 3.5b. At T1, JR named correctly 86% of the manipulable artifacts and his performance was the same at T4. In the picture association task, as far as function knowledge is considered, JR's performance was always within the normal range of performance [all modified *t*s (7) > -1.6; all *p*s > 0.15] and did not significantly decrease between 2009 and 2012 (McNemar test, $\chi^2 < 1.12$, $p > 0.25$). However, when probing manipulation knowledge, JR's performance was in the normal range at T1 [modified t (7) = -1, $p = 0.35$], almost significantly below the controls' at T2 [modified t (7) = -1.97, $p = 0.09$], and significantly below the controls' at T3 and T4 [both modified *t*s (7) = -6.28; both *p*s < 0.001]. This decrease of performance was significant (McNemar test, $\chi^2 = 6.67$, $p < 0.01$). A similar decrease of performance was observed in the object/manipulation matching task (McNemar chi² = 3.76, $p = 0.05$). In this task, JR made numerous errors that consisted in choosing the finger configuration foil (8%, 14%, and 26% of the trials at T1, T3, and T4, respectively) or the movement foil (12%, 28%, and 32% of the trials at T1, T3, and T4, respectively), but rarely the semantic foil (4%, 6%, and 4% of the trials at T1, T3, and T4, respectively). The increase of errors on finger configuration and movement foils from T1 to T4 was significant (both McNemar chi² > 5, $p < 0.05$). In the pantomime on verbal command task, 13 artifacts which pantomime of use needed a stand-up position were removed from the analysis due to JR's balance problems (e.g., the rake, the fork). At T1, JR performed correctly 70.27%

of the pantomimes but only 19% at T3, a decrease of performance that was significant (McNemar test, $\chi^2 = 15.43$, $p < 0.01$). In all sessions, errors were mainly spatio-temporal inaccuracies (65% at T1; 88.57% at T2; 94.54% at T3) resulting mostly from wrong finger configuration, hand orientation or position in respect to the body, and from the movement being elicited by the wrong articulator (often from the shoulder only while the wrist and the elbow did not move).

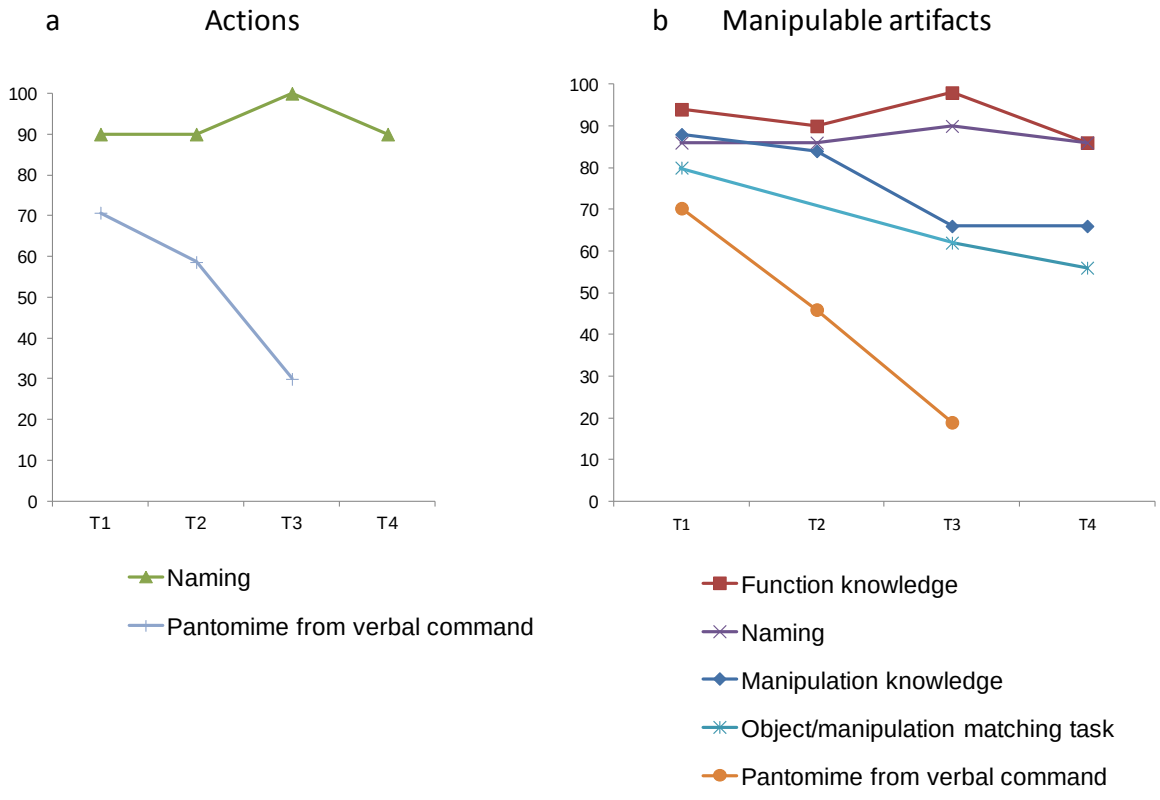

Figure 3.5| JR's percentage of correct responses at the different tasks of the "Production/comprehension" battery when considering the actions (a) or the manipulable artifacts (b).

2.2.6. Discussion

At T1, JR presented with a diffuse bilateral brain atrophy with right parietal predominance. From T1 to T4, he presented grey matter volume loss in 16 of the 20 ROIs we identified within the motor system. The asymmetric bilateral atrophy affected mostly the superior, inferior and posterior frontal cortex, the superior parietal cortex, and the

basal ganglia, a pattern that is typically found in CBD (Dickson et al., 2002). Four regions did not show abnormal volume loss throughout the study: the inferior parietal lobes, the right superior parietal lobe, the right caudal middle frontal gyrus, and the left pallidum. The relative preservation of the inferior parietal lobes is, again, typical of this condition (Dickson et al., 2002). However, whether the brain regions that showed no clear volume loss throughout the three-year period of the study were "functional" is difficult to know. Since JR presented already diffuse atrophy at T1, at least some of these regions may have underwent atrophy before the study began. Furthermore, decreases of metabolism may be present in regions where no atrophy was found.

At the behavioral level, JR was still independent in everyday activities at T1 but he presented already with motor disorders that affected both hands but mostly the left one. His motor disorders then increased. At T4, JR had very severe motor disorders that affected all everyday activities and functional independence. Among all the tests used in this part of the study, only his right hand grip strength remained in the normal range.

As typically reported in CBD, JR presented with both motor and praxic disorders (e.g., Stamenova et al., 2009). At the initial stage of the disease (T1 and T2), JR's pattern was mostly characterized by loss of hand and finger dexterity, which could partly explain his impairment in producing meaningful gestures on both imitation and verbal command. According to Rothi et al.'s (1991) model, impaired performance in both these tasks is likely to originate from damage to the processes of formation of "innervatory patterns". Furthermore, that JR's performance was more impaired when pantomiming on verbal command than on imitating meaningful gestures suggests that he presented additional damage to the stored representation of gestures or damage to the transformation of those representations into "innervatory patterns" caused by a disconnection of the frontal motor centers from the parietal systems involved in gesture representation (e.g., Jacobs, 1999).

Such pattern of praxis impairment is typically found in CBD (see for review, Stamenova et al., 2009).

Whether movement production disorders resulting from degradation of the final stages of the movement organization is a "praxic" or a "motor" deficit is sometimes debated (Stamenova et al., 2009). Hence, one could ask whether JR had apraxia at that initial stage of the disease. However, at the subsequent sessions of assessment, JR's movement production disorders clearly went beyond a mere motor disorder, since he also showed impaired performance in two tasks that required retrieving gesture representations without requiring any movement execution, i.e., the manipulation condition of the picture association task and the object/manipulation matching task. JR's impaired performance in the manipulation condition of the picture association task cannot be ascribed to a visuo-perceptual or a conceptual impairment since he was not impaired in naming or retrieving the function of these artifacts. His impaired performance in the object/manipulation matching task could not be due to an impairment in processing visually-presented gestures since he was not impaired in the gesture recognition task of the Battery of limb apraxia. On the whole, JR's pattern of performance with manipulable artifacts across tasks suggests that, at least from T2, he had damage to the representations of manipulation gestures or to the transformation of such representations into innervatory patterns. Actually, even if actual gesture execution is not demanded in these tasks, they may nevertheless rely on the formation of innervatory patterns. One can assume that some covert execution of the retrieved gestures is needed in order to achieve comparisons between the four manipulation patterns accessed from visually-presented artifacts (in the picture association task) or between the manipulation pattern accessed from a visually-presented artifact and two visually-presented pantomimes of object use (object/manipulation matching task).

In contrast to motor and praxic disorders that progressively increased throughout the period of the study, JR performed within the normal range, at every time period, in tasks assessing implicit (naming) or explicit (function condition of the picture association task) comprehension of actions and manipulable artifacts. Throughout the study, JR was always as accurate as the control participants in naming actions and manipulable artifacts. As regards non-motor-related stimuli, we found that, unexpectedly, JR's performance was impaired in naming animals and, to a lesser extent, plants, although it was not impaired in naming non-manipulable artifacts. Whether this pattern indicated a true category-specific deficit for animals and plants affecting either the structural or the conceptual level of processing (see Capitani et al., 2003 for a review) or only low personal familiarity with these categories of stimuli is unclear. Answering this question would have required additional testing, which was beyond the scope of this study.

To sum up, in this section, we have reported on the neuropsychological, morphometric, motor, praxis, and comprehension evaluations of a patient, JR, presenting with CBD, during a three-year period. Our aim was to test two predictions drawn from MTC, namely, (1) that damage to the motor system should impair selectively or disproportionately the comprehension of actions and manipulable artifacts in comparison to non-motor-related stimuli; and (2) that a progressive motor or/and praxic disorder in the context of a progressive bilateral atrophy of cortico-subcortical structures sustaining the motor system should be associated with progressively increasing difficulties to comprehend actions and manipulable artifacts. None of these predictions were confirmed. First of all, we found evidence that JR presented with a progressive grey matter volume loss in most of the cortico-subcortical areas sustaining the motor system and that this was indeed accompanied by progressive motor and praxis disorders. Then, we found that, in spite of this evolutionary pathological pattern, JR's comprehension of actions and

manipulable artifacts remained stable and unimpaired throughout the same testing period. This pattern of dissociation between progressive and severe motor/praxic disorders and stable and unimpaired comprehension of actions and manipulable artifacts is clearly at odd with MTC.

2.3. Additional investigation of JR's comprehension of motor-related stimuli at T4

With the following experiments, we sought additional evidence that, at T4, when the motor and praxic disorders were the most severe, JR's performance in naming motor-related stimuli did not significantly differ from the performance of control participants. Two additional naming tasks were used. The first assessed naming of actions, manipulable artifacts, and non-manipulable artifacts with a much larger sample of items. The purpose of the second naming task was twofold. First, it was presented in a way that allowed us to measure JR's naming speed. In spite of JR's normal naming accuracy for motor-related stimuli throughout the longitudinal study, he could nevertheless be slower than the controls in naming them. Second, the material allowed us to test an additional prediction drawn from MTC, namely, that JR could have a deficit affecting at least, among actions, those actions whose execution requires a lot of movement or those actions that are difficult to execute (e.g., Herrera, Rodríguez-Ferreiro, & Cuetos, 2012) and, among manipulable artifacts, those whose manipulation is associated with motor movements that unambiguously allow their identification (Mahon et al., 2007).

All the picture stimuli used in these additional tests were colour photographs with no context. Each task was preceded by a few examples designed to familiarize the patient with the task.

2.3.1. The "Artifacts/Actions 2" (AA2) picture naming task

Method

Table 3.7. Mean and standard deviation of the items of the "Motor Content" naming task (SM actions = Strongly Motor actions; WM actions = Weakly motor actions; SM artifacts = Strongly manipulable artifacts; WM artifacts = Weakly manipulable artifacts) for image agreement (IA), visual complexity (VC), imageability (IMAG), age of acquisition (AoA), number of letters (LETT), spoken word frequency of the lemma (Freq), concept familiarity (Fam), name agreement (NA), mean spoken naming latency (RLs), amount of movement implied in the execution of an action (Quant), complexity of the movement implied in the execution of an action (Compl) and, for objects, manipulability rating (Manip).

		IA[1]	**VC[1]**	**Imag[1]**	**AoA[1]**	**LETT**	**Freq[2]**	**Fam[3]**	**NA[4]**	**RLs[7]**	**Quant[5]**	**Compl[6]**	**Manip[1]**
ACTIONS	Mean	3.62	2.15	3.98	2.40	6.78	40.29	2.60	82.62	1511.70	2.93	2.59	
	SD	0.78	0.58	0.60	0.53	1.33	52.34	0.92	15.91	339.11	0.76	0.91	
SM actions	Mean	3.58	2.07	3.93	2.32	6.80	45.65	2.70	80.92	1585.52	2.33	1.86	
	SD	0.75	0.58	0.69	0.54	1.29	53.88	0.80	18.12	368.89	0.33	0.38	
WM actions	Mean	3.66	2.23	4.04	2.49	6.76	34.93	2.49	84.31	1437.88	3.53	3.33	
	SD	0.83	0.58	0.50	0.52	1.39	51.28	1.03	13.50	295.56	0.57	0.64	
ARTIFACTS	Mean	3.71	2.27	4.15	2.57	6.60	23.60	2.69	86.17				2.78
	SD	0.47	0.36	0.50	0.74	2.18	49.84	1.24	17.82				0.73
SM artifacts	Mean	3.60	2.27	4.10	2.56	6.56	26.38	2.68	87.23				2.16
	SD	0.43	0.31	0.56	0.73	2.33	60.87	1.11	12.89				0.25
WM artifacts	Mean	3.82	2.27	4.20	2.59	6.64	20.82	2.69	85.10				3.40
	SD	0.48	0.41	0.44	0.76	2.06	36.74	1.39	21.91				0.49

[1] Obtained from Bonin et al. (2004) for the actions and from Brodeur et al. (2010) for the objects according to similar consigns. [2] From the French database "Lexique 3" (New et al., 2004). [3] 22 control subjects were presented with each word (noun or verb) and asked to evaluate on a 5-point scale (1= very unfamiliar; 5 = very familiar) how usual or unusual each object or action is in their realm of experience. Following Bonin et al., (2004), concept familiarity was defined as "the degree to which you come into contact with or think about the concept". [4] For name agreement (NA) rating, 27 participants were presented with all the preselected photographs of actions and objects and asked to identify the action or objects each photograph referred to, and to write down their response on a sheet of paper. The measure of NA corresponded to the percentage of participants giving the most common name. [5] We asked 25 subjects to rate them as to the quantity of motor movement they implied on a five-point scale (where 1=very low amount of movement and 5=very high amount of movement). [6] We asked 25 other subjects to rate them as to the complexity of the motor movement entailed by the action on a five-point scale (where 1=very low motor complexity and 5=very high motor complexity). [7] Obtained on a sample of 30 undergraduate students by Bonin et al. (2004).

This picture naming task was presented to JR and 12 control subjects matched with JR in gender, age [mean = 63.16; modified t (11) = 1.06, p = 0.31], and years of education [mean = 15.17; modified t (11) < 1]. The material was composed of 150 actions and 120 artifacts. The 150 actions contained 30 actions made by an actor on an artifact (e.g., to dribble), 30 actions that did not include any object (e.g., to crawl), 60 actions made with an object in hand (e.g., to hammer), and 30 interpersonal actions not involving artifacts (e.g., to slap). The 120 artifacts were divided in 30 tools (e.g., a sickle), 30 non-tool little objects (e.g., a stopwatch), 30 means of transport (e.g., a locomotive), and 30 furniture items (e.g., an easel). For the purpose of this study, the 120 artifacts were submitted to a manipulability judgment made by three judges according to the same criteria as those applied for the items of the AA1 naming task. Only items that reached 100% agreement across the judges were retained for analysis. These criteria resulted in 54 manipulable artifacts and 51 non-manipulable artifacts. As shown in Table 3.7, actions, manipulable artifacts, and non-manipulable artifacts retained in the analysis were matched in concept familiarity [F (2, 252) = 1.10, p = 0.33], but not in log frequency [F (2, 252) = 10.89, p < 0.01]. Bonferroni post-hoc tests showed that manipulable artifacts had a significantly lower log frequency than actions and non-manipulable artifacts (ps < 0.01), which did not differ from each other (p = 1).

Results

Both target responses and acceptable alternatives (synonyms, nominal and verbal phrases, and more specific words) were considered as correct. Acceptable alternatives represented 10.36% of JR's correct responses and 6.46% of the correct responses of the controls, a difference that is almost significant (t (11) = 1.95, p = 0.08). However, this difference was in fact due to more non target response being considered as accurate in JR

for non-manipulable artifacts (t (11) = 3.09, p = 0.01). In contrast, the percentage of acceptable alternative responses was not different in JR and the controls for manipulable artifact (t (11) = - 0.09; p = 0.92) and actions (t (11) = 1.05, p = 0.31). The main results are displayed in Figure 3.6. JR's naming performance for the three categories of items was within the normal range [all modified ts (11) > -0.70; all ps > 0.5]. In addition, the discrepancy in JR's performance between manipulable and non-manipulable artifacts did never significantly differ from that found in control participants (RSDT, t (11) < 1).

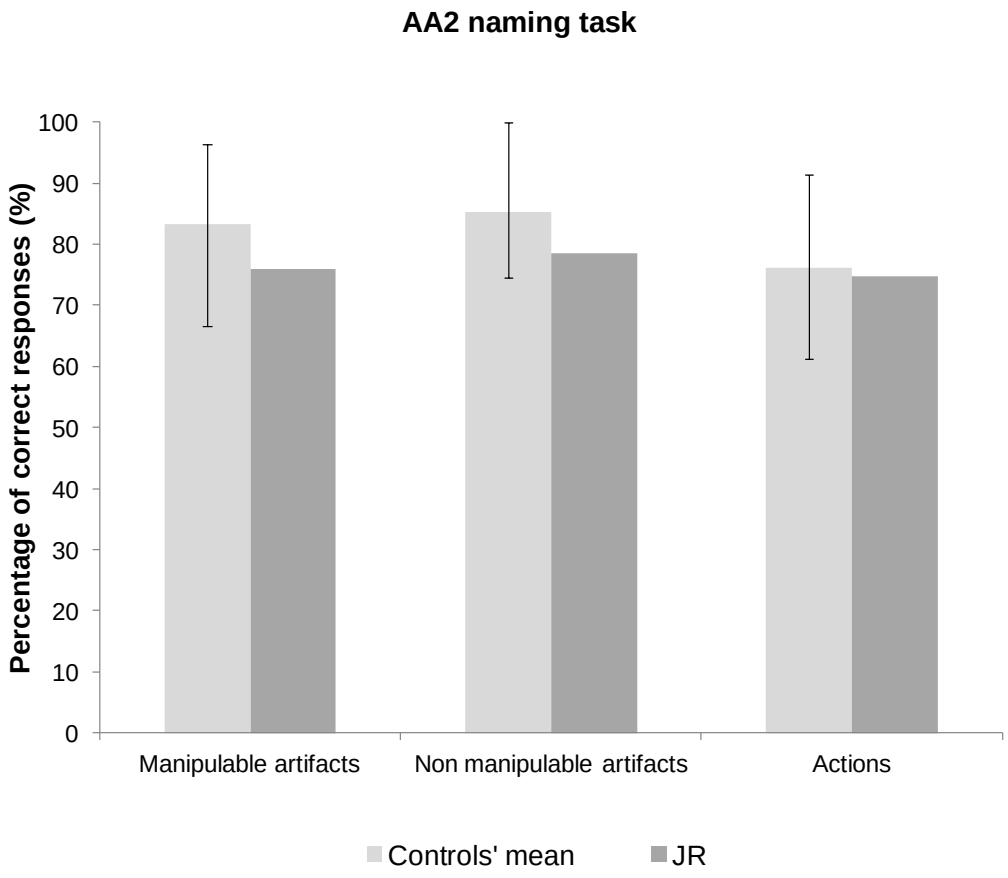

Figure 3.6| JR's and control participants' percentage of correct responses in the naming task of the « Artifacts/Actions 2 » battery. Error bar = range.

2.3.2. The "Motor Content" timed picture naming task

Method

This task was presented to JR and to 8 age, gender, and education-matched control participants [mean age = 76.25; modified t (7) < 1; mean education = 16.87; modified t (7) < 1]. These control participants were members of the "University for the Elderly", had a preserved cognitive functioning (all MMSE ≥ 28), a normal visual acuity (Parinaud's test), normal visuo-perceptive abilities (Riddoch & Humphreys, 1993; Birmingham Object Recognition Battery: test 7: all = 25/25; test 8: all = 25/25; test 11: all ≥ 30/32), and performed above the mean performance of their age category in a standardized object naming task (de Partz et al., 2002; all z > 0). Furthermore, none of these controls had movement production complaints.

The material included 50 actions divided equally in "strongly motor" actions (SM) and "weakly motor" actions (WM) and 50 artifacts divided equally in "strongly manipulable" (SM) artifacts and "weakly manipulable" (WM) artifacts. Among the SM actions, 20 are performed with an artifact, 21 are performed predominantly with the upper limbs without any object, and 4 implied the whole body. Among the WM actions, 9 are performed with an artifact, 16 are performed predominantly with the upper limbs without any object, 5 implied the whole body, and 4 the mouth. These items were selected from a preliminary set of 116 actions and 219 artifacts for which photographs and norms in image agreement, visual complexity, imageability, age of acquisition, number of letters, spoken word frequency (Bonin et al., 2004; Brodeur, Dionne-Dostie, Montreuil, & Lepage, 2010) and, for artifacts, manipulability (Brodeur et al., 2010) were available in extant databases. Manipulability ratings for artifacts in Brodeur et al.'s (2010) normative study were collected with the following instruction: "Could you easily mime the action usually associated with this object so that any person looking at you doing this action could

decide which object goes with this action". We also collected ratings of concept familiarity and name agreement for the actions and artifacts and, for the actions, ratings of the quantity of movement (where 1=very low amount of movement and 5=very high amount of movement) and movement complexity (where 1=very low motor complexity and 5=very high motor complexity) entailed by each action. The four categories of stimuli were matched in image agreement [F (3, 96) < 1], concept familiarity [F (3, 96) < 1], visual complexity [F (3, 96) = 1.03; p = 0.38], imageability [F (3, 96) = 1.05, p = 0.38], age of acquisition [F (3, 96) < 1], number of letters [F (3, 96) < 1], log spoken word frequency [F (3, 96) = 1.11, p = 0.35], and name agreement [F (3, 96) < 1]. SM actions were rated with a significantly higher amount of movement [t (48) = 9.07, p < 0.001] and significantly more complex movements [t (48) = 9.96, p < 0.001] than WM actions. SM artifacts were rated higher in manipulability than WM artifacts [t (36.11) = 11.36, p < 0.001].

For each item, its corresponding color photograph with no context (Bonin et al., 2004; Brodeur et al., 2010) was used in the timed picture naming task. Participants were presented with all the stimuli in the same session and were asked to name them as fast and as accurately as possible. A fixation point was presented in the center of a computer screen for 200 ms; then the screen was cleared for 500 ms and the stimulus was displayed until the voice key was triggered. The next trial began after an interval of 1000 ms. The experiments were controlled by the E-Prime software (Psychological Software, 2002, Pittsburgh, PA). The participants were equipped with a sensitive built-in microphone connected with an RT-measuring PST (Psychology Software Tool) serial response box. Malfunctioning of the voice key and participants' responses were checked by the experimenter.

Results

The main results are displayed in Figure 3.7. Trials with malfunctioning of the voice key were first removed (Controls = 4.37%; JR = 3%). Then, both target responses and acceptable alternatives (synonyms, nominal and verbal phrases, and more specific words) were considered as correct in the accuracy analysis. Acceptable alternatives represented 2.46% of JR's correct responses and 4.47% of the correct responses of the controls. In the response latency (RL) analysis, however, only trials corresponding to the expected name were considered. RLs were visually checked for abnormally fast or slow response latency but no latency below 300 msec or above 5000 msec was observed. The results showed that JR's performance did not significantly differ from the controls' for any of the four categories of items, neither in accuracy [all modified *t*s (7) > -0.51; all *p*s > 0.50] or in speed[8] [all modified *t*s (7) < 1.88; all *p*s > 0.1]. In addition, the discrepancy in JR's performance between WM and SM items did never significantly differ from that found in control participants (RSDT, all *t*s (7) < 1).

To corroborate the outcome of the modified *t* tests that are, by essence, by-subject analyses, we carried out a by-item analysis of variance (ANOVA) over the response latencies of JR and the median response latencies of control participants. We analyzed actions and artifacts separately. ANOVAs were carried out with response latency as the dependent variable, items as the random factor, Group (JR vs. Controls) as within-item factor, and Set of items (SM vs. WM) as between-item factor. RLs for action items were then log transformed and RLs for artifact items inverse transformed, for satisfying the ANOVA's normality assumptions (all Shapiro-Wilk *p*s > 0.05). For actions, the analysis showed no significant effect of Group [F (1, 36) = 1.89, p = 0.18], no significant effect of

[8] Similar results were obtained when all correct responses (target and acceptable alternatives) were considered in the RL analysis. Thus, JR was still not different from the controls' for any of the four categories of items, [all modified *t*s (7) < 1.83; all *p*s > 0.1].

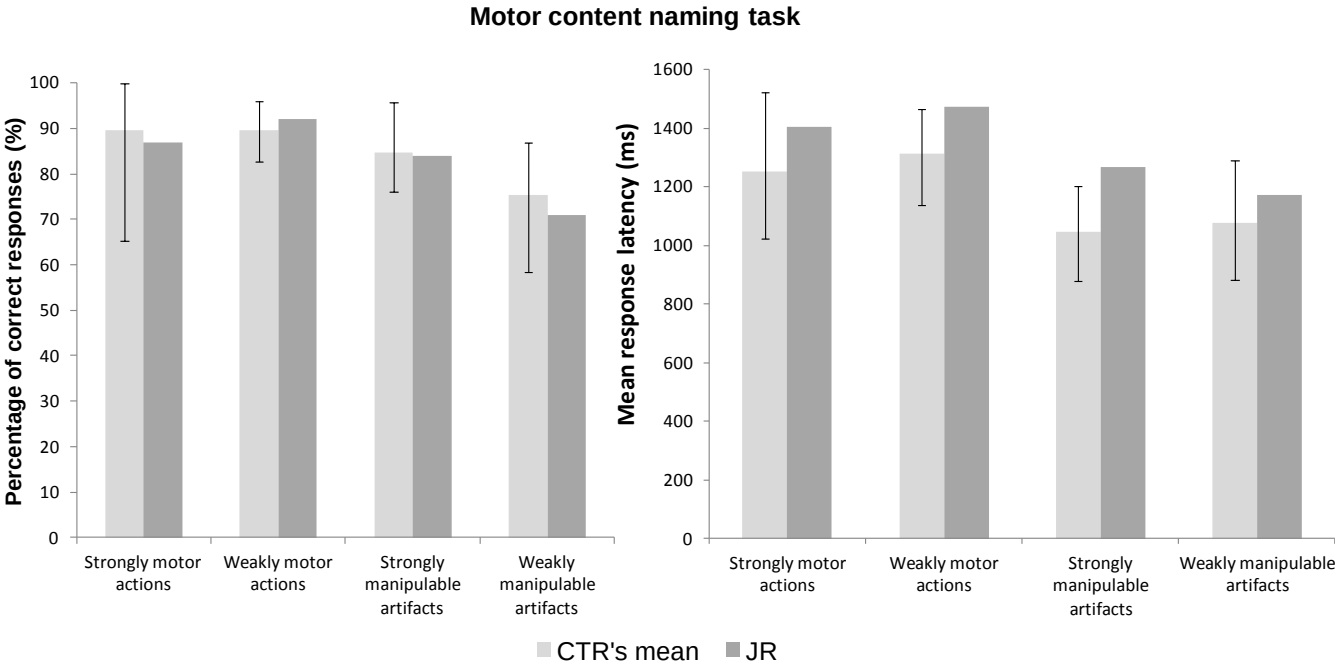

Figure 3.7| JR's and control participants' percentage of correct responses (Left) and mean response latency (Right) for the timed naming task of the "Motor Content" battery. Error bar = range.

Set of items [F (1, 36) < 1], and no significant interaction of Group x Set of items [F (1, 36) = 1.29, p = 0.26]. For artifacts, the analysis showed no main effect of Group [F (1, 35) = 1.08, p = 0.31], no main effect of Set of items [F (1, 35) < 1], and no significant interaction of Group x Set of items [F (1, 35) = 1.16, p = 0.29].

Finally, we performed a Bayesian analysis to seek positive evidence that the effect of Set of items (SM vs. WM) was equivalent in JR and control participants. The Bayesian analysis allowed us to estimate the likelihood of the null hypothesis being true (Masson, 2011; Wagenmakers, 2007) for the Group x Set of items interaction. This analysis was based on the sum-of-squares values for the interaction effect from the by-item ANOVA. The results indicated that the probability of the null hypothesis (H0; no interaction) being true was of 76% for actions and 76% for artifacts. According to Raftery's (1995) classification of evidence into « weak » (.50–.75), « positive » (.75–.95), « strong » (.95–

.99), and « very strong » (> .99), the probability values obtained here provides positive support for H_0 (interaction absent).

2.3.3. Discussion

JR's results in these additional naming tasks were clear-cut and corroborated the findings from the longitudinal study: JR did not have difficulty in comprehending actions and manipulable artifacts. Two additional pieces of evidence was also obtained. First, the results showed that JR was not only as accurate as the controls in naming actions and manipulable artifacts, but also *as fast as* them. Second, JR's naming performance was not significantly poor (less accurate or slower) for actions and artifacts with strong motor content (SM) than for those with weaker motor content (WM). Also, positive evidence was found that the effect of this variable on naming times was similar in JR and control participants. Thus, these findings showed that JR's movement production disorder was not associated with an impairment in comprehending actions and manipulable artifacts, even when speed of processing was considered and when the stimuli included actions implying a lot of movements or/and complex movements and manipulable artifacts whose identity are highly predictable from their manipulation pattern.

3. GENERAL DISCUSSION

A clear dissociation emerged from the results of this study. On one hand, over the three-year period of investigation, JR presented with a progressive volume loss of grey matter in bilateral cortico-subcortical brain areas sustaining the motor system, which resulted in an increasingly severe motor and praxic disorder. On the other hand, JR's ability to name actions and manipulable artifacts and to retrieve explicitly function knowledge about manipulable artifacts did not decrease over time and remained

consistently in the normal range of performance. Furthermore, additional testing at T4 showed that JR's performance in naming motor-related stimuli was not only as accurate as the control participants' performance, it was also as fast as theirs. These findings are clearly problematic for MTC.

The evidence provided in this study against MTC could not be rejected on the ground that we just failed to find evidence for a comprehension impairment in JR. It is indeed very unlikely that JR had a subtle comprehension impairment for motor-related stimuli that we failed to detect. First of all, one can rule out that we failed to detect a subtle impairment because JR could have presented exceptionally good premorbid comprehension abilities or, its corollary, because control participants had exceptionally poor performance. JR's naming performance was compared either to highly-educated *younger* participants (in the AA1 and AA2 naming tasks and in the picture association task) or to age-matched individuals attending the "University of the Elderly" (in the "Motor-Content" naming task) and who performed above the mean performance of their age group in naming pictures of objects in a standardized naming task. If JR's unimpaired comprehension performance in comparison to controls' were due to one of these reasons, then his comprehension performance still should have decreased throughout the three-year period of testing if the motor system indeed supported comprehension of motor-related stimuli. Second, there are reasons to believe that our tasks and measures were appropriate and sensitive enough to disclose a mild comprehension impairment if present. As we mentioned before, the picture naming task is known as a sensitive task to disclose even mild comprehension impairments and we found that JR performed the picture naming tasks not only with normal accuracy but also with normal speed. Furthermore, consistent results were obtained across 5 different naming tasks using different sets of

actions and manipulable artifacts and even for actions associated with a complex motor pattern and artifacts associated with a highly specific manipulation pattern.

Our findings are at odd with those reported previously with similar patients, who showed impaired comprehension of actions and manipulable artifacts (Cotelli et al., 2006; Silveri & Ciccarelli, 2007; Spatt et al., 2002). One possible account for our discrepant finding is that damage to the motor system in JR is not severe enough to cause an impairment in comprehending motor-related stimuli. Actually, the patients reported in these previous studies were likely at a later stage of the disease, as suggested by their mean performance at the MMSE, which was 19.5 in Silveri and Ciccarelli (2007), 15.2 in Spatt et al. (2002), and 25.3 in Cotelli et al. (2006), while JR had a MMSE score of 28 at T4. However, we think that this account is not plausible. JR did have extensive and bilateral atrophy in parietal, motor, and premotor brain areas and very severe motor disorders increasing throughout the study. Although assessed with different tasks, JR's performance in the pantomime imitation task (mean imitation score with the best hand = 17.5%) at T4 was at least as impaired as that of the patients reported by Silveri and Ciccarelli (2007) and Spatt et al.'s (2002) (mean imitation score with the best hand = 45% and 23%, respectively).

On the other hand, a closer look at the individual data provided in the studies of Silveri and Ciccarelli (2007) and Spatt et al. (2002) suggests that other cognitive impairments could be at the origin of the comprehension impairment in these cases. In Spatt et al. (2002), for instance, the patients' global performance in movement production tasks (imitation of meaningful and meaningless gestures and production of pantomimes on verbal command) was in fact *negatively* correlated with their mean performance in the tool naming task (r = -0.18) and the other tool comprehension tasks (r = -0.60). In contrast, other cognitive measures and, especially, the patients' performance in an

object/non object decision task was *positively* correlated with their performance in the tool naming task (r = 0.57) and in the other tool comprehension tasks (r = 0.67). Likewise, in Silveri and Ciccarelli (2007), the patients' performance in naming actions was more related to a general index of cognitive functioning (MMSE: r = 0.47) than to their performance in a gesture imitation task (r = 0.25). JR, in contrast to the patients of these studies, presented, even at T4, only slight cognitive impairments beyond his motor and praxic disorders. On this basis, a plausible account for the conflicting results obtained with JR and the patients of these previous studies is that the comprehension impairment, in these patients, originated from non-motor cognitive impairments, resulting from brain atrophy extending outside the motor system.

Our findings corroborate the results obtained with CBD patients by Chainay and Humphreys (2003) and Graham et al. (1999) and other similar results obtained with patients suffering from apraxia following focal brain damage (Negri et al., 2007; Papeo et al., 2010; Pazzaglia, Smania, et al., 2008; Pazzaglia, Pizzamiglio, et al., 2008; Rumiati et al., 2001), motor neuron disease (Hillis et al., 2006), and progressive supra-nuclear palsy (Cotelli et al., 2006; Daniele et al., 2012). In all these studies, patients showed a preserved ability to comprehend motor-related stimuli despite a mild to severe movement production disorder and damage affecting different parts of the motor system. In these studies, however, only patients' accuracy in comprehending motor-related stimuli was reported. Furthermore, evidence from apraxia has been discussed on the ground that apraxic patients did not suffer from sufficiently low level motor damage to hamper comprehension of motor-related stimuli (Meteyard et al., 2012) or that they suffer from damage affecting parts of the motor system that do not play a critical role in comprehension (e.g., Rizzolatti & Sinigaglia, 2010). The present findings add to previous neuropsychological evidence the observation that widespread damage to the motor system

affecting, at least, the bilateral caudate, putamen, superior frontal lobes, inferior frontal lobes (pars opercularis and triangularis), precentral gyri, supramarginalis gyri as well as the right putamen, left caudal middle frontal gyrus and left superior parietal lobe, and resulting in both severe motor and praxic disorders, has no impact on the ability to comprehend efficiently (accurately and fast) actions and manipulable artifacts.

CHAPTER 4

A DOMAIN-SPECIFIC SYSTEM FOR REPRESENTING KNOWLEDGE OF BOTH MAN-MADE OBJECTS AND HUMAN ACTIONS. EVIDENCE FROM A CASE WITH AN ASSOCIATION OF DEFICITS[9]

Abstract

We report the single-case study of a brain-damaged individual, JJG, presenting with a conceptual deficit and whose knowledge of living things, man-made objects, and actions was assessed. The aim was to seek for empirical evidence pertaining to the issue of how conceptual knowledge of objects, both living things and man-made objects, is related to conceptual knowledge of actions at the functional level. We first found that JJG's conceptual knowledge of both man-made objects and actions was similarly impaired while his conceptual knowledge of living things was spared as well as his knowledge of unique entities. We then examined whether this pattern of association of a conceptual deficit for both man-made objects and actions could be accounted for, first, by the "sensory/functional" and, second, the "manipulability" account for category-specific conceptual impairments advocated within the Feature-Based-Organization theory of conceptual knowledge organization, by assessing, first, patient's knowledge of sensory compared to functional features, second, his knowledge of manipulation compared to functional features and, third, his knowledge of manipulable compared to non-manipulable objects and actions. The later assessment also allowed us to evaluate an account for the deficits in terms of failures of simulating the hand movements implied by manipulable objects and manual actions. The findings showed that, contrary to the predictions made by the "sensory/functional", the "manipulability", and the

[9] This section is a modified version of an article with identical title by Vannuscorps and Pillon, which has been published in *Neuropsychologia*, 2011, 49: 2331-2341.

"failure-of-simulating" accounts for category-specific conceptual impairments, the patient's association of deficits for both man-made objects and actions was not associated with a disproportionate impairment of functional compared to sensory knowledge or of manipulation compared to functional knowledge; manipulable items were not more impaired than non-manipulable items either. In the general discussion, we propose to account for the patient's association of deficits by the hypothesis that concepts whose core property is that of being a mean of achieving a goal — like the concepts of man-made objects and of actions — are learned, represented and processed by a common domain-specific conceptual system, which would have evolved to allow human beings to quickly and efficiently designing, planning, and understanding means to achieve goals.

1. INTRODUCTION

Neuropsychological reports of category-specific conceptual deficits have constituted an important source of evidence for theories of conceptual knowledge organization in the human mind and brain. The most frequently reported cases were those of brain-damaged individuals who presented a selective or disproportionate conceptual impairment for one category of objects, like animals, plant life, or man-made objects, compared to another (see for review, Capitani, Laiacona, Mahon, & Caramazza, 2003), thereby informing theories about the organization of *object* knowledge in the mind and brain (Caramazza & Shelton, 1998; Humphreys & Forde, 2001; Martin, Ungerleider & Haxby, 2000; Simmons & Barsalou, 2003; Warrington & McCarthy, 1987). Much less neuropsychological evidence has been gathered as regards how conceptual knowledge pertaining to human actions[10] may break down after brain damage and, in particular, how

[10] Throughout this paper, the term "actions" will refer to categories of human goal-directed activities that are expressed by a single verb (e.g., *drinking* or *grating*). It thus will not refer to single movements (e.g.,

such knowledge is related to object knowledge. We report here the single-case study of a brain-damaged individual, JJG, whose pattern of conceptual impairment, which included impaired action knowledge, provided evidence relevant to this issue.

Three main positions may be distinguished across extant theories of conceptual knowledge organization, as regards the issue of how object and action conceptual knowledge is related at the functional and/or neural level — the first positing segregated conceptual representations for objects and actions, the second positing partly overlapping representational or processing systems for knowledge of one category of objects, i.e., man-made objects, and of actions, and the third, a shared but unspecific system for both man-made objects and actions.

The first position was formulated within the context of studies reporting on grammatical category-specific deficits, that is, naming and/or comprehension deficits that selectively or disproportionately impaired one grammatical category of words, nouns or verbs, compared to the other (for recent reviews, see Druks, 2002; Mätzig, Druks, Matterson, & Vigliocco, 2009). Because in almost all these reports, the material included concrete nouns and concrete verbs, which correspond to objects and actions, respectively, a number of authors advanced that, for at least some of these reported cases, the double noun/verb dissociation in fact reflected an underlying segregation between object and action concepts within the conceptual system (Damasio & Tranel, 1993; Kable, Kan, Wilson, Thompson-Schill, & Chatterjee, 2005; Laiacona & Caramazza, 2004; McCarthy & Warrington, 1985; Rapp & Caramazza, 1998; Vigliocco, Vinson, Lewis, & Garrett, 2004; see for discussion, Pillon & d'Honincthun, 2011a). However, in the studies reporting grammatical category-specific deficits, the set of nouns/objects that was

raising the arm**)** or more specific activities like the ones expressed by verbal phrases (e.g., *drinking wine* or *grating cheese*).

contrasted to the set of verbs/actions in fact included, most of the times and in various proportions, both living and non-living objects. The results were not reported or analyzed according to each category of nouns/objects, like it was assumed that all categories of objects shared a common representational system. Nonetheless, it is well known that, within the category of objects, knowledge of living and non-living things may dissociate following brain damage. It is thus unclear how the term "object" must be understood in this proposal of a conceptual fractionation along the "object/action" dimension. In the more recent proposal by Vigliocco and colleagues (Vigliocco et al., 2004), this point was made clearer. Thus, according to their "Featural and Unitary Semantic Space" (FUSS) hypothesis, the conceptual representations of each category of objects — animals, vegetables, man-made objects — occupy distinct areas within the "lexico-semantic space", which are themselves still more segregated from the areas sustaining the conceptual representations of actions. In that way, a focal "lesion" to this heterogeneous space may impair the conceptual representations of all or only one of the categories of objects by sparing the conceptual representations of actions or the reverse, i.e., impair the conceptual representations of actions by sparing those of all or only one category of objects.

The second position — partly overlapping representational or processing systems for knowledge of man-made objects and of actions — can be found within two different theoretical frameworks. First, within the currently most influential view on conceptual knowledge organization, which we will call here the Feature-Based Organization (FBO) theory, knowledge of one category of objects, that is, man-made objects, and knowledge of actions would be represented in overlapping systems by virtue of their being both weighted of a specific kind of conceptual features, like functional or manipulation features. There are several variants of this theory, which differ on a number of points. For

example, conceptual knowledge may be conceived of as amodal representations (e.g., Farah & McClelland, 1991) or modality-specific representations encoded nearby (e.g., Martin et al., 2000) or in the sensory and motor systems (e.g., Allport, 1985; Warrington & McCarthy, 1987). The number and kind of property dimensions driving the organization of conceptual knowledge may also vary across the various formulations of the theory, from one dimension like "sensory vs. non-sensory" (e.g., Bird, Howard, & Franklin, 2000) or "visual vs. functional" (Farah & McClelland, 1991; Warrington & McCarthy, 1983; Warrington & Shallice, 1984) properties, to multiple dimensions like form, color, motion, function, and motor properties (e.g., Allport, 1985; Humphreys & Forde, 2001; Martin et al., 2000; Warrington & McCarthy, 1987). However, all the variants share the two following assumptions: first, knowledge is represented in a distributed way over various functional and neural systems each representing a distinct kind of featural knowledge, say, sensory (visual, auditory, somato-sensory, olfactory), functional, manipulation, or motor knowledge; second, the various categories of concepts are differentially weighted of each kind of feature and, hence, represented in partially distinct systems. The differential weighting of features reflects the relative importance of the various types of semantic properties within the definition of a given concept (Bird et al., 2000; Farah & McClelland, 1991; Warrington & McCarthy, 1983; Warrington & Shallice, 1984) or the relative involvement of the various sensory-motor modalities of experience during the acquisition of that concept (Allport, 1985; Crutch & Warrington, 2003; Damasio & Tranel, 1993; Gainotti, Silveri, Daniele, & Giustolisi, 1995; Warrington & McCarthy, 1987). Thus, for example, Bird et al. (2000) assumed that the concepts of living things have a greater weighting of sensory compared to functional features and the concepts of actions a greater weighting of functional compared to sensory features, while the concepts of nonliving things (man-made objects) have an intermediate sensory-to-

functional ratio. This proposition predicts that, in case of damage to the functional system, man-made objects as well as actions should be impaired, although man-made objects would be *less* impaired than actions, while living things should be relatively spared. In another variant of the theory, the primary dimension determining the organization of conceptual knowledge is manipulability (Gerlach, Law, & Paulson, 2002; Kellenbach, Brett, & Patterson, 2003; Noppeney, Josephs, Kiebel, Friston, & Price, 2005; Saccuman, Cappa, Bates, Arévalo, Della Rosa, Danna, & Perani, 2006). According to this view, whether the utilization of an object (plant or artifact) involves fine hand movements or not (i.e., whether it is a manipulable or non-manipulable object) or whether an action involves fine hand motion or the whole body, is a crucial conceptual feature determining how (and where in the brain) the corresponding concepts are processed and represented. Thus, conceptual representations of both man-made objects and actions that are weighted of manipulation features would mainly rely on a shared system, a manipulation knowledge system (see also Buxbaum & Saffran, 2002). In case of selective damage (or sparing) to this system, the expected pattern of separation between conceptual categories thus would not be between the concepts of man-made objects and the concepts of actions, but between the concepts that are weighted of manipulation features (i.e., both man-made objects and actions which utilization or realization requires fine hand movements) and those that are not (i.e., both man-made objects and actions that do not involve hand movements). Whatever the proposal made within the FBO theory, however, it is expected that any category-specific conceptual deficit should be associated with a feature-specific conceptual deficit, that is, a disproportionate deficit for the type of feature (sensory, functional, manipulation) that is assumed to be crucial in the processing of the disproportionately impaired category.

Second, within the framework of the motor simulation theory (e.g., Gallese & Lakoff, 2005; Rizzolatti & Craighero, 2004; Rizzolatti, Fogassi, & Gallese, 2001), accessing the conceptual content of both manipulable objects and actions would be dependent on *motor production* processes involved in the actual use of objects and the actual execution of actions. The conceptual content of manipulable objects and actions would be retrieved by the covert simulation of the production of the movements implied by object manipulation or action execution. Thus, within this perspective, conceptual processing of manipulable objects and, specifically, manual actions should both depend on the ability to covertly simulate hand/arm movements. Therefore, in case of damage to these motor simulation processes, knowledge of both manipulable objects and manual actions should be impaired and such impairment should be associated with upper limb apraxia, in particular, an impairment in recognizing and performing the hand/arm movement associated with manipulable objects and manual actions.

In other words, both the above variants of the FBO theory and the motor simulation theory assume that the concepts of man-made objects and of actions share a specific kind of representation or processes that has a crucial role in their overall representation and processing — functional or manipulation feature representations, within the "sensory/functional" or the "manipulability" variant of the FBO theory, and hand/arm movement simulation processes, within the motor simulation theory. The third position, derived from the domain-specific knowledge theory (Caramazza & Shelton, 1998), would also predict that, in case of brain damage, knowledge of man-made objects should pattern with knowledge of actions, but for another principled reason. This theory assumes that the organization of conceptual knowledge in the brain results from evolutionary pressures that led to specific adaptations for solving, quickly and efficiently, computationally complex survival problems (for example, avoiding predators and finding

food). These adaptations would consist in specialized perceptual and cognitive processes and dedicated domain-specific neural circuits for processing knowledge of animals, plant life, and conspecifics, three domains in which quick and efficient recognition are thought to have fitness value. On this view, man-made objects as well as actions are not *a priori* candidate domains for dedicated circuits. Knowledge related to both these categories would thus be represented and processed by domain-general, non-specialized, cognitive processes and neural circuits. Thus, this theory predicts that, everything else being equal, brain damage should not differentially disrupt the concepts of man-made objects and the concepts of actions although both categories of concepts could dissociate from the concepts of animal and/or plant. Furthermore, in such a context, other kinds of concepts that are not assumed to be sustained by a specialized system, say, geographical knowledge, should be damaged as well.[11] In other words, the association of a knowledge deficit for man-made objects and for actions should in fact result from the selective preservation of animal and plant knowledge, which are processed by specialized conceptual systems. Recently, the proponents of the theory suggested that tools, within

[11] These predictions may seem too strong and could be qualified if additional assumptions were made about the internal organization of the domain-general conceptual system. Actually, the domain-specific knowledge theory does not exclude the possibility that some heterogeneity emerges within the conceptual space of semantic features as a result of systematic differences in the distribution of semantic features across the various categories of concepts, which could lead to dissociations in case of damage. Thus, concepts from one category (i.e., man-made objects) may have more strongly intercorrelated semantic features than concepts from another category (i.e., actions), and this could have significant consequences in the condition of brain damage. For example, the category with strongly intercorrelated features could be more vulnerable and more likely to be damaged as a category (Caramazza & Shelton, 1998) or, on the contrary, more resilient to mild damage compared to the category with more weakly correlated features (Devlin, Gonnerman, Andersen, & Seidenberg, 1998). Moreover, it may be assumed that clusters of concepts sharing properties are represented in close proximity in the conceptual space and, thereby, would be impaired together while other clusters of concepts would be spared, in case of damage (Caramazza, Hillis, Rapp, & Romani, 1990). Based on a feature cluster analysis (Vigliocco et al., 2004), this assumption would predict — like the "Featural and Unitary Semantic Space" hypothesis (Vigliocco et al., 2004) — that knowledge of man-made objects and of actions could be damaged separately.

the broader category of man-made objects, also could be a category of objects whose efficient recognition and use had fitness value in human evolution and, hence, could be processed by a dedicated domain-specific conceptual system (Mahon & Caramazza, 2009). In that case, knowledge of tools could dissociate from knowledge of other man-made objects (i.e., furniture, vehicles, clothing) in the condition of brain damage. However, in any case, within this theoretical framework, selective damage to a category of concepts will equally affect all types of knowledge about that category.

In the single-case study we are to report here we assessed knowledge of living things, of man-made objects, and of actions in a brain-damaged patient, JJG, presenting with a conceptual deficit. After a detailed case report, we will show that JJG's conceptual knowledge of both man-made objects and actions was severely impaired while his conceptual knowledge of living things was spared as well as his knowledge of unique entities. We then examined whether this pattern of association of a conceptual deficit for both man-made objects and actions could be accounted for, first, by the "sensory/functional" (Bird et al., 2000) and, second, the "manipulability" (e.g., Gerlach et al., 2002; Kellenbach et al., 2003; Noppeney et al., 2005; Saccuman et al., 2006) account for category-specific conceptual impairments advocated within the FBO theoretical framework by assessing, first, the patient's knowledge of sensory compared to functional features, second, his knowledge of manipulation compared to functional features and, third, his knowledge of manipulable compared to non-manipulable items. The later assessment also allowed us to evaluate an account for the deficits in terms of failures of simulating the hand movements implied by manipulable objects and manual actions.

The "sensori/functional" account for category-specific conceptual impairments predicts that a conceptual deficit for man-made objects and actions in the presence of spared knowledge of living things should (i) affect all types of man-made objects (i.e.,

both manipulable and non-manipulable man-made objects) and actions (i.e., both manipulation/manual and non-manipulation/manual actions), although man-made objects should be less severely impaired than actions, and (ii) be associated with a disproportionate loss of knowledge of functional compared to sensory features whereas the "manipulability" account predicts that the deficit should be (i) selective to manipulable man-made objects and manipulation actions, and (ii) associated with a disproportionate loss of manipulation compared to functional knowledge. As for the "failure-of-simulating" account, it predicts that a conceptual deficit for man-made objects and actions should be (i) selective to manipulable man-made objects and manual actions, and (ii) associated with upper limb apraxia.

The findings showed that, contrary to the predictions made by the "sensory/functional", the "manipulability", and the "failure-of-simulating" accounts for category-specific conceptual impairments, the patient's association of deficits for both man-made objects and actions was not associated with a disproportionate impairment of functional compared to sensory knowledge or of manipulation compared to functional knowledge; the patient was not more impaired for manipulable compared to non-manipulable items either, although he did present with upper limb apraxia. In the general discussion, we will propose to account for the patient's association of deficits by the hypothesis that all kinds of concepts whose core property is that of being a mean of achieving a goal are learned, represented and processed by a common domain-specific conceptual system, which would have evolved to allow human beings to quickly and efficiently design and understand means to achieve goals and purposes.

2. Case report

JJG is a right-handed man with a Master Degree in Engineering, and was 59-years-old in October 2007, when this study began. In 1999, he had suffered from an ischemic stroke in the region of the right posterior artery, without apparent sequel. In December 2005, he suffered from a second ischemic stroke in the region of the left middle cerebral artery which left him with a right hemiplegia, upper limb apraxia, and global aphasia. In 2009, an MRI scan showed micro- and macrocystic gliosis involving almost the whole profound and superficial left sylvian territory. This included the putamen, part of the pallidum, the caudate nucleus, a large part of the thalamus, the corona radiata, the centrum ovale, the insula, the superior and middle temporal gyri and part of the inferior temporal gyrus, the supramarginal and angular gyri, the precentral gyrus, the middle frontal gyrus and part of the inferior frontal gyrus. Subcortical gliosis also extended to the superior frontal gyrus and the root of postcentral gyrus. An important atrophy of the left cortico-spinal tract was observed as well as a passive enlargement of the left lateral ventricule (Figure 4.1).

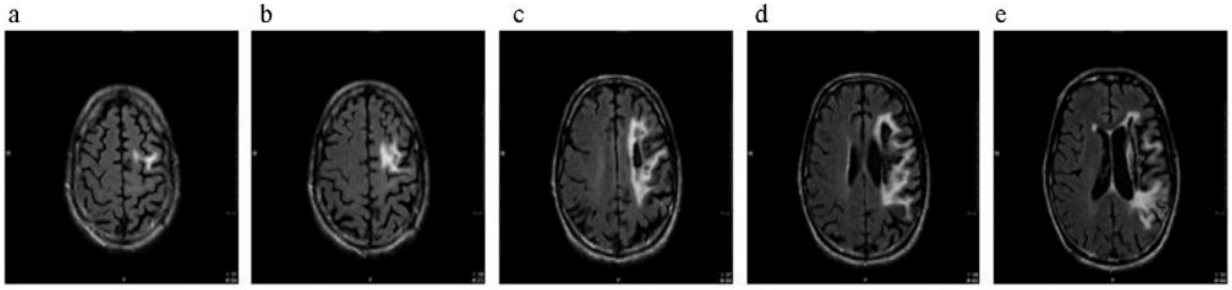

Figure 4.1| Transversal sections of JJG's brain, showing the lesion in the left prefrontal cortex (a, b) and th extensive superficial and deep lesion in the left temporal lobe (c, d, e).

The neuropsychological examinations performed in October 2007 (see Table 4.1) identified preserved visual episodic and short-term memory (verbal memory could not be tested because of JJG's word-finding and reading difficulties) and no executive dysfunction. Low-level visual processing was preserved on the Minimal Feature View

task (B.O.R.B., Riddoch & Humphreys, 1993). JJG's ability to access the structural description system (Humphreys, Riddoch, & Quinlan, 1988) was also preserved: he performed in the normal range with the items of the *Batterie de Décision Visuelle d'Objets* (Bergego, Pradat-Diehl, & Ferrand, 2006) containing 28 living and 44 man-made objects and 72 non-objects, as well as with another 144-items decision task comprising four subcategories of objects and non-objects (animals, fruit/vegetables, vehicles, and implements; Samson, Pillon, & De Wilde, 1998).

JJG's visual processing of gestures and access to the stored representation of gestures was good: he performed similarly to control subjects when presented with a videotaped presentation of 30 meaningful and 30 meaningless gestures and asked to tell whether they were meaningful or not (Peigneux & Van der Linden, 2000). He also performed almost flawlessly when asked to reproduce displayed postures on a model, which shows that his visuo-gestural analysis and knowledge of the body was intact (Goldenberg, 1995). However, JJG showed severe difficulties in gesture production, whatever the modality of presentation of the stimuli (i.e., producing gestures on verbal command or on imitation) and the type of gestures (i.e., meaningful or meaningless). He scored between 0 and 3/20 across the various production tasks (Table 4.1). The error analysis, performed with Peigneux and van der Linden's (2000) scheme (adapted from Rothi, Ochipa, & Heilman, 1997), first revealed a similar rate of partial perseveration errors (mostly, perseveration of the manual or digital configuration or of the movement of the preceding gesture) in producing gestures to verbal command (17%) and in imitating meaningless (17%) or meaningful (21%) gestures, which suggested an impairment located at the level of the output gestural buffer (Cubelli, Marchetti, Boscolo, & Della Sala, 2000). In the imitation task, the other main types of errors were temporal and spatial errors for both meaningless (80%) and meaningful (66%) gestures. However, in producing gestures on verbal

command, the temporal and spatial errors were less frequent (33%) while hesitation errors and non-responses appeared fare more frequently (42%) than in imitation tasks (3% and 5% hesitation errors in imitating meaningless and meaningful gestures, respectively). This error pattern suggested additional impairments in retrieving stored information about how to perform actions or manipulate objects and in planning accurately-recognized gestures for production.

Language examination (see Table 4.2) was undertaken in November and December 2007. JJG's spontaneous speech was non-fluent, and was interspersed with frequent episodes of word-finding difficulties, in the context of correct articulation, prosody, and syntax. Repetition of phonemes, syllables, and words (both verbs and nouns) was preserved although repetition of pseudowords was impaired. There was also evidence for severe anomia, speech comprehension difficulties, and impaired reading and writing. Thus, JJG was severely impaired both in a picture naming and a spoken word-to-picture matching task comprising the same set of concrete objects. His erroneous responses in naming were mainly non-responses and semantic paraphasias, and in matching, they mainly consisted in choosing the semantically-related foil. This pattern suggested that JJG presented with a conceptual deficit.

Because difficulties in understanding verbs was noted in clinical settings, verb compared to noun processing was further assessed in JJG. The patient's performance was within the normal range in an auditory lexical decision task including nouns and verbs matched in spoken word frequency and pseudo-nouns and pseudo-verbs differing from real nouns and real verbs from one or two phonemes. The patient recognized most nouns (34/36) and rejected most pseudo-nouns (35/36); he also accepted all verbs (36/36) and rejected most pseudo-verbs (35/36). In a translated version of the "Kissing and Dancing Test" (KDT; Bak & Hodges, 2003) and the "Pyramid and Palm Trees test" (PPT; Howard

& Patterson, 1992), which evaluate verb/action and noun/object processing, respectively, JJG was impaired with verbs/actions in both the spoken word (45/52; controls' mean=51.8; SD=0.45) and the picture (48/52; controls' mean=52, SD=0) version. He was also impaired with nouns/objects in both the spoken word (48/52; controls' mean=51.8, SD=0.45) and the picture (47/52; controls' mean=51.8, SD=0.45) version. No significant difference was observed between the picture and the word version either on the verbs/actions or the nouns/objects ($\chi^2 < 1$) or between verbs/actions and nouns/objects ($\chi^2 < 1$). We presented JJG with an additional association task similar to the KDT, which included 20 action items and in which the target response and the foil were selected so that they were matched in familiarity [t (38) < 1] and spoken word frequency [t (38) < 1]. JJG was again impaired both with the picture version (13/20) and the spoken word version (14/20), $\chi^2 < 1$, of this association task.

Given the sparing of spoken word, object, and gesture recognition processes in JJG (Cf. Supra), the results of the object and action association tasks suggested that JJG's difficulty in understanding verbs resulted from a conceptual deficit affecting action knowledge, and that he actually also presented with a conceptual deficit impairing object knowledge. The experimental study presented below was carried out in order to delineate more precisely and with a more controlled material the classes of concepts affected by the conceptual deficit and, then, to test different accounts for the pattern of cooccurrence of deficits for various classes of concepts within extant theories of conceptual organization.

Table 4.1. Neuropsychological data of patient JJG (October 2007)

Tests	JJG's score	Control's mean (CM) or JJG's percentile (P) or z-score
Short term memory		
Spatial Span [1]		
Forward	5	NS 7
Backward	5	NS 9
Long term memory		
Doors test [2]		
Part A	10	P25
Part B	7	P25-P50
Total	17	P25
Executive functions		
Trail making test		
Part A		
Time	70 sec	-0.4 σ
Errors	0	
Part B		
Time	206 sec	
Errors	(Interrupted 7G)	
Luria's graphic series [3]	26.5	Normal
Visual processing		
B.O.R.B [4]		
Minimal feature view	25/25	0.85 σ
Batterie de décision d'objets [5]	70/72	Control mean: 68/72
Object/Non-Object decision [6]	71/72	Control mean: 68/72
Praxis [7]		
Visual recognition of gestures	57/60	.
Posture reproduction on a mannequin	9/10	.
Pantomiming the use of a pictured object	0/10	.
Use of familiar man-made objects	5/9	.
Delayed imitation		
Meaningless gestures		
Blocked condition[2]	2/19	.
Mixed condition	0/20	.
Meaningful gestures		
Blocked condition	3/20	.
Mixed condition	0/20	.
Gesture production on verbal command	0/20	.

[1] Smirni, Villardita, and Zappala (1983); [2] Baddeley, Emslie, and Nimmo-Smith (1994); [3] Luria (1980); [4] Riddoch and Humphreys (1993); [5] Bergego, Pradat-Diehl, and Ferrand (2006); [6] Samson et al. (1998); [7] *Batterie d'Evaluation des Praxies*, Peigneux and Van der Linden (2000). This test took place in December 2007.

Table 4.2. Language evaluation in JJG (November-December 2007)

Tasks	JJG's score	JJG's z-score
Repetition [1]		
Words	17/18	n.a
Pseudo-words	1/6	n.a
Writing on dictation [1]		
Letter	4/8	n.a
Words	2/12	n.a
Pseudo-words	0/4	n.a
Oral Spelling [1]		
Words	0/8	n.a
Pseudo-words	0/3	n.a
Reading aloud [1]		
Regular words	8/36	n.a
Irregular words	2/6	n.a
Pseudo-words	0/10	n.a
Spoken Picture Naming [2]	28/80	-21.7 σ
Spoken word/picture matching [2]	70/80	-20.2 σ

[1] *Batterie d'évaluation du langage* (Cliniques universitaires Saint-Luc, Brussels). [2] de Partz, Bilocq, De Wilde, Seron & Pillon (2001).

3. EXPERIMENTAL STUDY

3.1. General method

The experimental investigations were carried out from September 2007 to July 2009 in sessions lasting between 60 and 120 minutes. Unless otherwise indicated, the tasks were presented to the same group of 8 control subjects, matched with the patient for age (mean = 62.6; range = 60-64), gender, and years of education (mean = 16.2; range = 15-17).

Crawford and Howell's (1998) modified *t*-test was used to test whether the patient's performance on the various categories of items was significantly impaired in comparison to the control group (test for the presence of a deficit). Crawford and Garthwaite's (2007) Bayesian Standardized Difference test (BSDT) was applied to test whether the discrepancy between two item categories in the patient's performance was significantly different from the discrepancy between them in the control group (test for the presence of a dissociation). We used BSDT rather than the Revised Standardized Difference test

(RSDT, Crawford & Garthwaite, 2005) because BSDT provides better protection against Type I errors when the size of the control group is small and, especially, when the patient's scores are extreme (z-score < -3.0), which was the case for JJG.

All the picture stimuli used in this study across the different batteries, unless otherwise indicated, were color photographs with no or minimal context presented in full-screen mode (15.4 inch screen) using PowerPoint software. The photographs of actions depicted all the persons, objects and instruments typically involved in the action. The characteristics of these stimuli in terms of spoken word frequency, subjective word frequency, concept familiarity, imageability, and age of acquisition, when available, are displayed in Table 4.3.

The general procedure used for the naming, word/picture matching, and word/picture verification tasks included in the different batteries presented to the participants was as follows:

- In the naming tasks, the participants were presented with all the items in one session and were asked to name them within 20 seconds. The naming of actions was elicited by the phrase *en train de* which requires being completed by the infinitive form of a verb ("*en train de* $Verb_{inf}$" is the French equivalent of English "$Verb_{ing}$").
- In the word/picture matching and the word/picture verification tasks, nouns were presented without their articles and verbs were presented in the infinitive form with the phrase *en train de*. In the word/picture matching tasks, each spoken word was presented simultaneously with an array of pictures (the correct picture and the semantic foils) in a balanced-order design and the participants were asked to point to the picture of the object or of the action that corresponded to the spoken word. In the word/picture verification tasks, each spoken word was presented once with the correct picture, and once with each of the foils, during the same session, and the participants were asked to

Table 4.3. Mean and standard deviation of the spoken word frequency, subjective word frequency, concept familiarity, imageability, and age of acquisition for the various subsets of items in the batteries used in the study.

	N	Spoken word frequency [1]	Subjective word frequency [2]	Familiarity [3]	Imageability [4]	Age of acquisition [5]
"Objects/Actions"						
Objects						
Living Things	18	26.21 (34.19)	2.92 (0.72)	2.88 (0.75)	4.74 (0.18)	n.a.
Man-made Objects	18	22.85 (33)	3.03 (0.58)	3.16 (0.68)	4.68 (0.28)	n.a.
Total Objects	36	24.53 (33.16)	2.97 (0.65)	3.02 (0.72)	4.71 (0.23)	n.a.
Actions						
Object-directed Actions	18	41.78 (49.74)	3.12 (0.61)	3.13 (0.65)	3.46 (0.44)	n.a.
Person-directed Actions	18	41.74 (49.74)	3.10 (0.83)	3.16 (0.91)	3.46 (0.67)	n.a.
Total Actions	36	41.76 (47.58)	3.11 (0.72)	3.14 (0.78)	3.46 (0.56)	n.a.
'Concrete Objects"						
Animals	25	10.19 (10.57)	2.53 (0.50)	2.69 (0.80)	4.39 (0.48)	2.46 (0.57)
Plants	25	6.66 (7.16)	2.77 (0.56)	2.83 (0.76)	4.48 (0.42)	2.54 (0.56)
Man-made Objects	25	8.59 (8.89)	2.68 (0.76)	2.71 (0.92)	4.45 (0.38)	2.66 (0.59)
"Man-made Objects/Actions"						
Man-made Objects	28	12.56 (15.30)	n.a.	3.02 (1.02)	4.20 (0.53)	2.62 (0.67)
Actions	28	14.34 (20.10)	n.a.	2.96 (0.85)	4.10 (0.51)	2.38 (0.58)
"Living things/Made-made objects"						
Living Things	32	9.44 (22.38)	2.60 (0.62)	n.a	4.45 (0.50)	n.a
Man-made Objects	32	35.65 (87.20)	3.01 (0.91)	n.a	4.47 (0.34)	n.a
"Manipulable/Non-manipulable Items"						
Manipulable						
Man-made Objects	16	5.63 (8.12)	n.a.	2.79 (0.64)	4.56 (0.56)	n.a.
Actions	16	23.98 (48.99)	n.a.	3.07 (0.49)	3.68 (0.51)	n.a.
Total Manipulable	32	14.80 (35.78)	n.a.	2.93 (0.58)	4.12 (0.69)	n.a.
Non-manipulable						
Man-made Objects	16	11.25 (16.80)	n.a.	3.01 (1.33)	4.62 (0.32)	n.a.
Actions	16	57.24 (70.27)	n.a.	3.34 (0.69)	3.82 (0.42)	n.a.
Total Non-manipulable	32	34.24 (55.42)	n.a.	3.18 (1.05)	4.22 (0.55)	n.a.
Total Man-made Objects	32	8.44 (13.29)	n.a.	2.90 (1.03)	4.59 (0.45)	n.a.
Total Actions	32	40.61 (61.94)	n.a.	3.20 (0.61)	3.75 (0.46)	n.a.
Manipulable/Non-manipulable items of the "Man-made Objects/Actions" battery						
Manipulable items	30	13.62 (19.18)	n.a.	3.04 (1.04)	4.15 (0.46)	2.64 (0.65)
Non-manipulable items	26	13.26 (16.11)	n.a.	2.93 (0.81)	1.14 (0.58)	2.34 (0.58)

n.a=non-available

[1] Number of lemma occurrences per million in a corpus of subtitles of films (New, Brysbaert, Pallier & Veronis, 2007); [2] From Bonin, Boyer, Meot, Fayol and Droit (2004) and Bonin, Meot, Aubert, Malardier, Niedenthal and Capelle-Toczek (2003) for the items of the "Concrete Objects" and the "Living Things/Man-made Objects" batteries; rated on a five-point scale (1=low, 5=high frequency) by 25 subjects for half of the items and 29 subjects for the second half (mean age=66; SD=8.9) for the items of the "Objects/Actions" battery. [3] From Alario and Ferrand (1999), Bonin, Peereman, Malardier, Meot and Chalard (2003), and Bonin et al. (2004) for the items of the "Concrete Objects", "Living Things/Man-made Objects" and "Man-made Objects/Actions" batteries; rated on a five point scale (1=low, 5=high familiarity) by 20 subjects (mean age=35.95; SD=11.01) for the items of the "Manipulable/Non-manipulable Items" battery and by 27 subjects for half of the items and 26 subjects for the second half (mean age=67; SD=9.7) for the items of the "Objects/Actions" battery.[4] From Bonin et al. (2004) and Bonin, Meot et al. (2003) for the items of the "Concrete Objects", "Living Things/Man-made Objects" and "Man-made Objects/Actions" batteries; rated on a five point scale (1=low, 5=high imageability) by 20 subjects (mean age=29.15; SD=7.47) for the items of the "Manipulable/Non-manipulable Items" battery and by 27 subjects (mean age=58.22) for the items of the "Objects/Actions" battery. [5] From Alario and Ferrand (1999), Bonin, Peereman et al. (2003), and Bonin et al. (2004).

tell whether the spoken word and the picture matched. An item was scored correct if, for that item, both the correct picture was accepted and each of the foils rejected. In both these tasks, there was no time limit set for the response, the photograph was displayed until the participant's response, and repetition of the word stimulus was allowed if necessary.

- Each task and session was preceded by a few examples designed to familiarize the participants with the task.

3.2. Delineating the scope of JJG's conceptual impairment

3.2.1. Material and method

In order to delineate the classes of concepts that were impaired/spared by conceptual damage in JJG, four sets of tasks were presented to him and the control subjects: (1) A "Objects/Actions" battery assessing knowledge of objects and actions; (2) a "Concrete Objects" battery assessing knowledge of three categories of objects, i.e., animals, plants, man-made objects; (3) a "Man-made Objects/Actions" battery assessing knowledge of man-made objects compared to actions; (4) a "Unique Entities" battery assessing knowledge of famous people, countries, and famous buildings.

"Objects/Actions" battery

This battery was composed of a spoken picture naming and a spoken word/picture verification task. It contained 72 items, i.e., 36 objects and 36 actions. Among the 36 objects, half were living things, i.e., 9 animals and 9 plants, and half man-made objects, i.e., 9 tools and 9 other man-made objects. Among the 36 actions, half were "object-directed' actions and half "person-directed" actions. "Object-directed actions" involved a man-made object either as the goal (n=9; e.g., crushing) or as the instrument/tool (n=9; e.g., hammering) of the action, while the "person-directed actions" included 9 whole-

body actions (e.g., dancing) and 9 interactions (e.g., strangling). The object and the action set were matched for spoken-name frequency [t (62) = -1.78; p = 0.08], subjective frequency (t < 1), and concept familiarity (t < 1); however, the objects were more imageable than the actions [t (47.1) = 12.34; p < 0.001]. The living things and man-made objects, on the one hand, the object-directed and person-directed actions, on the other hand, were matched for spoken word frequency (t < 1), familiarity (t < 1), and imageability (t < 1). A color photograph with no or a minimal context was selected for each object and action and used in the naming task. Three additional photographs per item were selected as foils for the word/picture verification task: one corresponding to a "close" semantic coordinate of the item, one to a "far" semantic coordinate of the item, and one that was semantically unrelated to the item. Filler items were added to increase the yes/no response ratio, which reached 0.34. Given the scoring procedure adopted (Cf. General method), the correct response probability at chance was 0.0625.

The same set of action items was further assessed both in naming and word/picture verification with videotaped stimuli instead of photographs in the naming and the word/picture verification task. Videotaped clips were prepared so that they resembled the corresponding photographs as closely as possible, with no additional information except from movement and duration. The participants were asked to wait until the end of each video clip before responding.

"Concrete Objects" battery

This battery was composed of a spoken picture naming, a word/picture matching, and a word/picture verification task including the same set of 75 items equally divided among the categories of animals (n=25), plants (n=25), and man-made objects (n=25). The items from the three categories were matched in concept familiarity (F < 1), age of acquisition

($F < 1$), imageability ($F < 1$), subjective word frequency ($F < 1$), and objective spoken word frequency ($F < 1$). In the word/picture matching and the word/picture verification task, the foils were two semantic coordinates. These were selected on the basis of the ratings made by 30 subjects who were asked to evaluate on a 5-point scale the degree to which pairs of coordinates and targets presented as written words shared semantic characteristics (where 1 = no and 5 = a lot of characteristics in common). The foils did not differ in their mean semantic proximity with the targets across the three categories of items ($F < 1$). In the word/picture verification task, filler items were added to increase the yes/no response ratio, which reached 0.39. Given the scoring procedure (Cf. General method), the correct response probability at chance was 0.125.

"Man-made Objects/Actions" battery

This battery contained a spoken picture naming, a word/picture matching, and a word/picture verification task composed of the same set of 28 man-made objects (15 tools, e.g., a compass, and 13 non-tools, e.g., skirt, hammock, bike) and actions (15 manual actions, e.g., drawing, and 13 non-manual actions, e.g., licking), matched for age of acquisition [t (54) = 1.42; p = 0.16], concept familiarity ($t < 1$), imageability ($t < 1$), and spoken word frequency ($t < 1$). Note also that the items of this battery were matched in familiarity ($F < 1$), spoken word frequency [F (4,126) = 1.35; p = 0.25] and age of acquisition ($F < 1$) with the items of the "Concrete objects" battery. In the word/picture matching and the word/picture verification task, the foils were two close semantic coordinates that were selected after an assessment of their semantic proximity with the targets, made by 33 control subjects who were asked to rate the degree to which pairs of concepts presented as written words shared common characteristics on a 5-point scale (1 = no to 5 = a lot of characteristics in common). No significant difference in mean

semantic proximity between targets and foils was observed between the man-made object (Mean = 3.35; SD = 0.72) and the action (Mean = 3.08; SD = 0.77) sets [t (110) = 1.89; p = 0.06]. In the word/picture verification task, the yes/no response ratio reached 0.39 once filler items were added. With our scoring procedure, the correct response probability at chance was 0.125.

To assess the consistency of his performance, JJG was tested on the naming and the word/picture verification task three times in separate sessions over a six-month period.

"Unique Entities" battery

This battery was composed of three sets of tasks assessing knowledge of unique entities; the first set related to famous people, the second to countries, and the third to famous buildings. To assess knowledge of famous people, two tasks were prepared. In the first task, the participants were auditorily presented with the first name and surname of 60 famous people from different fields (sports, national and international politics, music, film or television) and had to point to the color photograph corresponding to the spoken name (e.g., *Johnny Depp*), among a array of five, i.e., the correct picture, a semantic foil (i.e., same profession, e.g., Ben Affleck), a visual foil (similar facial features, e.g., Stephan Eicher), a visuo-semantic foil (e.g., Vincent Pérez), and a phonological foil (similar name, e.g., Johnny Clegg). The second task was a binary choice task aimed at evaluating conceptual knowledge about 50 other famous people. Three properties of each famous person were assessed, namely, their profession, the country they were from, and a specific feature. In each trial, the name and surname of the famous person was auditorily presented with a phrase describing a correct property and a phrase describing an incorrect property (in a balanced order). Foils for the profession were in the same domain (e.g., Politician: Prime minister or President; Sport champion: Boxing or Cycling) and foils for

the specific feature were a plausible coordinate (e.g., *Alfred Nobel invented the dynamite or the revolver?*). The participant had to tell which phrase was correct. One point was given for success on all three properties of a given person. Two tasks were also prepared to assess knowledge of countries. In the country pointing task, the participants were presented with four blank maps each depicting a continent (America, Europe, Asia, Africa) and were asked to point successively toward the four auditorily presented continents, and then to six countries in America, Asia, and Africa and eight in Europe. In the second country task, the participants had to tell, among two choices, which was the capital, the specialty (both presented auditorily) or the flag (presented visually) of 20 countries worldwide. Foils for the capital were an important city of the same country (e.g., Switzerland: Bern or Geneva), foils for specialties were selected from the same category (e.g., Russia: Vodka or Whiskey), and foils for flags were chosen for their visual similarity (e.g., Greece: Greek or Uruguayan flag). One point was given for success on all three properties of a given country. Finally, knowledge of famous buildings was assessed through a binary choice task including 20 famous buildings. Three auditorily presented properties of each building, namely the country, the city, and name, were assessed on presentation of a color photograph of the building. For example, with the photograph of the *Sagrada Familia*, the examiner asked whether it was in Australia or Spain, whether it was located in Madrid or Barcelona, and whether it was named *La Casa Battlo* (another building from Gaudi) or *La Sagrada Familia*. One point was given if the three properties of a given building were all successfully identified.

3.2.2. Results

"Objects/Actions" battery

As shown in Table 4.4, JJG was significantly impaired in the naming and the word/picture verification task, but he was not differentially impaired for objects and actions in either task (BSDT: $p = 0.53$ and $p = 0.73$, in the naming and the verification task, respectively). JJG was also significantly impaired with the videotaped version of the naming and the word/picture verification task, with no significant difference between the videotaped and the photograph version in the naming task (BSDT: $p = 0.93$) but significantly *worse* performance in the videotaped compared to the photograph version in the verification task (BSDT: $p = 0.01$).

Within the object set, both living things and man-made objects were significantly impaired in naming, and there was no significant difference between both categories of objects (BSDT: $p = 0.75$). Likewise, within the action set, both person-directed and object-directed actions were significantly impaired, and there was no significant difference between both categories of actions (BSDT: $p = 0.28$).

However, a different pattern of performance emerged in the verification task. Within the object set, JJG's performance was *not* significantly impaired for living things although it was significantly impaired for man-made objects. In fact, JJG's performance for man-made objects was significantly worse than his performance for living things (BSDT; $p < 0.005$). Then, it turned out that JJG's performance for man-made objects did not significantly differ from his performance for actions (BSDT: $p = 0.36$), while his performance for living things significantly differed from his performance for actions (BSDT: $p < 0.02$). Within the action set, no significant difference was found between person-directed and object-directed actions either in the photograph (BSDT: $p = 0.42$) or the videotaped (BSDT: $p = 0.23$) version.

Table 4.4. JJG's and control group's number of correct responses in the picture naming and the word/picture verification tasks for the items on the "Objects/Actions" battery, as well as in the video clip naming and verification tasks for the action items of the battery.

Task	N	JJG	Control Subjects			Modified
			Mean	SD	Range	*t* test
Picture Naming						
Objects						
Living Things	18	9	17.87	0.35	17-18	-23.90***
Man-made Objects	18	6	17.62	0.51	17-18	-21.49***
Total Objects	36	15	35.50	0.75	34-36	-25.77***
Actions						
Person-directed Actions	18	5	16.37	1.06	15-18	-10.11***
Object-directed Actions	18	2	16.25	0.88	15-17	-15.26***
Total Actions	36	7	32.63	1.19	31-34	-20.47***
Video clip Naming						
Person-directed Actions	18	3	17.37	0.51	17-18	-26.57***
Object-directed Actions	18	4	17.00	1.06	15-18	-11.56***
Total actions	36	7	34.37	1.30	32-36	-19.85***
Word/picture Verification						
Objects						
Living Things	18	16	17.50	0.75	16-18	-1.88
Man-made Objects	18	14	17.87	0.35	17-18	-10.43***
Total Objects	36	30	35.37	0.74	34-36	-6.84***
Actions						
Person-directed Actions	18	7	16.37	1.59	14-18	-5.55***
Object-directed Actions	18	6	16.87	1.35	15-18	-7.59***
Total Actions	36	13	33.25	2.43	29-36	-7.95***
Video clip Verification						
Person-directed Actions	18	5	17.65	0.51	17-18	-23.33***
Object-directed Actions	18	6	17.75	0.70	16-18	-15.82***
Total Actions	36	11	35.37	1.06	33-36	-21.68***

*** = $p < 0.001$

"Concrete Objects" battery

The results are displayed in Table 4.5**.** In naming, JJG's performance was significantly impaired for the three categories of objects, but it was significantly more impaired for man-made objects than for both animals (BSDT: $p < 0.01$) and plants (BSDT: $p < 0.01$) which themselves were not differentially impaired (BSDT: $p = 0.54$). In the word/picture matching task, JJG's performance was not significantly different from controls' for animals and plants but was significantly impaired for man-made objects. His

performance was significantly poorer for man-made objects than for both animals (BSDT: $p < 0.01$) and plants (BSDT: $p < 0.01$) and it was not significantly different between animals and plants (BSDT: $p = 0.18$). Likewise, in the word/picture verification task, JJG's performance did not differ from controls' for animals and plants but was significantly impaired for man-made objects. Once again, his performance was significantly poorer for man-made objects than for both animals (BSDT: $p < 0.01$) and plants (BSDT: $p = 0.01$), and there was no significant difference in his performance between animals and plants (BSDT: $p = 0.98$).

Table 4.5. JJG's and control group's number of correct responses in the picture naming, word/picture matching, and word/picture verification task of the "Concrete Objects" battery.

Task	N	JJG	Control Subjects			Modified *t* test
			Mean	SD	Range	
Naming						
Animals	25	7	23.13	1.55	20-25	-9.20***
Plants	25	5	23.00	1.41	21-25	-12.03***
Man-made Objects	25	7	24.00	0.53	23-25	-30.24***
Word/picture Matching						
Animals	25	25	24.62	0.38	23-25	0.90
Plants	25	24	24.62	0.76	23-25	-0.79
Man-made Objects	25	17	24.75	0.38	24-25	-19.74***
Word/picture Verification						
Animals	25	19	20.87	2.64	16-23	-0.67
Plants	25	20	21.12	1.80	19-24	-0.59
Man-made Objects	25	7	21.00	1.85	19-25	-7.13***

*** = $p < 0.001$

"Man-made Objects/Actions" battery

The results are displayed in Table 4.6. In picture naming, JJG's performance was significantly impaired relative to the control group in all three sessions and for both man-made objects and actions. There was no significant difference between his impairment for man-made objects and for actions in any of the three sessions (all BSDTs: $p > 0.58$). In

the word/picture matching task, JJG's performance was significantly and similarly impaired for man-made objects and actions (BSDT: $p = 0.69$). In the word/picture verification task, JJG's performance was again significantly impaired for both man-made objects and actions in all three sessions, with none of the differences between these two categories being significant (all BSDTs: $p > 0.35$). When the scores from the three sessions were averaged, JJG's performance still did not show any significant difference between man-made objects and actions, either in naming (BSDT: $p > 0.75$) or in the word/picture verification task (BSDT: $p > 0.87$).

Table 4.6. JJG's and control group's number of correct responses in picture naming, word/picture matching, and word/picture verification for the "Man-made Objects/Actions" battery and at the three sessions of testing.

Task	Items	N	JJG	Control group			Modified *t* test
				Mean	SD	Range	
Naming							
Session 1	Man-made Objects	28	11	26.50	0.93	25-27	-15.88***
	Actions	28	6	26.00	1.19	24-28	-15.85***
Session 2	Man-made Objects	28	14	26.50	0.93	25-27	-12.81***
	Actions	28	7	26.00	1.19	24-28	-15.05***
Session 3	Man-made Objects	28	15	26.50	0.93	25-27	-11.79***
	Actions	28	8	26.00	1.19	24-28	-14.26***
Word/picture Matching	Man-made Objects	28	21	27.75	0.46	27-28	-13.83***
	Actions	28	19	27.12	0.64	26-28	-11.97***
Word/picture Verification							
Session 1	Man-made Objects	28	8	26.75	1.28	25-28	-13.81***
	Actions	28	5	25.50	1.41	24-28	-13.71***
Session 2	Man-made Objects	28	12	26.75	1.28	25-28	-10.86***
	Actions	28	7	25.50	1.41	24-28	-12.37***
Session 3	Man-made Objects	28	8	26.75	1.28	25-28	-13.81***
	Actions	28	9	25.50	1.41	24-28	-11.03***

*** = $p < 0.001$

Distribution of JJG's errors

Whatever the battery ("Objects/Actions", "Concrete Objects", or "Man-made Objects/Actions" battery) and the category of items (living things, man-made objects, or actions), JJG's errors in naming mainly consisted in non-responses or unrelated words, followed by semantic paraphasias; in the word/picture verification tasks, his errors the

most often consisted in accepting a semantic foil (see Appendix for detailed results). (In the word/picture matching tasks, the only possible type of error was pointing to a semantic foil.).

Additional analyses of the "Man-made Objects vs. Actions" contrast

We performed an analysis with all the man-made object and action items from the previous batteries.[12] In that way, the set of man-made objects amounted to 71 (18+25+28) and the set of actions to 64 (36+28). JJG' and the control's performance for this item set is displayed in Table 4.7. The results showed again a not significantly different

Table 4.7. JJG's and control group's number of correct responses in picture naming and word/picture verification for the two sets of man-made object and action items combined from the different batteries.

Task	N	JJG	Control group			Modified
			Mean	SD	Range	*t* test
Naming						
Man-made Objects	71	24	68.12	1.12	66-69	-37.01***
Actions	64	13	58.60	1.68	57-62	-25.60***
Man-made Objects	103	41	96.37	2.44	92-100	-21.34***
Actions	96	19	85.75	1.90	82-88	-33.12***
Word/picture Verification						
Man-made Objects	71	30	65.62	2.92	61-71	-11.50***
Actions	64	18	58.75	3.10	53-63	-12.39***
Man-made Objects	103	53	95.37	3.20	91-102	-11.89***
Actions	96	38	89.25	2.96	84-92	-16.32***

*** = $p < 0.001$

impairment for man-made objects and actions in the naming (BSDT: $p = 0.18$) or the verification task (BSDT: $p = 0.78$). If we again increased the number of items by adding to the previous set the set of 32 man-made objects and 32 actions from the

[12] In these additional analyses, the naming data for the action items from the « Objects/Actions » battery were those of the naming from photographs and the data from the « Man-made Objects/Actions » battery were those of the first presentation.

"Manipulable/Non-manipulable Items" battery that will be presented in the next section (Cf. Infra), thereby obtaining a set of 103 man-made objects and 96 actions (see Table 7 for JJG's and the control's performance for this set), still no significant difference was found between the impairment for man-made objects and actions in the naming task (BSDT: $p = 0.24$) or the word/picture verification task (BSDT: $p = 0.38$).

"Unique Entities" battery

In the famous people tasks, JJG scored 51/60 (controls: 42-59, Mean = 50.7, SD = 6.50) when he had to point to the picture of a named person, which was an unimpaired performance (modified $t < 1$), and he scored 35/50 (controls: 33-46, Mean = 39.6, SD = 4.30) when he had to retrieve semantic properties about famous people, again an unimpaired performance [modified t (7) = -1, p = 0.18]. When asked to identify continents and locate countries on maps, JJG scored 27/30, which was within the control subjects' range of performance (27-30, Mean = 28.1, SD = 1) and indicated no significant deficit [modified t (7) = -1.03, p = 0.17]. He also identified accurately all the three features of the countries for 17/20 countries, which was again within the control group's range of performance (15-20, Mean = 17, SD = 2), and not significantly impaired (modified $t < 1$). Finally, in accessing the semantic properties of the famous buildings, JJG scored 16/20 (controls: 15-19, Mean = 17.5, SD = 1.69), which was not significantly different from the control group (modified $t < 1$).

3.2.3. Discussion

The results of this first set of tasks first indicated that JJG presented with a conceptual impairment that *selectively* and severely affected his knowledge of man-made objects and of actions although his naming performance suggested that he probably

presented with an additional deficit in retrieving the phonological word forms, which affected his performance and caused similar naming errors in all classes of words. Thus, with the three different sets of items including man-made objects ("Objects/Actions", "Concrete Objects", and "Man-made Objects/Actions" batteries), the results showed that JJG was significantly impaired in the comprehension tasks (word/picture matching or word/picture verification tasks) with man-made objects. Furthermore, in these comprehension tasks and in the two different sets of items where both living things and man-made objects were present ("Objects/Actions" and "Concrete Objects" batteries), his performance with man-made objects appeared disproportionately impaired compared to his performance with living things, both animals and plants that, in fact were spared. Likewise, in both the item sets including action items ("Objects/Actions" and "Man-made Objects/Actions" batteries), JJG's knowledge of actions appeared significantly impaired. A summary of the results obtained in the comprehension tasks (word/picture verification) with the living thing, man-made object, and action items from the various item sets, together with the results obtained in the tasks assessing knowledge of unique entities, is displayed in Figure 4.2.

Two interpretations of the pattern of association of a deficit for man-made objects and for actions already can be rule out on the basis of the results of this set of tasks. First, the associated conceptual impairment for both man-made objects and actions cannot be explained simply by an across-the-board conceptual deficit with a selective *preservation* of living things, say, as a preservation of knowledge sustained by specialized domain-specific processing systems (Caramazza & Shelton, 1998). Knowledge of other classes of entities were indeed preserved in JJG, that is, unique entities like countries and famous buildings (The preservation of famous people knowledge was also preserved, but this could be explained, within the DSK framework, as a preservation of a specialized system

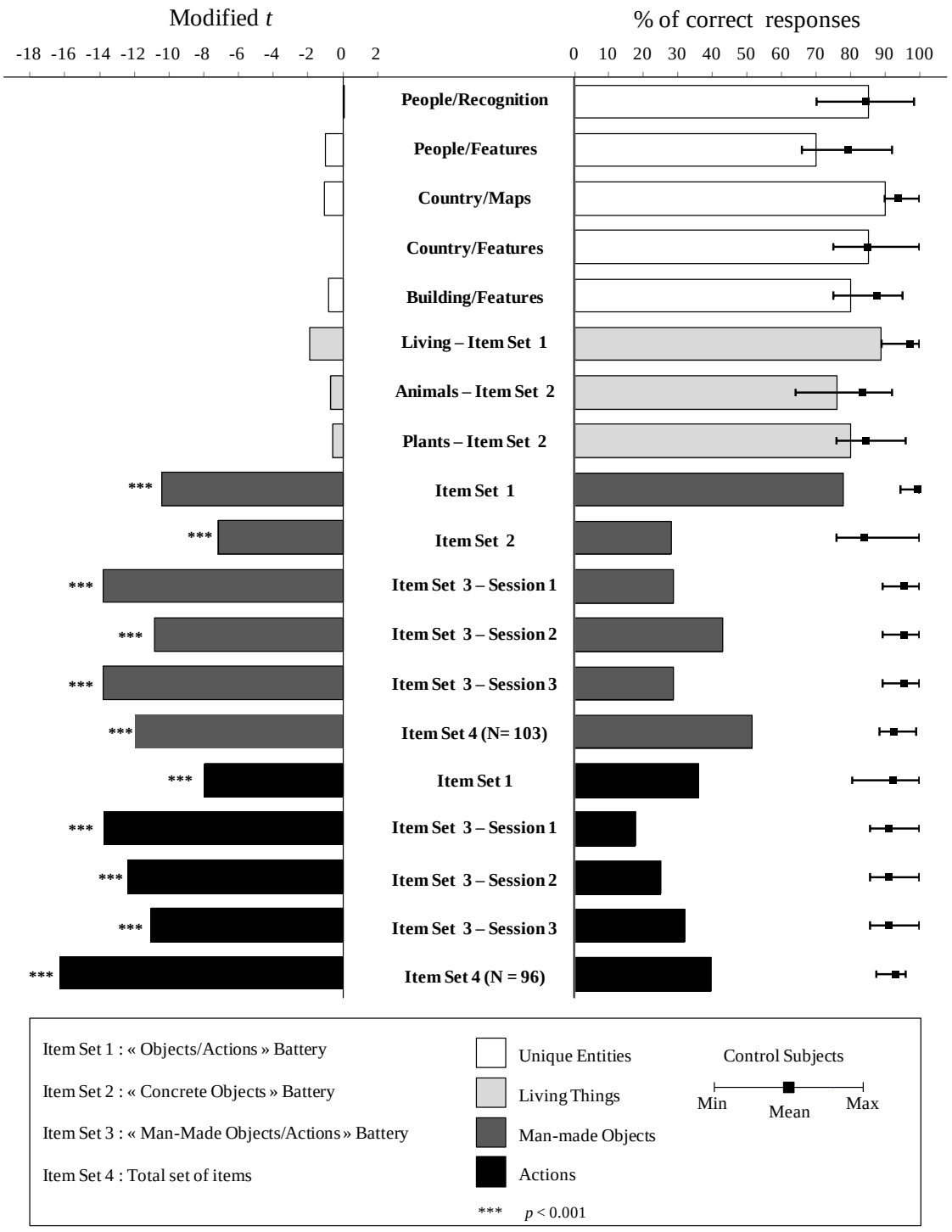

Figure 4.2| Summary of JJG's and control subjects' results in the word/picture verification task with the living thing, man-made object, and action items from the various item sets ("Objects/Actions", "Concrete Objects", "Man-made Objects/Actions" batteries, and total item set), and in the tasks assessing knowledge of unique entities. On the right, the figure displays the percentage of JJG's correct responses with the mean percentage and range (min-max) of correct responses of the control subjects and, on the left, the results of the modified *t*-tests for the comparison between JJG's and control subjects' performance.

for representing conspecifics.) Second, the associated conceptual impairment for both man-made objects and actions cannot be explained either by the processing of actions being impaired because of a deficit in accessing knowledge of the man-made objects that are involved in the actions. Like the results of the "Object/Actions" battery showed, actions that involve man-made objects ("object-directed" actions) were no more impaired than actions that do not involve man-made objects ("person-directed" actions).

Now the question is whether JJG's pattern of conceptual impairment should be considered as a mere co-occurrence of deficits resulting from two independently-damaged functional components within the conceptual system or rather as a theoretically-relevant association of deficits due to the selective impairment of a single component involved in the conceptual processing of both man-made objects and actions. Although the two independent component account cannot be formally ruled out, we believe that JJG's pattern of conceptual impairment presented several features that are more naturally accounted for within a single component hypothesis. First, the deficits JJG presented for both man-made objects and actions presented a specific feature that was absent in most associations of deficits reported on or discussed in the neuropsychological literature (e.g., Gerstmann, 1940; Warrington & McCarthy, 1987; Warrington & Shallice, 1984): both deficits were of a similar degree of severity. Both in the "Objects/Actions" battery and in the "Man-made Objects/Actions" battery, we found no evidence for JJG's impairment being of a different degree of severity for man-made objects and actions. Second, this pattern of similar severity was found with two different samples of items ("Objects/Actions" and the "Man-made Objects/Actions") and, third, it was found consistently across three examinations during a six-month period. Again, none of these facts provides compelling evidence to reject a two independent component account for

the association of deficits in JJG. However, taken together, they strongly suggest a more parsimonious account in term of a single component deficit.

We may add that the same outcome was found when we gathered the data from all the action and man-made object items from the various batteries used in this study, which increased statistical power. Thus, the consistently negative result of the man-made objects vs. actions contrasts obtained in each set was unlikely due to a lack of statistical power or a sample bias. Therefore, in the following section, we tested several hypotheses that could account for the association of deficits in JJG's pattern of conceptual impairment by assuming damage to a single functional component.

3.3. Assessing knowledge of sensory, functional, and manipulation features

Within both the Feature-Based Organization and the motor simulation theories, the association of a conceptual deficit for man-made objects and for actions could be accounted for by both classes of concepts being mainly (albeit not solely) represented and processed by a shared system which would be selectively damaged in the case of JJG. This shared system would be a conceptual system representing functional knowledge, within the "sensory/functional" account (Bird et al., 2000)[13], or manipulation knowledge within the "manipulability" account (e.g., Gerlach et al., 2002; Kellenbach et al., 2003; Noppeney et al., 2005; Saccuman et al., 2006) or a motor system involved in hand/arm movement simulations, within the "failure-of-simulating" account (e.g., Gallese & Lakoff, 2005; Rizzolatti & Craighero, 2004; Rizzolatti et al., 2001).

[13] Already, the absence of evidence for a differential impairment for man-made objects and actions in JJG is problematic for the sensory-functional theory. However, it could be objected that, in the sets of items used previously, the actions had fewer functional features than average and/or the man-made objects had more functional features than average, leading to a similar impairment of both categories.

Let us remind here that the "sensory/functional" account predicts that a selective conceptual deficit for man-made objects and actions should be associated with a selective or disproportionate deficit for functional compared to sensory knowledge in all categories of concepts (i.e., living things, man-made objects, and actions). The "manipulability" account instead predicts that a selective conceptual deficit for man-made objects and actions should be associated with a selective or disproportionate impairment of manipulation compared to other kinds of knowledge, say, functional knowledge, and that manipulable objects and manipulation actions should be more impaired than non-manipulable objects and non-manipulation actions. As for the "failure-of-simulating" account, it predicts that a selective conceptual deficit for man-made objects and actions should be selective or disproportionate to manipulable objects and manual actions compared to non-manipulable objects and non-manual (i.e., whole-body) actions.

3.3.1. Material and method

Sensory vs. Functional features of Objects and Actions

Sensory and functional features were assessed with a property verification task (Pillon & d'Honincthun, 2011b) comprising the object and action items of the "Objects/Actions" battery. Four statements were associated with each item. Two statements (one true, one false) expressed a sensory property, and two statements (one true, one false) expressed a functional property of the item. The sensory vs. functional properties were defined, following Bird et al. (2000), as knowledge that can vs. cannot be derived from the senses ("functional" thus refers to all "non-sensory" information). Thus, for objects, sensory properties mainly referred to the visual properties of objects (their shape, parts, color, or material), but also to features such as the taste of fruit and the feel of a plant; functional properties were eating habits, living environments, or utilization (e.g., transportation or

rearing) for animals, growing environments or modes of cooking for fruit and vegetables, function for implements and, for means of transport, what is transported or the specific place where it is used. For actions, sensory properties described the typical visual motion associated with the action and functional properties described the causes, goals, or results of the actions. Each statement was spoken aloud to the participants who had to tell whether it was true or false. A sensory or functional property of an item was scored correct if, for that given property, both the true statement was accepted and the false statement rejected. An item was scored correct overall if both the functional and sensory statements related to that item were succeeded.

For this task, the control group was the group of five healthy participants from the study by Pillon and d'Honincthun (2011b). These participants were a bit younger than JJG (Mean age = 43.2; SD = 2.28) but matched with him for gender and education level (Mean number of years = 16.4; SD = 0.89).

Sensory vs. Functional features of Living Things and Man-made Objects

A further property verification task was prepared with 64 items corresponding to concrete objects (hereafter, "Living Things/Man-made Objects" battery), half living things (16 animals and 16 fruit and vegetables), and half man-made objects (16 implements and 16 means of transport), matched for spoken word frequency [$t(35) = 1.65$, $p = 0.1$] and imageability ($t < 1$). Each item was associated with two statements (one true, one false) describing a sensory property and two statements (one true, one false) describing a functional property. Sensory and functional properties were defined as above. (These items and the corresponding statements were a subset of those used by Samson et al., 1998.) The statements were submitted to 9 control subjects (aged between 19 and 27) who were asked to verify the properties and to rate on a five-point scale how easy each was to answer (1 = very easy; 5 = very difficult). The mean difficulty of the

statements did not differ between living things and man-made objects [t (62) = 1.04, p = 0.3] or between sensory and functional properties (t < 1). (See mean ratings per category in Table 4.8.) The instructions and the scoring procedure were the same as in the previous property verification task.

Table 4.8. Control subjects' mean ratings of difficulty of responding to the sensory and functional features in the property verification task for the items of the "Living Things/Man-made Objects" battery.

Category of items	N items	Mean difficulty	SD
Sensory Features			
Living Things	32	1.69	0.57
Man-made Objects	32	1.95	0.71
All Sensory Features	64	1.82	0.65
Functional Features			
Living Things	32	2.12	0.47
Man-made Objects	32	1.61	0.50
All Functional Features	64	1.86	0.55
Living Things	32	2.00	0.36
Man-made Objects	32	1.89	0.49

Manipulation vs. Functional knowledge

A picture association task was prepared with 50 pictures of manipulable man-made objects that, in one condition, the participants had to associate with an object that is manipulated in a similar way (manipulation condition) and, in a second condition, with an object that had a similar function (functional condition). The two conditions were presented in an ABBA order: in the first session, the participants were presented with the first half of the items in the functional condition and the second half of the items in the manipulation condition; in the second session, they were tested with the second half of items in the functional condition and the first half of the manipulation items. The same material was used in both conditions, that is, the same test items and the same array of choices were displayed in the same order in both the functional and the manipulation conditions. This allowed us to match perfectly the material used in both conditions. Thus,

in both the functional and the manipulation condition, the test item (e.g., a cigarette lighter) was presented with, below it, a picture of an object having a similar function (e.g., a match), a picture of an object that is manipulated in a similar way (e.g., a chronometer), and a visually-related object (e.g., a salt shaker). In order to prevent the participants to discard the picture s/he previously chosen in the first presentation of the test item when presented with that item the second time, the same picture served as the correct associate for both the functional and the manipulation conditions in 28% of the trials; in these trials, the two other choices were visually-related objects (e.g., the test item was a tiller, the functional and manipulation associate was a steering wheel and the two visually-related objects were a ring and a lifebuoy). The test objects, their functional and manipulation associates, and the visually-related objects were matched in imageability ($F < 1$), age of acquisition ($F < 1$), familiarity ($F < 1$), and subjective name frequency ($F < 1$).

"Manipulable vs. Non-manipulable Items" battery

This battery comprised a picture naming and a word/picture verification task including 32 manipulable (16 man-made objects and 16 actions) and 32 non-manipulable (16 man-made objects and 16 actions) items. Manipulability was estimated by three independent judges who were asked to tell whether 60 man-made objects and 60 actions entailed manipulation, i.e., whether the utilization of the object or the realization of the action entailed specific and fine hand motion (Saccuman et al., 2006).[14] Only items that reached 100 % agreement across the judges were selected. Manipulable and non-manipulable

[14] They were provided with the following instructions: "An object is manipulable if it is typically associated with a specific hand action involving either grasping the object to use it as a tool (e.g., a brush) or a manipulation of the object in order to achieve a result. Non-manipulable objects are impossible to grasp and cannot be used as tools (e.g., a carpet). An action is considered a manipulation if it involves the grasping or other fine hand movements performed on an object (e.g., peeling). Non-manipulation actions are performed either with the whole body moving through space (e.g., jumping) or with another body part than the hand (e.g., smiling)".

items were matched in spoken word frequency [t (62) = 1.67; p = 0.10], concept familiarity [t (62 = 1.15; p = 0.25], and imageability (t < 1). Within the set of man-made objects, the 16 manipulable and 16 non-manipulable items were also matched in familiarity [t (21.7) = -0.60; p = 0.55], imageability [t (30) = -0.39; p = 0.70], and spoken word frequency [t (30) = -1.20; p= 0.24]. The same was true within the set of actions (0.86 < t < 1.55; 0.13 < p < 0.40). In the word/picture verification task, one semantic and one unrelated foil were selected. The yes/no response ratio reached 0.4 once the filler items were added. With our scoring procedure (Cf. General method), the correct response probability at chance was 0.125.

"Manipulable vs. Non-manipulable Items" of the "Man-made Objects/Actions" battery

We applied the same analysis to the items of the "Man-made objects/Actions" battery, by splitting the set of items into manipulable (15 man-made objects and 15 actions) and non-manipulable (13 man-made object and 13 actions) items, according to the same criteria as those applied in the previously presented task. The manipulable and non-manipulable items were matched in spoken word frequency (t < 1), familiarity (t < 1), age of acquisition [t (54) = 1.79; p = 0.08], and imageability (t < 1). These variables were also matched between manipulable and non-manipulable man-made objects (all ts < 1.44; all ps > *0.16*) and between manipulable and non-manipulable actions (all ts < 1.95; all ps > 0.06).

3.3.2. Results

Sensory vs. Functional features of Objects and Actions

In the property verification task (see results in Table 4.9), JJG's overall performance was significantly impaired for both objects and actions and there was no significant

difference between objects and actions (BSDT: p = 0.37). Like in the word/picture verification task with the same items, JJG's performance was however less impaired for living things than for man-made objects within the object set[15] and it did not significantly differ between man-made objects and actions (BSDT: p = 0.52) while it differed between living things and actions (BSDT: p = 0.01). As regards the sensory/functional contrast, the results showed that JJG was significantly impaired for both sensory and functional properties, with no evidence of a differential impairment between both kinds of properties, either for the whole set of items (BSDT: p = 0.21), for objects (BSDT: p = 0.82), or for actions (BSDT: p = 0.87).

Sensory vs. Functional features of Living Things and Made-made Objects

The overall results (see Table 9) showed that, in this property verification task, JJG performed within the normal range for living things but was significantly impaired for man-made objects and that his performance was significantly poorer for man-made objects than for living things (BSDT: $p < 0.01$). Moreover, his performance was significantly worse for the sensory than the functional properties, on the whole (BSDT: p = 0.02) and for the man-made objects (BSDT: p = 0.005), but not for the living things (BSDT: p = 0.95). Thus, contrary to what the sensory/functional account for the category-specific deficit for man-made objects predicts, JJG performed better on the functional than on the visual properties of man-made objects.

[15] See the modified *t*s values in Table 8. BSDT could not be computed because the SD in controls was nil.

Table 4.9. JJG's and control group's number of correct responses according to the type of feature and the category of items in the property verification tasks with the items of the "Objects/Actions" battery and of the "Living Things/Man-made Objects" battery.

TASK	N	JJG	Control group			Modified *t* test
			Mean	SD	Range	
"OBJECTS/ACTIONS" BATTERY						
Sensory Features						
Living Things	18	12	17.00	0.71	32-36	-6.42**
Man-made Objects	18	5	17.20	0.84	16-18	-13.25***
All Objects	36	17	34.40	1.51	32-36	-10.52***
Person-directed Actions	18	5	16.20	1.48	14-18	-6.9**
Object-directed Actions	18	2	16.80	0.45	16-17	-30.02***
All Actions	36	7	33.00	1.41	31-35	-16.83***
All Sensory Features	72	23	64.70	1.82	65-70	-20.92***
Functional Features						
Living Things	18	13	16.80	0.84	16-18	-4.12**
Man-made Objects	18	8	15.60	0.55	15-16	-12.61***
All Objects	36	21	32.40	0.89	31-33	-11.69***
Person-directed Actions	18	5	15.20	0.84	14-16	-11.08***
Object-directed Actions	18	3	15.40	0.89	14-16	-12.71***
All Actions	36	8	30.60	1.14	29-32	-18.09***
All Functional Features	72	29	63.00	1.00	62-64	-31.03***
All features						
Living Things	18	11	16.00	0.70	15-17	-6.52**
Man-made Objects	18	2	15.20	0.83	14-16	-14.50***
All Objects	36	13	31.20	1.09	30-33	-15.24***
Person-directed Actions	18	0	14.60	0.55	14-15	-25.18***
Object-directed Actions	18	2	14.60	1.52	12-16	-7.86***
All Actions	36	2	29.20	1.30	27-30	-19.10***
"LIVING THINGS/MAN-MADE OBJECTS" BATTERY						
Sensory Features						
Living Things	32	27	27.89	1.17	26-30	-0.72
Man-Made Objects	32	14	28.44	1.74	25-31	-7.87***
All Sensory Features	64	41	56.33	2.17	53-59	-6.70***
Functional Features						
Living Things	32	28	29.33	1.58	27-31	-0.79
Man-made Objects	32	26	30.89	1.27	28-32	-3.67**
All Functional Features	64	54	60.22	2.22	57-63	-2.65*
All Features						
Living Things	32	23	25.78	1.79	23-29	-1.48
Man-made Objects	32	13	27.78	2.59	22-31	-5.43***

* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$

Supplementary analyses: Sensory vs. "strictly functional" features

Functional knowledge related to objects has been characterized in different ways (e.g., Caramazza & Shelton, 1998; Cree & McRae, 2003; Farah & McClelland, 1991; McRae, de Sa, & Seidenberg, 1997). In our two property verification tasks, following Bird et al.'s conception, the functional statements associated with the object items expressed their "functional" properties in the broad sense of "non-sensory" properties, which encompasses the function of an object (e.g., *The kettle is used for heating water*) but also its typical location (e.g., *The pouffe usually stands in a lounge*), its utilization (e.g., *Cows are reared for milk*) and associative and encyclopaedic knowledge (e.g., *Foxes chase hens).* Likewise, the functional statements associated with the action items expressed various properties that were not strictly related to the "function", i.e., the purpose of the action (e.g., *Grating something is for reducing it into powder or small pieces* or *Stretching is for relaxing*), but also to its cause (e.g., *When one pushes somebody away, it is because this person bothers him/her*) or consequence (e.g., *When one pinches somebody, this hurts him/her a bit*). One might object that the kind of features that the most crucially distinguishes living things from man-made objects and actions are not functional features defined in this broad sense, but "strictly" functional features, namely, properties pertaining to the *function* of the objects and the purpose of the actions — in a word, "what for" information. To address this issue, we re-analyzed the results of both property verification tasks by only keeping the items for which both the true and the false functional statement corresponded to this narrower definition. The results are displayed in Table 4.10.

In the property verification task with the items from the "Objects/Actions" battery, 12 man-made objects and 27 actions (10 person-directed and 17 object-directed) could be kept in the analysis (no statement related to living things conformed to the strict definition

of function). The overall results showed that JJG was significantly impaired for both man-made objects and actions and that there was no evidence for a differential impairment between both categories (BSDT: $p = 0.18$). As for the sensory/functional contrast, the results showed that JJG was significantly impaired for both the sensory and functional properties; moreover, there was no evidence of a differential impairment between both kinds of properties, either in the whole set of items (BSDT: $p = 0.46$) or in the man-made object set (BSDT: $p = 0.47$). Only for the action set was there a significant difference in JJG's performance for sensory compared to functional features, which went however in the reverse direction of that predicted by the sensory/functional account: JJG was significantly *less* impaired for the functional compared to the sensory properties of actions (BSDT: $p < 0.02$).

In the property verification task with the items of the "Living things/Man-made Objects" battery, 24 man-made object items (no living things) remained once only functional statements conforming to the strict definition were kept. The results showed that JJG was significantly impaired for both the sensory and functional properties of man-made objects and that he was significantly *less* impaired for the functional compared to the sensory properties of these objects (BSDT: $p < 0.02$) — a pattern that is, again, the reverse of that predicted by the sensory/functional account for the category-specific deficit for man-made objects.

Manipulation vs. Functional knowledge

The results indicated that JJG was significantly impaired both in the manipulation [20/50; controls' mean = 46.1, SD = 1.95; modified t (7) = -12.63, $p < 0.01$] and in the functional [26/50; controls' mean = 46.87; SD = 2.41; t (7) = -8.16. $p < 0.01$] condition and that there was no significant difference between both conditions (BSDT: $p = 0.19$).

Table 4.10. JJG's and control group's number of correct responses according to the type of feature and the category of items in the property verification tasks with the items of the "Objects/Actions" battery and of the "Living Things/Man-made Objects" battery, with a strict definition of the functional features.

Task	N	JJG	Control group			Modified *t* test
			Mean	SD	Range	
"OBJECTS/ACTIONS" BATTERY						
Sensory Features						
Man-made Objects	12	3	11.20	0.84	10-12	-9.81***
Person-directed Actions	10	3	9.60	0.55	9-10	-11.17***
Object-directed Actions	17	2	15.80	0.44	15-16	-28.63***
All Actions	27	5	25.40	0.55	25-26	-34.36***
All sensory features	39	8	36.60	1.14	35-38	-22.90***
Functional Features						
Man-made Objects	12	4	10.40	0.89	9-11	-7.15**
Person-directed Actions	10	4	8.60	1.14	7-10	-3.68*
Object-directed Actions	17	2	14.20	1.30	12-15	-8.57***
All Actions	27	6	22.80	1.64	21-25	-9.35***
All Functional Features	39	10	33.20	1.30	32-35	-16.29***
All Features						
Man-made objects	12	1	10.00	1.00	9-11	-8.22***
Person-directed Actions	10	1	8.40	0.89	7-9	-7.59***
Object-directed Actions	17	1	13.60	1.51	11-15	-7.62***
All Actions	27	2	22.00	1.22	20-23	-14.96***
"LIVING THINGS/MAN-MADE OBJECTS" BATTERY						
Sensory Features						
Man-made Objects	24	10	21.00	1.32	19-23	-7.91***
Functional Features						
Man-made Objects	24	20	23.11	0.92	21-24	-3.18**

* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$

"Maipulable vs. Non-manipulable Items" battery

The results (Table 4.11) showed that JJG was not differently impaired for manipulable and non-manipulable items both in the naming and the word/picture verification task, whether for man-made objects (BSDT: $p = 0.26$ and $p = 0.39$, in the naming and verification task, respectively), actions (BSDT: $p = 0.09$ and $p = 0.15$), or the whole set (BSDT: $p = 0.79$ and $p = 0.76$). For actions, the non significant trend was toward better performance for actions involving a manipulation than actions non involving manipulation, in both naming and word/picture verification.

Table 4.11. JJG's and control group's number of correct responses in picture naming and word/picture verification for the items of the "Manipulable/Non-manipulable Items" battery and the manipulable and non-manipulable items of the "Man-made Objects/Actions" battery.

Task	N	JJG	Control group			Modified *t* test
			Mean	SD	Range	
"MANIPULABLE/NON-MANIPULABLE" BATTERY						
Naming						
Manipulable man-made Objects	16	8	14.50	1.19	12-16	-5.12***
Manipulable Actions	16	1	12.25	1.98	9-15	-5.35***
All Manipulable	32	9	26.75	2.71	22-31	-6.16***
Non-manipulable man-made Objects	16	9	13.75	1.67	11-16	-2.68*
Non-manipulable Actions	16	5	14.87	0.83	14-16	-11.21***
All Non-manipulable	32	14	28.65	1.99	25-31	-6.90***
Word/picture Verification						
Manipulable man-made Objects	16	11	15.00	1.07	13-16	-3.52**
Manipulable Actions	16	10	14.87	0.83	14-16	-5.53***
All Manipulable	32	21	29.87	1.13	28-31	-7.40***
Non-manipulable man-made Objects	16	12	14.75	1.28	13-16	-2.02
Non-manipulable Actions	16	10	15.62	0.52	15-16	-10.20***
All Non-manipulable	32	22	30.37	1.19	29-32	-6.63***
"**MAN-MADE OBJECTS/ACTIONS" BATTERY**						
Naming						
Session 1						
Manipulable items	30	9	27.85	1.34	26-30	-23.42***
Non-Manipulable items	26	8	24.42	1.61	22-26	-15.75***
Session 2						
Manipulable items	30	12	27.85	1.34	26-30	-19.74***
Non-manipulable items	26	9	24.42	1.61	22-26	-14.79***
Session 3						
Manipulable items	30	13	27.85	1.34	26-30	-18.52***
Non-manipulable items	26	10	24.42	1.61	22-26	-13.83***
Word-picture Matching						
Manipulable items	30	23	29.25	0.70	28-30	-8.42***
Non-manipulable items	26	17	25.62	0.74	24-26	-10.99***
Word/picture Verification						
Session 1						
Manipulable items	30	8	27.85	1.34	26-30	-13.97***
Non-Manipulable items	26	5	24.42	1.61	22-26	-11.37***
Session 2						
Manipulable items	30	12	27.85	1.34	26-30	-11.15***
Non-manipulable items	26	7	24.42	1.61	22-26	-10.20***
Session 3						
Manipulable items	30	10	27.85	1.34	26-30	-12.56***
Non-manipulable items	26	7	24.42	1.61	22-26	-10.20***

* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$

Manipulable vs. Non-manipulable items from the "Man-made Objects/Actions" battery

The results (Table 4.11) showed that there were no significant differences between manipulable and non-manipulable items across the three sessions on either the naming (BSDTs: $0.18 < p < 0.33$), the word/picture matching (BSDT: $p = 0.45$), or the word/picture verification (BSDTs: $0.43 < p < 0.73$) tasks.

3.3.3. Discussion

The main findings of this section are summarized in Figure 4.3. They are clear-cut: JJG's conceptual impairment for both man-made objects and actions was not associated with a greater impairment of functional compared to sensory knowledge or to a greater impairment of manipulation compared to functional knowledge. Furthermore, manipulable items were not more impaired than non-manipulable items. These findings thus provided no support for the "sensory/functional", the "manipulability", or the "failure-of-simulating" account for the pattern of association of conceptual deficits found in JJG. Moreover, we found additional evidence that knowledge of man-made objects and actions was similarly affected by brain damage in a task where knowledge of the properties of items was directly assessed, i.e., the property verification task, which showed that the JJG's difficulties were not confined to naming or comprehending words from these semantic categories but indeed reflected impaired conceptual knowledge of man-made objects and of actions.

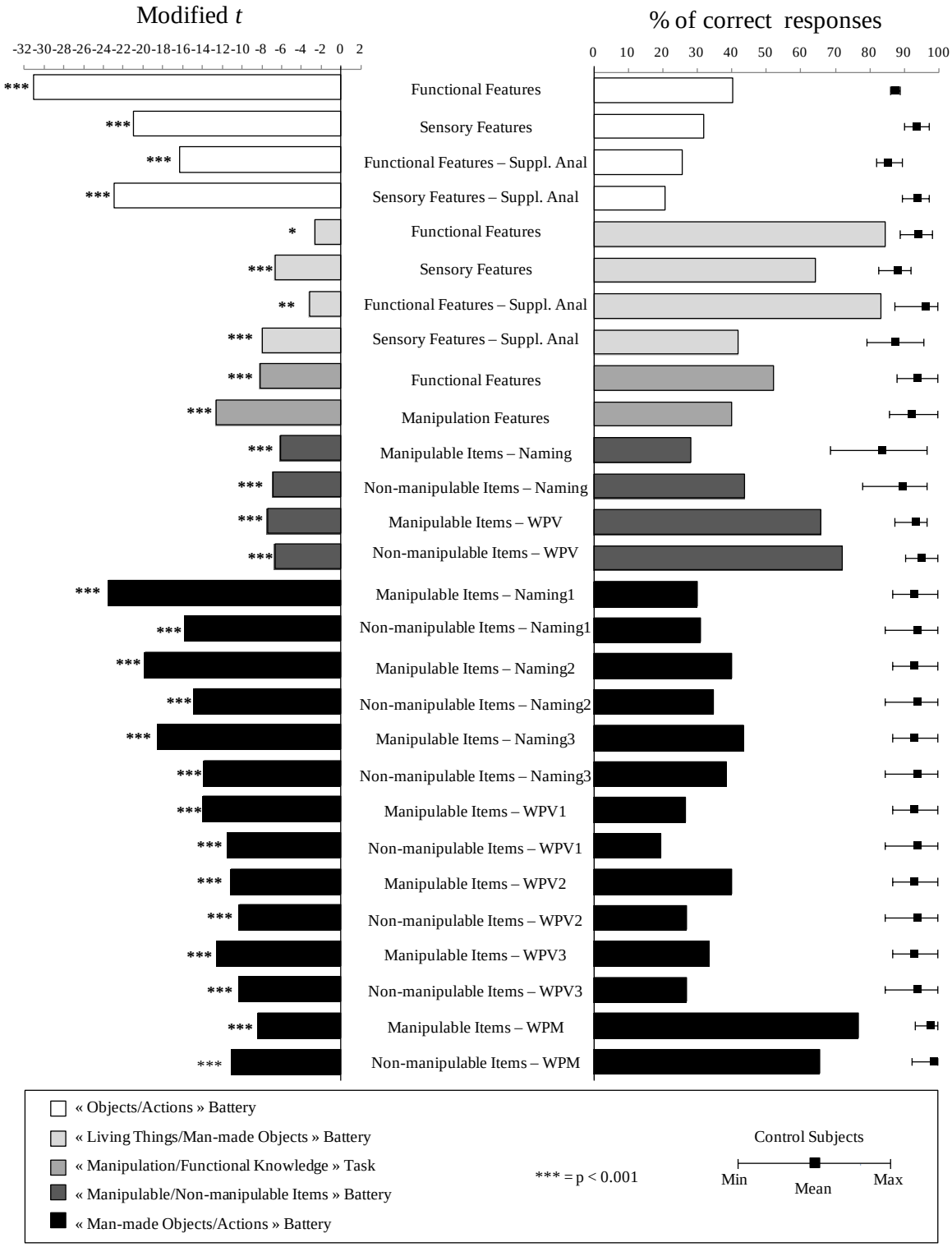

Figure 4.3| Summary of JJG's and control subjects' results in the tasks assessing knowledge of sensory, functional, and manipulation features (i.e., in the property verification task with the items of the "Objects/Actions" and of the "Living Things/Man-made Objects" batteries and the "Manipulation/Functional Knowledge" task), and in the word/picture verification task contrasting manipulable to non-manipulable items (from the "Manipulable/Non-manipulable Items" and the "Man-made Objects/Actions" batteries). On the right, the figure displays the percentage of JJG's correct responses with the mean percentage and range (min-max) of correct responses of the control subjects and, on the left, the results of the modified *t*-tests for the comparison between JJG's and control subjects' performance.

4. GENERAL DISCUSSION

4.1. Main findings

We have reported the case of a brain-damaged individual, JJG, who was referred to us because of his difficulties in understanding verbs. We found that his impairment with verbs was likely due to a conceptual impairment affecting action concepts although there was no significant dissociation in the patient's performance between verbs/actions and nouns/objects, when the nouns/objects set comprised both living and non-living (i.e., man-made objects) things. We then found that the patient's performance in comprehension tasks (word/picture matching and word/picture verification) presented in fact a classical dissociation within the set of objects, with a significant impairment for the category of man-made objects and a sparing of the category of living things. Knowledge related to other categories of entities, like famous people, countries, and famous buildings, was also spared, which indicated that the selective impairment for man-made objects could not be interpreted, like for example within the domain-specific knowledge theory (Caramazza & Shelton, 1998), as a selective preservation of living things. Finally, it turned out that the concepts of actions and of man-made objects were both impaired to a similar degree and that this pattern did not simply result from many actions involving man-made objects, since both actions involving and not involving man-made objects were impaired (and they were impaired to a similar degree). This finding of an association between a deficit for man-made objects and for actions seems problematic for the hypothesis that objects and actions are separated at the conceptual level of processing (e.g., McCarthy & Warrington, 1985; Vigliocco et al., 2004). Not only our findings showed that a dissociation may occur within the class of "objects" (which is already a well-known fact) but also that a subclass of objects, that is, man-made objects, may pattern with actions following brain damage.

Admittedly, the association of a conceptual deficit for both man-made objects and actions in JJG could be explained by the mere cooccurrence of two deficits arising from two independent functional systems (or two distinct regions within a single semantic space; e.g., Caramazza et al., 1990; Vigliocco et al., 2004) being fortuitously damaged, one affecting a system (or a region within the semantic space) representing and processing knowledge of man-made objects, the other impairing a system (or a region) representing and processing knowledge of actions. In that case, our findings would be no more problematic for the hypothesis of a conceptual separation between objects and actions.[16] However, we presented several arguments supporting the view that the association of a conceptual deficit for both man-made objects and actions in JJG was likely not arising by chance. We found that knowledge of man-made objects and of actions was consistently impaired to a similar degree of severity in various tasks like word/picture matching, word/picture verification, and property verification, with different subsets of items, and at different time periods. If we acknowledge that the empirical value of an association of deficits is weak when the deficits are not of similar severity or when their relative severity is not reported (e.g., Warrington & McCarthy, 1987; Warrington & Shallice, 1984), we believe that this is not or, at least, less the case when, like in this study, the severity of the deficits appears similar across various tasks, item sets, and time. An additional argument supporting the view that the association of conceptual deficits in JJG may not arise by chance is the existence of the inverse pattern of conceptual impairment, recently reported by Pillon and d'Honincthun (2011b). The case GC they reported on showed a significantly disproportionate conceptual impairment for living things compared to man-made objects and actions, which were similarly impaired. Thus,

[16] Provided that the hypothesis specifies that, within the conceptual system, the representation of *each* of the three categories of objects (animals, plants, and man-made objects) is separate from the representation of actions.

GC's performance showed a consistent pattern of similar level of impairment for both man-made objects and actions in a variety of tasks such as naming photographs, understanding words and pictures, verifying verbally-presented semantic properties, and pantomiming the way in which the objects are used or the actions performed. The double dissociation represented by JJG' and GC's pattern (observed in part with the same material) not only weakens a chance account for the association of a deficit for man-made objects and a deficit for actions found in JJG, it also allows us to rule out an account for the association in terms of higher sensitivity to conceptual damage of these classes of concepts.

In a second step, we asked whether the "sensory/functional" or the "manipulability" account for category-specific conceptual deficits, both formulated within the framework of the FBO theory of the organization of knowledge in the mind and brain, and the "failure-of-simulating" hypothesis could account for the association of deficits observed in JJG. Within these three accounts, concepts of man-made objects and of actions would pattern together in the condition of damage to the conceptual system by virtue of their sharing a representational/processing system that is crucial for both these classes of concepts, that is, respectively, the functional property representational system, the manipulation representational system, and the hand movement production system. None of these accounts was supported by the data: JJG's conceptual impairment for man-made objects and actions was not associated with a disproportionate impairment for functional compared to sensory knowledge or manipulation compared to functional knowledge, and it did not affect manipulable more than non-manipulable items. In particular, even if JJG indeed had damage to motor processes involved in the planning and execution of hand/arm movements, which caused him upper limb apraxia (Cf. Case Report), such damage could not explain his impairment for man-made objects and actions that also

concerned objects and actions that do not involve manual motor representation (i.e., non-manipulable objects and non-manual actions).

4.2. A domain-specific knowledge account for JJG's association of deficits

If these accounts within the FBO theory and the motor simulation framework are to be rejected, how can we explain the pattern of association found in JJG's conceptual impairment? We will propose here, following Pillon and d'Honincthun (2011b), that conceptual knowledge of man-made objects and of human actions share a common, specialized, domain-specific representational and processing system which is responsible for the human ability to creatively, quickly, and efficiently design and understand means to achieving specific goals and purposes.

Currently most popular theories of the organization of conceptual knowledge in the mind and brain assume that the organization of conceptual knowledge is determined by the intrinsic properties of the stimuli that are to be recognized and categorized, such as the kinds of features they involve (Humphreys & Forde, 2001; Martin et al., 2000; Warrington & McCarthy, 1987; Warrington & Shallice, 1984) or the sensory and motor images they evoke (Barsalou, 1999, 2008; Barsalou, Simmons, Barbey, & Wilson, 2003; Damasio, 1989; Gallese & Lakoff, 2005; Meyer & Damasio, 2009). Instead, we propose that one organizing principle for conceptual knowledge could be an extrinsic property of stimuli like the reason why, for a given organism, conceptual knowledge about different kinds of stimuli is acquired, stored, and processed. Under this assumption, concepts of man-made objects and of human actions would be learned, stored, and processed by a common conceptual system whose function would be to provide human beings with a highly efficient problem-solving system needed for quickly and efficiently designing and understanding means to achieve specific goals and purposes.

This view, that the mind and brain have evolved cognitive and neural subsystems not because of the intrinsic characteristics of the input but because of the different functions to be achieved, is not new. Since 1980, psychologists have defended the view that the brain has evolved specialized devices designed to cope with specific types of problems (Fodor, 1983; Gardner, 1983; Marr, 1982). A core assumption in evolutionary functionalist research (Cosmides & Tooby, 1994, 1995; Tooby & Cosmides, 1995) is that functional circuits have evolved to perform specialized functions so that they are primarily composed of problem-solving devices. The same idea could be found in cognitive neuroscience. Milner and Goodale (Goodale & Milner, 1992; Milner & Goodale, 2006), for example, criticized the input-driven initial conception of the ventral and dorsal visual streams proposed by Ungerleider and Mishkin (1982) and instead defended that the ventral/dorsal organization was driven by the outputs of the two visual processing systems. Thus, separate processing streams would have evolved to sustain different behaviors, that is, the perceptual representation of our surrounding world, on the one hand, the visual control of actions, on the other hand.

We propose that the organization of conceptual knowledge for man-made objects and actions has been determined by such a principle. It is easy to agree, indeed, that designing actions according to one's purpose and understanding others', first, are very important functions in everyday life, second, rely on conceptual knowledge of both man-made objects and actions, and third, would benefit from the joint processing of action and man-made object knowledge. Thus, a specialized device designed to process altogether concepts of man-made objects and of actions could have evolved to achieve these functions.

This hypothesis seems reasonable also in light of empirical evidence in the developmental literature that shows that the acquisition of concepts of man-made objects

and of actions is mediated by very similar learning principles. Thus, infants show a tendency to apprehend both actions (e.g., Csibra & Gergely, 2007; Gergely, Bekkering & Kiraly, 2002; Gergely & Csibra, 2003) and man-made objects (e.g., Hernik & Csibra, 2009; Kelemen, 1999) in terms of the *goals* they permit to achieve. For example, Gergely et al. (2002) have shown that infants, among several elements, primarily pay attention to the physical features of the action, that causally contribute to the achievement of a goal. Thus, when 14 month children watch to an adult, whose hands are tied, using his head to turn on a light, and are asked to imitate the action, they imitated the action with their hands, revealing that they understand actions on the basis of a rationale analysis of the goal to be achieved.

A similar goal-based principle is used to construct concepts of man-made objects. Träuble and Pauen (2007), for example, have shown that, after being presented with the use of unfamiliar man-made objects, infants are able to attend to their functionally relevant physical features, i.e., the features that causally contribute to the achievement of a goal, to categorize them. In their study, 11- to 12-month-old infants were presented with short demonstrations in which various novel man-made objects with a common functional part (a T-shaped projection) were used to achieve a common goal (e.g., pulling a pair of hooks out of the apparatus). After this familiarization phase, when presented with new pairs of objects, infants explored more shortly objects with the previously seen functionally relevant feature (orientation of the critical T-shaped part) than objects that lacked this feature. This was not the case when they were not demonstrated the use of the objects or in a group who watched non-functional demonstrations (producing no effect). This suggests that infants are able to categorize new man-made objects on the basis of their functional features as soon as they had been shown the functional use of the objects. Later on, verbal children, when confronted to a novel man-made object, immediately try

to catch its intended function by asking questions about its functions, i.e., the goal-directed action in which it is used (Greif, Kemler Nelson, Keil & Gutierrez, 2006; Kemler Nelson, Egan, & Holt, 2004); furthermore, they rely on a "common-function" principle to extend the name of a man-made object to a novel one (Kemler Nelson, 1995).

In sum, thanks to his/her early ability/tendency to consider actions and man-made objects as means to achieve goals, the child builds his/her conceptual knowledge by discovering the several possible goals of actions, the functions of man-made objects, and how actions with man-made objects may enable a goal to be achieved (Csibra & Gergely, 2007). We assume that this learning principle lies at the heart of the acquisition and storing of knowledge about man-made objects and human actions by a common, domain-specific, conceptual system. This system would represent and process all kinds of concepts whose core property is that of being a mean of achieving a goal. Because both tools or other manipulable objects (e.g., a hammer or a coat) and non-manipulable objects (e.g., a bookcase or a car) and both manual (e.g., cutting) and whole-body (e.g., running) actions are conceptualized as means to achieve a goal, knowledge of the various categories of man-made objects and of goal-directed human actions is assumed to be not segregated within this common, specialized, domain-specific system. Within this specialized system, tools would thus not have a special status compared to other man-made objects. Contrary to the suggestion made within the domain-specific knowledge theory (Mahon & Caramazza, 2009) with which we share the evolutionary perspective, we propose here that this specialized domain-specific system has evolved in humans not because adaptation for efficiently *using* tools had fitness value but rather because adaptation for efficiently *designing* these tools had fitness value and this would be part of a more general adaptation for efficiently designing means to achieving specific goals and needs. Indeed, in our hunter-gatherer ancestors, it is likely that the ability to

design and manufacture artifacts (e.g., weapons, containers, clothing, shelters, and tools to manufacture these artifacts) had survival and reproductive value.

Furthermore, we propose that this system is domain-specific in the sense that it would store and process all kinds of conceptual knowledge related to man-made objects — not only their function but also knowledge of their shape, texture, color, weight, typical location, approximate cost, and so on — and to human actions — not only their typical cause, goal, consequences but also the typical agent involved, the needed energy, the approximate duration, emotional valence, and so on (e.g., Tranel, Kemmerer, Adolphs, Damasio, & Damasio, 2003). Planning and understanding means to achieve goals indeed would benefit from such an extended base of knowledge about man-made objects and actions.[17] Therefore, in case of damage to this domain-specific conceptual system, all types of knowledge about any type of man-made objects and goal-directed human actions should be similarly impaired (everything else being equal).

The proposal of a shared conceptual system for man-made objects and actions is compatible with extant findings from neuroimaging studies that consistently reported a bilateral although left dominant fronto-parieto-temporal network involved in processing knowledge of both man-made objects (the most often but not always, tools) and actions in a great variety of tasks (see the meta-analysis by Binder, Desai, Graves, & Conant, 2009,

[17] Our proposal has some resemblance to the praxis conceptual system suggested by Roy (1983; see also Roy & Square, 1985) since this praxis conceptual system is also assumed to represent some aspects of both man-made object and action knowledge (see also the "action semantics" of Rothi, Ochipa, & Heilman, 1991). However, this system, which is actually part of a model of limb praxis, only represents knowledge relevant to limb praxis, that is, knowledge of the specific mechanical advantages provided by tools or of the specific mechanical requirements to achieve a manual action goal on an object, whereas, in our view, any kind of conceptual knowledge (e.g., perceptual, functional, associative knowledge) related to all man-made objects and actions, be they relevant to limb praxis or not (e.g., be they transitive manual actions or intransitive actions performed with the whole body) would be represented in the domain-specific conceptual system.

and the review by Noppeney, 2008). Thus, when contrasted to the processing of living things in tasks like picture naming or word or picture association, processing man-made objects resulted in specific activity in the mostly left premotor/motor cortex, inferior parietal cortex, and/or posterior middle temporal regions (e.g., Chao & Martin, 2000; Creem-Regehr & Lee, 2005; Kalénine, Peyrin, Pichat, Segebarth, Bonthoux, & Baciu, 2009; Lewis, Brefczynski, Phinney, Janik, & DeYoe, 2005; Moore & Price, 1999; Mummery, Patterson, Hodges, & Price, 1998). The same three regions showed specific activity during action observation compared to non-action stimuli and during naming, auditory word comprehension, and conceptual judgment of action names compared to non-action names (Bedny, Caramazza, Grossman, Pascual-Leone, & Saxe, 2008; Damasio, Grabowski, Tranel, Ponto, Hichwa, & Damasio, 2001; Grèzes & Decety, 2001; Kable et al., 2005; Noppeney et al., 2005). The precise function of each part of this network is still poorly understood. However, specific activity within the left middle posterior temporal region was found during retrieval of conceptual knowledge related to both manipulable and non-manipulable man-made objects (Kellenbach et al., 2003) and during retrieval of conceptual knowledge related to both manual and whole-body actions (Corina, Chiu, Knapp, Greenwald, San Jose-Robertson, & Braun, 2007; Noppeney et al., 2005). Strong activity within the same region was also found during semantic judgments related to five classes of verbs (running, speaking, hitting, cutting, and change of state verbs) varying with respect to the semantic features of action, motion, contact, change of state, and tool use (Kemmerer, Gonzalez Castillo, Talavage, Patterson, & Wiley, 2008). These results suggest that activity in the left middle posterior temporal region is not dependent on the specific sensori-motor features of man-made objects and actions and may thus reflect the retrieval of property- and modality-independent representations of man-made objects and actions (see also Bedny et. al, 2008; Binder et al., 2009; Mummery

et al., 1998). It is reasonable to put forward the hypothesis that the left middle posterior temporal region — which was damaged in JJG — constitutes the neural substrate of a domain-specific conceptual system representing knowledge of all kinds of man-made objects and human actions.

4.3. Is there empirical evidence that contradicts the hypothesis of a common system for representing knowledge of man-made objects and of actions?

To the best of our knowledge, no previous neuropsychological study, either in the field of category-specific conceptual disorders or in the field of grammatical category-specific deficits, has investigated the issue addressed in this study (except Pillon and d'Honincthun, 2011b). Therefore, no one separately assessed knowledge of living things, man-made objects, and actions in the same design. There is thus no direct evidence available to date, but a few studies reported some results related to the assessment of man-made object and action processing in brain-damaged patients.

Thus, Ferreira, Giusiano, and Poncet (1997) reported on three patients whose performance in both naming and comprehension tasks was worse for animals than tools. The patients' performance in naming action photographs was also reported and showed that action naming was relatively spared in comparison with naming animals, which suggested that tools and actions patterned together in comparison with animals in naming. However, no statistical contrast was reported between the naming of tools and actions and, furthermore, the comprehension of actions was not tested.

Three studies may seem to report a different pattern, that is, a pattern suggesting that tool and action concepts may be separately damaged. The first one, by Tranel et al. (2003), reported that among 26 patients with impaired action concepts, only 6 also showed impaired concepts of tools. However, there are several aspects in the

methodology used in this study that may be questioned. First, knowledge of tools and of actions was assessed with different tasks, which were likely to differ both in the processing components involved and in difficulty. Thus, tool knowledge was assessed by presenting the patients with a picture of a tool and asking them to identify it (i.e., either to name it or to provide a detailed description of the object). On the other hand, action knowledge was assessed, first, with a "Picture Attribute Test", in which the patients were presented with two color photographs of actions and asked to choose the one that best met certain criteria (e.g., Which action would make the loudest noise?; Which action would require moving hands closer together?) and, second, with a "Picture Comparison Test", in which the patients had to select one from among three photographs that is different from the other two. Second, a patient was deemed to have impaired concepts of actions if her/his performance was below a cut-off score for either one or both of the tests. Among the 26 subjects that fit this criterion, 6 were impaired on just the Picture Attribute Test, 11 on just the Picture Comparison Test and only 9 were impaired on both tests. The question could be raised whether the subjects who were impaired on only one test did have damage to action conceptual knowledge rather than to some other processing component specifically involved in each test. Third, tool and action items were not matched on relevant variables such as familiarity or imageability and performance for both categories of items was not compared within each patient. Yet if a patient were slightly impaired for one category and not impaired for another, the difference between both categories might turn out to be non-significant. Finally, the functional locus of the deficit for actions and/or tools was not assessed. In particular, one cannot rule out that a number of patients with impaired action processing presented a pre-conceptual deficit in recognizing or inferring the movements in the static pictures of actions (d'Honincthun & Pillon, 2008).

Bi, Han, Shu, and Caramazza (2007) reported on the single case study of ZBL and claimed that his pattern of performance supported the hypothesis that tool and action concepts can be damaged independently. This conclusion was, however, not at all warranted by the results. First of all, there was no one task, in that study, that specifically comprised tool items. Tool items were always mixed with other man-made objects like clothing, furniture, kitchenware, vehicles, etc. and no separate result for tools compared to other man-made objects was reported. Second, and more importantly, action and man-made object items never were directly matched or contrasted in any task or by any statistic analysis: actions vs. (both living and man-made) objects were tested in two noun/verb picture naming tasks and man-made objects vs. animals were tested in another picture naming and an attribute judgment task. The results showed that ZBL's performance in naming was impaired for both nouns and verbs, although it was worse in naming nouns (41% and 37%, depending on the naming task) than verbs (68% and 80%). Moreover, the patient's performance was impaired in naming both animals and man-made objects and it was more impaired for man-made objects (44%) than animals (57%). In the attribute judgment task, ZBL's performance was impaired for man-made objects (73%) but not for animals (83%). This pattern suggested that ZBL probably had a conceptual impairment for man-made objects and a further impairment in retrieving the phonological word-form of both nouns and verbs, but especially nouns. There are no data, however, that could inform us about the status of verbs/actions at the conceptual level and, in particular, no data that could rule out that actions might be impaired like man-made objects.

The third case report that has to be discussed here is the case EA (Laiacona & Caramazza, 2004). EA presented with a category-specific conceptual deficit for animals. Moreover, like ZBL, EA showed worse performance in naming nouns (42%) than verbs

(82%); he was also worse at naming the man-made objects (22%) than the actions (85%) presented in the same pictures. However, EA was unimpaired in a word/picture matching task for both man-made objects (98%) and actions (100%), which suggest that his disproportionate impairment in naming nouns/objects compared to verbs/actions was caused by a word-form retrieval deficit affecting nouns more than verbs, not by a conceptual deficit affecting man-made objects more than actions, a pattern of a grammatical category-specific deficit that is far from being uncommon (e.g., Berndt, Mitchum, Haendiges, & Sandson, 1997; Bird et al., 2000; Breedin, Saffran, & Schwartz, 1998; Miceli, Silveri, Nocentini, & Caramazza, 1988; Shapiro & Caramazza, 2003a, 2003b; Zingeser & Berndt, 1988).

Overall, the patterns of performance shown by ZBL and EA might indicate the existence of two independent functional loci of deficit in both patients. ZBL had a deficit at the conceptual level of processing affecting man-made objects (and, possibly, actions) more than animals and an additional deficit at the level of the phonological form retrieval affecting nouns more than verbs. On the other hand, EA had a deficit at the conceptual level affecting animals more than man-made objects and actions, further to an additional deficit at the level of the phonological form retrieval affecting nouns more than verbs, like in ZBL. We acknowledge that these interpretations are speculative because of the lack of relevant data. It is clear that further single and multiple case studies of patients with a conceptual impairment, whose knowledge of various categories of objects and actions should be carefully tested across distinct tasks, are needed to evaluate the hypothesis of a common conceptual system for man-made objects and actions.

Finally, there are findings in the tradition of apraxia research that may seem to contradict the hypothesis of a common conceptual system for representing knowledge of man-made objects and of actions. Patients have been reported who could name and

recognize man-made objects — which suggested that conceptual knowledge of man-made objects was spared in these patients — while they could not demonstrate how to use them — which suggested that "action-related knowledge" for man-made objects was impaired (e.g., Negri, Rumiati, Zadini, Ukmar, Mahon, & Caramazza, 2007; Rosci, Chiesa, Laiacona, & Capitani, 2003). However, in these cases with apraxia, "action-related knowledge" that was impaired in the patients does not refer to the same notion as our notion of "concepts of action". "Action-related knowledge" refers to knowledge or/and execution of the skilled movements that must be performed to achieving a given activity with a given object while by "concepts of action" we mean all kinds of conceptual knowledge related to a category of goal-directed activities (an action), which includes knowledge of its goal, causes and consequences, the objects, people and instruments its generally involves, the typical context in which it takes place, its emotional content, etc. (Tranel et al., 2003). Our hypothesis could be rejected if it were shown that patients could name and recognize man-made objects without retrieving conceptual knowledge about the action they serve to realize (e.g., if it were shown that they could name a knife without knowing that it is for "cutting" and knowing what "cutting" is about).

5. CONCLUSION

We have reported on the single-case study of a brain-damaged patient presenting with a severe impairment of conceptual knowledge of man-made objects and of actions while his knowledge of plant-life, animals, and other categories of objects like famous people, countries, and famous buildings, was spared. We then showed that, contrary to the predictions made by the "sensory/functional", the "manipulability", and the "failure-of-simulating" accounts for category-specific conceptual impairments, the patient's association of deficits for both man-made objects and actions was not associated

with a disproportionate impairment of functional compared to sensory knowledge or of manipulation compared to functional knowledge; manipulable items were not more impaired than non-manipulable items either. We propose to account for the patient's association of deficits by the hypothesis that concepts whose core property is that of being a mean of achieving a goal — like the concepts of man-made objects and of actions — are learned, represented and processed by a common, domain-specific conceptual system, which would have evolved to allow human beings to creatively, quickly, and efficiently designing and understanding means to achieve goals and purposes.

APPENDIX. Distribution of JJG's errors (in % of total errors) in the naming and the word/picture verification tasks of the "Objects/Actions", "Concrete Objects", and "Man-Made Objects/Actions" battery.

Battery	NAMING Error Types			WORD/PICTURE VERIFICATION Error Types			
	Non-Response and Unrelated	Semantic Paraphasia	Other	Rejection of the Correct Picture	Acceptance of a Close Semantic Foil	Acceptance of a Far Semantic Foil	Acceptance of an Unrelated Foil
"Objects/Actions"							
Living Things	78	22	0	0	100	0	0
Man-made Objects	73	27	0	25	50	25	0
Action/Photographs	72	24	4	3	47	32	18
Actions/Videos	62	28	10	9	50	28	12
"Concrete Objects"							
Animals	61	39	0	0	90	n.a.	0
Plants	65	35	0	0	100	n.a.	0
Man-made Objects	56	44	0	0	100	n.a.	0
"Man-Made Objects/Actions"							
Man-made Objects	53	39	8	0	100	n.a.	0
Actions	55	36	9	0	92	n.a.	0

CHAPTER 5

EFFECT OF BIOMECHANICAL CONSTRAINTS IN THE HAND LATERALITY JUDGMENT TASK: WHERE DOES IT COME FROM?[18]

Abstract

Several studies have reported that, when subjects have to judge the laterality of rotated hand drawings, their judgment is automatically influenced by the biomechanical constraints of the upper limbs. The prominent account for this effect is that, in order to perform the task, subjects mentally rotate their upper limbs toward the position of the displayed stimulus in a way that is consistent with the biomechanical constraints underlying the actual movement. However, the effect of such biomechanical constraints was also found in the responses of motor-impaired individuals performing the hand laterality judgment task, which seems at odds with the "motor imagery" account for this effect. In this study, we further explored the source of the biomechanical constraint effect by assessing the ability of an individual (DC) with a congenital absence of upper limbs to judge the laterality of rotated hand or foot drawings. We found that DC was as accurate and fast as control participants in judging the laterality of both hand and foot drawings, without any disadvantage for hands when compared to feet. Furthermore, DC's response latencies for hand drawings were influenced by the biomechanical constraints of hand movements in the same way as control participants' response latencies. These results suggest that the effect of biomechanical constraints in the hand laterality judgment task is not strictly dependent on "motor imagery" and can arise from the visual processing of body parts being sensitive to such constraints.

[18] This section is a modified version of an article with identical title by Vannuscorps, Pillon and Andres, which has been published in *Frontiers in Human Neuroscience*, 2012, 6: 299.

1. INTRODUCTION

In the past twenty years, an increased interest has been devoted to the study of motor imagery. Most research has been achieved by the means of the hand laterality judgment (HLJ) task (Cooper and Shepard, 1975; Parsons, 1987, 1994; Sekiyama, 1982). In this task, participants are asked to decide whether drawings of different hand postures rotated with different angles from the upright view depict a left or a right limb (see Figure 5.1). If a hand drawing were processed like any other visual object response latencies should increase as a function of the angular disparity between the hand drawing and its upright view, as evidenced for other 2D or 3D stimuli (Cooper and Shepard, 1975). Instead, it has been shown that the impact of the angular disparity on the speed of hand laterality judgments was strongly modulated by the biomechanical limits that constrain the movement of the hand toward the displayed position (Parsons, 1987; Sekiyama, 1982). This observation was taken as evidence that, to solve the task, participants internally simulate a movement of their own hand and, moreover, that mental imagery of human movements — i.e., motor imagery — relies on the same representations and processes as those involved in action planning and/or control (Fiorio et al., 2006; Helmich et al., 2007; Jeannerod and Frak, 1999; Kosslyn et al., 2001; de Lange et al., 2006, 2008; Munzert et al., 2009; Nico et al., 2004; Parsons, 1987, 1994; Wraga et al., 2005). Furthermore, neuroimaging studies showed that hand laterality judgments induced increased activity in a parieto-frontal network known for its contribution to the planning and execution of hand movements (Kosslyn et al., 1998; de Lange et al., 2006; Parsons et al., 1998). On the basis of this behavioral and neural evidence, the HLJ task was considered as a privileged tool to read out the unconscious and normally covert process of motor planning (Fiorio et al., 2006; Jeannerod, 1994; de Lange et al., 2008; Munzert et al., 2009). In this paper, we report evidence that calls for a re-examination of the

prominent "motor imagery" account of the effect of biomechanical constraints in the HLJ task.

The effect of biomechanical constraints on participants' judgments in the HLJ task is characterized by three features unveiled by the analysis of the response latency pattern (Funk and Brugger, 2008; Parsons, 1987; Pelgrims et al., 2009). First, the response latencies (RLs) for the hand drawings depicted in the various rotation angles (from 0° to 360° in a clockwise direction) from the upright display (0°) are modulated by both the specific posture of the depicted hand (e.g., view of the hand side from the thumb vs. view of the palm from the wrist) and its laterality (right vs. left hand). This three-way interaction reflects the different biomechanical constraints that limit the amplitude of the rotation angle of each hand in a given posture. Thus, for instance, the recognition of a side view takes more time for right than left hands if the drawing is rotated at 150° clockwise given that such an angle corresponds to the outcome of a possible left hand movement but it is almost impossible to achieve with the right hand in this position. Likewise, the palm of a right hand viewed from the wrist, with the thumb pointing down toward the right side of the screen (i.e., between 210° and 270° clockwise) is recognized more slowly than a left hand displayed in the same orientation, in line with the fact that it is much more difficult to reach this orientation with the right than with the left hand in this posture. The second feature indexing the effect of biomechanical constraints on participants' responses is the overall chronometric advantage for judging the laterality of hands oriented in medial positions (stimuli rotated toward the mid-sagittal plane) when compared to lateral positions (away of the mid-sagittal plane). This effect, called the "MOLA" (Medial Over Lateral Advantage) effect, reflects the impact of the biomechanical constraints of hand movements that make it easier to move one's hand toward medial than lateral directions. The third feature is the significant correlation

between the response latency to a given stimulus and its degree of awkwardness that is, how difficult participants rated it to actually place their own hand in the displayed position (Parsons, 1987).

There is, however, evidence showing that the effect of biomechanical constraints in the HLJ task can be observed even in the condition of impaired motor planning or execution processes. After transient disruption of motor-related areas with transcranial magnetic stimulation (TMS), the performance in the HLJ task was either normal (Sauner et al., 2006) or characterized by a small RL increase that nevertheless did not hamper the effect of biomechanical constraints (Ganis et al., 2000; Pelgrims et al., 2010). Furthermore, studies of patients suffering from motor disorders that prevent normal execution of hand movements such as congenital hemiparesis (Steenbergen et al., 2007), Parkinson's disease (Helmich et al., 2007), dystonia (Fiorio et al., 2006), conversion paralysis (de Lange et al., 2008), amputation of an upper limb (Nico et al., 2004), or chronic arm pain (Schwoebel et al., 2001) showed that these conditions delayed hand laterality judgments but, again, without affecting the effect of biomechanical constraints. Finally, a study using the HLJ task with two individuals suffering from bilateral upper-limb aplasia reported an effect of biomechanical constraints on response latencies in at least one individual (Funk and Brugger, 2008).

Evidence for an effect of biomechanical constraints in the HLJ task despite impaired motor planning or execution raises the possibility that the effect does not arise from motor but instead from visual processes that ensure the perception of human body parts. Several authors indeed suggested that, when representing the human body in whole or in parts, the visual system encodes information about the biomechanical constraints of body part movements, information that in turn constrains whole body or body part perception (Kourtzi and Shiffrar, 1999; Marr and Vaina, 1982). Evidence advanced in

support of this view includes findings from the apparent motion paradigm. When an object is displayed sequentially in two different positions, it elicits in participants the perception of an apparent motion along the shortest pathway (Kolers and Pomerantz, 1971). However, the apparent motion induced by two hand postures presented sequentially can follow a longer pathway when the shortest one is not biomechanically possible (Shiffrar and Freyd, 1990, 1993). According to some authors (Chatterjee et al., 1996; Shiffrar and Freyd, 1993), this effect indicates that implicit perceptual knowledge of how the body moves impacts how body parts are perceived (but see Stevens et al., 2000, for an alternative account in terms of motor simulation).

However, before considering the perceptual hypothesis as an alternative account for the effect of biomechanical constraints in the HLJ task, a number of ambiguities that are present in the aforementioned studies of motor-impaired or aplasic individuals must be addressed. First, one cannot rule out that the motor-impaired patients in whom the effect of biomechanical constraints was found actually suffered from a deficit affecting processes that take place *after* the stage where biomechanical constraints influence motor planning and/or execution. Indeed, motor execution was not totally abolished in these patients. At first sight, the effect found in a bilateral aplasic individual (Funk and Brugger, 2008) should not present this ambiguity since, in such condition, none of the processes involved in the planning and execution of hand movements is functional. Nevertheless, this individual (AZ) reported vivid phantom sensations of her missing body parts that include phantom movements corresponding to those of normal upper limbs (Funk et al., 2005). One thus cannot rule out the existence of limb representations in AZ, which could explain her ability to carry out motor imagery for congenitally absent limbs (Brugger et al., 2000; Funk and Brugger, 2008). Furthermore, and this is also true for the studies with motor-impaired patients, the issue of whether mere visual familiarity with the

various hand positions could have contributed to the observed pattern of RLs in the HLJ task was not addressed. What looks like an effect of awkwardness might in fact be an artifact of the differential occurrences of the various hand positions — awkward hand positions are also likely to be less often seen than easy ones. Within this visual familiarity account, the RLs in the HLJ task would mainly depend on how often a given hand position has been seen in everyday settings, with the more frequent hand positions being recognized faster as a right or a left hand than the less frequent ones.

In this study, we sought further evidence for the presence of the effect of biomechanical constraints in the HLJ task in the context of a motor disability to plan and execute hand movements. We presented the HLJ task to DC, a man born without upper limbs, as well as to 7 normally limbed control participants, and analyzed their pattern of RLs vis-a-vis the main features indexing the effect of biomechanical constraints. Because of the congenital disability of DC, who has also never experienced any phantom limb sensation, the present study overcomes the difficulties raised by previous studies with motor-impaired patients or aplasic individuals. In the case of DC, no hand motor planning or execution ability of any kind could be invoked to explain, if any, an effect of biomechanical constraints in the HLJ task. Furthermore, we examined the effect of biomechanical constraints on the RLs of DC and control participants by taking into account the potential effect of the rated visual familiarity of hand positions.

2. MATERIAL AND METHODS

2.1. Participants

DC is a 51 year-old man with a Master's Degree in Psychology. He presents a congenital bilateral upper limb aplasia (right side: two fingers attached to a foreshortened humerus; left side: completely aplasic) due to in-utero thalidomide exposure. He had no

experience of prosthesis or phantom limb sensations. His performance was compared with that of 7 right-handed, normally limbed control participants matched in gender, age (mean age = 53.5), and educational level. All participants had a normal or corrected to normal vision and no 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 written informed consent prior to the study.

2.2. Tasks and stimuli

Participants were presented with drawings of a hand outlined in black on a white background and asked to decide as fast as possible whether the drawing corresponded to a right or a left hand.

Stimuli were left or right hands, presented according to 4 different postures (dorsal view, palm view, side from thumb view, and palm from wrist view) and at 7 different rotation angles (Upright-0° and 30°, 90°, 150°, 210°, 270°, and 330° in a clockwise direction, from Parsons, 1987; see Figure 5.1). The total number of different stimuli was thus of 56 hands (2 laterality x 4 postures x 7 angles). Ratings of motor awkwardness for each hand drawing were extracted from a previous study (Parsons, 1987), in which judges were asked to position their own hand or foot at the orientation of each stimulus and, afterwards, to estimate the awkwardness of the reached position on a 5-point scale (1=easy to place the appropriate limb into the orientation of the stimulus and 5=difficult to place the appropriate limb into the orientation of the stimulus). Ratings of visual familiarity were collected in 25 students of the *Université catholique de Louvain* (8 males) who were asked to rate how often they saw a hand in each posture and angle of rotation in everyday life (1=very unfamiliar and 5=very familiar). DC's personal visual familiarity was collected separately following the same procedure; it was highly

correlated to the students' ratings [r (56) = 0.53; $p < 0.001$]. As a control, we also tested foot laterality judgments using stimuli that were found to evoke implicit activation of the biomechanical constraints of foot movements in seminal studies of mental imagery (Parsons, 1987). Fifty-six drawings of left and right feet were presented at the same angle of rotation as hand drawings, according to 4 similar postures (sole view, top view, view from inside, and sole from heel view).

Participants seated in front of a computer screen located at a distance of about 60 cm; their feet were lying at rest on the ground and the hands of control participants were placed palms down on their knees without visual feedback.

During the experiment, participants performed 5 blocks of 56 trials with hand drawings and then 5 blocks of 56 trials with foot drawings. In each block, all postures and rotation angles were mixed in a different pseudo-randomized order. The first blocks of hand and foot laterality judgments included a familiarization with the four postures and 10 practice trials. Within each block, each trial started with the presentation of a central cross for 200 ms followed by a hand or foot drawing displayed until a response was recorded. Trials were separated by a blank screen of random duration between 500 ms to 1000 ms.

The experiment was controlled with the E-Prime software (Psychological Software, 2002, Pittsburgh, PA). Stimuli were presented on a 15.4 inch laptop screen set at 1024 x 768 pixels and subtended 5° of visual angle. During the testing, participants were asked to produce a verbal response ("right" or "left"). The RLs corresponded to the post-stimulus onset latency of the subject's vocalization, whose amplitude was electrically compared to a trip level voltage using a voice key controlled by E-prime. Malfunctioning of the voice key and response accuracy were monitored on-line by the experimenter.

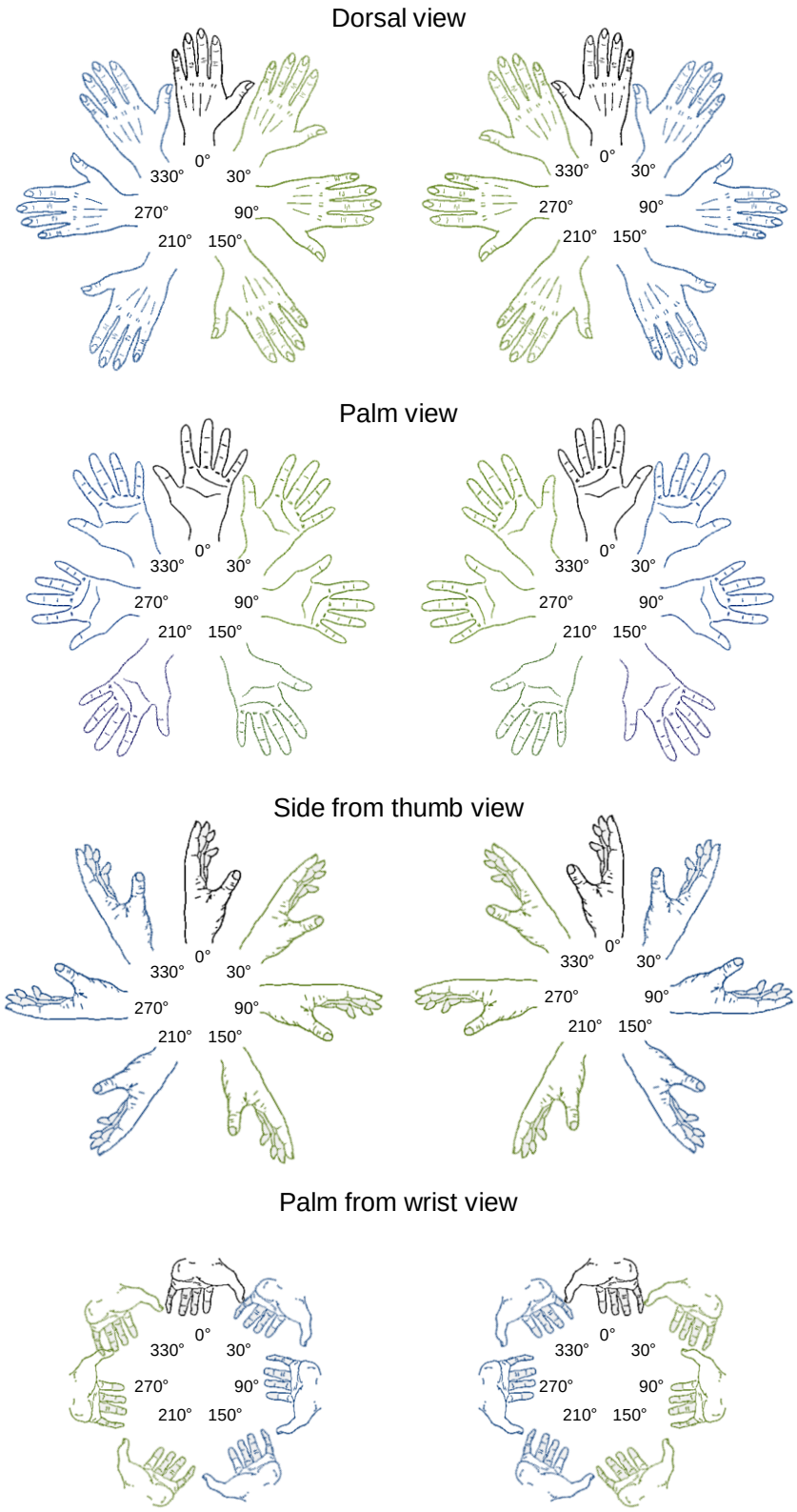

Figure 5.1| Line drawings of left and right hands in four postures and seven rotation angles. In blue: lateral orientations; in green: medial orientations.

3. RESULTS

Voice key failures (0% and 0.6% of the data in DC and controls, respectively), trials with RLs deviating more than 2 standard deviations from the mean RL within each participant (5.14% and 4.43% of the data in DC and controls, respectively), and trials with errors were discarded from RL analyses.

3.1. General analysis of DC's and controls' performance

First of all, we performed Crawford and Howell's (1998) modified *t*-test to test whether DC's performance (accuracy and speed) in hand and foot laterality judgments was impaired in comparison to the control group's performance. In hand judgments, no significant difference was observed between the performance of DC (correct responses: 97 %; mean RL: 1237 ms) and control participants [mean % correct responses ± S.D.: 91% ± 4%, modified t (6) = 1.56, $p > 0.1$; mean RL ± S.D.: 1277 ms ± 345 ms, modified t (6) = -0.11, $p > 0.9$]. The analysis of foot judgments showed a similar pattern, with a non significant difference in accuracy or RLs between DC (correct responses: 97 %; mean RL: 1512 ms) and controls [mean % of correct responses ± S.D.: 90% ± 6%, modified t (6) = 1.13, $p > 0.3$; mean RL ± S.D.: 1446 ms ± 386 ms, modified t (6) = 16, $p > 0.8$]. Second, Crawford and Garthwaite's (2005) Revised Standardized Difference Test (RSDT) was applied to test whether the difference between hand and foot laterality judgments in DC deviated from the difference observed between hand and foot judgments in the control group. The results showed that DC's difference in performance between hand and foot drawings was not significantly different from that found in the control participants, either in accuracy [RSDT: t (6) = 0.31, $p > 0.7$] or speed [RSDT: t (6) = 0.4, $p > 0.7$]. Third, independent samples *t*-tests were performed in order to compare the RLs across posture, laterality, and angle of rotation for foot and hand judgments in DC and

controls, respectively. The results indicated that both DC [t (67.76) = -2.99, $p < 0.01$] and control participants [t (84.1) = -4.29, $p < 0.01$] were significantly faster for hand than for foot judgments.

3.2. Effect of biomechanical constraints on DC's and controls' RLs

Having shown that the performance of DC in hand laterality judgments was within the normal range, we looked for the presence of the three behavioral features that were classically reported as evidence for an effect of biomechanical constraints in the HLJ task.

First, we investigated the presence of a three-way interaction between LATERALITY, ANGLE, and POSTURE in the chronometric data gathered for all participants. To do so, the RLs of control participants were entered in a repeated measure analysis of variance (ANOVA) with SUBJECT as the random factor and LATERALITY (left vs. right), POSTURE (dorsal view vs. palm view vs. palm from the wrist view vs. side from the thumb view), and ANGLE with respect to the upright view (0° to 330°, in a clockwise direction) as within-subject factors. The data of control participants required a log transformation to satisfy the ANOVA's homoscedasticity and normality assumptions. In order to explore the effects of biomechanical constraints in DC's judgments, we performed an ANOVA with ITEM as the random factor and LATERALITY (left vs. right), POSTURE (dorsal view vs. palm view vs. palm from the wrist view vs. side from the thumb view), and ANGLE with respect to the upright view (0° to 330°, in a clockwise direction) as between-item factors. For the analysis of DC's performance, the data were inverse transformed to fulfill the criteria of homoscedasticity and normality. The results replicated the significant three-way interaction between LATERALITY, ANGLE, and POSTURE, not only in control participants [F (18, 108) = 3.77, $p < 0.001$] but also in DC [F (18, 202) = 2.69, $p < 0.001$]. This three-way interaction showed that the effect of the angle of rotation on RLs was not

symmetric for left and right hands, with the angle associated to the maximal increase varying as a function of hand posture.

In order to further exemplify the effect of biomechanical constraints, we decomposed the three-way interaction as a function of hand posture. In control participants, the log transformed data were analyzed separately for each hand posture using repeated measure ANOVAs with SUBJECT as a random factor and LATERALITY and ANGLE as within-subject factors. The inverse transformed data of DC were entered in similar ANOVAs with ITEM as a random factor and LATERALITY and ANGLE as between-item factors. In control participants, a significant LATERALITY by ANGLE interaction was found for the palm from the wrist view [F (6, 36) = 4.32, $p < 0.01$] and for the palm view [F (6, 36) = 7.68, $p < 0.001$]. A near significant interaction effect was observed for the side from the thumb view [F (6, 36) = 2.15, $p = 0.07$] but, for the dorsal view, no significant interaction was found [F (6, 36) = 1.38, $p > 0.2$]. The performance of DC also revealed a significant LATERALITY by ANGLE interaction for the palm from wrist views [F (6, 51) = 3.98, $p < 0.01$] as well as for the side from the thumb view [F (6, 56) = 2.5, $p < 0.05$], but not for the palm [F (6, 41) = 1.49, $p > 0.2$] or dorsal view [F (6, 54) < 1]. In Figure 5.2, we represented the pattern of RLs of control participants (upper panel) and DC (lower panel) for the two postures that showed a significant LATERALITY by ANGLE interaction in DC after decomposition of the three-way interaction. The Figure clearly illustrates that the angle of rotation had a different effect on RLs depending on hand laterality. In both controls (Figure 5.2A) and DC (Figure 5.2C), the side view of a left hand led to maximal RLs at angle 210°, whereas the slowest responses for the side view of a right hand were observed at angle 150°. In contrast, the palm from the wrist views showing the highest RLs ranged from angles 90° to 150° for the left hand and from angles 210° to 270° for the right hand (Figure 5.2B and 5.2D). The comparison of Figure 5.2B and 5.2D showed that

maximal RLs for the palm from the wrist views were not observed exactly at the same angles in controls and DC, with a RL curve skewed to angle 150° for DC. Except for this slight difference, the angles associated to maximal RLs in DC and controls reflect the most difficult positions to reach while adopting the displayed posture with one's left or right hand (see the awkwardness estimates provided by Parsons, 1987).

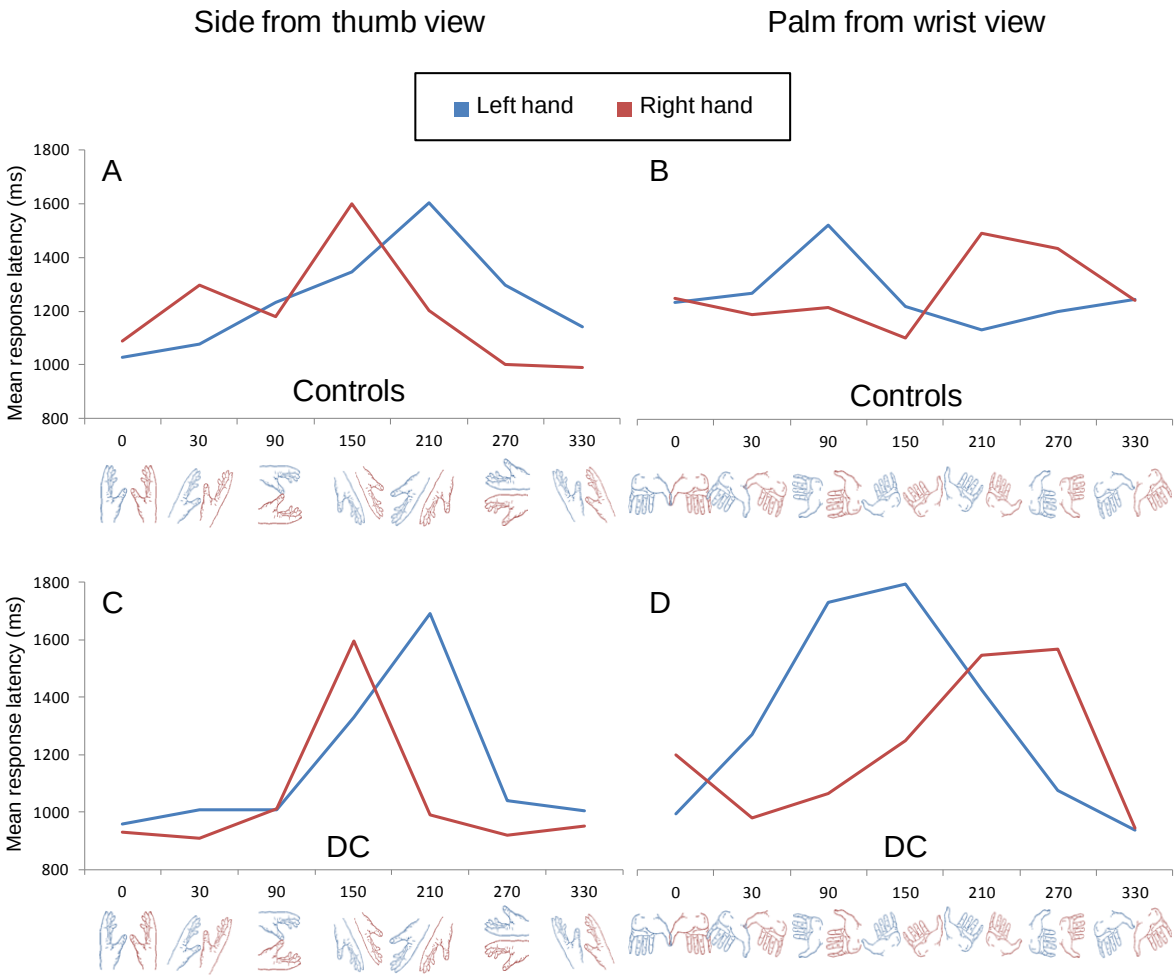

Figure 5.2| Mean response latency for left (blue) and right (red) hand drawings rotated clockwise by steps of 60° viewed from the side (A, C) and from the wrist (B, D). The pattern of response latency in control participants and DC are shown in the upper (A, B) and lower (C, D) panels, respectively.

DC did not show the expected pattern of asymmetric RL curves for the left and right hands viewed from the dorsal or from the palm view. However, the absence of LATERALITY by ANGLE interaction for these two postures was already pointed out in

previous experiments with normally limbed participants (Parsons, 1987; see for discussion ter Horst et al., 2010). Likewise, in our control participants, the effect of angular disparity was not modulated by hand laterality for dorsal views and a look at the individual data for the palm views revealed that the expected interaction was observed in only 3 out of 7 participants.

Second, in order to test for the presence of the MOLA effect, we recoded the trials according to the "medial" or "lateral" orientation of the displayed hand posture with respect to the body mid-sagittal plane (Cf. Figure 5.1: medial orientations are displayed in blue and lateral orientations in green). In that way, the analyses were performed on the mean RLs calculated for each 24 medial and each 24 lateral hand displays (2 hands x 3 angles x 4 postures). Figure 5.3 shows the mean RLs associated to medial and lateral orientations in DC and every control participant. Independent samples *t*-tests revealed that both control participants [medial: 1191 ms ± 134 ms; lateral: 1345 ms ± 139 ms; t (46) = 3.89, $p < 0.001$] and DC [medial: 1205 ms ± 274 ms; lateral 1378 ms ± 335; t (46) = 1.95, $p = 0.057$] responded faster to hand drawings in medial than in lateral orientation, which mimicked the effect of biomechanical constraints on actual hand movements. Furthermore, RSDT indicated that the MOLA effect did not significantly differ in size between DC and controls [RSDT: t (6) = 0.13, $p > 0.9$].

Third, we calculated the correlation between the mean RL obtained for each of the 56 items and the estimates of motor awkwardness collected independently for the same items (Parsons, 1987). The correlation plots are displayed in Figure 5.4 A and 5.4 B. The analyses showed that the RLs of both controls [r (56) = 0.55, $p < 0.001$] and DC [r (56) = 0.52, $p < 0.001$] were significantly correlated to the motor awkwardness of the hand drawing. A final set of analyses was performed in order to partial out the influence of motor awkwardness and visual familiarity on RLs (see Figures 5.4 C and 5.4 D).

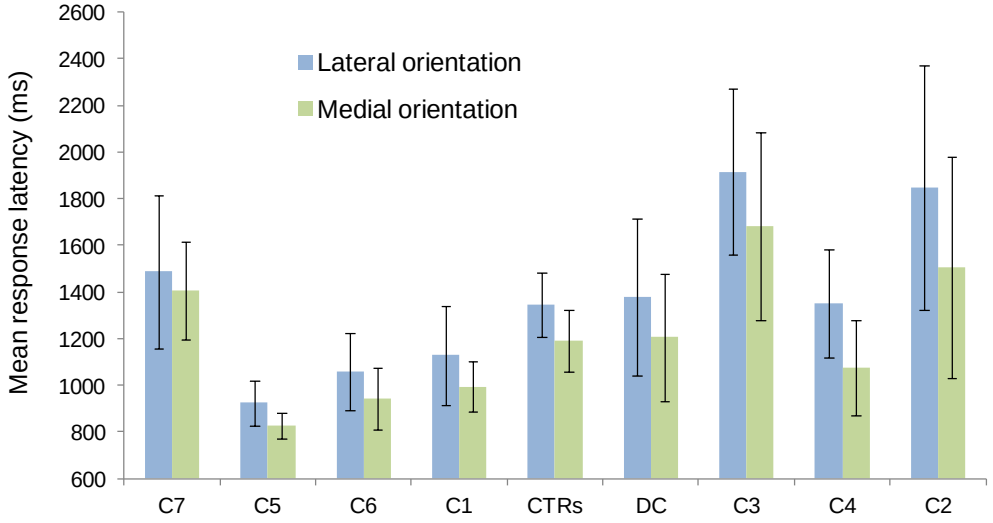

Figure 5.3| Mean response latency and standard deviations (vertical bars) are shown as a function of hand orientation (lateral vs. medial). The data for the lateral and medial orientation were obtained by pooling the data from all postures and rotation angles corresponding to the lateral (blue) and medial (green) positions depicted in Figure 5.1. Individual data (C = Control; CTRs = mean of controls) are aligned in ascending order on the X axis as a function of the size of the medial over lateral advantage.

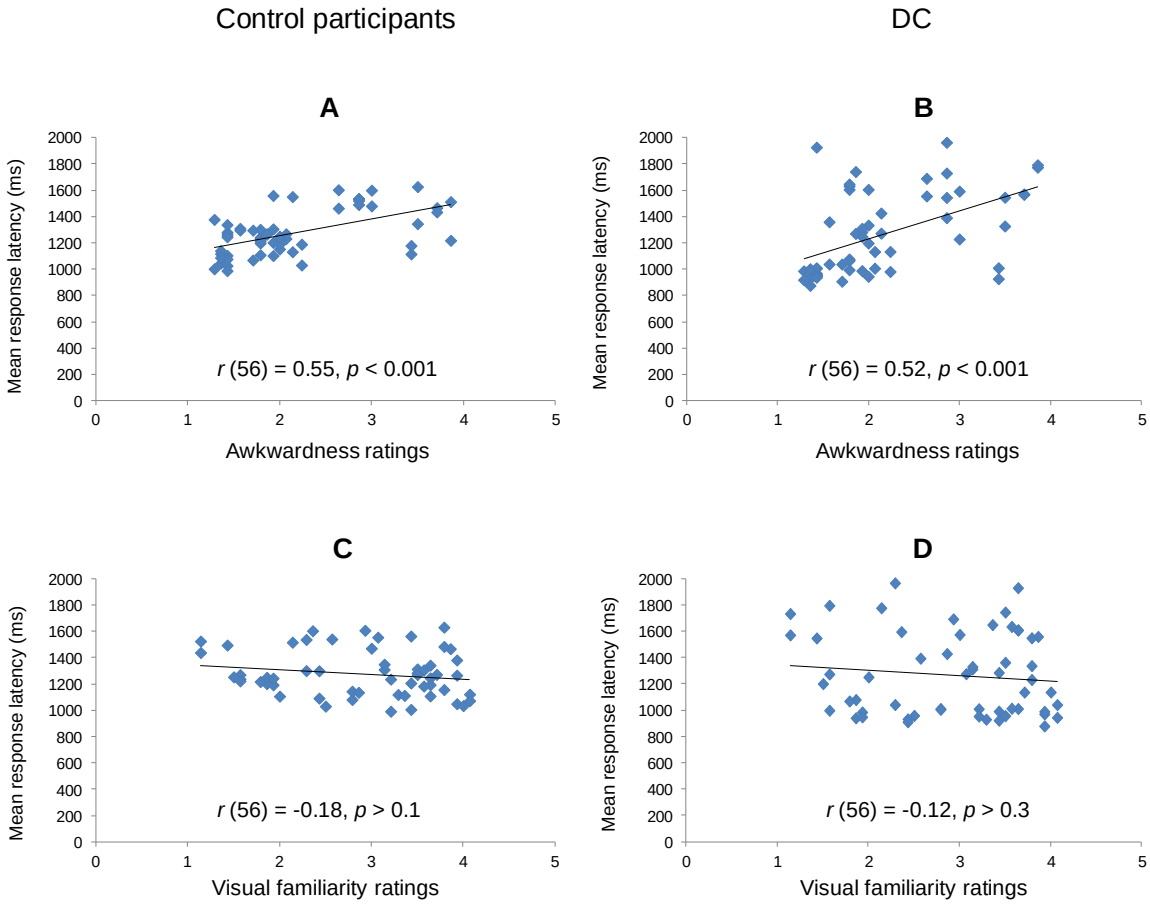

Figure 5.4| Correlation plots between the mean response latency of controls (left panels) and DC (right panels) for each hand stimulus in relation to rated awkwardness (A, B) and visual familiarity (C, D).

We conducted stepwise regression and partial correlation analyses between RLs and, respectively, ratings of motor awkwardness and visual familiarity. The regression analysis performed in control participants [F (1,54) = 23.94, $p < 0.001$, $R^2 = 0.31$] showed that the motor awkwardness associated to a given hand drawing was the best predictor of the observed RLs (ß = 0.55, t = 4.89, $p < 0.001$). The contribution of visual familiarity was not significant (ß = -0.04, t = -0.35, $p > 0.7$). Likewise, the regression of DC's RLs [F (1,54) = 19.87, $p < 0.001$, $R^2 = 0.27$] revealed a significant effect of motor awkwardness (ß = 0.52, t = 4.46, $p < 0.001$) in the context of a non-significant contribution of visual familiarity (ß = 0.01, t = 0.11, $p > 0.9$). Similar results were observed when DC's own ratings of visual familiarity were taken into account in the regression equation [F (1,54) = 19.87, $p < 0.001$, $R^2 = 0.27$]. Furthermore, partial correlations showed that the correlation between RLs and awkwardness estimates remained significant in controls [r (53) = 0.54, p < 0.001] and DC [r (53) = 0.51, $p <$ 0.001] after controlling for the part of variance explained by the effect of visual familiarity.

3.3. Summary

The goal of this study was to test whether the effect of biomechanical constraints in the HLJ task is strictly dependent on hand motor planning and execution abilities. To do so, we compared the performance of DC, a bilateral aplasic individual, with the performance of control participants in the HLJ task. First, we looked at the overall performance and found that DC was as fast and accurate as the control participants. Second, we found (1) that DC's RLs were influenced by the laterality, the angle and the posture of hand stimuli, in a way that mirrors the biomechanical limits imposed by each posture on left and right hand movements; (2) that DC's RLs showed a chronometric

advantage of medial over lateral hand orientations, reflecting the difference of movement amplitude allowed by these two orientations; and (3) that DC's RLs were strongly predicted by the motor awkwardness of the stimuli but not by their visual familiarity. To sum up, DC showed the three behavioral features that were classically reported as evidence for an effect of biomechanical constraints in the HLJ task. These effects were qualitatively and quantitatively comparable to the effects observed in control participants and they cannot be explained by the differential occurrences of the various hand positions in everyday life.

4. DISCUSSION

The effect of biomechanical constraints in the HLJ task is commonly assumed to reflect a process of motor simulation anchored in the same processes and representations as those involved in actual action planning and execution (Fiorio et al., 2006; Helmich et al., 2007; Jeannerod and Frak, 1999; Kosslyn et al., 2001; de Lange et al., 2006, 2008; Munzert et al., 2009; Nico et al., 2004; Parsons, 1987, 1994; Wraga et al., 2005). In this paper, we found that a person born without upper limbs was as accurate and fast as a group of control participants in performing the HLJ task and that his RLs in this task were significantly influenced by the biomechanical constraints of upper limb movements, just like normally limbed participants. These findings show that the effect of biomechanical constraints in the HLJ task is not strictly dependent on representations and processes involved in the planning and execution of hand movements. Given his total lack of motor experience with upper limb movements, and also of phantom limb experience, DC is not endowed with such motor representations and processes and could therefore not rely on them to perform the task.

Two kinds of accounts for the effect of biomechanical constraints in DC can be dismissed. First, this effect is not an artifact of the visual familiarity of the various hand positions. We found that DC's RLs were better predicted by the degree of motor awkwardness associated to each hand drawing than by their visual familiarity. Furthermore, the correlation between his RLs and motor awkwardness estimates remained significant even after removing the influence of visual familiarity on the data, which indicated that the influence of motor awkwardness and visual familiarity does not fully overlap in hand laterality judgments. Second, our data allow us to rule out that the effect is due to DC performing the HLJ task by mentally rotating the representation of his feet. Seminal studies in fact showed that the motor awkwardness estimates associated to certain foot positions correlate with those gathered for the homologue hand positions (see Tables 3 and 4 in Parsons, 1987). However, DC was 275 ms faster for hand than foot judgments. This advantage of hand over foot responses even reached an average of 583 ms for the side views, which showed the typical effect of biomechanical constraints.

Our findings thus provide strong evidence for the presence of an effect of biomechanical constraints in the HLJ task in a condition that totally prevents the planning and execution of hand movements. Uncovering the source of this effect in such condition was beyond the scope of this study and we have no direct evidence that speaks to this issue. Nevertheless, the finding that knowledge of biomechanical constraints was implicitly and automatically recruited in DC's hand laterality judgments is consistent with the view that such knowledge is an intrinsic component of body part visual perception processes. These perceptual processes would provide us with a representation of the human body that takes into account information about the range of movement allowed by the different body parts (Kourtzi and Shiffrar, 1999; Marr and Vaina, 1982; Shiffrar and Freyd, 1990, 1993). Such information might have an adaptive value for humans because it

facilitates the anticipation of the outcome of movements performed by others (Kourtzi and Shiffrar, 1999). The body representation we propose to explain the results of DC should not be confused with the « body schema » because this representation refers specifically to one's own body (de Vignemont, 2010; Corradi-Dell'Acqua et al., 2010). It is also different from the « body structural description » (i.e., a visuospatial representation of body parts) and the « body image » (i.e., a conceptual representation of the body) because none of these representations include knowledge of the biomechanical constraints of the body (Schwoebel and Coslett, 2005; Sirigu et al., 1991).

The role of visual processes in the effect of biomechanical constraints[19] in the perception of body parts was already emphasized by Brugger and colleagues in order to explain the influence of such constraints on hand laterality judgments (Brugger et al., 2000; Funk and Brugger, 2008) and apparent motion perception (Funk et al., 2005) in an bilateral aplasic individual, AZ, who experienced phantom limb movement sensations. It should be noted, however, that this proposal deviates from the idea that biomechanical knowledge is an intrinsic component of visual perception. In Brugger and colleagues' proposal, visual experience is assumed to activate pre-existing limb representations common to both action observation and execution, thereby allowing AZ to engage in a process of motor imagery in the HLJ task. Our finding that biomechanical constraints also

[19] Several authors (e.g., Daprati et al., 2010; ter Horst et al., 2010; Tomasino, Rumiati and Umilta, 2003; Steenbergen et al., 2007) argued that, when motor simulation is not possible (e.g., aplasia or severe motor deficit), alternative strategies may be used to perform the HLJ task. These strategies imply, for instance, mental rotation of the visual stimulus (Tomasino et al., 2003), visual analysis based on non-motor features of the hands such as the number of visible fingers or the position of the thumb and/or pinkie (Daprati et al., 2009), or third-person visual imagery of the action "as if someone else performed the action" (Steenbergen et al., 2007). It is important to note, however, that all these visually-based strategies predict no effect of biomechanical constraints on response latencies. Thus, any account for DC's pattern in the HLJ task in terms of such alternative strategies would be inappropriate.

affect the performance of a bilateral aplasic individual *without* phantom limb sensations in the HLJ task makes it unnecessary to assume that the role of visual experience is mediated by processes involved in action planning or execution.

In their study, Funk and Brugger (2008) also presented the HLJ task to a bilateral aplasic individual, CL, who did *not* experience phantom limb sensations, like DC, but, contrary to the results we reported here, they found no evidence for an effect of biomechanical constraints in CL's response pattern. These discrepant results in the HLJ task deserve some methodological considerations. While performing the task, CL was influenced by the rotation angle but not by the biomechanical constraints, as evidenced by an absence of interaction with hand laterality and angle of rotation. However, CL was tested with a short version of the HLJ task including only two postures (palm vs. back) and four rotation angles (from 0° to 270° by steps of 90°). Previous research in healthy participants showed that minor modifications in the stimulus set, such as the reduction of the number of rotational axes, can suppress the effect of biomechanical constraints (ter Horst et al., 2010). Furthermore, laterality judgment for hands viewed from the back and the palm are less regularly associated with an effect of the biomechanical constraints, even in normally limbed participants (e.g. Parsons, 1987; this study). It is therefore unclear whether the effect of biomechanical constraints in CL's performance was not observed because he had no motor experience or because the stimulus set allowed him to base his responses on strategic processes that do not make use of biomechanical knowledge. This observation underlines the need to assess the influence of biomechanical knowledge on HLJ with an extended set of hand drawings.

Finally, our findings call for re-examining the motor imagery account for the effect of biomechanical constraints in normally limbed individuals performing hand laterality judgments. Obviously, the effect observed in DC and controls could be driven by distinct

kinds of representations and processes, i.e., visual vs. motor processes, both being sensitive to the biomechanics of the human body. Nevertheless, we find it unlikely that an implicit and automatic access to biomechanics, such as the one revealed in DC's laterality judgments, would be totally suspended when normal subjects perform the task. Our findings thus encourage further empirical studies to entertain the hypothesis that visual in addition to motor processes, or even visual processes alone, contribute to the effect of biomechanical constraints in the HLJ task. In the meanwhile, the HLJ task should not be considered anymore as an unambiguous window on the covert stages of motor control and motor planning in normal or motor-impaired individuals.

CONCLUSION

This thesis was concerned with two issues. The first concerned the nature of conceptual knowledge mobilized in the process of comprehension. Embodied theories of concepts assume that concepts are composed of traces of previous sensory-motor experience directly stored as motor and sensory representations in sensory and motor representational systems. In contrast, "amodal" theories of concepts assume that concepts are represented in an "abstract" or "amodal" representational format within heteromodal cortex remote from the sensory and motor systems. The second issue concerned the role of motor representations and processes in the *comprehension of observed actions performed by others*. According to the "traditional view" in cognitive psychology, comprehension of observed actions relies on a visuo-perceptual analysis of the actor's body shape and motion which provides inputs to an "amodal" semantic system. However, recent "motor simulation" theories of action comprehension claim that comprehending an observed action relies on the observer's own motor representations of the same action, i.e., those that she uses when performing that action herself.

The empirical evidence reported in this thesis allowed us to make the two following conclusions:

(1) Conceptual knowledge relative to human actions and artifacts (manipulable and non-manipulable) is independent from the motor representations that specify how to execute actions and manipulate objects.

(2) Motor representations are not required to comprehend actions performed by others in normal viewing conditions efficiently. However, motor representations become critical when actions are perceived under adverse conditions.

Below, we will discuss these two conclusions in turn.

1. CONCEPTUAL KNOWLEDGE RELATIVE TO HUMAN ACTIONS AND ARTIFACTS IS INDEPENDENT FROM THE MOTOR REPRESENTATIONS THAT SPECIFY HOW TO EXECUTE ACTIONS AND MANIPULATE OBJECTS.

In this thesis, we have provided direct tests of two predictions of the embodied theories of concepts. The first prediction is that a loss or an absence of motor representations should prevent or, at least, hamper the comprehension of manipulable artifacts and/or human actions (Barsalou, 1999, 2008; Martin, 2007; Martin et al., 2000; Pulvermüller, 1999, 2005). The second prediction is that a category-specific conceptual deficit for actions and artifacts leaving preserved animals and plants should necessarily disproportionately affect manipulable artifacts in comparison to non-manipulable artifacts (Barsalou, 1999, 2008; Martin, 2007; Martin et al., 2000; Pulvermüller, 1999, 2005) and, in at least some variants, manipulation knowledge in comparison to visual and functional knowledge (Martin, 2007; Martin et al., 2000).

Neither prediction was held up by our empirical findings. In **chapter 1,** we found that an individual presenting with atypical motor development due to upper limb aplasia, DC, identified with a similar speed and accuracy manipulable artifacts that were and were not associated with motor knowledge (that he had or had never used). In **chapter 2**, we found that DC was perfectly able to name and comprehend upper limb actions displayed

in video clips and photographs. In **chapter 3**, we found that a patient presenting with a severe bilateral atrophy in the cortico-subcortical motor system resulting in a severe praxis and motor disorder was nonetheless as fast and accurate as control participants at naming actions and manipulable artifacts. In **chapter 4**, we reported the case-study of a brain-damaged patient, JJG, who presented with a conceptual deficit that affected selectively, but similarly, actions, manipulable artifacts and non-manipulable artifacts, as well as manipulation, functional and visual knowledge about them.

Admittedly, each of these studies is open to objections or alternatives interpretations. JJG's association of deficit for actions, manipulable artifacts, and non-manipulable artifacts, for instance, could be interpreted as a mere cooccurrence of two independent deficits arising from two independent modality-specific systems being fortuitously damaged in a comparable severity, one involved in the retrieval of motor representations and causing the conceptual deficit for actions and manipulable artifacts, and the other involved in the retrieval of a kind of sensory-motor representation that would be important for comprehending non-manipulable artifacts. It could be argued that JR's brain damage still leave preserved at least some parts of the motor system supporting comprehension of actions and manipulable artifacts. It may also be objected that DC could have acquired motor representations for upper limb actions and never used manipulable artifacts through the observation of others' actions and manipulations of objects. Several studies have indeed shown that observation of actions may improve (facilitate) their later execution in a variety of experimental conditions (e.g., Heyes & Forster, 2002; Mattar & Gribble, 2005) and that this improvement is linked to changes in the motor system of the observer (e.g., Stefan et al., 2005).

However, although each of these studies may be subject to caution, we believe that, when taken together, they provide a convergence of evidence legitimating the

conclusion that conceptual knowledge relative to human actions and artifacts is independent from the motor representations. In addition, if we acknowledge that we cannot formally rule out the objections/alternative interpretations raised here above, let us note that none of them seems very plausible. We have already presented in the discussion section of the chapter 4 several arguments supporting the view that the association of a conceptual deficit affecting similarly actions, manipulable artifacts and non-manipulable artifacts is unlikely to arise by chance. We have also already presented in the discussion section of the chapter 3 several arguments making it unlikely that JR's brain damage could spare parts of the motor system involved in comprehension. Let us here add that for at least three reasons, it is unlikely that DC could have acquired motor representations by observation. The first reason is that, to our knowledge, all current theories about motor learning by observation hold that such learning relies on visuo-motor conversions of an observed action into more elementary motor programs that already belong to the observer's motor repertoire (e.g., Buccino et al., 2004; Byrne, 2009). The acquisition of motor representations by observation, thus, must be understood in the sense of being able to re-combine pre-existing motor representations in novel sequences of movements, a condition that, in any case, DC does not fulfill for observed upper limb actions. The second reason is that there is evidence that in aplasic people, like DC, the motor part of the brain that normally represent "absent" limbs is reorganized and allocated to the control of adjacent body parts. Using fMRI, Funk and Brugger (2008) observed that in unilateral upper limb aplasic individuals, the deafferented/deeferented "hand" areas are colonized by the normally adjacent oro-facial motor areas. This observation suggests that DC's motor cortex does not contain a representation of the missing limbs. In line with that hypothesis, Reilly and Sirigu (2011) have shown that, in contrast to what is often found in amputees and is interpreted as an evidence of persistent motor representation,

TMS over the motor cortex (numerous activation sites) of congenital aplasic individuals does not elicit any sensations of the absent arm. Third, the hypothesis that DC would have acquired "normal" motor representations of upper limb actions by observation is difficult to reconcile with his selective difficulty at comprehending upper limb actions presented as point-light action (PLAs, chapter 3). In addition, be that as it may, current evidence indicates that motor representations acquired by observation are far from being equivalent to those built by actual physical experience. Cross and colleagues (Cross, Hamilton & Grafton, 2008), for instance, trained participants to learn sequences of dance movements by physically performing them or by observation and found that only sequences learned through physical practice were significantly better executed than new sequences at post-test. Mattar and Gribble (2005) have shown that participants who had observed someone else manipulating a mechanical device 96 times were subsequently faster when they had to learn to use the same device, but that observation was far from leading to similar performance than physical experience. In sum, the acquisition of motor representations by observation is very unlikely in DC and, even if he had acquired some motor representations, they would not be comparable to that developped through physical experience by normally limbed participants.

It is important, here, to add that it is sometimes hypothesized that aplasic individuals may have intact motor representations on the grounds that some (scarce) congenital aplasic individuals feel the presence of "phantoms" of the absent limbs and that some of them are even able to "command" the movements of their phantom limbs (Brugger et al., 2000; Price, 2006). However, recent findings suggest that the phantom sensations reported by bilateral upper limb aplasic individuals in fact recruit a hand movement representation that does not develop within the motor cortex and that is different from the motor representation that develop in healthy controls (see for

discussion Reilly & Sirigu, 2011). Phantom limb sensations in aplasic individuals, for instance, are dissimilar to the phantom sensations reported by amputees who have had motor experience before the amputation (Reilly & Sirigu, 2011) and involve a network of parietal areas (SPL, IPL, IPS), whereas primary motor and somatosensory cortices are inactive (Brugger et al., 2000). Be that as it may, to avoid this potential source of ambiguity, we selected an individual, DC, who *had no* experience of phantom limbs.

Our conclusion is consistent with previous reports of other patients who, despite lesions to the motor system, did not have difficulties in comprehending or naming actions or manipulable artifacts (Chainay and Humphreys, 2003; Cotelli et al., 2006; Daniele et al., 2012; Graham, Zeman, Young, Patterson, & Hodges, 1999; Hillis et al., 2006; Negri et al., 2007; Papeo, Negri, Zadini, & Rumiati, 2010; Pazzaglia, Smania, et al., 2008; Pazzaglia, Pizzamiglio, et al., 2008; Rumiati, Zanini, Vorano, & Shallice, 2001). In these studies, however, only patients' accuracy was reported. Furthermore, evidence from apraxia has been discussed on the grounds that apraxic patients could suffer from damage affecting parts of the motor system that do not play a critical role in comprehension (e.g., Rizzolatti & Sinigaglia, 2010). The findings reported in this thesis allow us to go a step farther by demonstrating that neither a widespread damage to the whole cortico-subcortical motor system, nor a complete absence of motor representations for some artifacts and actions, affected the ability to name actions and manipulable artifacts quickly and accurately.

Furthermore, the pattern of association found in JJG's conceptual impairment corroborated these findings and allowed us to propose an alternative hypothesis – that knowledge of actions and artifacts is represented in a common, domain-specific, conceptual subsystem representing means to achieve goals. We have already developped in the discussion of chapter 4 several theoretical and empirical justifications in favor of

this hypothesis. Here, let us simply note that this domain-specific hypothesis receives empirical support from developmental research showing that concepts of actions and artifacts are learned according to very similar principles (Csibra & Gergely, 2007; Gergely, Bekkering, & Kiraly, 2002; Gergely & Csibra, 2003; Hernik & Csibra, 2009; Kelemen, 1999). This hypothesis obviously needs to be empirically confirmed by future neuropsychological research.

Where are represented concepts of actions and artifacts, if not in the sensory-motor systems? It is likely that concepts of actions and artifacts depend on a network of brain areas supporting both domain specific and domain general components of conceptual processing. Among these areas, that certainly include temporal, parietal and frontal regions, the left posterior middle temporal gyrus (pMTG) seems to play a particularly central role in the retrieval of property- and modality-independent representations of artifacts and actions (see also Bedny CaramazzaGrossman, Pascual-Leone, & Saxe, 2008; Binder, Desai, Graves, & Conant, 2009; Mummery, Patterson, Hodges, & Price, 1998). A first source of evidence in favor of this hypothesis comes from functional brain imaging studies. Activity in the left pMTG has indeed consistently been reported in studies contrasting the processing of actions (verbs) and/or artifacts (nouns) to other categories of concepts (the most often animals) in a range of tasks including, among others, passive observation, hearing of action and tool-related sounds, reading, naming, lexical decision, semantic similarity judgments and synonym judgments (see for meta-analyses, Binder et al., 2009; Caspers, Zilles, Laird, & Eickhoff, 2010; Chouinard & Goodale, 2009; Lewis, 2006; see for reviews Martin, 2007 and Noppeney, 2008). Moreover, action and artifacts activations in the pMTG has been reported irrespectively of the stimulus modality or material such as written and spoken words (Bedny et al., 2008; Kellenbach, Brett & Patterson, 2003; Mummery et al., 1998), pictures and video-

clips (see Caspers et al., 2010 and Chouinard & Goodale, 2009 for meta-analyses) and sounds (see Lewis, 2006 for a meta-analysis). Finally, the left pMTG is activated regardless to the type of artifacts or action that is processed. Thus, it is activated when participants make judgments about the function of both manipulable and non-manipulable artifacts from their nouns (Kellenbach et al., 2003), judge on a scale the similarity of verbs referring to actions implying a very low or very high amount of motion (Bedny et al., 2008), or decide which two of three action verbs are the more "similar" for five different classes of verbs (running, speaking, hitting, cutting, and change of state verbs) varying with respect to the semantic features of action, motion, contact, change of state, and tool use (Kemmerer, Gonzalez Castillo, Talavage, Patterson, & Wiley, 2008). Note that pMTG activation is often interpreted by proponents of the embodied view of concepts as reflecting retrieval of modality-specific visual motion information acquired through past experience of action and tool use observation (Beauchamp, Lee, Haxby, & Martin, 2002, 2003; Kemmerer et al., 2008; Martin & Chao, 2001; Martin, Haxby, Lalonde, Wiggs, & Ungerleider, 1995; Noppeney, 2008; Patterson, Nestor, & Rogers, 2007 Tranel, Kemmerer, Adolphs, Damasio, & Damasio, 2003). pMTG, indeed, is just anterior to the area MT/V5 which supports basic motion processing and just inferior to the posterior Superior Temporal Sulcus (pSTS) which plays a important role in the perception of biological motion (Giese & Poggio, 2003; Blake & Shiffrar, 2007). However, Bedny and colleagues (2012) have recently found that the same parts of the pMTG are activated when sighted or congenitally blind participants perform a similarity judgment task about action verbs (how similar are "run" and "jump"), thereby ruling out the modality-specific visual information account.

A second source of evidence allowing the inference that the pMTG is critical in retrieving conceptual knowledge about artifacts and actions are the neuropsychological

studies that have reported anatomo-clinical correlations between pMTG lesions and the conceptual processing of actions and/or artifacts (e.g., Brambati et al., 2006; Kalenine, Buxbaum, & Coslett, 2010; Kemmerer et al., 2010; Tranel et al., 2003). Tranel and colleagues (2003), for instance, observed that the highest area of lesion overlap in patients who had impaired knowledge for both tools and actions was in the left middle posterior temporal region. Kalénine et al. (2010) tested 43 patients with left hemisphere brain damage and found that impaired performance in a conceptual task (word to video-clip matching task with a conceptual foil), but not a visual task (same task but the foil was the same action performed incorrectly), was associated with damage to the pMTG. In another study that comprised 152 patients suffering from various neurodegenerative diseases, Brambati and colleagues found that naming accuracy for pictures of different kinds of artifacts (household items, vehicles and manipulable objects), but not the naming accuracy for animals and fruit, correlated with grey matter volume in the pMTG (Brambati et al., 2006).

To sum up, we claim that concepts of actions and manipulable artifacts are independent from motor representations and from the motor system. As an alternative hypothesis, we suggest that knowledge of actions and artifacts could be represented in a common conceptual system that would have evolved to represent means to achieve goals. Further, building on the brain functional imaging and neuropsychological literature, we suggest that the pMTG, rather than the motor system, plays a central role in the conceptual processing of artifacts and actions. To avoid misunderstanding, let us note that this hypothesis does not preclude that knowledge about how actions are executed or objects manipulated could be part of the concepts of actions and artifacts and be involved in their comprehension. It seems indeed obvious that comprehending an observed action requires that we have knowledge about the movements involved in executing it. However,

such knowledge must be distinguished from motor representations and processes, supported by the motor system and to which embodied theories of concepts attribute a role in comprehension.

2. MOTOR REPRESENTATIONS ARE NECESSARY ONLY TO COMPREHEND OBSERVED ACTIONS UNDER ADVERSE CONDITIONS.

Traditionally, the debate about the role of motor representations in the comprehension of observed actions sets two extreme positions, variously suggesting that motor representations are very important to comprehend others' actions (Blackemore & Decety, 2001; Jeannerod, 2001; Rizzolatti & Craighero, 2004; Rizzolatti, Fogassi, & Gallese, 2001), or that they have no role at all (e.g., Rothi, Heilman, & Ochipa, 1991). In this thesis, we have put forward a middle ground hypothesis.

First, we reported several results that allow to refute the hypothesis that motor representations and processes are required for the efficient comprehension of observed actions. We showed, indeed, that neither the loss (chapter 1), nor the complete absence (chapter 3) of motor representations affects the ability to name observed actions efficiently (i.e., quickly and accurately). Furthermore, we showed that, as normally limbed controls, DC's judgments in the hand laterality judgment task were slower when a hand was displayed on the screen in a position that would be difficult to reach with one's own hand. This result indicate that, in contrast to a current viewing in the field of body part and movement perception, "motor-like" influence on visual tasks does not require interpretation in terms of the involvement of motor processes and representations in perception (chapter 5). In addition, this showed that implicit knowledge of how a body part moves may be extracted by the visual system and then used to constrain visual processing.

One could wonder whether the study of a patient with a developmental disorder is relevant for the purpose of developing a model of the cognitive architecture supporting the comprehension of observed actions in typically developped individuals. After all, it is known that congenitally blind people develop superior abilities in some non-visual perceptual tasks, such as pitch-change direction discrimination (Gougoux et al., 2004), verbal memory (Amedi, Raz, Pianka, Malach, & Zohary, 2003), speech discrimination (Muchnick, Efrati, Nemeth, Malin, & Hildesheimer, 1991), sound localization (Gougoux, Zatorre, Lassonde, Voss, & Lepore, 2005) or tactile discrimination (Van Boven, Hamilton, Kauffman, Keenan, & Pascual-Leone, 2000). By analogy, DC's lifelong absence of upper limbs could have allowed him to develop "exceptional" visual skills for the recognition of upper limb movements.

However, the results obtained with DC converge with the results obtained with JR (chapter 3) whose preserved ability to name actions despite severe motor and praxis deficits is not subject to the same ambiguity. Together, these findings legitimate the conclusion that motor representations do not support action comprehension in normal healthy participants. Furthermore, the results obtained with DC nonetheless allow the inference that the visual system "alone", at least in his case, is able to support efficiently the comprehension of actions and to use knowledge about the biomechanical constraints of the human body to constrain visual perception. This demonstrates that there is no need to assume that the motor system contribute to action comprehension to account for our ability to comprehend actions efficiently.

The hypothesis that motor representations are not necessary to comprehend observed actions also receives support from studies reporting on the ability of people with Möebius syndrome (MS), a syndrome characterized by a congenital paralysis of facial muscles, to recognize facial expressions. Several studies, indeed, have found that individuals with

MS, despite being congenitally unable to perform facial movement, are still able to recognize facial expressions (Calder, Keane, Cole, Campbell, & Young, 2000; Bogart & Matsumoto, 2010). Calder et al. (2000), for instance, examined emotion recognition in three individuals with MS and found no significant deficits in facial expression recognition. Bogart and Matsumoto (2010) corroborated these findings and found that a group of 37 adults with MS did not differ from 37 age and gender matched control participants in a facial expression recognition task.

The neuro-anatomical basis of visual action recognition would rely on two different pathways: one specialized in the processing of motion information and the other in the processing of body postures information, converging in the pSTS (Giese, 2004; Giese & Poggio, 2003). Cells in the macaque STSa, which is the homologue of the human pSTS (Jellema & Perrett, 2005), respond to multiple views of the same specific actions such as walking towards or away, head turning, movement into or out of view, arm movements, reaching for an object, picking an object, tearing an object and holding an object (e.g. Jellema, Baker, Oram, & Perrett, 2002; Logothetis, Pauls, & Poggio, 1995; for review, see Jellema & Perrett, 2005). In humans, the pSTS is consistently activated by the observation of human body motion (Bonda, Petrides, Ostry, & Evans, 1996; Grossman et al., 2000; Grossman & Blake, 2002; Beauchamp et al., 2003; Saygin, Wilson, Hagler Jr, Bates, & Sereno, 2004; Pelphrey et al., 2003, see for review, Allison, Puce, & McCarthy, 2000; Blake & Shiffrar, 2007; Caspers et al., 2010; Giese & Poggio, 2003; Puce & Perrett, 2003) and its transient lesion by TMS affects the perception of biological motion (Grossman, Battelli, & Pascual-Leone, 2005).

However, we have also shown that having motor representations constitutes an important advantage when actions are perceived under particularly adverse conditions. We found indeed that although he had no difficulty at comprehending lower-limb actions

presented as PLAs, DC could not recognize upper limb actions (for which he lacked of motor representations) presented in similar perceptual conditions (chapter 2). As discussed in the discussion section of the chapter 2, this result is compatible with the extant neuropsychological evidence gathered in the field of action comprehension/perception (Arrighi, Cartocci, & Burr, 2011; Casile & Giese, 2006; Serino et al., 2010) and the field of speech perception (Meister, Wilson, Deblieck, Wu, & Iacoboni, 2007; Moineau, Dronkers, & Bates, 2005).

All together, these empirical observations encourage us to put forward the hypothesis that, under normal viewing circumstances, brain regions involved in visual aspects of action recognition (pSTS) and in the retrieval of conceptual knowledge about actions (pMTG) are sufficient for action comprehension. However, under conditions in which the visual signal is degraded or ambiguous, or that perception is difficult for any reason, the activation of motor representations and processes may augment the recognition of observed body movements. In this view, the contribution of motor representations and processes to the comprehension of observed actions could thus be nothing more than an instance of supra-modal or multi-modal integration of information from different modalities like, for instance, the integration of the auditory and visual information that allows improving speech comprehension under adverse perceptual conditions. By analogy, motor contribution is not required to comprehend observed actions in natural (sufficiently informative) condition such as visual information is not required to the comprehension of speech in sufficiently informative conditions. In such circumstance, motor involvement could play no role at all, or could "enrich" or "augment" comprehension by allowing the retrieval of traces of personal experience with a given action (Mahon & Caramazza, 2008; Hickok, 2010; Rumiati, Papeo & Corradi-Dell'Acqua, 2010). However, this "additional" information would not be necessary to

"comprehend" actions as defined herein, i.e., being able to recognize the action and to retrieve knowledge about it. Under adverse perceptual conditions, however, additional information from motor representations and processes would become critical to deal with ambiguity in the visual stimulus, like visual information conveys additional information allowing improving speech perception in a noisy environment (e.g., Calvert et al., 1997).

Future research should endeavor to corroborate our findings. To his aim, other patients with atypical motor development could be tested. Another possibility could be to measure the response times of normally limbed participants when they are asked to name actions presented in video-clips (natural condition) or in PLAs (adverse conditions) while rTMS is applied on their ventral premotor cortex (vPM) and left inferior parietal lobule (IPL). Visuo-motor interactions, indeed, are likely to rely on recurrent reciprocal connections between the pSTS and the vPM by the bias of the IPL (Rizzolatti & Craighero, 2004). We predict that action identification will be slowed down only for the point-light actions (not for the video-clips) and only when the TMS interferes with visuo-motor interactions (not in a control stimulation).

In parallel, future research should also try to specify what make an "adverse condition", or in other words, what modulates the impact of motor representations and processes on action comprehension. To address this issue, future studies could ask individuals with atypical motor experience (e.g., aplasia, cerebral palsy) to identify as fast and accurately as possible actions they have already performed or never performed presented in various visual conditions: motionless, strobe and full versions of actions performed by an actor represented by point-lights, a moving skeletons or a natural human body. These conditions differ in the presence and continuity of movement (motionless versus strobe versus full stimuli), body structure (point-light display versus moving skeletons) and body shape (skeletons versus video-clips of natural actions). By

identifying the conditions in which individuals with atypical motor experience are less efficient than matched participants in identifying actions they have never performed, we will be able to specify the visual conditions under which achieving action identification needs motor involvement and, thereby, develop a theory about the respective contribution of the visual and motor system in action recognition.

Finally, further research should also attempt to dissociate the processing level(s) that is (are) influenced by motor representations during the process of action identification. At least four different processing levels may be considered in this process: detection of the presence of human body motion, configural processing of the moving body, recognition (access to a stored visual description of the action, if familiar), and identification of a specific action. Future research could address this issue by assessing the ability to process already performed and never performed actions in individuals with atypical motor experience in tasks that differ as regards the level of processing they are assumed to tap. In a detection task, for instance, the participants would be presented with a display containing a number of randomly moving dots of the same size and color as the dots used in the point-light actions and asked to decide as fast as possible whether a point-light action is camouflaged within the other dots. In a configural processing task, they would see point-light actions of an actor viewed from his left or right profile and be asked to judge as fast as possible if the actor faces the left or the right side of the screen. In a recognition task, point-light displays of familiar actions (e.g., "hammering" or "waving goodbye") would be presented within a stimulus set also containing "invented" gestures and the participants would be asked to say as fast as possible whether they have already seen the presented action. Finally, in an identification task, they would have to identify which particular action is being performed by naming it (e.g. "running"). Specifying the task(s) for which individuals with atypical motor experience show, or do not show, poorer

performance for never performed as compared to already performed actions, would inform us about the processing level(s) that is (are) complemented or influenced by motor representations and processing.

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