SISSA

Scuola Internazionale Superiore di Studi Avanzati
International School for Advanced Studies

The Tie between Action and Language Is in Our Imagination

Candidate:

Liuba Papeo

Supervisor:

Raffaella I. Rumiati

Thesis submitted for the degree of Doctor of Philosophy in
Cognitive Neuroscience
Trieste, 2010

Jury

Alfonso Caramazza

Harvard University, Cambridge, MA, US and

Center for Mind/Brain Sciences (CIMeC), Università di Trento, Trento, Italy

Peter Hagoort

Donders Institute for Brain, Cogntion and Behavior, Radboud University, Nijmegen and

Max Planck Institute for Psycholinguistics, Nijmegen, The Netherlands

Raffaella I. Rumiati

Cognitive Neuroscience Sector,

International School for Advanced Studies (SISSA/ISAS), Trieste, Italy

Tim Shallice

Cognitive Neuroscience Sector,

International School for Advanced Studies (SISSA/ISAS), Trieste, Italy

Alessandro Treves

Cognitive Neuroscience Sector,

International School for Advanced Studies (SISSA/ISAS), Trieste, Italy

Contents

8. Appendices

Acknowledgements

My deepest gratitude to Raffaella Rumiati, who believed in me before anyone else, even before I believed in myself, who has been a guide and a friend throughout the past years, throughout the ups and downs that brought me here. Thank you Raffaella!

I would like to thank Antonella Zadini (Azienda Ospedaliero-Unversitaria “Ospedali Riuniti” di Trieste) for making available her expertise for the neuropsychological study, for medical assistance in the TMS studies, and for her generosity and encouraging words in difficult moments. It has been a pleasure for me to work with Barbara Tomasino (I.R.C.S.S. “E. Medea”, Polo Friuli Venezia Giulia), who taught me all I know about fMRI. For help in these last months, I am grateful to Cinzia Cecchetto, a young student with a surely promising career on her horizon. I would also like to thank Antonino Vallesi for introducing me to TMS, the funniest toy I have ever experienced. This thesis would not have been possible without Alessio Isaja, who followed me day by day, even in some crazy experimental setups and against the hostility of my computer.

Special thanks to Corrado-Corradi Dell’Acqua for being always there for me with his expertise and generosity; to Gareth Bland’s challenging mind that pushed me to continuously dispute my own ideas, and to Claudia Civai for thousands of words about science and life.

Alan Langus, Elisa Tunini, Rosaria Calvaruso and Carlo Apostoli, thank you for having made Trieste a very special place over all those years!

All my gratitude and love to my mother Sabina and my father Michele, who taught me the power of knowledge, as the only capital to be free.

Jean-Remy Hochmann’s incredible wisdom gave me invaluable insights for every single study in this thesis; thank you for all time and the laughs inside and outside of this building!

To Emiliana Papeo, the beautiful angel who is always at my side, I dedicate this thesis.

Abstract

In this thesis, the embodied cognition proposal that action words are directly and automatically mapped into the perceiver's sensorimotor system, and understood via motor simulation, has been put under the lenses of neuropsychology, psychophysics, transcranial magnetic stimulation (TMS), and functional magnetic resonance imaging (fMRI) investigation. The objective was to establish whether the tie between language understanding and motor simulation is necessary for the former to be effective, to the extent that a virtual identity can be recognized between action and language systems.

In Chapter 1, the ability of left-damaged patients to perform actions and comprehend their names, was assessed under those stimulus- and task-conditions (i.e., equally early-acquired verbal and motor tasks involving perceptually and conceptually identical stimuli) that are held to increase maximally the degree of overlap between the two systems. Even so, I found double dissociations between action and action-language performances, and no relationship between deficits in action-word comprehension and lesions in motor and premotor regions. These findings clearly show that motor substrates (and processes) are not essential for action-word understanding.

Building on this finding, I proposed that motor simulation in language reflects one imagery-based interface mediating strategically (i.e., when needed) the information transfer from one system (action) to an independent one (language). To corroborate this interpretation, I had to demonstrate that, first, motor activity does not always occur in action-language processing and, second, that it is triggered by the same conditions that elicit motor imagery. Indeed, imagery recruits motor processes and substrates only

when people mentally represent, or stimuli evoke, bodily movements in an egocentric (embodied), first-person perspective.

Using TMS, I found that motor simulation, as reflected in primary motor (M1) activity, steps in language processing only when the task required the explicit retrieval of action knowledge (versus other aspects) associated with a word (Chapter 3). Importantly, M1 activity enhanced only after 400 ms, a time interval beyond that for lexical-semantic encoding, and within that for imagery. A second TMS study (Chapter 4) shows that M1 activity increased selectively for actions attributed to the self versus a third subject/agent. Not only can the motor system distinguish the self from another, but it can also disentangle humans from non-human motion. In chapter 5, I provided evidence that action-language affects a subsequent motor behavior when the sentential context describes human action versus mechanical motion. These findings resticted from all to certain the conditions that make the cross-talk between language and motor system possible, compatibly with the circumstances that elicit a motor strategy of imagery. An fMRI study (Chapter 6) provides decisive demonstration that simulation in language is so truly a strategy that it can be prevented by context-dependent factors, even for tasks and stimuli with salient sensorimotor components, and can be readily learnt and imposed top-down to the processing of (nonaction) words that do not normally elicit it.

Motor simulation, in action-word understanding, is defined by the reliance on top-down higher-level factors, such as the individuals’ attention to sensorimotor aspects of stimuli, the representation of self as distinct from others, the sentential and the cognitive (neural) context. That is, the engagement of this modality of processing in language requires a cognitive mediation that is not predicted by the direct matching between a perceived word and the corresponding motor representation. This research whishes to contribute to our understanding of how information flows from basic (motor) to specific (linguistic) domains, within the flexible, creative, distributed architecture, which is the human brain.

“No, Ernest, don't talk about action.

It is a blind thing dependent on external influences, and moved by an impulse of whose nature it is unconscious. It is a thing incomplete in its essence, because limited by accident, and ignorant of its direction, being always at variance with its aim. Its basis is the lack of imagination. It is the last resource of those who know not how to dream.”

Oscar Wilde - The critic as artist - 1891

Chapter 1. Introduction

What is the nature of conceptual representations? Are they symbolic or innate? What is the role of physical experience in human knowledge of the world? These questions have structured the history of ideas for thousands of years, opposing Plato to Aristotle, the rationalism of Descartes to the empiricism of Locke and Hume, the nativism of Chomsky to the constructivism of Piaget. Recently, cognitive science and neuroscience have addressed this issue by trying to establish how knowledge is acquired and represented in the human brain. In the latest version of this debate, an *embodied* approach to human cognition has been opposed to a *disembodied* one.

1.1. Embodied cognition

Although with no unique definition (see Chrisley & Ziemke, 2002; Wilson, 2002), the idea of "embodiment", since the mid-1980s, has been developed in cognitive science and artificial intelligence (AI), promoting the view that physical experience with the world is a *condition sine qua non* for any form of intelligence or knowledge (Pfeifer & Scheier, 1999). According to this view, meaningful concepts arise from the history of humans' bodily interaction with the environment and from humans' innate capacity to project from sensorimotor and social experience to conceptual structures (Lakoff, 1987; Lakoff & Johnson, 1980; 1999). A typical example can be found in the abstract concept of "grasping the idea" that may be grounded in the bodily experience of grasping a physical object with one's own hand. This view is not novel, but stems from a tradition of Motor Theories of Cognition in psychology, which dates back at least to the eighteenth century (Berkeley, 1709; Liberman et al., 1967; Washburn, 1914; Watson, 1913; see Scheerer, 1984, for an overview). The first detailed articulation of the new generation of embodied theories was by Allport (1985), who proposed that conceptual knowledge is organized according to sensory and motor modalities, and that the information represented within different modalities was format-specific. In other words, the same neural processes that are involved in coding the sensory attributes of an object presented to senses, also constitute the basis for the conceptual representation of objects in (semantic) memory. Accordingly, the comprehension process is *modal*, as it corresponds to the *re*-enactment (Prinz, 1997) of previous experience associated with a perceived stimulus, including its sensory and motor aspects, and introspective and affective states that typically accompanied interaction with that entity (Barsalou, 1999; 2009; Damasio et al., 2004; Gallese & Lakoff, 2005; Prinz 2002; Zwaan 2004). The specific stance of embodied accounts of language is that all words *always and necessarily* activate the *internal simulation* of the perceptual or motor experience implied by words, because conceptual representations are directly mapped onto the neural substrates for action and perception, without any cognitive mediation (Rizzolatti & Craighero, 2004). Importantly, this view predicts that perception and action are functionally linked in the brain, and share mechanisms in a frontoparietal sensorimotor system (Braitenberg & Schüz, 1998; Fadiga et al., 2000; Rizzolatti & Craighero, 2004). This system, and particularly its frontal motor aspect, would the basis and the seat of action understanding.

1.2. Disembodied cognition

The disembodied approach corresponds to the *classic* view of cognitive science thst concepts are stored in the form of abstract, modality-independent representations or symbols, within dedicated cerebral structures, remote from the mechanisms of perception and action (Fodor, 1983; Shallice, 1988). Symbols retrieve much of their meaning by their association with other symbols, and processing their meaning is *amodal*, in that it does not engage, in the first place, modality-specific systems involved in the perception of, or interaction with the physical referent (Fodor, 1975; Kintsch, 1998; Landauer & Dumais, 1997; Pylyshyn, 1984).

The symbolic nature of conceptual representations, however, does not exclude that sensorimotor experience can play a role in conceptual organization. In various “disembodied” theorizations, in fact, symbolic representations of objects are largely shaped and organized by sensory and motor experience. For instance, on one account, conceptual organization is held to be constrained by the modality in which individuals interact with objects (i.e., sensory/perceptual or motor/functional), resulting in modality-specific subsystems that parallel the sensory and motor modalities of input and output (the Sensory/Functional Theory; Warrington & McCarthy, 1983; 1987; Warrington & Shallice, 1984). On another account, conceptual organization is suggested to reflect object domains (e.g., living animate, living inanimate, conspecifics and tools) that result from the evolutionarily relevant history of interaction with the environment (Caramazza & Shelton 1998; Carey, 2009; Carey & Spelke, 1994). A third class of theories is based on the Correlated Structure Principle, whereby semantic memory is organized as to represent statistical regularities, namely, the co-occurrence of different types of features or properties in the world, which determines different categories of objects (Caramazza et al., 1990; Devlin et al., 1998; McClelland & Rogers, 2003; Tyler & Moss, 2001; refer to Mahon & Caramazza, 2009, for a more extensive review of theories of concepts). The specific stance of disembodied accounts is that conceptual content, while tied in important ways to sensory and motor systems, is more abstract than the token-based information contained within the sensory and motor (or sensorimotor) systems.

Thus, the crucial difference between embodied and disembodied theories concerns the nature of conceptual representations in the brain, modal or *embodied* in sensorimotor experience on one hand, symbolic and amodal on the other hand.

Traditionally, the literature on the debate about whether language comprehension is fundamentally symbolic or embodied has largely followed the distinction between psycholinguistic and computational linguistic approaches. Psychophysics has provided instruments for investigating the embodiment of language by showing the effects of word contents on motor behavior, or the effects of motor or perceptual processes on language processing (e.g., Boroditsky, 2000; Glenberg & Kaschak, 2002; Zwaan et al., 2002; Zwaan & Taylor, 2006). On the other hand, the majority of symbolism publications are computational, showing how data are related to corpus linguistic findings (Burgess, 1998; Howard & Kahanna, 2002; Kintsch, 1998; Landauer, 2002; Landauer & Dumais, 1997; Steyvers et al., 2004). This debate and the related empirical investigation have recently received new impetus by the discovery of neural underpinnings that may subserve the embodiment, and by the availability of a range of techniques (e.g., functional and structural neuroimaging and transcranial magnetic stimulation) that allow exploring more or less deeply these neural mechanisms.

1.3. Language in the body: a perfect story

To the earlier theorizations of motor involvement in cognition (i.e., the motor theories of cognition; see Scheerer, 1984), the renewed framework of embodied cognition has added the description of a mechanism, the *mirror matching*, and its neural underpinnings, the *mirror neurons*, which have the potential to explain how comprehension meets action. According to the mirror matching, action understanding results from the automatic mapping of a perceived action onto the perceiver’s motor system (“self-other shared representation”), where an *internal simulation* of that action is carried out (Rizzolatti et al., 2001). This process may be accomplished by a population of neurons in the sensorimotor circuitry that display the characteristic to respond both when individuals observe another’s action and when they perform the same action on themselves. Thus, motor areas may be endowed with a mechanism that matches a perceived action on the perceiver's internal representation of that action.

Studies on monkey brain have described neurons in the posterior motor area F5 with such *mirror* properties between action and vision (di Pellegrino et al., 1992; Gallese et al., 1996) or between action and audition (i.e., hearing the sound associated with an action; Kohler et al., 2002), suggesting that the same mechanism applies to action processing, regardless of the modality thorough which the action is perceived or inferred. In humans, left-lateralized motor activity has been found not only when an action is observed (Fadiga et al., 1995), but also when a word implying an action is presented (Hauk et al., 2004), to the extent that the mirror matching has been generalized to action-language comprehension (see Pulvermüller & Fadiga, 2010, for a recent overview) [1]. On this view, the lexical-semantic processing of an action word, just like the processing of any action-stimulus, may depend upon the early, *automatic* and *necessary* activation of the agent-neutral (i.e., the same for self and other's actions) motor representation involved in the execution of the same physical act, via motor simulation (Barsalou, 2009; Gallese & Lakoff, 2005; Rizzolatti et al., 2001; Rizzolatti & Craighero, 2004; see Pulvermüller, 1999, for different but compatible proposal). Notice that this theorization rests upon the assumptions that word representations are *modality-specific*, while sensorimotor system for word processing is *modality-neutral*, in that it treats any action-

---

[1] Here, we focus on the extent to which the motor system is involved in semantic representations of words and in word understanding, although the debate touches other levels of language processing too, including phonemic (Liberman, 1967; Wilson et al., 2004), orthographic (Galantucci, 2005) and syntactic processing (Glenberg & Kaschack, 2004; Fogassi & Ferrari, 2007), as well as conversation or pragmatics (Scott et al., 2009).

related stimulus in a similar manner, regardless of its modality (verbal, auditory, motor or perceptual).

While the existence of mirror neurons in humans is still hotly debated and, given the available evidence, very unlikely (Dinstein et al., 2007; 2008; Lingnau et al., 2009; see Hickok, 2009; Turella et al., 2009; for critical reviews), a mirror matching-*like* mechanism in humans, whereby actions are understood via motor simulation, could be inferred by several lines of evidence. First, the monkey area F5, where mirror neurons were first found, is the homologue of the language-related Broca's region in the human brain (see Hagoort, 2005). Both F5 and Broca's region have similar location within the frontal cortex (i.e., in the inferior precentral cortex), and cytoarchitectonic similarities (Patrides & Pandya, 1994). Moreover, a positron emission tomography (PET) experiment showed that Broca's area may be also actived during action observation (Rizzolatti et al., 1996), leading to the conjectural account that this region is the missing ring, in evolution, between an archaic manual communication system to human language (Rizzolatti & Arbib, 1998).

Second, "the 90% of apraxics is aphasic" (Ajuriaguerra et al., 1960): when damage affects the left hemisphere, aphasia, the disturbance of linguistic function, is often accompanied by apraxia, a disorder affecting the purposeful performance of actions. Moreover, systematic studies have reported correlations between the severity of aphasia and apraxia (De Renzi, Pieczuro & Vignolo, 1966; Dee et al., 1970; Hecaen, 1962; Kertesz & Hooper, 1982; Liepman, 1905). Even when motor performance is spared in aphasics, verbal impairment is often associated with deficits in nonverbal processing. Critically, impaired pantomime recognition is reported as a common correlate of aphasia.

For instance, Duffy and colleagues (Duffy & Duffy, 1981; Duffy, Duffy & Pearson, 1975) reported that, in aphasics, deficits in naming ability, auditory comprehension and general linguistic competence were tightly correlated with pantomime recognition and expression. In a group of 40 aphasics, Varney (1978) documented that, except for 4 cases, all patients exhibited a close relationship between deficits in pantomime recognition and reading comprehension. Aphasic patients can also exhibit the disturbance of symbolic gesture comprehension (Gainotti & Ibbia, 1972), and this impairment was found to correlate with verbal semantic impairment (Gainotti & Lemmo, 1976). Ferro et al. (1980) replicated the correlation between impairments on gesture recognition and auditory comprehension in 111 aphasics, and proposed that the type of aphasia could have an effect on gesture recognition, in that impairment on this ability was more pronounced in cases of global, Wernicke's and transcortical aphasia than in Broca's, conduction and anominc aphasics (but see Daniloff et al., 1982). Gainotti (1980) proposed a link between impairments on nonverbal abilities of aphasics (e.g., gesture recognition) and the failure of lexical-semantic process, as the poorest performance on nonverbal tests was obtained by patients with pronounced lexical-semantic impairments. More recently, in a group of 29 aphasics, Saygin et al. (2004) identified a sub-group of 23 patients, with correlated impairments of action understanding in verbal (i.e., reading) and non-verbal modality (i.e., pantomime interpretation). Likewise, tool-use pantomimes of a group of 40 aphasics correlated significantly with their performance on linguistic tests (Goldenberg, Hartmann & Schlott, 2003). A correlation has been also observed between aphasia and the ability to perform naturalistic actions involving technical devices (e.g., making a coffee; Hartmann, Goldenberg et al., 2005). The embodied hypothesis of language arguing for a *virtual* identity of conceptual and sensorimotor representations seems to represent the obvious explanation for associated deficits in linguistic and nonlinguistic domains.

A third line of evidence in favor of the embodied account of language consists in empirical demonstration of the phenomenon of *motor resonance*, i.e. the modulation of motor behavior or motor activity during language processing. A number of behavioral studies have shown that language content influence motor response. For instance, Glenberg and Kaschak (2002) reported that moving the arm toward or away from the body was facilitated when preceded by sentences describing a transfer-action in a congruent direction, such as “Andy delivered the pizza to you” (see also Zwaan & Taylor, 2006). Tucker and Ellis (2004) showed that merely presenting people with the name of a manipulable object facilitated a manual (power or precision) grip, consistent with that required to actually manipulate the object (see also Bub, Masson & Cree, 2008, for consistent results). Gentilucci and Gangitano (1998) showed that reading words such as “long” and “short” affected the kinematics of reaching movements (e.g., peak acceleration, peak velocity, and peak deceleration of the arm), suggesting that even the processing of words with no obvious motor content can interact with the motor system. Complementary evidence exists for the influence of perception and action on language comprehension: typically, the comprehension of a verbally described action is facilitated by a visual prime specifying that action (Klatsky et al., 1989; see also Zwaan et al., 2002). Taken together these studies suggest that language comprehension can activate perceptual and motor representations that interact with concurrent sensorimotor processes.

Imaging, electrophysiological and transcranial magnetic stimulation studies provide physiological support to those behavioral phenomena. Using fMRI, Hauk, Johnsrude and Pulvermüller (2004) showed that passive reading verbs denoting hand-, leg- and face-actions (e.g., to pick, kick and lick) activated left motor and premotor regions for hand-, leg- and face-actions, respectively. Similar *somatotopic* activations were found in the premotor cortex using sentences rather than words (e.g., Aziz-Zadeh et al., 2006; Tettamanti et al., 2005). Further evidence for motor activation upon exposure to action verbs came from a study using highdensity MEG (Pulvermüller, Shtyrov, & Ilmoniemi, 2005). Here subjects were engaged in a distracting task while listening to words denoting leg- or face-actions. Different patterns of activation were found for leg and face words in frontocentral regions, within 200 ms after word onset, a temporal delay that well matches that for lexical-semantic access (Pulvermüller et al., 2005). TMS over the primary motor cortex (M1) elicits motor-evoked potentials (MEPs) in peripheral muscles responding to the stimulated area, providing a measure of corticospinal excitability. With this technique, Oliveri et al. (2004) found increased left M1 activity when participants performed a morphological transformation task involving concrete nouns (i.e., producing either the singular or the plural form) and action verbs (producing either the third person singular or plural inflected form), relative to abstract nouns and verbs. Using sentences, Buccino et al. (2005) reported a somatotopic modulation of the left M1 activity, in either the hand or leg area, when participants listened to hand-action and leg-action sentences, respectively (see also Glenberg et al., 2008)

This ensemble of findings (see for a more extensive review, Fisher & Zwaan, 2008; see also Willems & Hagoort, 2007, for a critical review) supports the stance that language processing recruits the motor systems, where action meanings, just like bodily movements, are somatotopically represented (Pulvermüller, 2005). Moreover, motor responses appear as automatic as lexical-semantic word processing (Pulvermüller, 2005), to the extent that the mere exposure to a single action-word is sufficient to activate the motor system. The question is: is the motor system sufficient (and necessary) for processing action language?

1.4. Language in the body?

Despite overwhelming evidence, there is one good reason to accept that embodiment is the whole story about language understanding, against a number of questions that remain unanswered. The embodied stance that we understand action because we can perform and, therefore, simulate that action, is simple to comprehend and easy to believe, given that the influence of bodily experience on the most abstract thoughts is a daily experience of everyone. "*The only question that any one cares to raise is how much of it will the known facts permit one to accept*" (Pillsbury, 1911, p. 84, quoted in Hickok, 2009).

If the system for motor production plays a constitutive role not only in action perception but also in conceptual processing of action, then one should expect that damage to this system should always be accompanied by defective language and conceptual processing of action words. The study of neurological populations, therefore, provides the most stringent test of the causal relationship between sensorimotor and language/conceptual processes.

Although the embodied account relies (also) on the aforementioned associations between apraxia and aphasia, these findings cannot be assumed as a proof of causal relationship between sensorimotor and language/conceptual deficits (or processes). The reported associations were found in groups of stroke patients, who is the pathological population the most frequently studied by cognitive neuropsychologists, given the dramatically high incidence of cerebrovascular accidents, worldwide (Hachinsky, 2002). However, following a stroke, a cognitive deficit rarely comes in isolation. Particularly in right-handed individuals, ideomotor apraxia (IMA) and ideational apraxia (IA) are mainly associated with lesions in the language-dominant left hemisphere. The main symptom associated with IMA is a reduction in action imitation while the main symptom of IA is a deficit in object use (deficit in pantomiming the use of objects has been found in association with either imitation deficit or object use deficit). Thus, the association between apraxia and aphasia may merely reflect the encroachment of the lesion upon contiguous structures, which are differentially dedicated to language and praxis. Alternatively, the association can result from a failure of a third component that is involved both in verbal and nonverbal abilities, as suggested by a number of studies (Goldenberg, Hartmann, & Schlott, 2003; Lehmkuhl & Poeck, 1981; Rumiati et al., 2001). For this reason, any conclusion driven from associated linguistic and nonlinguistic impairments cannot imply necessarily a functional dependence between systems (Saffran, 1982; Schwartz, 1984). The ambiguity of relying on symptom association is further suggested by reports of uncorrelated performances in groups of aphasics, for instance, between production of transitive and intransitive pantomime versus their comprehension (Goodglass & Kaplan, 1963; Wang & Goodglass, 1992), verbal comprehension versus pantomime recognition (Bell, 1994), and comprehension of sentences describing actions versus comprehension of the same actions when visually presented (Saygin et al., 2004).

On the whole, evidence of correlated or uncorrelated performance based on group analysis can reflect an overall trend, while masking individual cases with dissociations that go in the opposite direction relative to this tendency (see Caramazza, 1986; Shallice, 1988). Indeed, when the performance of single patients was considered, double dissociations were reported, which are held to constitute the most solid basis to infer the organization of cognitive abilities in patients, and processes in models (Shallice, 1988). For instance, Liepmann (1905) described 7 non-aphasic patients with apraxia, 6 of whom had right-sided hemiplegia. Kertesz, Ferro and Shewan (1984) found that of 177 left-stroke patients, 6 had severe aphasia but normal praxis abilities. De Renzi et al. (1980) studied 100 left-damaged patients and found a positive, significant correlation between imitation scores and a measure of verbal competence (measured with the Token test). However, the study of individual cases showed that 12 of the 60 aphasics in the group were not impaired in the imitation task, while of the 40 non-aphasic patients, 2 showed a selective deficit in performing the imitation task. Papagno, Della Sala and Basso (1993) reported that 10 out of 699 patients exhibited a deficit in imitating actions without aphasia, and 149 of them were aphasic but not apraxic. Recently, Mengotti et al. (2009) described, in a group of 61 left-damaged patients, 6 with a selective impairment in language and 5 with a selective deficit in imitation. This functional independence between language and praxis related to their anatomical segregation. In fact, using the Voxel-based Lesion Symptom Mapping (VLSM), the authors found that imitation deficit was associated with lesion in the angular gyrus and bordering white matter, while aphasia was associated with lesion in superior temporal and insular cortex (Mengotti et al., 2009). Consistently, in a group of 37 unilateral stroke-patients double dissociations at the behavioral level (Negri et al., 2007), and anatomical dissociations (Mahon et al., 2007) were found, when the ability to imitate and use objects was compared with the ability to name and recognize (in name-to-picture matching task) pantomimes of object-use and objects. Dissociation between apraxia and aphasia well matches reported double dissociation between deficits in motor production versus deficits in recognition of visual actions and objects, or in their conceptual knowledge (e.g., Cubelli, Marchetti, Boscolo, & Della Salla, 2000; Mozaz, Rothi, Anderson, Crucian, & Heilman, 2002; Ochipa, Rothi, & Heilman, 1989; Rapcsak, Ochipa, Anderson, & Poizner, 1995; Rosci et al., 2003; Rothi et al., 1986, Rumiati, Zanini, Vorano, & Shallice, 2001; see Mahon & Caramazza, 2005).

As noted by Gainotti and Lemmo (1976), nonverbal impairment is highly variable among aphasic subjects, so that, in the spectrum of possible relationships between verbal and nonverbal impairments, there are aphasic patients who can still produce high rates of effective nonverbal (motor) behavior and retain nonverbal competence. Double dissociations cast serious doubt on the hypothesis that motor system, via simulation, sustains a general and necessary mechanism for processing language with motor content.

At very least, neuropsychological dissociations make the conclusion that action and language representational systems are virtually identical unlikely. Neither opportunely justified is the conclusion that, in normal individuals, language-induced motor activity (or simulation) truly served lexical-semantic encoding of action-related language. In fact, based on the imaging studies reporting motor activations during passive exposure to action language (e.g., Hauk et al., 2004; Tettamanti et al., 2005), it is not clear which type of processing participants were engaged in, because an online measure of participants' performance was not recorded (or provided). What is more, no TMS study proved that when M1 activity was disrupted by the TMS-induced neural noise, the processing of action language was altered or abolished (a possibility that appears unlikely, given the neuropsychological results!). In fact, the above TMS studies (e.g., Buccino et al., 2005; Oliveri et al., 2004) failed to provide a measure of participants' performance on action language during TMS delivery. Finally, the effects of congruence between language and motor behaviour can only suggest that language and motor systems interact at some *unspecified* level (Kornblum et al. 1990); however, in this sort of experiments, participants are often cued explicitly to activate sensorimotor modalities by tasks that involve skills such as visuo-spatial analysis of pictorial information and movement to button press, or require deep semantic analysis (e.g., semantic judgments, sensibility ratings, memory load) focusing participants' attention on the sensorimotor content of language. This consideration suggests that, under *certain* circumstances, language understanding may be supported by sensorimotor processes, without implying that language is solely embodied.

1.5. The working hypothesis

A theory is warranted to integrate the neuropsychological evidence of distinct representational systems and processes for action and language, with the phenomenon of language-induced motor resonance. This objective poses the primary question to establish whether motor simulation in language is really a component of the lexical-semantic processing of action words.

The initial discovery of mirror neurons in premotor - but not in primary motor - regions of monkey brain led some scholars to claim that ‘‘mirror’’ responses to action observation reflected a higher-level function, beyond the mere implementation of a motor command, resulting in covert motor activity (Rizzolatti & Craighero, 2004; Rizzolatti et al., 2001). Despite so, Tkach et al. (2007) have recently described mirror neurons M1 of macaques, leaving open a possibility that “mirror” activity indeed reflects covert generation of a motor command in response to action-stimuli, via learned associations.

This argument may extend to the role of motor system in language. The embodied view interprets language-induced motor simulation in terms of lexical-semantic processing for language processing. Again, this conclusion seems to overlook the possibility that the *motor* system in language supports *motor* functions. Motor imagery, the ability of humans to generate, manipulate and transform mental images of actions, is a cognitive state that can be experienced by everyone in everyday life, and can be *strategically* engaged to assist virtually any cognitive task, by recalling perceptual information from memory when a stimulus is not physically present (Kosslyn, Behrmann & Jeannerod, 1995). This process, though complex it might be, largely relies on the mechanisms for overt action execution, including motor brain network, keneasthetic sensations and autonomic activation (Decety, Jeannerod, Durozard & Baverel; 1993; Jeannerod, 2001), to the extent that it is defined a “true motor behavior”.

Thus, the proposal of an intense exchange between motor system and higher-level cognition (language as well as learning, memory, abstract or concrete reasoning) is neither novel, nor surprising. Embodied cognition goes beyond this, claiming that the tie between language processing and motor system is necessary for the former to be effective. However, no evidence can so far rule out the possibility that motor activity in language reflect imagery, providing a *strategic* interface between two independent systems to achieve or facilitate comprehension.

The evaluation of the two alternatives (necessary or strategic simulation) asks to establish, in the first place, whether or not it always occurs in language. However, proving that action language processing is not always accompanied by motor activity is not sufficient to support the interpretation based on motor imagery. One should also demonstrate that the conditions that trigger motor activity in language are the same that trigger motor imagery. Imagery is not a single, undifferentiated ability, but can rely on different sets of processes, or *strategies*, which can be independently employed (Kosslyn et al. 2001) or disrupted (Tomasino & Rumiati, 2004). Imagery is “motor” and is therefore accompanied by motor activity when people mentally transform, or the stimuli evoke, movements of human body parts or their interactions with objects (Ehrsson et al., 2003; Kosslyn et al., 1998; Tomasino et al., 2010). This occurs when motion is mentally represented in an egocentric reference frame, or first-person perspective, so that a virtual identity has been established between kineasthic motor imagery and first-person imagery (Jackson et al., 2006; Solodkin et al., 2004).

On the one hand, the embodied account of language implies that: first, motor activation is as early as the activation of the lexical-semantic network for word processing; second, motor activation occurs automatically, in response to *any* action word, regardless of the task or the context in which the word occurs, and regardless of whether words refer to oneself or another’s action. On the other hand, the “strategic imagery“ account poses a number of constraints to the recruitment of motor activity in language. First, it enhances only when required by the task-context cueing concrete, motor representations of words; second it is most likely to take place when the stimulus content activates the representation of human body-part motion or human actions; third, motor activation is greater when the stimuli activate an egocentric, first-person perspective (versus a third-person perspective) representation of motion.

The following studies have been carried out with the objective to address directly each of these predictions. This research may contribute to lay the foundation of a theory that will be able to explain the mental operations that make the cross-talk between language and motor processes possible, to the extent that embodied representations go along with –or even supersede - more abstract representations of meanings.

This work also represents an attempt to break out of the current impasse reached by the debate between advocates of either embodied or disembodied hypothesis, which runs the risk to arrest research on other (more crucial) questions concerning, for instance, what the sensorimotor experience actually adds to human cognition, and what is missed in conceptual representations, when such experience is lacking. Finally, this work was also motivated by one practical and ethical reason: the generalization of embodied theories to a surprisingly wide range of abilities and disorders (e.g., language, empathy, altruism, emotion, theory of mind, imitation, autism spectrum disorder, tabagism and alcoholism) is leading to the proliferation of clinical work using motor simulation, action observation and/or action imitation therapeutically, for instance, after stroke to stimulate recovery of language abilities. Given the state of the art, one may think that treating an aphasic with action observation is not bad *per se*; but is there enough reason to believe that it is right?

Chapter 2.

Tool-use actions, action verbs and tool nouns: Evidence from neuropsychology

2.1. Introduction

Action and language are traditionally considered paradigmatic examples of independent brain systems (Fodor, 1983; Shallice, 1988). Accordingly, a wealth of neuropsychological studies has documented dissociations between linguistic and nonlinguistic deficits in single patients, and uncorrelated performance on linguistic and nonlinguistic in groups of left-damaged patients (see Rumiati, Papeo, & Corradi-Dell'Acqua, 2010 for a review; refer also to Chapter 1). However, the association of aphasia and apraxia is the most common scenario in neuropsychological population, and linguistic deficits often co-occur with deficits in nonverbal action domains such as signs, gestures and pantomimes (Duffy & Duffy, 1981; Pickett, 1974; Seron, van der Kaa, Remitz, & van der Linden, 1979; Varney, 1982) and object recognition (De Renzi, Pieczuro, & Vignolo, 1968). Likewise, individuals with a specific disturbance affecting motor functions, such as the Motor Neurone Disease, may also show communication problems, particularly with verbs (Bak, O'Donovan, Xuereb, Boniface, & Hodges, 2001; Bak, Yancopoulou, Nestor, Xuereb, Spillantini, & Pulvermüller, 2006), although the major implication of frontal lobes, as shown by radiological exhibits of these patients, casts doubt on the motor origin of their cognitive impairments (see Neary et al., 1990; Talbot et al., 1995; see also Hickok, 2010, for a critical review).

While past conceptualizations have interpreted associations in terms of damage to a single underlying factor, common to both functions ("asymbolia" hypothesis; Finkelnburg, 1870), the involvement of motor system in apparently unrelated processes, such as word comprehension, has been differently framed within the embodied hypothesis of language. In its strongest – and latest - version, embodied hypothesis holds action meanings are encoded, with no cognitive mediation, in the motor system, with a prominent involvement of inferior frontal, precentral motor regions (see Rizzolatti & Craighero, 2004).

However, while accounting for symptom associations, the embodied hypothesis cannot explain why patients are observed as suffering from aphasia or apraxia selectively. Saygin, Wilson, Dronkers, and Bates (2004) attempted to overcome the discrepancy between the associative and dissociative view, testing the ability of 29 aphasics to understand transitive pantomimes (actions involving objects) depicted in line drawings or described by sentences. These authors found that the performances on the two tasks did not correlate at group level, but did in a subgroup of patients. They proposed that these conflicting results might reflect different degrees of representational overlap in linguistic and nonlinguistic domains, depending on how similar verbal and nonverbal tasks are in terms of perceptual and conceptual properties and developmental stages of acquisition. In particular, the authors argued that the overall dissociation between verbal and nonverbal performances could be attributed to reading being acquired much later in life than nonverbal action comprehension (but see Hickok, 2009; 2010, for a critical discussion of these findings). Therefore, "if the systems are acquired and related skills are honed at such different stages in development, the resulting brain networks subserving processing in the two domains will also be rather different, and patients with brain injury will not show tightly correlated deficits" (*ibidem*, p. 1082). It follows that, when the linguistic and nonlinguistic task involve identical stimuli and are served by networks acquired at similar (early) stages in development, tightly correlated deficits should be observed in brain-damaged patients' performance.

The aim of the study reported in this chapter was threefold. First, I investigated whether a causal relationship exists between processing action-related words and the ability to perform actions, when tasks and stimuli are matched for perceptual, conceptual and developmental characteristics. Second, I examined the patients' lesions in order to *describe* the neural correlates of action-word comprehension. One insight to this question can be primarily provided by patients' performances on motor and linguistic task. Dissociations between tasks would strongly suggest that the *distributed* networks that maintain action performance (Rumiati et al., 2010) and action-word comprehension (Hickok & Poeppel, 2007; Price, 1998) are independent (Shallice, 1988). The idea of a distributed architecture for complex functions implies that networks can sometimes interact (i.e., the same anatomical region can be involved in both functions), as depending on a given task context (see Price & Friston, 2002). In this light, it is not surprising that, for instance, areas involved in tool use can *sometimes* be recruited when naming tools (see Johnson-Frey, 2004). The embodied hypothesis goes beyond this, suggesting that the motor system is *always* a necessary correlate of action-word comprehension. Thus, an evaluation – and eventually the acceptance - of this hypothesis requires to demonstrate not only that all patients with action-word comprehension deficits cannot perform actions, but also that their impairment is associated with damage centered in those regions of the motor system (inferior frontal, precentral and central gyri) that are held to encode action meanings. The combination of evidence from patients' behavior and lesion analysis can shed light on this issue.

Third, I examined the alleged differences in processing action verbs and tool nouns. In fact, neuropsychological studies showed that these two word classes can be selectively affected by brain injury (Berndt, Mitchum, Haendiges, & Sandson, 1997; Caramazza & Hillis, 1991; Damasio & Tranel, 1993; Daniele, Giustolisi, Silveri, Colosimo, & Gainotti, 1994; Luzzatti et al., 2002; Miceli, Silveri, Nocentini, & Caramazza, 1988; Shapiro, Shelton, & Caramazza, 2000; Warrington & McCharty, 1987). Moreover, imaging studies have indicated that while noun processing is centred in left temporal regions, verb processing is associated with the activity of left frontoparietal regions (Corina et al., 2005; Martin, Haxby, Lalonde, Wiggs, & Ungerleider, 1995; Tranel, Adolphs, Damasio, & Damasio, 2001; but see Perani et al., 1999; Tyler, Russell, Fadili, & Moss, 2001; Warburton et al., 1996), although it is not clear whether this verb-noun distinction reflects a grammatically-based principle of lexicon organization (Caramazza, 1997; Levelt, Roelofs, & Meyer, 1999), or emerges from semantics. This latter hypothesis follows from the observation that nouns have more semantic features in common with other nouns as they typically denote objects, while verbs share more features with other verbs as they typically denote actions (Bates

& MacWhinney, 1982; Langacker, 1987). Contrasting with the view that nouns and verbs enjoy different lexical-semantic status, embodied theories of cognition predict that information related to actions or objects we use, is represented and encoded in the motor system responsible for action production (Gallese & Lakoff, 2005).

To these ends, the current study examined the ability of 12 left-damaged patients and 17 healthy participants to imitate and name actions, to use and name tools, and to recognize words (verbs and nouns), using the same stimuli in verbal and nonverbal tasks. As the main objective of this study was to assess the embodied prediction of shared substrates and processing for motor and action-word representations, naming and word recognition were both employed to test action-language comprehension. Indeed, naming impairment, on its own, is not sufficient to conclude that a word representation is disrupted, as it can also reflect a failure of lexical-phonological retrieval that can take place even when the semantic representation of a word is spared (see Caramazza, 1997). Notice also that naming, which has been used in most of the abovementioned studies, involves a strong motor (articulatory) component that brings a confounding factor in the interpretation of association between motor and language disease (see Hickok, 2010).

Importantly, the abilities recruited in performing our motor and linguistic tasks are supposedly acquired at comparable developmental stages. I had no instrument to establish when exactly our participants acquired the ability to perform a given tool-directed motor program, or to comprehend (or produce) its associated label. However, our claim is well grounded in a wealth of developmental studies showing that motor control required to perform deictic gestures, gestural routines and tool use, develops synchronously with word acquisition, and particularly with word comprehension (Bates & Dick, 2002; Lenneberg, 1967; Siegel, 1981). To avoid the risk of group analysis ignoring cases that do not follow the group-level trend but can provide a basis for inferring functions (Caramazza, 1986; Shallice, 1988), the patients’ performance was analyzed at both group and single-case level. Multiple single-case analysis was conducted to look for potential dissociations between verbal and motor abilities, as well as between action-verb and tool-noun processing.

2.2. Material and Methods

2.2.1. Participants

A group of 12 consecutive patients (mean age 70±8 years, mean education 10±4 years) took part in the study. They were recruited in the rehabilitation and neurological unit of the Ospedali Riuniti in Trieste. To be included in the study, patients had to meet the following criteria: to have a single focal unilateral lesion in the left-hemisphere; to have al least 5 years of education; to be right-handed (Oldfield, 1971) and native Italian speakers. They had all normal or corrected-to-normal vision, no hearing difficulties and neurological or psychiatric history. The inclusion criteria did not contemplate patients’ symptoms or lesion site in the left-hemisphere. Nine out of 12 patients were still in the acute epoch of recovery (i.e., within 3 months post lesion-onset), when tested. Demographic variables are summarized in Table 1. Seventeen healthy right-handed Italian speaking adults (mean age 69±8 years, mean education 12±4 years) served as controls for experimental tests after taking the Mini Mental State Examination (Folstein, Folstein, & McHugh, 1975) to ensure that they were not suffering from any form of cognitive decline. All participants confirmed their voluntary participation signing the informed consent. The study was approved by SISSA Ethics Committee.

2.2.2. Neuropsychological assessment

Patients were given the Aachen Aphasia Test (AAT, Italian version; Luzzatti *et al.*, 1996) to assess type and severity of aphasia, and standardized tests to evaluate praxis, visuo-spatial abilities (and in particular, to ensure they had no visual agnosia), executive functions and memory. Patients and controls performed additional verbal tasks to assess lexical access (Luzzatti, Willmes, & De Bleser, 1996), reading (Toraldo, Cattani, Zonca, Saletta, & Luzzatti, 2006) and potential noun-verb dissociation (object and action picture naming, Crepaldi et al., 2006). Details about the neuropsychological screening and the scores obtained by each patient are reported in Table 1.

Table 1. Demographic variables and patients'scores on the neuropsychological evaluation.

Part 1.

Case	*Sex*	*Age*	*Education (years)*	*Testing post-onset (months)*	*EHI*	*LTM words*	*LTM faces*	*Span forward*	*Span backward*	*Corsi*	*TMT A*	*TMT B*	*Weigl*	*Raven's CPM*
BB	M	72	18	3	100	n.a.	**10**	-	-	**4**	-	-	t.i.	t.i.
BS	M	60	8	1.5	100	43	21	**4**	4	**4**	36	144	10	32
CF	M	80	8	1.5	100	32	23	6	3	5	92	t.i.	7	24
CG	M	77	17	1	100	n.a.	-	-	n.a.	n.a.	**194**	-	**3**	20
DC	F	62	10	1	100	39	-	5	5	**4**	47	106	13	29
DBM	F	58	13	11	100	35	25	-	-	4	48	76	13	31
IN	F	71	8	2	100	34	24	-	-	4	**117**	t.i.	**5**	**18**
MB	M	70	8	2	62	**31**	20	**3**	**2**	5	45	**285**	**4**	-
NP	F	75	5	1	100	35	21	5	**2**	4	**125**	n.a.	**3**	**11**
SA	F	83	8	1	100	36	19	4	**2**	4	89	t.i.	6	**13**
SN	F	64	8	7	100	28	21	n.a.	n.a.	6	94	n.a.	9	28
UL	M	71	6	4	83	29	**9**	4	n.a	**3**	n.a.	n.a.	**5**	19
Maximum score					100	-	**-**	-	-	**-**	-	-	15	36

Part 2.

Case	*AAT token*	*AAT repet*	*AAT written*	*AAT naming*	*AAT compreh*	*Lexical decision*	*Reading*	*Picture naming*	*VOSP screen*	*VOSP o.d.*	*IMA*	*IA*	*Type of aphasia*
BB	**46**	**66**	**10**	**23**	**49**	t.i.	n.a.	N>V	t.i.	**9**	**60**	**10**	severe global
BS	15	**127**	85	**94**	110	144	**109**	N>V	20	20	64	14	mild amnesic
CF	14	139	82	109	109	134	114	N>V	20	18	70	14	severe unfluent
CG	**50**	n.a.	n.a.	n.a.	**22**	122	n.a.	n.a.	19	12	**31**	**7**	severe Wernicke's
DC	2	149	90	117	117	144	116	N>V	19	18	**58**	14	-
DBM	**23**	**111**	**77**	**95**	111	138	**110**	V>N	20	16	66*	14	mild anomic
IN	**28**	**65**	**27**	**60**	**93**	128	**23**	V=N	20	16	**43**	**11**	mild Broca's
MB	**17**	110	73	100	86	142	**108**	N>V	20	**12**	66	14	mild Broca's
NP	**20**	**139**	**37**	**93**	**90**	126	**108**	N>V	18	**13**	**52**	**10**	**-**
SA	5	143	62	105	100	141	115	N>V	20	16	**46**	**9**	mild amnesic
SN	**28**	**137**	**53**	**69**	**93**	125	**100**	n.a.	20	**13**	-	-	severe Broca's
UL	**29**	**132**	31	**93**	**84**	101	**65**	N>V	20	17	**48**	14	mild Broca's
UL	**29**	**132**	31	**93**	**84**	101	**65**	N>V	20	17	**48**	14	mild Broca's
Maximum score	50**	120	90	120	120	144	116	-	20	17	72	14	

Standardized tests used in the neuropsychological assessment: EHI = Edinburgh Handedness Inventory (Oldfield; 1971); LTM words = long-term memory, word recognition (Warrington, 1984); LTM faces = long-term memory, face recognition (Warrington, 1996); Span forward = digit span forward for verbal short-term memory; Span backward = digit span backward for short-term memory and working memory; Corsi = Corsi test for spatial short-term memory (Spinnler & Tognoni, 1987); TMT A = Trail making tests for attention; TMT B = Trail making test for executive functions (Giovagnoli *et al.*, 1996); Weigl = Weigl's tests for executive functions (Spinnler & Tognoni, 1987); Raven's CPM = Raven Coloured Progressive Matrices for general intelligence (Carlesimo, Caltagirone and Gainotti, 1996); AAT = Aachener Aphasie Test, Italian norms (Luzzatti et al., 1996); AAT token = subtest for comprehension; AAT repetition = subtest for repetition; AAT written language = subtests for reading and writing; AAT name = subtest for production; AAT comprehen = subtests for auditory and visual comprehension; Lexical decision (Luzzatti et al., 2002); Reading (Toraldo et al., 2006); Picture naming = object and action picture-naming (Crepaldi et al., 2006); VOSP screen = Visual object and space perception, screening task; VOSP o.d. = VOSP object decision task (Warrington & James, 1991); IMA = Test for ideomotor apraxia (Tessari & Rumiati, 2004), * = test by De Renzi, Motti & Nichelli (1980); IA = Ideational Apraxia (De Renzi & Lucchelli, 1988). Patients are sorted alphabetically by their initials. F=female. M=male. t.i. = test interrupted because the patient was not able to perform the task. n.a. = test not administered. Pathological scores are reported in bold. Maximum scores are reported where applicable (** Maximum error).

2.2.3. Experimental design and materials

A 3x2x2 experimental design was used: 3 tasks (Motor production, Naming and Comprehension), 2 stimulus-types (Action and Tools) manipulated within-subjects, and 2 groups (Patients and Controls) (see Table 2).

Stimuli were selected with series of preliminary, norming studies. First, I choose 87 tool-use pantomimes, presented in the form of colour video clips of 3 sec each, in which a male actor carried out pantomimes of tool use with his right hand (the tool itself was not shown), and 87 colour photographs of the corresponding tools, portrayed in their prototypical view. A panel of 45 healthy adults (age 21-86 years, education 5-18 years) was then asked to name the actions shown in the clips and the tools shown in the photographs, using verbs and nouns, respectively. Notice that the panel covered also the age and educational level typical of patient population. Items that were named with the same label by at least 85% of participants[1], were subjected to a second norming phase, in which a group of 30 healthy adults (age 21-41 years) was asked to name each of them, as fast as possible. Only action-tool pairs in which both items were named in less than 3 sec were selected. Finally, 19 healthy adults (age 21-31 years) rated the age of acquisition (AoA) of verbs and nouns corresponding to actions and tools thus selected, using a 7-point Likert-*type* scale with 1 corresponding to acquisition within the third year of life, 2 between the fourth and the fifth years, and so on up to 7 (after 13 years). Action-verbs and tool-nouns were thus matched for AoA ($t(14) = -0.31$, $p = 0.7$), which is closely related with word frequency, but predict better naming performance in adults (Perez, 2007), as well as for word length ($t(14) = -0.63$, $p = 0.5$). Thus, this multi-phase

---

[1] A second response to any of each items, provided by at least 5% of the panel was considered as an alternative correct response in the experimental phase.

norming study reduced the initial set of 87 actions and 87 tools, to 15 items for each category, which achieved the 85% of agreement on their label and were named in less than 3 sec. The set of stimuli is listed in Appendix A.

The selected 15 video-clips of pantomimes and 15 corresponding real tools were used in the imitation and tool-use task, respectively. The same actions and tools were presented in a naming task. Video-clips were preferred to static line drawings because the latter require inferences to be made about action movements, a process that is not required in tool naming (see Corina et al., 2005). For the verb comprehension task, 15 photographs were derived from the video-clips, depicting the frame that best described the action. Each target photograph was presented with two distractor photographs depicting, respectively, an action semantically related and one visually similar to the target. The second distractor could be either a real or a nonexistent action, obtained by modifying a kinematic aspect of the target action such as the hand/arm orientation (e.g., target action: eating with a spoon; semantic distractor: filling a dish; visual distractor: hand in the configuration required for eating with a spoon but near the actor's forehead). In the noun comprehension task, the 15 photographs of the above 15 tools were taken. Each target photograph was presented together with a semantically related and a visually related object (e.g. target: spoon; semantic distractor: ladle; visual distractor: a round mirror with handle). The semantic distance between targets and distractors was assessed on a 7-point Likert-*type* scale by 10 healthy adults.

Photographs, instead of video-clips, were used in the comprehension task in order to present all three actions simultaneously and, thus, avoid the influence of confounding factors, such as great memory load or great demand to working memory, on participants' performance. In each trial of the two comprehension tasks, the verb or the noun corresponding to the target was spoken aloud by the experiment simultaneously with the appearance of the three photographs on the screen (see below).

Table 2. Experimental design: two types of action-related stimuli (pantomimes and tools) were processed across motor and linguistic tasks by all participants (patients and controls).

	Trigger	
	Pantomimes of tool-use (*N*=15)	Tools (*N*=15)
Motor performance to visual stimuli	Imitation	Use
Naming to visual stimuli	Action-verb retrieval	Tool-noun retrieval
Name-to-picture matching	Action-verb comprehension	Tool-noun comprehension

2.2.4. Procedures

All patients and controls completed the three types of tasks with actions and tools, for a total of six experimental conditions. Five controls performed the praxis tasks with the non dominant-left hand in order to match them with the patients who showed right-sided hemiparesis following left-hemisphere injury. As all tasks involved the same stimuli, their order was counterbalanced across participants to control for carryover effects. Comprehension tasks were always presented at the end of the experimental session. Items in each condition were presented to all participants, in a fixed order. The six conditions are described below.

Pantomime imitation. Video-clips of tool-use pantomimes were presented on a computer screen placed in front of the participant. S/he was asked explicitly to imagine holding and using the tools. Each item was presented once and, if the participant failed to imitate, it was shown again for a maximum of two times. Performances were videotaped and analyzed offline by one of the authors (LP), and two neuropsychologists unaware of the experimental hypotheses, as follows. Each rater judged each trial as “correct” or “incorrect”. If at least 2 of the 3 raters judged the performance as “correct”, two points were assigned to that trial. If at least 2 of the 3 raters judged the performance as “incorrect”, one rater, who is an experienced neuropsychologist, trained in the error analysis of praxis tests, classified the error according to criteria established in previous studies (e.g., Negri et al., 2007; Tessari et al., 2007). The categories of errors included: spatial-hand or spatial-arm error, semantic error (“body-part use as a tool”, or substitution with a semantically-related action), visual error (substitution with a visually-related action), omission, and unrecognizable action. In particular, “1” was assigned when the participant made spatial errors (i.e., misorientation of hand/arm), but the action was still clearly recognizable; “0”was given in all the other cases of error. This procedure led to one score assigned to each trial (0, 1 or 2), the total score of a patient corresponding to the sum of scores assigned to each trial (maximum = 30/30).

Tool-use. Each tool was placed on a table in front of the participant, who was asked to demonstrate how s/he would use it. The participant’s performance was videotaped and subsequently scored by the same three raters as above. One point was assigned when at least 2 of the 3 raters judged the performance in a trial as correct, “0” was assigned, if at least 2 of the 3 raters judged the performance as incorrect. Then, an experienced neuropsychologist (the same as above) classified the error as misuse, mislocation, clumsiness, perplexity, or spatial error, according to previously established criteria (see Negri et al., 2007). The total score of a patient in this task corresponded to the sum of the scores assigned to each trial, the maximum being 15/15[2].

Action and tool naming tasks. In the first task, participants were requested to name, by producing a verb, 15 pantomimes presented in the form of video-clips, one at a time, on a computer screen. All but five pairs of verb- noun had phonologically unrelated roots (i.e., *penna-scrivere*, pen-to write vs. *timbro-timbrare*, stamp-to stamp),. To avoid confusion in assessing the performance in those five cases, patients were always encouraged to produce the infinitive form of the verb, for which a specific suffixation is needed (*timbr-are*). The response was scored 1 if the participant produced the correct verb or its acceptable alternative, and 0 if the response was incorrect. Self-repairs, dialect forms of the target-verb and phonological errors in which the target word was clearly recognizable were scored as correct. Semantic paraphasias, circumlocutions and latencies longer than 5 sec were scored as errors. In the case of multiple responses for a single item, the first was considered. The maximum score was 15/15. In the second task, participants were requested to name the 15 tools from photographs presented, one at a time, on a computer screen. The same scoring criteria were applied as for action naming.

Verb and noun comprehension tasks. Two separate word-picture matching tasks, one involving the 15 verbs and one the 15 nouns were used to assess participants' word comprehension. A verb (or noun) was spoken aloud by the experimenter in each trial, while three color photographs (the target and two distractors) appeared on the computer

---

[2] Inter-rater reliability was computed using the concordance correlation coefficient (Lin, 2000) for assessment of concordance in continuous data, as we used scores obtained by patients in each of the two tasks (imitation and tool-use). Correlation coefficient was 0.97 between rater 1 and rater 2, 0.97 between rater 2 and rater 3, and 0.98 between rater 1 and rater 3.

screen, with their relative position (left, center, right of the screen) being pseudo-randomly counterbalanced. In each matching task, participants had to indicate the photograph depicting the spoken item. One point was assigned for correct responses and 0 when the participant pointed at either distractor. The maximum score was 15/15 for each task.

2.3. Statistical analyses

2.3.1. Behavioral analysis

Group level. The data entered in this analysis corresponded to the individual percentage of correct responses in each experimental condition. As patients' and controls' data in the six experimental conditions were not normally distributed (Shapiro-Wilk's W-test, *p*s >.05), the non-parametric Wilcoxon test and Mann-Whitney-U-test were used to compare performances within and across groups (patients and controls), respectively. To measure the strength of association between performances at group level, Spearman's correlations were computed between imitation, naming and comprehension of pantomimes, and between use, naming and comprehension of tools. Separate Spearman's correlations were computed between action and tool naming and between action-verb and tool-noun comprehension.

Single-cases. The Revised Standardized Difference Test (RSDT, Crawford & Garthwaite, 2006) was used to detect dissociations, using the software released with the article by Crawford and Garthwaite (2005). The following comparisons between patients' scores on different tasks involving the same stimuli: 1) action imitation versus action naming; 2) action imitation versus action-verb comprehension; 3) tool-use versus tool naming; 4) tool-use versus tool-noun comprehension. The software provides a *t* score for each individual performance in the pair, which estimates the abnormality of the individual’s score (defined as the percentage of the population that would obtain a lower score), and 95% confidence limits on this percentage. In addition, based on the significance values of the *t* scores and taking into account the correlation within controls across the two tasks, the RSDT determines whether potential difference between the two scores reflects classical dissociation (compared to controls, the patient is impaired on task A but not on task B) or strong dissociation (the patient is impaired on both tasks relative to controls, but task A is more impaired than task B), according to Shallice’ criteria (1988) revised in Crawford et al. (2003). Both types of dissociation provide evidence that two functions are independent and rely on separate neural substrates. The same inferential method was applied to test possible dissociations between action versus tool naming, and between action-verb versus tool-noun comprehension.

2.3.2. Lesion analysis

A neuroradiologist, uninformed of the experimental hypotheses, mapped the lesioned areas on the computerized tomography (CT) or magnetic resonance imaging (MRI) scans for all patients but three (MB, SA and CF), onto a normalized MNI template (www.bic.mni.mcgill.ca/cgi/icbm_view) using MRIcro (http://www.mricro.com; Rorden & Brett, 2000). Lesion location in each patient was identified using the Automated Anatomical Labelling map (Tzourio-Mazoyer et al., 2002) provided by the software, and referring to the Duvernoy atlas (1991) (see Table 3). The following lesion analysis was performed with the same software, based on the logic of subtraction proposed by Rorden and Karnath (2004). This method is particularly suited for visualizing evident anatomical changes like those that typically follow strokes, even in relatively small sample size. Given the limited sample size, the following analyses were run with the objective to provide a description of regions that were damaged in all patients with impairment in a given task (task-specific regions), and regions that were possibly implicated in both verbal and nonverbal functions (shared regions).

Firstly, I overlaid all patients' lesions to ensure that those regions that are held to be crucially involved in our experimental tasks were actually affected in our sample. To show what region was specifically associated with deficit in each of the 6 tasks, lesions of all patients impaired in a given task (according to the Crawford's t scores) were overlaid, revealing the lesion site common to all patients in the group (i.e., lesion intersection). From the resulting lesion density plots, I subtracted the lesion sites of patients who were not impaired in the same task. This subtraction analysis, whereby lesions of patients with injuries in the same hemisphere and comparable neurological/neuropsychological characteristics but without the impairment of interest, are subtracted from lesions of patients with the impairment of interest, is based on the assumption that regions unrelated to the disorder of interest reflect vulnerability to injury (e.g. due to their vasculature or susceptibility to sheer and impact) and, therefore, tend to be equally damaged in patients with different symptoms (Rorden & Karnath, 2004). As subtractions were performed between groups of different sizes, relative percentages rather than absolute values were used. The automatic three-dimensional renderings of the subtraction analysis showed regions that were most frequently damaged in one group of patients, and typically spared in patients without that deficit.

Then, in order to investigate what region was possibly involved in both action performance and comprehension, lesions of group with praxis deficit were compared against lesions of group with comprehension deficit. This comparison assessed directly the embodied hypothesis that action-word comprehension relies on the same substrates for motor production. Two separate comparisons were performed, one contrasting group with imitative deficit against group with action-verb comprehension deficit, and the other contrasting group with tool-use deficit against group with tool-noun comprehension deficit. In each comparison, regions associated with both deficits resulted from the overlay of all patients with either deficit (lesion intersection), from which lesions of patients with no deficit in either task were subtracted. In this manner, I could clean off damaged regions with no specific effects on either task, while preserving those regions associated with both tasks. Lesion sites resulting from each of the described comparisons were identified using the Automated Anatomical Labelling map (Tzourio-Mazoyer et al., 2002) and verifying its output referring to the Duvernoy atlas (1991).

Table 3. Description of lesion for all patients. Numbers indicate Brodmann Areas.

	Cerebral regions affected by the lesion	BA involved in the lesion
BB	precentral gyrus, inferior frontal gyrus, insula, basal ganglia (putamen and caudate), superior temporal gyri and temporal pole.	4, 6, 22, 38, 42, 43 ,44, 47
BS	middle and superior temporal gyri, middle occipital gyri.	19, 20, 21, 22, 41, 42
CF*	small portions of precentral and postecentral gyri, rolandic operculum, subcortical white matter.	
CG	middle and inferior frontal gyri, rolandic operculum, insula, supramarginal and angular gyri, superior, middle and transverse temporal gyri, middle occipital gyrus.	2, 3, 19, 21, 22, 37, 39, 40, 41, 42
DC	small portion of inferior frontal gyrus, precentral and postcentral gyri.	2, 3, 4, 6, 43, 44
DBM	middle and superior temporal gyri.	20, 21, 22, 37, 41, 42
IN	rolandic operculum, insula, postcentral gyrus, inferior parietal lobule, supramarginal and angular gyri, superior, middle and transverse temporal gyri, superior and middle occipital gyri.	1, 2, 3, 7, 19, 21, 22, 37, 39, 40, 41, 42, 43
MB*	basal ganglia	
NP	insula, basal ganglia (caudate, putamen, pallidum)	
SA*	periventricular hypodensity	
SN	inferior frontal gyrus, rolandic operculum, insula, postcentral gyrus, temporal and transverse temporal gyri, temporal pole, basal ganglia (caudate, putamen, pallidum).	6, 20, 21, 22, 38, 42, 43
UL	insula, basal ganglia (caudate, putamen, pallidum), thalamus	

The location of the lesions was identified using the Automated Anatomical Labelling map (Tzourio-Mazoyer et al., 2002), and with reference to the atlas of Duvernoy (1991). * patients with no MRI or CT scan available: for these patients, the lesion site was defined with reference to the medical exhibit.

2.4. Results

2.4.1.Group-level performance

Figure 1 shows the results of both groups in all the experimental tasks.

Controls. Controls were better at naming tools than actions, and at comprehending tool nouns than action verbs (both Wilcoxon: p = .02). Their performance on naming and praxis tasks did not differ (ps > .05). Action-verb comprehension was better than imitation (Wilcoxon: p = .03) and tool-noun comprehension tended to be better than tool-use (Wilcoxon: p = .06). Overall, controls performed better on nouns than verbs, and on verb and noun comprehension relative to praxis tasks involving the corresponding actions and tools.

The difference between performance on nouns and verbs is consistent with evidence for a stable and significant noun advantage, which holds for normal children, older people and aphasic patients (DeBleser & Kauschke, 2003; but see below). The performance difference between comprehension and praxis may merely indicate that the former task was less difficult than the latter.

Patients. Mann-Whitney-*U*-Tests showed that, as a group and compared to controls, patients were impaired in imitation (p = .01), tool-use (p = .02), and in action (p =.0001) and tool naming (p = .0001). They did not differ from controls in action-verb and tool-noun comprehension (p > .1). Comparing patients' performance across the three tasks involving action-stimuli (imitation, action naming and comprehension) with Wilcoxon tests, they resulted similarly impaired at imitating and naming actions (p = .15). Comprehension was better than naming (p = .003) and imitation, although the latter difference did not reach significance (*p* = .08). Considering the performance with tool-stimuli, naming resulted more impaired than tool-use (*p* = .03) and tool-noun comprehension (*p* = .003), while performance on these two tasks did not differ (*p* = .2). Therefore, patients showed a prominent impairment in naming with no difference between action- and tool-stimuli (*p* = .34), and in praxis, imitation being more compromised than tool-use (*p* = .03). This is as expected because apraxic and aphasic symptoms are most common following left-side injury. Comprehension of verbs and nouns was relatively preserved, at group-level, with no difference between action verbs and tool nouns (*p* = .15).

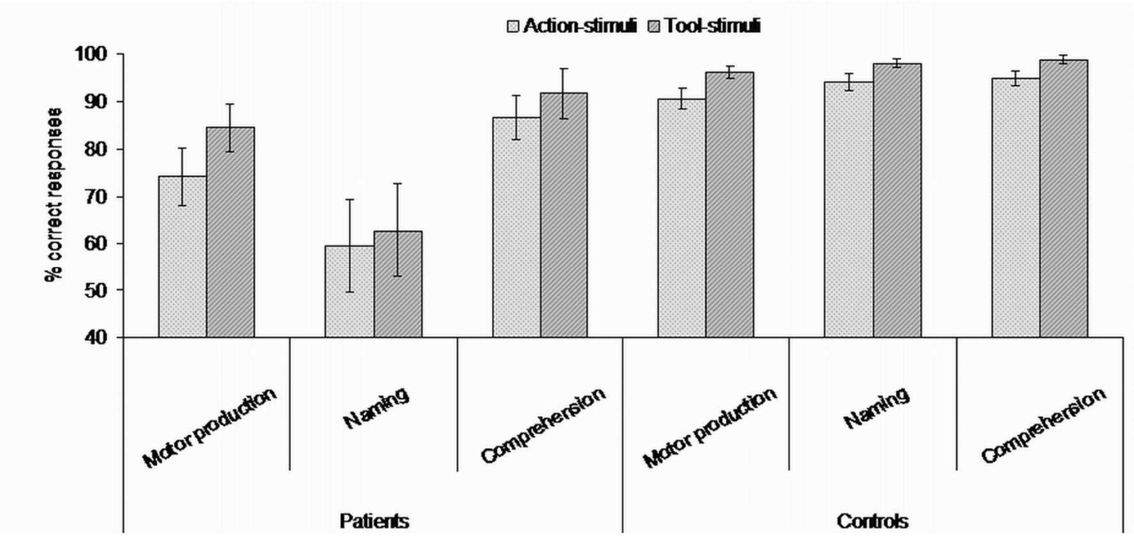


Figure 1. Performance (percentage of correct responses) of both groups (patients and controls) in the three types of tasks (motor production, naming and word comprehension) triggered by action-stimuli and tool-stimuli. Relative to controls, patients were significantly impaired on naming (no difference between action and tool naming) and motor production tasks (tool-use better than imitation). Vertical bars denote the standard error of the mean.

While overall performance on action naming correlated with both imitation (*N*=12, Spearman R=.59, *p*=.04) and action-verb comprehension (*N*=12, Spearman R=.67, *p* = .01), performance on imitation and action-verb comprehension did not (*N*=12, Spearman R=.42, *p* = .17) (Table 4). The same analysis performed on tasks involving tool-stimuli revealed only a significant correlation between naming and noun comprehension (*N*=12, Spearman R=.72, *p* = .008) (see Table 4). Significant correlations were found between action and tool naming (*N*=12, Spearman R=.83, *p* = .0008), but not between action-verb and tool-noun comprehension (*N*=12, Spearman R=.42, *p* = .17).

Table 4. Results of Spearman's correlation analyses computed on the raw scores of tasks involving pantomimes of tool-use and tools.

	Tasks with pantomimes of tool-use					Tasks with tools			
	Naming		Comprehension			Naming		Comprehension	
	Spear. R	N	Spear. R	N		Spear. R	N	Spear. R	N
Imitation	.59*	12	.42	12	Tool-use	.40	12	.19	12
Naming			.67**	12	Naming			.72**	12

*Correlation is significant at the .05 level. **Correlation is significant at the .001 level.

2.4.2. Single-case performance

Table 5 provides a summary of patients' performance across all experimental tasks.

Performance on action stimuli

Imitation versus action naming (Figure 2). Six patients showed a poorer performance on action naming relative to imitation: three (CG, MB, UL) showed a classical dissociation as, compared with controls, they performed pathologically on naming but normally on imitation; the remaining three (BB, IN, SN) exhibited a strong dissociation, with both performances being worse than controls but naming being more impaired than imitation. One patient (NP) showed the reversed (classical) dissociation, in that she was impaired on imitation but not on naming. Of the remaining five patients, one (SA) was more impaired on imitation than naming, but this difference did not approach significance, while the other four patients performed within the normal range on both action naming and imitation.

Imitation versus action-verb comprehension (Figure 2). Three patients exhibited a significantly worse performance on imitation than comprehension. In particular, two of them (IN, NP) showed a classical dissociation, as their comprehension was within normal range, and one patient (SA) showed a strong dissociation, as her comprehension was also impaired, but significantly less than imitation. On the contrary, two patients resulted more impaired in action-verb comprehension, relative to imitation, one of them (CG) exhibiting a classical dissociation (i.e., normal ability to imitate), and the other one (BB) exhibiting a strong dissociation. Of the remaining seven patients, six performed normally on both imitation and comprehension tasks; one (SN) was impaired in imitation but the performance difference between the two tasks did not reach significance.

Thus, when comprehension was tested through word-picture matching task, which did not entail phonological-retrieval and speech production ability, a greater imitative deficit, relative to word comprehension, became evident in three patients, while the comprehension deficit suggested by naming performance was confirmed in two patients.

Performance on tool-stimuli

Tool-use versus tool naming (Figure 3). Seven patients showed a single dissociation between the ability to use and the ability to name tools. Specifically, five patients (CG, DBM, BS, CF, SN) showed a classical dissociation with impaired naming but normal tool use, while two patients (BB and IN) showed a strong dissociation, performing poorly on both tasks, with naming being worse than tool use. In contrast, although patient NP was more impaired in tool use than naming, the performance difference did not approach significance. Of the remaining four patients, three showed no significant difference across tasks (although compared to controls their performance on naming was impaired, it did not differ significantly from tool use, which was within the normal range), and one (DC) performed normally on both tasks.

Tool-use versus tool-noun comprehension (Figure 3). While I failed to find a double dissociation between tool use and naming, as all patients resulted more impaired in naming, the word-picture matching task was revealing of patients' performances, which were poorer on tool use relative to comprehension. In particular, NP and IN showed a classical dissociation, with impaired tool-use and normal tool-noun comprehension. The reversed dissociation was shown by two patients, of whom CG was impaired in tool-noun comprehension with a normal ability to use tools (classical dissociation), and BB was impaired in both tasks, with comprehension being worse than tool use (strong dissociation). The performance of the remaining eight patients on both tasks was comparable with that of controls.

The word-picture matching task revealed that, of the seven patients who were impaired in tool naming (as compared to use), only in two patients comprehension was actually worse than use. Two other patients showed the opposite pattern of performance, resulting in a double dissociation between tool use and tool-noun comprehension.

Language performance

Action naming versus tool naming (Figure 4). Six patients were more impaired on tool naming relative to action naming: three of them (BS, DBM, NP) revealed a classical dissociation (normal performance on action naming), and the remaining three (BB, CG, IN) exhibited a strong dissociation[3]. No patient showed the opposite dissociation. Of the remaining six patients, BB, SA, SN and UL were equally and severely impaired in both tasks; CF and MB were more impaired in tool naming, relative to controls, but this performance did not differ significantly from that on action naming; finally, DC performed within the normal range on both tasks.

Action-verb comprehension versus tool-noun comprehension (Figure 4). Double dissociation was found when word comprehension was tested with the word-picture matching task. Indeed, while patients BB and CG exhibited a strong dissociation, with

---

[3] It should be noticed that patients BB and CG's performances on both action and tool naming were very extreme (near floor). In this cases, even though the RSDT showed a significant difference between the two tasks (i.e. dissociation), the results should be treated with caution (see Laws et al., 2004).

noun comprehension worse than verb comprehension, SA was impaired at comprehending action verbs, with normal tool-noun comprehension. All remaining patients performed normally with both word-classes.

Thus, only in patients BB and CG, impairment in tool naming and in the comprehension task could be due to brain damage affecting tool-noun representations more than action-verb representations; one patient (SA), who was dramatically impaired in naming both types of stimuli, showed a major damage to noun, relative to verb representations, in the comprehension task.

Age of acquisition (AoA) effect on actions and tool naming. I tested whether AoA of words affected noun and verb retrieval differentially. The AoA of a word is thought to determine the way in which the information is stored and accessed in the brain; therefore, it has been suggested that this variable affects differently, word classes for which segregated substrates are predicted (Ghyselinck, Lewis, & Brysbaert, 2004). The effect of AoA results in a better performance on early-acquired than later-acquired words, this being more reliable in naming, than in comprehension performance (Morrison, Ellis, & Quinlan, 1992). Naming ability also reveals that words learned at late childhood are typically more vulnerable to loss in elderly subjects and patients with neurological conditions (Morrison, Hirsh, & Duggan, 2003). I tested whether the AoA had a different impact on nouns and verbs using Pearson’s correlations between the mean AoA of nouns and verbs, as assessed in the rating study (see “Materials” section), and the mean percentage of patients’ correct responses in naming for the same items. Overall, AoA correlated with the patients’ ability to name items (N=30, r=-.43, p = .01): earlier-acquired words were named more accurately - or were more resistant to the deficit - than words acquired at a later age. However, when correlations were carried out separately for nouns and verbs, performance on action naming did not correlate with AoA (*N*=15, *r*=-.35, *p* = .2), whereas there was a significant correlation between AoA and tool naming (*N*=15, *r*=-.5719, *p* = .02).

Table 5. Individual performance of all patients across all experimental tasks.

	Action-stimuli						Tool-stimuli					
	Imitation		Naming		Comprehension		Tool-use		Naming		Comprehension	
Case	% corr	t score	% corr	t score	% corr	t score	% corr	t score	% corr	t score	% corr	t score
BB	56.67	**-3.63**	0	**-11.77**	46.67	**-7.24**	73.33	**-4.17**	0	**-24.31**	60	**-10.72**
BS	86.67	-0.42	93.33	-0.09	100	0.76	100	0.72	86.67	**-2.82**	100	0.32
CF	90	-0.06	86.67	-0.93	93.33	-0.23	100	0.72	86.67	**-2.82**	100	0.32
CG	80	-1.13	0	**-11.77**	66.67	**-4.24**	100	0.72	0	**-24.31**	46.67	**-14.40**
DBM	90	-0.06	86.67	-0.93	100	0.76	93.33	-0.50	46.67	**-12.73**	93.33	-1.51
DC	96.67	-0.65	93.33	-0.09	86.67	-1.21	93.33	-0.50	100	0.48	100	0.33
IN	40	**-5.42**	26.67	**-8.43**	93.33	-0.23	40	**-10.28**	33.33	**-16.04**	100	0.33
MB	100	1.00	73.33	**-2.59**	100	0.76	86.67	-1.72	86.67	-2.82	100	0.33
NP	60	**-3.28**	86.67	-0.93	100	0.76	66.67	**-5.39**	80	**-4.47**	100	0.33
SA	40	**-5.42**	60	**-4.25**	80	**-2.24**	86.67	-1.72	80	**-4.47**	100	0.33
SN	73.33	**-1.85**	46.67	**-5.93**	86.67	-1.21	86.67	-1.72	73.33	**-6.12**	100	0.33
UL	76.67	-1.50	60	**-4.25**	86.67	-1.21	86.67	-1.72	80	**-4.47**	100	0.33

Note: Patients are sorted alphabetically by their initials. Numbers in bold denote t-scores (Crawford & Garthwaite, 2002) significantly below the controls' mean.

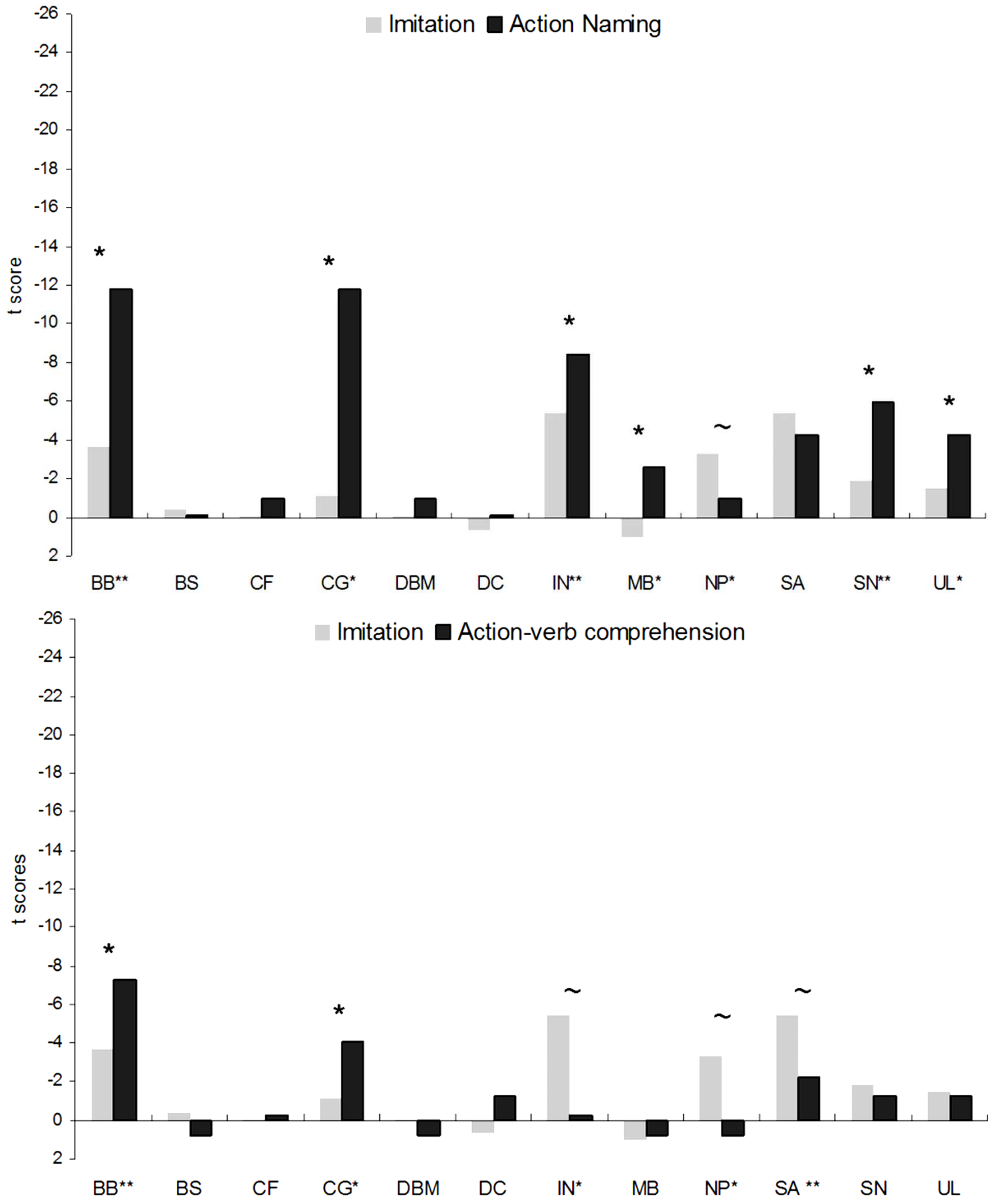


Figure 2. Upper part: patients' performance on action imitation versus action naming. Lower part: patients' performance on action imitation versus action-verb comprehension. Patients are shown in alphabetic order. Besides patients' initials: *indicates classical dissociation, **indicates strong dissociation (Crawford & Garthwaite's RTSD, *p* < .05). On the top of the columns: *indicates dissociation with better performance on imitation than on word-stimuli; ~ indicates dissociation with better performance on word-stimuli than on imitation.

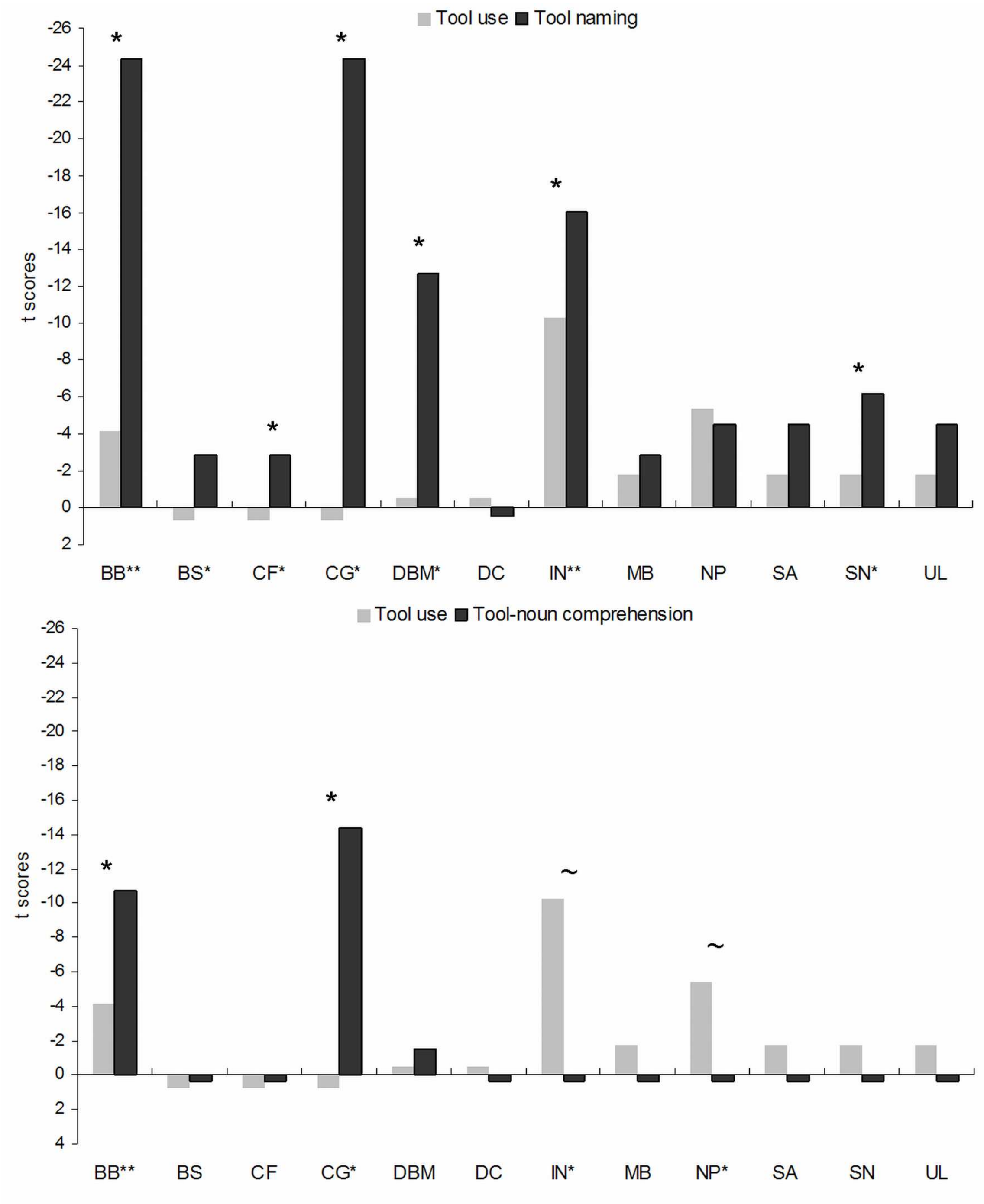


Figure 3. Upper part: patients' performance on tool use versus tool naming. Lower part: patients' performance on tool use versus tool-noun comprehension. Patients are shown in alphabetic order. Besides patients' initials: *indicates classical dissociation, **indicates strong dissociation (Crawford & Garthwaite's RTSD, *p* < .05). On the top of the columns: *indicates dissociation with better performance on tool use than on word-stimuli; ~ indicates dissociation with better performance on word-stimuli than on tool use.

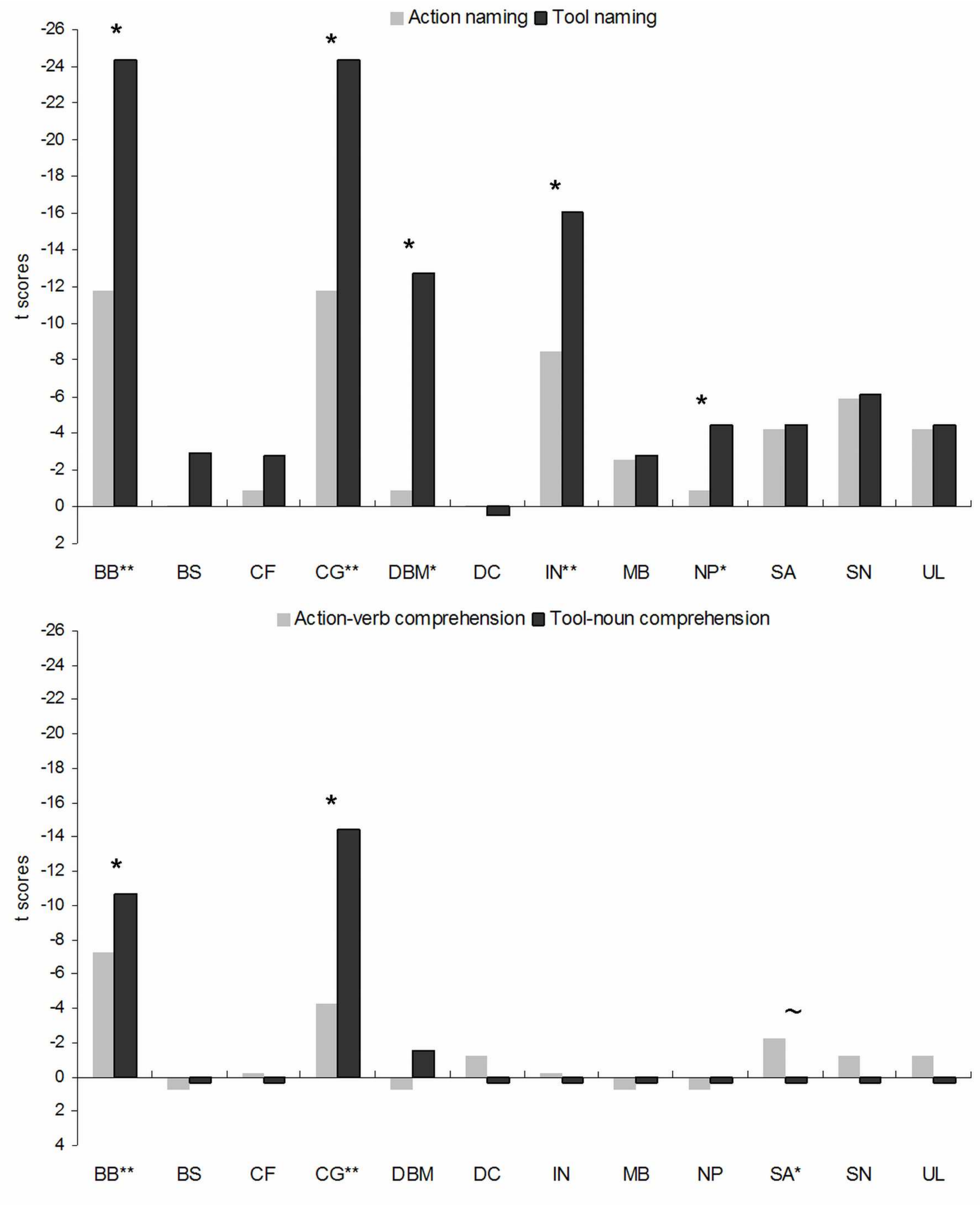


Figure 4. Upper part: patients' performance on action versus tool naming. Lower part: patients' performance on action-verb versus tool-noun comprehension. Patients are shown in alphabetic order. Besides patients' initials: *indicates classical dissociation, **indicates strong dissociation (Crawford & Garthwaite's RTSD, *p* < .05). On the top of the columns: *indicates dissociation with better performance on action-verbs than on tool-nouns; ~ indicates dissociation with better performance on tool-nouns than on action-verbs.

2.4.3. *Lesion results*

The lesion overlay of the 9 patients, for whom the CT or MRI scan was available, covered the classic perisylvian language-processing regions and the frontoparietal network sustaining sensorimotor functions (see Figure 5A; refer also to Table 3, where regions damaged in each patient are listed). In the following comparisons, patient NP, who had a prominent impaired in imitation and tool-use, was not included, as she had only subcortical lesion (Figure 5B). Although her performance was highly informative with respect to our hypothesis, including this patient in the groups with similar impairments would have "masked" the cortical regions that were affected in the remaining individuals. Indeed, the intersection plot only shows regions that are commonly affected in all patients in a group.

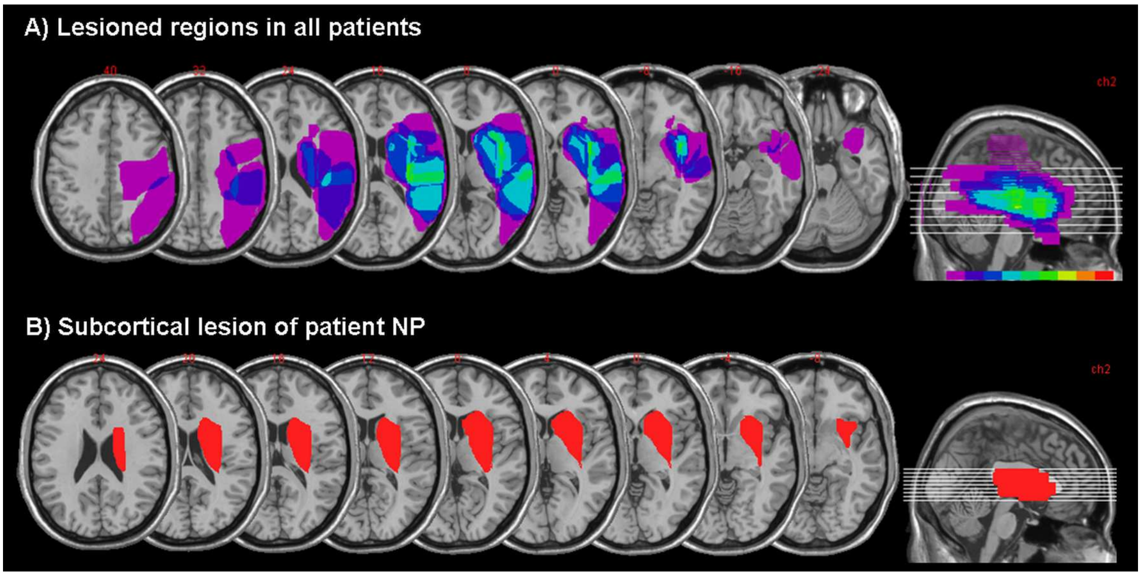


Figure 5. A) The lesion overlay including all 9 left-damaged patients for whom CT or MRI scan was available. **B)** NP's CT scan showing the lesion affecting the left hemisphere insula, basal ganglia, thalamus and surrounding white matter. Coordinates of the transverse sections are given. As customary, the neuroimage is reversed, the right hemisphere is on the left side of the picture.

Damaged regions in processing action-stimuli (Figure 6). Lesion overlay of all patients with imitative deficit (BB, IN, SN), after subtraction of damaged areas in the remaining patients with no imitative deficit, showed that imitation was specifically associated with insular cortex and postcentral gyrus extending to the opercular region (OP) of the parietal lobe. The lesion site associated with deficit in action-verb comprehension (impaired: BB, CG), after subtracting lesions of non-impaired patients, resulted centred in the insular cortex, pars opercularis and, marginally, pars triangularis of the inferior frontal gyrus (IFG), superior temporal pole (TP) and a small portion of superior temporal gyrus (STG). The intersection analysis involving patients with action-naming deficit (BB, CG, IN, SN, UL), after subtracting lesions of non-impaired patients, revealed no mutually shared coordinates. This result suggests that, as it could be expected, the naming deficit of our patients resulted from damage to different processes (from motor to semantic), and therefore to different brain regions. The contrast between lesion sites associated with deficits in imitation and action-verb comprehension confirmed the above task-specific regions. In addition, it showed that regions associated to both deficits overlapped in the insula and the posterior part of PO.

Damaged regions in processing tool-stimuli (Figure 7). The lesion overlay of patients with tool-use impairment (BB, IN), after subtraction of the remaining non-impaired patients, was centred in postcentral gyrus extending to the supramarginal gyrus (SMG). Lesion site specifically associated with tool-noun comprehension deficit of patients BB and CG (after subtraction of non-impaired patients) involved the insular cortex, pars opercularis of IFG, extending to the adjacent part triangularis, and superior TP, extending marginally to STG. Again, the same analysis applied to patients with action-naming deficit (BB, BS, CG, DBM, SN) revealed no mutually shared coordinates. The contrast between lesion sites associated with deficits in tool use and in tool-noun comprehension confirmed the above task-specific regions, and showed that regions associated to both deficits overlapped in the insular cortex and OP.

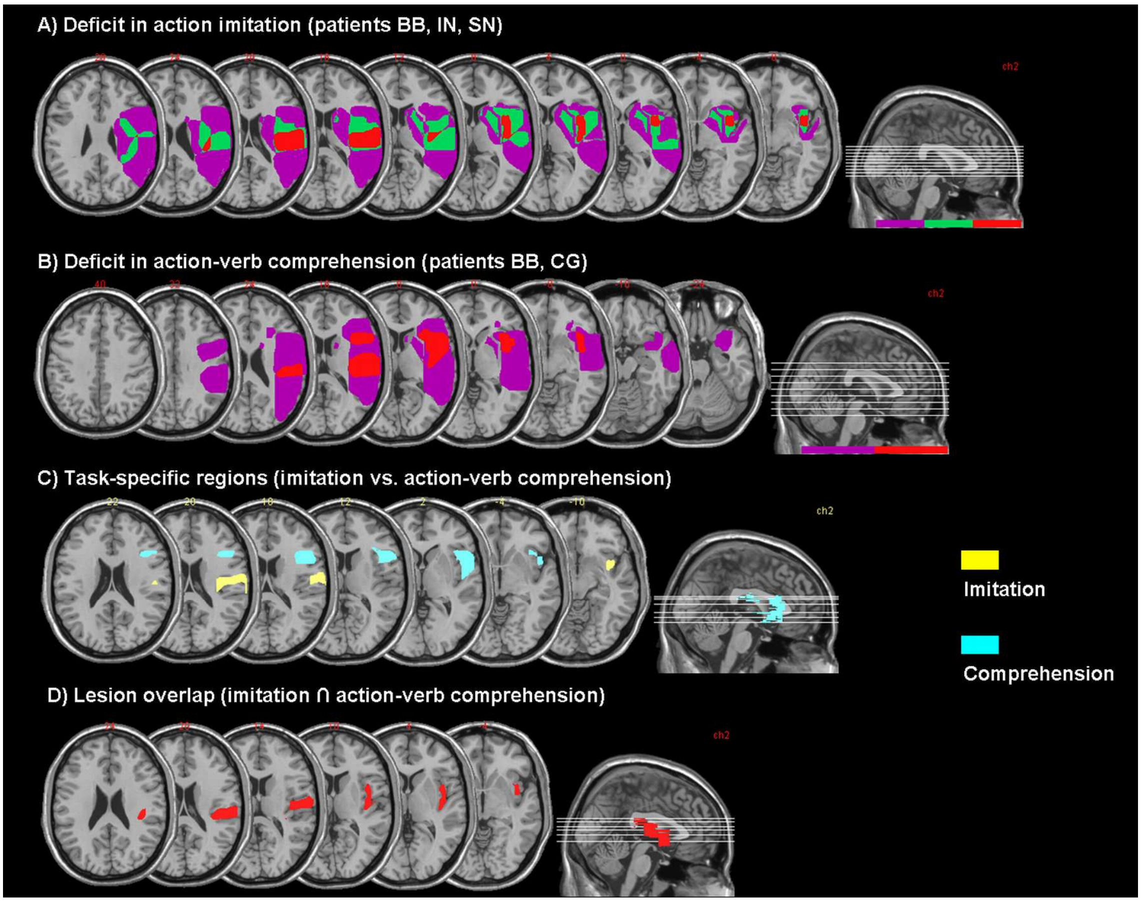


Figure 6. (A) Lesion overlay of three patients with imitation more impaired than action-word comprehension **(B)** Lesion overlay of two patients with action-word comprehension more impaired than imitation. The number of overlapping lesions is illustrated by a colour coding increasing frequencies from violet (n=1) to red (indicating the maximum number of subjects in each group) colour. **(C)** Damaged regions specifically associated with imitative deficit, after subtraction from non-impaired patients, are shown in yellow color. Damaged regions associated with deficit in action-verb comprehension, after subtraction from non-impaired patients, are shown in light-blue color. **D)** Intersection of damaged regions implicated in imitation and action-verb comprehension. Only those regions in which the percentage of overlapping lesions for a specific group of subjects (after subtraction from the other groups) was 100% are shown. Coordinates of the transverse sections of the brain are given.

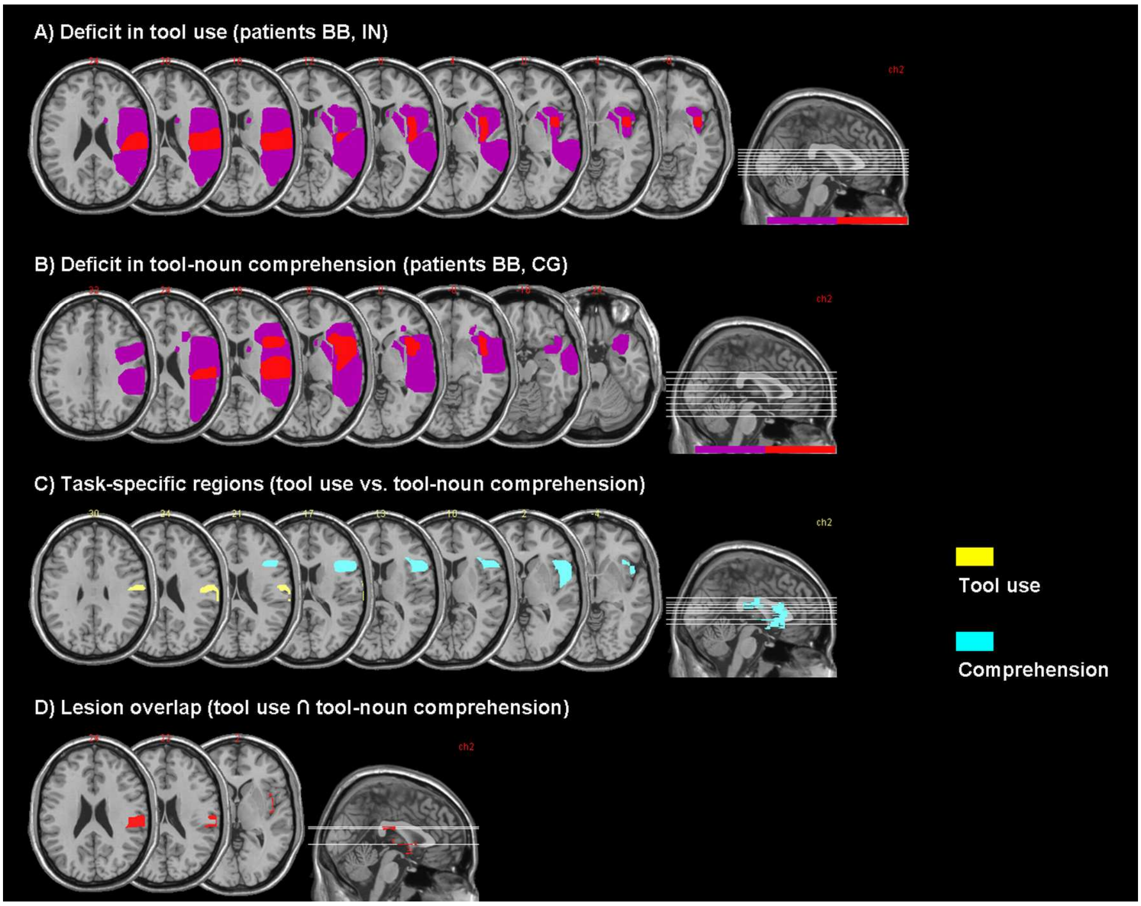


Figure 7. (A) Lesion overlay of three patients with tool use more impaired than tool-noun comprehension **(B)** Lesion overlay of two patients with tool-noun comprehension more impaired than tool use. The number of overlapping lesions is illustrated by different colours coding increasing frequencies from violet (n=1) to red (n=2) colour. **(C)** Damaged regions specifically associated with deficit in tool use, after subtraction from non-impaired patients, are shown in yellow color. Damaged regions associated with deficit in tool-noun comprehension, after subtraction from non-impaired patients, are shown in light-blue color. **D)** Intersection of damaged regions implicated in tool use and tool-noun comprehension. Only those regions in which the percentage of overlapping lesions for a specific group of subjects (after subtraction from the other groups) was 100% are shown. Coordinates of the transverse sections are given.

2.5. Discussion

In this chapter I tested the hypothesis that the action production system is causally involved in the comprehension of words related to action. One explanation of the conflicting neuropsychological and neuroimaging evidence about the relationship between action and language systems suggests that the extent to which the two systems overlap is a function of i) the perceptual and conceptual similarity between verbal and nonverbal stimuli employed in linguistic and nonlinguistic tasks, and ii) the temporal similarity of the development of skills underlying those tasks (Bates & Dick, 2002; Saygin et al., 2004).

Here, I showed that, although linguistic and nonlinguistic (motor) deficits in left-damaged patients may correlate, single-patients' performances on motor and word comprehension abilities double dissociated, even when identical action-related stimuli were used in tasks with comparable developmental stage. I will start by discussing patients' performance on linguistic and non-linguistic tasks involving actions and tools, and I will then consider their linguistic performance on action verbs versus tool-nouns.

2.5.1. Linguistic and non-linguistic abilities

The analysis of the patients' performance at group and at single-case level on action imitation and linguistic tasks with verbs (naming and comprehension) produced different results. Although at group-level a positive significant correlation between action naming and imitation seems to support the argument that action-word representations are related to representations for motor performance (Gallese & Lakoff, 2005), the single-case analysis revealed the limits of a logic based on correlations. A number of patients were, in effect, impaired on naming actions but relatively unimpaired when imitating them, while one patient showed the opposite pattern, suggesting that word representations can be disrupted despite preserved imitation, and *vice versa*.

On the other hand, action imitation and comprehension did not correlate at group-level but if I increased the sample size or the number of observations, this correlation could become significant, as reported in previous studies (see Buxbaum, Kyle, & Menon, 2005; Negri et al., 2007). However, when performance of individual patients was considered, comprehension and imitation double dissociated suggesting that the ability to comprehend action-verbs can be disrupted in the absence of deficit in producing the corresponding motor program, and *vice versa*. While it cannot be established unequivocally why two functions do - or do not - correlate (as any third factor or, merely, the lack of statistical power, can explain it), the observed double dissociation provides a solid basis for inferring that they are served by distinct substrates. Individual patients' performances challenge the embodied view of language: the basic ability to translate a visual input into a motor output required for imitation, does not seem necessary for the comprehension of verbs that denote the same motor act.

When I analyzed the relationship between the ability to use tools and the lexical-semantic processing of tool-nouns, at group level, I found that tool use did not correlate with either tool naming or tool-noun comprehension. As observed above, the lack of correlation may reflect, in the first place, the limited power of our analysis, due to a small-sized sample of participants or stimuli. However, previous studies involving larger samples suggest that, although tool use and tool recognition can correlate (e.g. Negri et al., 2007), this is not universal (see Tessari et al., 2007). The lack of correlation, in our study, is rather in keeping with double dissociation between the use of tools and the ability to comprehend their nouns, observed at individual level. Overall, our findings agree with studies that described selective deficits affecting one of these abilities at a time (De Renzi & Lucchelli, 1988; Negri et al., 2007; Rosci et al., 2003; Rumiati et al., 2001). Hence, the ability to use tools does not seem necessary for successfully comprehending their nouns.

The lack of double dissociation between verbal and motor tasks, when comprehension was tested with a naming task, does not weaken this conclusion. In fact, naming deficit does not necessarily reflect damage to word (semantic) representations. Based on the overall performance of patients on verbal tasks, we can safely conclude that the naming deficit was genuinely determined by a semantic breakdown only in two patients. In contrast, the naming disability of the remaining five patients could be due to a failure occurring at other stages of the processing, such as the lexical-phonological retrieval of a specific entry that did not abolish semantic activation required for performing the word-picture matching task (see Berndt et al., 1997). Notice that this independence of naming from word recognition, which is also predicted by influential models of language (Morton & Patterson, 1980; Seidenberg & McClelland, 1989), does not mean that a close relationship does not exist between them. Indeed, both functions, tap the same representations, as confirmed by the tight correlation I found in the group-level analysis, between action naming and action-verb comprehension, and between tool naming and tool-noun comprehension.

2.5.2. Tool-nouns and action-verbs

Although performances on action-verbs and tool-nouns correlated at group-level, they dissociated at the level of individual patients. When action-word representations were assessed with naming task, five patients named actions significantly better than tools, while none of the patients showed the opposite pattern of performance. However, double dissociation between action-verb and tool-noun representations emerged when they were assessed with the word-picture matching task, which is more reliable than naming in assessing comprehension. In the light of the double dissociation between action-verbs and tool-nouns, I conclude that the semantic (motor) content of words is not sufficient – or does not constitute the only principle - for determining their organizationin the brain. In line with previous neuropsychological and imaging studies (see Shapiro & Caramazza, 2003), the dissociation between verbs and nouns reported here maintains that word representations are (also) organized by word-form class, even when they share relevant semantic features.

Notice that, in the comprehension task, seeing static photographs, instead of video-clips, might have made the recognition of the ongoing action more difficult than the recognition of a tool. Luckily, having observed a double dissociation makes this event unlikely (e.g., Shallice, 1988). Moreover, the within-patient difference between accuracy rates in the two comprehension tasks was rather equivalent in the two patients with noun-verb dissociation, so that one task cannot be said significantly more difficult than the other.

The segregation between the two word-classes is also supported by the significant AoA effect on tool naming (noun retrieval) but not on action naming (verb retrieval). The AoA is held to affect differently words that belong to different classes, and are presumably represented in different brain networks (Ghyselinck et al., 2004)[4].

---

[4] Note that AoA can also affect verb retrieval (Colombo & Burani, 2002; Morrison *et al.*, 2003), depending on the aspects of word processing tapped by a given task (see Boulenger et al., 2007).

Although the lack of correlation between AoA and action naming can merely reflect the lack of power in this analysis, our results fully replicated those of Boulenger, Décoppet, Roy, Paulignan, and Nazir (2007), in a rating study on normal participants, involving similar stimuli (actions and concrete objects), the same task (naming), but a much larger number of observations, relative to our study.

I cannot exclude that action-verbs and tool-nouns share semantic features. As the task I used to test comprehension (matching a word to its corresponding action or tool) did not tap all aspects of action knowledge associated with a word (e.g., function, context), it remains possible that, under different task conditions, semantic similarities between word classes may become evident and their representations, closely interactive (and overlapping).

One final consideration concerns the numerical disproportion of patients with verb superiority, relative to those with noun superiority, in the naming task. This observation is contrary to the distribution of word-class effect in aphasics, which is predominantly in favor of nouns (e.g., DeBleser & Kauschke, 2003). I suggest that the apparent discrepancy between our results and those reported in literature depends on the fact that the inferential method I used to test dissociation in single-patients, takes into account controls' means, standard deviations and correlation between the same two tasks, while other methods (i.e., *z*-scores and within-patient χ^2) that are often used to test dissociations do not. Laws and colleagues (2005) showed that the higher incidence of deficits in processing living, relative to nonliving, items, did not hold when they employed the inferential method to compare a patient with controls, like in the RSDT. Indeed, as in their analysis controls also performed worse with living than with nonliving things, a patient's poor performance on living things resulted non-significantly worse or, paradoxically, less severe than performance on nonliving things, even when the row data show the opposite (Laws, 2005; Laws et al., 2005). This seems to be the case of our study, where controls performed better on tool naming (*M*=98 ± 3.9) that on action naming (*M*=94 ± 7.7). Therefore, along with Laws and colleagues', our results maintain that the use of inferential methods for dissociation, which do not take into account controls' performance, might have exaggerated the number of verb deficits, or underestimated the incidence of noun deficits in previous studies.

2.5.3. Linguistic and nonlinguistic action-related mechanisms

Task-specific regions

Action imitation. In our study, deficit in action imitation was associated with lesion in the insula, the postcentral gyrus housing the primary somatosensory cortex (SI), and extended to OP that forms the lower margin of the inferior parietal gyrus (IPG). The affected portion of OP fairly corresponds to the secondary somatosensory cortex (SII, Eickhoff et al., 2006; 2007) consistently with frequent observations of imitative deficit following damage to parietal regions (De Renzi & Faglioni, 1999; Rumiati, Papeo, & Corradi-Dell'Acqua, 2010, for a review). The left parietal regions had been found to be critically involved in executing hand configuration (Goldenberg & Hagmann, 1997). In particular, left SI and SII that hold somatotopic body representations may provide knowledge of one's own body structure to transforms the perceived action into one's own action, and somatosensory feedback to allocate the hand in the near-body space (e.g., Goldenberg, 1999; Hermsdorfer, Goldenberg, Wachsmuth, et al., 2001; Tanaka & Inui, 2002). Consistently with neuropsychological observations, imaging studies reported postcentral activation in the processing of referring to knowledge of one's own body during motor and conceptual tasks (Ruby & Decety, 2001; 2003), and SII activation in the encoding of hand position relative to one's own body (Corradi-Dell'Acqua, Tomasino & Fink, 2009).

A study on 44 apraxic linked the left insula to deficit in finger posture imitation, (Goldenberg & Karnath, 2006), and fMRI studies associated insular activation with the encoding of body schema (Chaminade, Meltzoff, Decety, 2005; Corradi-Dell'Acqua, et al., 2009), or, as part of limbic system, with the processing of the social/empathic component of imitation (Carr et al., 2003). Given the reciprocal connections of insula with many cortical (prefrontal, premotor, parietal and temporal) and subcortical (limbic) structures, it is difficult, at present, to establish what its specific functional contribution to imitation is.

Action-verb comprehension. In our patients, comprehension deficit was associated with lesion in the IFG and STG, which are *classic* components of the perisylvian-language network, in the superior TP, and in the insula. The role of the pars opercularis and triangularis of the IFG (Broca's area) in verb processing is largely documented in neuropsychological (Caramazza & Hillis, 1991; Damasio & Tranel, 1993; Daniele et al., 1994; McCarthy & Warrington, 1985; Miceli et al., 1988) and imaging studies (Kellenbach, Wijers, Hovius, Mulder, & Mulder, 2002; Shapiro et al., 2005). However, due to its involvement in a wide range of linguistic and non-linguistic tasks (Bookheimer, 2003; Fink et al., 2006; Friederici, 2002), recent neurobiological models of language assign the Broca's area an executive-*like* function in controlling the retrieval and binding together, into a coherent overall representation, lexical and non-linguistic information associated with a word, conveyed from posterior regions (e.g., Fiez, 1999; Hagoort, 2005; Thompson-Schill et al., 1997)

STG that was marginally encompassed by lesion is another typical correlate of comprehension (e.g., Chao, Haxby, & Martin, 1999; Friederici, Rüschemeyer, Hahne & Fiebach, 2003; Scott & Johnsrude, 2003; Vandenberghe, Price, Wise, Josephs, Frackowiak, 1996). Although traditional neurological models do not posit a role of TP, our findings go along with clinical studies on semantic dementia (see Jefferies & Lambon Ralph, 2006), and TMS studies on healthy participants (e.g., Lambon Ralph, Pobric & Jefferies, 2009), suggesting that this region is one crucial substrate within the neural network for conceptual knowledge. The involvement of TPs is held to be bilaterally, but evidence suggests that the left side is specialized for verbal modality (Lambon Ralph et al., 2001). Finally, while left insular lesions often elicit speech production deficit (Dronkers, 1996; Shuren, 1993), imaging studies have also linked this region to the semantic processing of words (Friederici, Rüschemeyer, Hahne & Fiebach, 2003; Mummery et al., 1999). Mummery et al. (1999) hypothesized that insular activation reflects automatic aspects of semantic processing; however, its precise role in word comprehension, as well as in speech production (see Hillis et al., 2004) remains unclear.

Tool use. Lesions of patients with tool-use impairment - a key symptom of ideational apraxia - overlapped in a relatively small region centered in postcentral gyrus and SMG that forms the anterior part of the inferior parietal lobule. A wealth of studies on patients suffering from ideational apraxia suggests that the capacity for highly skillful tool use relies on the left inferior parietal lobe (e.g., Rothi et al., 1991; Rumiati et al., 2001). Consistently, imaging studies with healthy subjects related the postcentral gyrus to execution of visually-guided grasping (e.g., Frey, Vinton, Norlund & Grafton, 2005), and the left SMG to the access of object-related action schemas during motor performance (Binkofski, 1999; Johnson-Frey et al., 2005; Rumiati et al., 2004), but also in non-motor tasks involving tools, such as semantic judgments (Canessa et al., 2008; Kellenbach et al., 2003), naming (Chao & Martin, 2000), or passive perception (Mahon et al., 2007).

Tool-noun comprehension. Regions implicated in deficit of tool-noun comprehension were the insular cortex, pars opercularis and, marginally, pars triangularis of the IFG (Broca's area), and superior TP. The fact that these regions matched those associated with deficit in action-verb comprehension is not surprising as the group of patients with impaired action-verb comprehension involved the same two patients (BB, CG) who formed the group with impaired tool-noun comprehension. As discussed above, these lesion sites have been related to processes that are *broadly* involved in comprehension, irrespective of task and word content.

However, while the deficit of our patients seems to reflect damage to *non-specific* semantic processing, this does not exclude the existence of neural systems dedicated to particular types of knowledge or word classes. The anatomo-functional distinction between verbs and nouns, as suggested in many studies (see Shapiro & Caramazza, 2003), might not have been appreciated here, due to limitations of our lesion analysis (i.e., small sample size and full overlap of groups with impaired action-verb and impaired tool-noun comprehension). Double dissociation observed in patients' behavioral implies that the – at least partial – independence of verb and noun representations, even when semantically related, is more than a possibility.

Shared regions for motor performance and action-word comprehension

Two regions resulted associated with deficits in both imitation and action-verb comprehension: OP and insula. As discussed above, the involvement of OP in imitation may reflect the encoding of spatial location of hand/harm in relation with one’s own body (schema) (e.g., Corradi-Dell’Acqua et al., 2009)[5]. Notice, however, that the overlap between imitation- and comprehension-related regions extends more caudally relative to the portion of OP associated with imitation deficit only. Therefore, other processes held in different portions of OP contributed to imitation deficit. This possibility takes into account evidence for four distinct cytoarchitectonic areas in human OP, which can be expected to contain separate body representations, or serve different functional aspects within the somatosensory system (Eickhoff et al., 2007).

In word comprehension, the involvement of OP may relate to the functional relevance of the left inferior parietal cortex in understanding written and spoken words, as acknowledged for more than a century in clinical investigation (Dajerine, 1892; Geshwind, 1965; Hart & Gordon, 1990; Heilman et al., 1982; Mesulam, 2008), and supported by imaging studies (Friederici et al., 2000; Price, 1998). OP has also been linked specifically to auditory processes for speech perception (Binder et al., 2010; Hickok & Poeppel, 2000).

OP and its adjacent parietal cortex is part of the frontoparietal circuitry that, in the embodied conception, is crucial for action performance (e.g., imitation), as well as for action comprehension (Rizzolatti, Fogassi & Gallese, 2001). Despite so, I did not find any apparent involvement of motor and premotor cortices in action-word comprehension. This is clearly contrary to the central claim of embodied hypothesis that action meanings are encoded in these anterior motor regions (see also Hickok, 2009, for a similar argument). Thus, I have to conclude that the motor system does not necessarily

---

[5] Notice that this specific function of PO is coherent with the predominant proportion of hand/arm spatial errors (95%) or unrecognizable gestures observed in our patients in action production tasks (i.e. action imitation and tool use), relative to semantic or visual errors.

support this processing. Moreover, while all our patients with imitative and comprehension deficits had damage to OP, it should be reminded that many of them (i.e., all but BB) had impaired imitation without comprehension deficit, and one of the two patients with impaired comprehension (CG) had preserved imitation. In other words, the portion of OP, where networks for imitation and comprehension overlap, does not seem necessary for either task. This observation is better accommodated within the frame of a distributed architecture of complex functions (McIntosh, 2000; Price & Friston, 2002) predicting that, when there is localized damage, there may be no evident cognitive deficit, although the damaged region may be part of the network. As Price and Friston (2002) observed, "[i]maging can, in principle, identify the set of regions that are sufficient for a cognitive operation and the lesion-deficit model identifies which of these areas are necessary" (p. 418). That is, the involvement of a given region in a task does not imply that that region is necessary for that task! The recruitment of OP in several tasks may be one instance of "one-to-many structure-function" relationship predicted within the same perspective, whereby a particular area may be part of different networks depending on the task context (McIntosh, 2000; Price & Friston, 2002). Consistently with that, for instance, OP is activated in disparate linguistic tasks and irrespective of the word content, leaving open a possibility that distinct neural systems overlap in the same anatomical region (Price, 1998).

A similar reasoning applies to the insula that is recruited in surprisingly large number of tasks, suggesting that there is no one, but many functions to which insula – or different portions of insula – contributes, as a part of different networks.

The same two regions, OP and insular cortex, resulted from the intersection-analysis between tool use- and tool-noun comprehension-related lesions. OP has been independently related both to tool-use ability, as a part the grasp-specific cortical network to guide hand-object interactive movement (Frey et al., 2005; Naito & Ehrsson, 2006), and to word comprehension/perception, as discussed above. Likewise, insular cortex has been linked to both (and many other) functions. Again, the lesion analysis combined with the behavioral observations, leads to the conclusion that networks for tool-use and tool-noun comprehension may overlap in some anatomical regions, (or the same regions can be part of the two networks). It remains that no evidence in our findings indicates a critical function of motor system in word comprehension.

One may observe that, in our patients, none of the praxic deficits was specifically associated with damage to motor and premotor areas, but rather resulted from disruption of posterior (parietal) components of the sensorimotor circuitry. Hence, it can be argued that the *interruption* in any point of the circuitry contributes to word-semantic impairment. This possibility has to be excluded on the basis of our patients' behavior: two patients (IN, SN) with damage to OP and impaired imitation could still comprehend words (denoting the same actions), and patient IN who was also impaired in tool use could still comprehend tool-nouns. I do not mean to exclude that language and action are highly interactive systems, especially because our comprehension task (word-picture matching) did not exhaust all aspects of action knowledge associated with a word. It is plausible that, in other task contexts, sensorimotor regions can gain greater relevance for achieving comprehension, a possibility that well meshes with the notion of a distributed architecture of cognitive functions. What our results mean is that a complex cognitive process, such as word comprehension, cannot be localized to the motor cortices, as stated in the strictly embodied view (Rizzolatti et al., 2001; Pulvermüller & Fadiga, 2010). Moreover, the reported double dissociations imply that, even if one assumes that, not the motor cortices, but the whole sensorimotor circuitry sustains comprehension, this cannot be regarded as a necessary component of the processing.

As last remark, results of lesion analyses discussed so far must be taken as descriptive and, possibly, suggestive of the neural underpinnings of the investigated functions. The limited sample size did not allow us to employ more sophisticated methods (i.e., voxelwise lesion mapping), for which power is a major concern (Kimberg, Coslett & Schwartz, 2007). Thus, our analysis relied only on evident anatomical changes in the patients' brain. The same limitation resulted in comparisons between lesions of small-sized groups, often restricted to two individuals. Moreover, a very few patients exhibited deficit in only one task. In particular, the susceptibility of naming ability to impairments at many processing levels can explain why I failed to detect naming-specific regions. This objective would require having a larger number of patients with anomia and spared semantic or motor abilities.

A case of deep apraxia. Patient NP was a case of *deep* apraxia, as her disorder resulted from damage to subcortical structures (see Figure 8), including insular cortex, basal ganglia (head of caudate nucleus, globus pallidus and putamen), thalamic nucleus (lateral portion) and surrounding white matter (internal capsule and peristriatal white matter). Her deficit in both tool-use and imitation, suggests a functional breakdown at the level of the output gestural buffer that temporarily holds the whole action to be performed (Cubelli et al., 2000; Rumiati et al., 2010). This diagnosis is consistent with the lesion affecting the basal ganglia (and their connections to prefrontal areas), which are held to be involved in online action monitoring (Botvinick & Plaut, 2006). On the other hand, Pramstaller and Marsden (1996), in a meta-analysis of single-cases, suggested that deep apraxia reflects the interruption of information flow from the left inferior parietal lobule to frontal motor regions, due to lesion of white matter (arcuate fasciculus and internal capsule) adjacent to basal ganglia and thalamus. For the sake of our study, NP's performance was highly informative as her praxis dysfunction left completely unaffected word comprehension. This instance brings further support to our conclusion that neither the motor system, nor the whole frontoparietal sensorimotor circuitry that in this patient was apparently interrupted in a crucial point, can be regarded as a substantial correlate of action-word comprehension.

2.6. Conclusions of chapter 1

Our findings show that producing actions and processing words related to the same actions rely on independent representational systems and dissociable neural substrates. This is true even when verbal and nonverbal abilities are acquired equally early in life and deal with identical stimuli. Previous neuropsychological studies have reported patients with preserved action and object comprehension and apraxia, and others with no apraxia but impaired action and object knowledge (e.g. Negri et al., 2007; see Mahon & Caramazza, 2005, for a review). Here, I have extended this dissociation to the relationship between action and action-word representations. A productive investigation of the role of basic modality-specific systems in cognition should start from the evidence that a person may lose her ability to physically use a broom, while she can still be able to *grasp* what the D.F. Wallace's "*Broom of the System*" is!

Chapter 3.

The “when” of motor simulation: Timing and task-dependency of motor activity in word processing

3.1. Introduction

The hypothesis that motor simulation is the mechanism for understanding action-words implies that motor activation occurs *automatically*, even when a subject’s attention is diverted from the motor content of a word (Pulvermüller, 2005). On the contrary, recent imaging studies have shown that M1 was activated only in some – but not all – tasks involving action language (e.g., Tomasino, Werner, Weiss & Fink, 2007; Willems, Haggort & Casasanto, 2010). Establishing whether motor activation is automatic in word processing can provide insight on the question as to whether it serves lexical-semantic encoding or not.

Insight on this question can also be gained by establishing the precise time interval in which M1 activity enhances. Word recognition is, in fact, a multistage processing, characterized by lexical, syntactic, semantic and post-conceptual stages, each with its own specific time course. If it is true that M1 is an integral part of word representation, it should be active during the lexical-semantic stages of word recognition, i.e., within 200 ms. Some electrophysiological studies seem to support this hypothesis (Hauk, Davis, Pulvermüller & Marslen-Wilson, 2006; Penolazzi, Hauk & Pulvermüller, 2007; Pulvermüller, Shtyrov & Ilmoniemi, 2005). For instance, Pulvermüller *et al.* (2005), using magnetoencephalography (MEG), while participants listened passively to a stream of action-words and pseudo-words, reported that a short-lived activity occurred in frontocentral regions within 200 ms after action words appeared. However, given the limited spatial resolution of the technique employed, the authors could only conclude that the processing of action words was maintained in "*different parts of frontocentral cortex, possibly including the prefrontal, premotor and motor areas*" (*ibidem*, p. 889). On the other hand, in TMS studies, where temporal resolution is combined with a more precise spatial resolution, language-induced modulation of M1 was found to be either an early (Buccino, Riggio, Melli, et al., 2005[1]) or a late phenomenon (500 ms post-word; Oliveri et al., 2004).

In this chapter I addressed two questions. First, does motor activation occur *automatically*, even when participants perform a task that barely requires the explicit retrieval of the motor content of the word? Second, what stage of word recognition is most likely to activate the motor cortex? Given its intrinsic characteristics, TMS provided the ideal instrument to address these questions. In fact, when supra-threshold TMS is applied to

---

[1] The authors reported that TMS was applied 500-700 ms after the sentence-onset, which always corresponded to the second syllable of the action verb (Buccino et al., 2005).

M1 at a given point in time, it elicits motor-evoked potentials (MEPs) in peripheral muscles responding to the stimulated area. MEPs provide a direct measure of motor excitability at that time, as their amplitude is proportionate to the level of motor activity. Moreover, TMS delays or disrupts the ongoing behavior in the stimulated areas (Harris, Clifford & Miniussi, 2008), thus, investigating whether and to what extent behavioral performance changes when M1-activity is temporarily disrupted can throw light on the question as to whether M1 activity critically (necessary) contributes to processing action-word.

TMS was applied to the left hand-M1 and MEPs were recorded from hand muscles while participants performed a semantic and a syllabic-segmentation task. The semantic task, where participants were instructed to judge whether each verb was action-related, required the explicit retrieval of the implied motor representation. The syllabic-segmentation task asking participants to decide on the number of syllables in each verb, primarily directed their attention to the sub-lexical (orthographical-phonological) features of a word (e.g., Carreiras, Vergara & Barber, 2005). Semantic activation is rather automatic in visual word recognition, but it might be only implicit when the retrieval of word meaning is not necessary in order to perform the task, as is in the syllabic segmentation (MacLeod, 1991; Neely, 1977). If M1 activation is automatic in response to action words, MEPs should be greater for action than for non-action verbs irrespective of the task, i.e. syllabic segmentation and semantic encoding.

Three separate experiments were carried out, in which TMS was applied at different timings after word onset (hereafter, post-stimulus). In Experiment 1, TMS was delivered 170 ms post-stimulus, as Event-related Potential (ERP) studies indicate that lexical access occurs already at 100-200 ms after the visual presentation of a word, in posterior regions

(Sereno, Rayner & Posner, 1998), and early semantic processes may start prior to 200 ms, in anterior regions (Pulvermüller, Harle & Hummel, 2001). In Experiment 2, TMS was triggered 350 ms post-stimulus, the time when the brain is thought to encode category-specific attributes of word meaning. Over the 300-350 ms latency range, in fact, a greater negativity (N400 component) in posterior regions was found for motor words compared to visual or abstract words (Kellenbach, Wijers, Hovius et al., 2004). With a similar latency, parietal and frontal positivity (P300-*like*) correlate with more fine-grained aspects of action-word meaning, such as the body segments involved in the implied action (Pulvermüller et al., 2001). In Experiment 3, TMS was applied 500 ms post-stimulus, i.e. in post-conceptual stages of word recognition.

Manipulating the delay between stimulus onset and magnetic stimulation across experiments served to investigate the time-course of M1 activity when participants performed different linguistic tasks. It also provided a methodological control for distracting/alerting effects and acoustic and tactile sensations associated with TMS. This control is based on the assumption that nonspecific effects of TMS are independent, whereas the behavioral effects are highly dependent on the precise interval between the event and the stimulation (Robertson, Théoret & Pascual-Leone, 2003). This procedure proves to be particularly appropriate for single-pulse TMS protocols, where stimulus and pulse are not delivered simultaneously (Walsh & Rushworth, 1999). In addition to MEPs, accuracy rates and reaction times (RTs) were collected as measures of participants' performance. Thus, besides identifying the mental operations that most likely modulate M1 (explicit or implicit encoding of motor content), insight was gained as to *when* M1 is recruited and *what* the nature of its relationship (causal?) is with linguistic performance.

3.2. Materials and Methods

3.2.1. Participants

Eleven individuals (7 men, 4 women; mean age = 24.5 ± 4 years) took part in Experiment 1, fourteen (5 men, 9 women; mean age = 25.7 ± 3.5 years) in Experiment 2, and eleven (5 men, 6 women; mean age = 26.3 ± 5 years) in Experiment 3. All the participants were right-handed (mean laterality quotient: Experiment 1, 83, range 65-100; Experiment 2, 80, range 60-100; Experiment 3, 86, range 65-100; Oldfiled, 1971), and had normal or corrected-to-normal vision. None of them had ever participated in a TMS experiment before. The participants were provided with an explanatory leaflet on TMS prior to the experiment, and filled in a questionnaire to ensure they were clear of contraindications to TMS (Wessermann, 1998). They confirmed their voluntary participation in writing, gave their written consent, and received compensation for their collaboration. The study was approved by the local ethics committee.

3.2.2. Stimuli

A norming study was conducted, in which a list of 375 verbs was shown to ten healthy university graduates or undergraduates who were not involved in the main experiments. This set of items was selected following the criteria of the linguistic tradition that distinguishes between action verbs referring to physical acts, and state or psychological verbs with no reference to a physical object (Taylor, 1977; Vendler, 1957). Participants were asked to decide whether each verb was related to an action, and for those that were judged so, to specify the associated body effector among the following alternatives: “upper limb”, “lower limb”, “head” or “whole body”. Verbs indicated as action-related by at least 80% of the panel were included in the TMS study, resulting in a final set of 256 items. This set included 128 action-verbs (64 associated with hand, e.g., *“mescolo”*, *I stir;* and 64 associated with other body effectors, *“salto”*, e.g., *I jump*) and 128 non-action verbs (e.g., “*medito*”, *I wonder*), presented in the first person singular of the present tense (see Appendix B). Fifty percent of verbs in each category (hand-action, non-hand action and non-action) were 3-syllable words; the remaining 50% was divided equally between 2- and 4-syllable words. In addition to length (i.e., number of syllables), hand-action, non-hand action and non action verbs were matched for written frequency (Dizionario di frequenza della lingua italiana, Consiglio Nazionale delle Ricerche, C.N.R.- I.L.C.), *t-tests* n.s.

3.2.3. Procedure

Participants performed two tasks, a semantic and a syllabic segmentation task, both involving action and non-action verbs. In the semantic task, they were asked to judge explicitly whether each verb implied a physical act (e.g. *“mastico”*, *I chew*) or not (e.g. *“adoro”*, *I adore*). In the syllabic-segmentation task participants decided on the number of syllables in each verb (3 or different from 3, i.e., 2 or 4). They sat on a height-adjustable chair at approximately 1 meter from a 17’ CRT screen that displayed the stimuli (font: Arial 38). The height of the chair was regulated to align the participants’ gaze with the centre of the display. Each trial began with an acoustic alert of 1500-Hz pure tone followed by a blank screen for 100 ms and then, by a fixation cross displayed in the centre of the screen for 1750 ms. After a 200-ms blank, the verb was projected in the centre of the screen for 375 ms, which gave the participants sufficient time to read the stimulus (Sereno et al., 1998). The verb was then substituted by three dots which were displayed for 3975 ms, to allow participants to provide the vocal response. On conclusion of this cycle, the next trial began. Each trial lasted 6200 ms from start to finish, a time sufficiently long to prevent interaction between consecutive TMS-pulses (Robertson et al., 2003).

Participants were instructed to give yes-or-no vocal responses to all the stimuli in both tasks. Half of the participants had to respond “yes” to action-related verbs and “no” to non action verbs in the semantic task, while in the syllabic task the yes-response was to correspond to 3-syllable verbs and the no-response to 2- or 4-syllable verbs. The other half of the participants received opposite instructions. The voice-onset time was recorded as a measure of RTs, using a microphone connected to the external response box of an E-prime PC-controlled system (Psychology Software Tools, Inc., Pittsburgh, PA). Response accuracy was recorded online by the experimenter who pressed one of the two mouse keys: the right for yes-responses and the left for no-responses.

The experiment consisted of four blocks of 64 trials each, for a total of 256 items: semantic task (64 verbs) and syllabic task (64 verbs) with TMS, and semantic task (64 verbs) and syllabic task (64 verbs) with sham stimulation, as control. I obtained 128 MEPs for each participant, as one magnetic pulse was applied for each item (pulses delivered during the two sham-blocks did not elicit MEPs). Hand-action, non-hand action and non-action verbs were randomly presented within each block, and a pause was administered after every 32 items. Participants were given four practice trials before each block. The order of the two tasks, the mapping of the verb type (action vs. non-action verb and 3 vs. 2/4 syllables) to a response (“yes” or “no”), and the verb lists in TMS and the sham condition were all counterbalanced across participants.

3.2.4. Single-pulse TMS protocol

TMS site and TMS intensity. Single-pulse TMS was applied to the left M1, using a Magstim 200 stimulator (Magstim Company, Withland, UK) connected to a figure-of-eight coil (70 mm in diameter). The coil was positioned by mapping the cortical representation of the first dorsal interosseus muscle (FDI) of the right hand, starting from the Cz reference point of the international 10-20 EEG system (Jasper, 1958) and moving the center of the coil approximately 6 cm to left, i.e., position C3/C4. The optimal scalp position for the induction of MEPs with maximum amplitude in the right FDI muscle was individuated for each participant. The coil rested tangential to the scalp surface. The target site was marked on the participant's head with a cosmetic pencil, and the coil was maintained in position by an articulated, metallic arm.

TMS intensity was adjusted to 120% of the motor threshold at rest, which is defined as the minimum intensity to evoke MEPs with ≥ 50 μV peak-to-peak amplitude in the relaxed FDI, in 3 out of 5 consecutive pulses (Rossini et al., 1994). The mean motor threshold for participants of Experiment 1 was 37.6 ± 1.4% of the maximum stimulator output. The means in Experiment 2 and 3 were 38.7 ± 1.4 and 38.9 ± 2.2 respectively. Participants were instructed to keep their right arm/hand and head motionless and the muscle relaxation was monitored throughout the experiment to check for involuntary movements. A visual feedback consisting of a muscle twitch, i.e. an abduction movement of the right forefinger, was always present after actual TMS delivery.

The same intensity was used for sham stimulation. In this condition, the coil was held perpendicularly to the surface of the scalp over the left M1, so that it mimicked the noise and the mechanical vibration of TMS, although no magnetic stimulation actually reached the scalp (Robertson et al., 2003). The order of the two stimulation conditions (TMS and sham) was counterbalanced across subjects according to Latin square. Participants were not informed whether they were going to receive TMS or sham stimulation.

Timing of TMS delivery. The same protocol was adopted for all three experiments, the only difference being the timing of the TMS application. In Experiment 1, TMS pulses were triggered 170 ms after the onset of each stimulus. In Experiments 2 and 3, TMS was applied 350 and 500 ms post-stimulus, respectively. TMS-induced MEPs were recorded by a pair of gold surface electrodes placed over the FDI (active electrode) and the metacarpophalangeal joint of the index finger (reference electrode). The ground electrode was placed on the ventral surface of the right wrist. The electromyographic (EMG) signal was amplified and filtered (bandpass 20 to 2000 Hz) through a Grass amplifier (P122 Series) and recorded with the Biopac system (MP150 model) at a sampling rate of 5 kHz. EMG data were transferred to a personal computer for offline analyses run with Matlab (The MathWorks, Natick, Massachusetts, USA). The delay of TMS delivery in each experiment was replicated in the sham condition.

3.3. Statistical analysis

The same statistical analyses on RT, accuracy and MEP data were performed in Experiments 1-3 as the experimental design itself was identical. Practice trials, trials with RTs shorter than 100 ms and longer than 2500 ms, and those in which the participants made errors in the syllable count or in semantic judgement (according to the norming study), were excluded from the offline analysis. Mean RTs and accuracy were submitted to a 2 x 2 x 3 analysis of variance (ANOVA), with TMS condition (left M1 vs. Sham), task (semantic vs. syllabic) and verb category (hand-action vs. non-hand action vs. non action) as within-subjects factors.

Notice that, although both action-related, hand-action and non-hand action verbs were considered as separate levels of the verb-category factor. Indeed, while some studies reported increased hand-M1 activity associated with rather heterogeneous stimuli (e.g., action verbs related to several body effectors and nouns of manipulable objects; Oliveri et al., 2004; concrete nouns such as “house” and “collar”; Meister et al., 2003), other studies showed that M1 was activated in a somatotopic fashion, according to the body-effector of the implied-language action (see Pulverüller, 2005). Given the uncertainty on the involvement (general or specific) of hand-M1 in language, I considered, in this analysis, that TMS to the hand-M1 might affect differently hand- and non-hand action verbs.

The peak-to-peak amplitude (mV) of each MEP was computed by an automatic Matlab script and then normalized. MEP amplitudes inferior to 0.1 mV were not included. Z-scores were calculated using the individual mean and standard deviation of each mini-block of 32 trials. Given the high variability of individual MEPs, Z-scores were used to increase the comparability of mini-blocks, within- and between-participants. Normalized MEP peak-to-peak amplitudes were subjected to a 2 x 2 repeated measures ANOVA with task (semantic vs. syllabic) and verb-category (action hand-action vs. non-hand action vs. non-action) as within-subject factors. All post-hoc comparisons between single factors were carried out using LSD Fisher’s test ($\alpha \leq .05$).

3.4. Results

Table 1, 2 and 3 summarize the results of the RT, accuracy and MEP analyses for the three experiments.

3.4.1. Experiment 1: M1 activity during lexical access (TMS 170 ms post-stimulus)

RTs. The main effect of task was significant, $F(1,10)=6,27$, $p=0.03$, revealing that semantic judgments were given, on average, 106 ms faster than syllabic judgements. The effect of category was also significant, $F(2,20)=10.33$, $p<0.001$, with action verbs (both hand and non-hand related) being processed faster than non action verbs (ps<0.001). The task x category interaction was significant, $F(2,20)=10.33$, $p<0.001$, suggesting that the effect of verb category was dependent on the type of task performed (see Figure 1A). Post-hoc tests revealed that, in the semantic task, participants responded faster to hand- and non-hand action verbs than non action verbs, (ps<0.001), with no difference between the two action-verb categories ($p>0.1$). Instead, the three verb categories did not differ in the syllabic task (ps>1). This effect was independent of TMS, as the interaction between stimulation condition, task and category did not approach significance, $F(2,20)<1$, *n.s.* Thus, the semantic encoding was faster for action than for non-action verbs; the syllabic segmentation did not give rise to difference across verb categories.

Accuracy. The effect of task resulted significant, $F(1,10)=5.13$, $p<0.05$, the semantic judgments being more accurate than the syllabic judgments. There was a trend for the interaction between task and category, $F(2,20)=2.77$, $p=0.08$ (see Figure 2A). Post-hoc comparisons showed that semantic judgments were more accurate on the two action-verb categories, relative to non-action verbs (*p*s<0.05), whereas the syllabic task was performed equally well with the three categories (*p*s>0.1). This pattern of results allowed us to rule out that a speed-accuracy trade-off could explain participants' performance.

MEPs. The analysis of the normalized MEPs led to no significant effect or interaction (all *p*s>0.2).

3.4.2. Experiment 2: M1 activity during semantic processing (TMS 350 ms post-stimulus)

RTs. The effect of task was significant, *F*(1, 13)=13.53, *p*=0.003, as well as the effect of category, *F*(2,26)=12.00, *p*=0.001. RTs in the syllabic task were slower than those in the semantic task, and hand-action verbs were processed faster than non-hand action and non-action verbs (*p*s<0.01). The task x category interaction was significant, *F*(2, 26)=10.4, *p*<0.01 (see Figure 1B). In the semantic task, hand-action and non-hand action verbs were processed faster than non-action verbs (*p*s<0.01), and hand-action verbs were judged also faster than non-hand action verbs (*p*<0.01). The three categories did not differ in the syllabic task (*p*s>0.2). The three-way interaction between TMS, task and category was also significant, *F*(2, 26)=4,27 *p*=0.02 (Table 1), showing that in the semantic task, TMS further delayed participants' performance on non-action verbs compared with the sham condition (*p*=0.02). No TMS effect was observed in the semantic task for the two action-verb categories (*p*s>0.1). Conversely, in the syllabic task TMS slowed down responses to both action-verb categories compared with the sham condition (*p*<0.05).

Thus, like in Experiment 1, here, participants processed action verbs faster than non-action verbs in the semantic but not in the syllabic task. In addition, the three-way interaction revealed that TMS delivery to M1 delayed participants' responses when they performed the semantic task on non-action verbs, and when they performed the syllabic task on action verbs.

Accuracy. The effect of TMS was significant, *F*(1, 13)=6,83, *p*=0.02, participants being less accurate during TMS than sham stimulation. The main effect of category was also significant, *F*(2, 26)=10,59, *p*<0.001, whereby hand-action verbs were processed more accurately than non-hand action and non-action verbs (*p*s<0.001). There was also a significant task x category interaction, *F*(2, 26)=4,71, *p*=0.02 (see Figure 2B). Accordingly, participants were more accurate with hand-action than non-hand action and non-action verbs, in the semantic task (*p*s=0.001), while no difference was found across verb-categories in the syllabic task (*p*s>0.1). The agreement between accuracy and RT results excluded the speed-accuracy trade-off effect as explanation of participants' performance.

MEPs. The ANOVA revealed only a trend for the effect of category, *F*(2, 26)=3,26, *p*=0.05, according to which MEPs were the greatest for non-action verbs. However, the lack of interaction between task and category, *F*(2, 26)<1, *n.s*., did not allow any obvious conclusion concerning the involvement of left M1 in word processing.

3.4.3. Experiment 3: M1 activity during post-conceptual processing (TMS 500 ms post-stimulus)

RTs. The analysis revealed a significant main effect of task, *F*(1, 10)=13.95, *p*<0.01, the semantic task being faster than the syllabic, and a main effect of the verb-category, *F*(2, 20)=6.03, *p*<0.01, whereby hand-action verbs were processed faster than non-hand and non-action verbs (*p*s<0.05). Although the interaction between task and category did not approach significance, *F*(2,20)<1, n.s., the pattern of participants performance was qulitatively comparable to that of Experiments 1-2 (see Figure 1C).

Accuracy. The ANOVA revealed a significant main effect of task, *F*(1,10)=5,27, *p*=0.04: the semantic task was performed better than the syllabic task (0.90 ± 0.02 vs. 0.83 ± 0.004). Qualitatively, the pattern of participant's performance in the two tasks, with the three verb-categories was consistent with that of Experiments 1-2 (see Figure 2C), but no interaction approached significance (*p*s>0.1).

MEPs. The effects of task and category were not significant (*p*>.05), but the interaction between the two factor was, *F*(1, 10)=8.872, *p*=0.01. Post-hoc tests showed that the semantic processing of hand-action verbs elicited greater MEPs, as compared with non action verbs (*p*=0.03), whilst the MEP amplitude for non-hand action verbs did not differ from that for non-action verbs (*p*>0.1). In the syllabic task, M1 excitability verbs was significantly smaller following hand-action than non-hand action and non-action verbs (*p*s<0.03). Again, there was no difference in the MEP amplitude between non-hand action and non-action verbs (*p*=0.6).

A difference was also observed in the MEP amplitude between the semantic and syllabic processing of hand-action verbs (*p*=0.001): M1 activity significantly increased and decreased, depending on whether the same verbs were processed semantically and syllabically, respectively. A similar difference between tasks was not observed for the other two verb-categories (*p*s>0.1). Thus, the enhancement of M1 activity occurred only when participants explicitly encoded the content of the hand-action verbs, but not when they encoded their phonology. In the latter condition, M1 activity resulted to be rather inhibited.

Table 1. Mean RTs (ms) in all experimental conditions of Experiments 1-3.

		Semantic task			Syllabic task		
		Hand-act	Non-hand act	Non-act	Hand-act	Non-hand act	Non-act
Experiment 1	TMS	730	726	853	948	905	909
	Sham	722	705	882	818	844	836
Experiment 2	TMS	781	845	**962**	**1156**	**1166**	1105
	Sham	774	848	**886**	**1065**	**1101**	1111
Experiment 3	TMS	627	683	713	843	856	862
	Sham	560	612	683	767	814	762

Tabled mean RTs (ms) following the semantic and the syllabic processing of the hand-action (*Hand-act*), the non-hand action (*Non-hand act*) and the non action (*Non-act*) verbs, during TMS and sham stimulation, in Experiments 1-3. The regions in bold type showed the only significant differences between TMS and sham (Experiment 2).

Table 2. Mean Accuracy (proportion of correct responses) in all experimental conditions of Experiments 1-3.

		Semantic task			Syllabic task		
		Hand-act	Non-hand act	Non-act	Hand-act	Non-hand act	Non-act
Experiment 1	TMS	0.93	0.93	0.83	0.87	0.84	0.87
	Sham	0.94	0.91	0.84	0.86	0.86	0.86
Experiment 2	TMS	0.97	0.88	0.88	0.89	0.86	0.88
	Sham	0.99	0.92	0.88	0.93	0.90	0.93
Experiment 3	TMS	0.94	0.90	0.84	0.83	0.84	0.82
	Sham	0.93	0.90	0.90	0.84	0.84	0.82

Tabled mean accuracy (proportion of correct responses) following the semantic and the syllabic processing of the hand-action (*Hand-act*), the non-hand action (*Non-hand act*) and the non action (*Non-act*) verbs, during TMS and sham stimulation, in Experiments 1-3. A difference between TMS and sham stimulation was never observed.

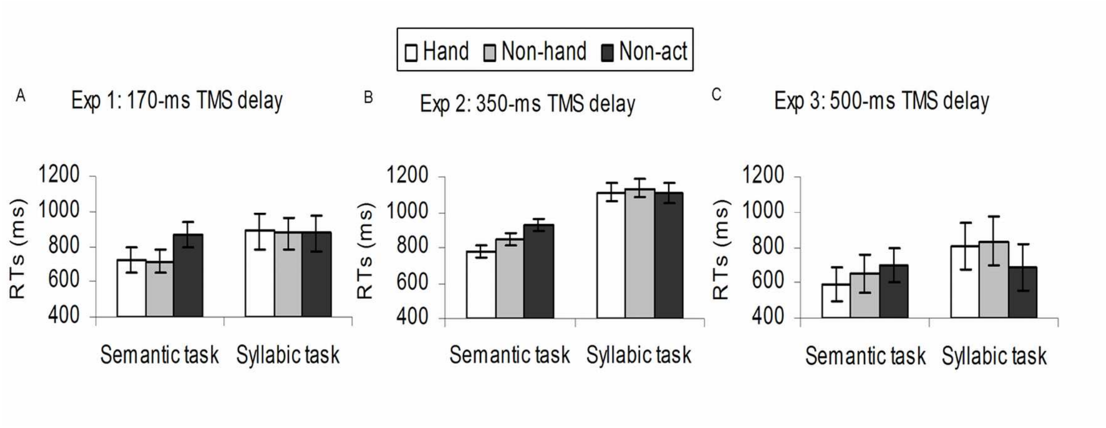


Figure 1. Mean RTs (ms) as a function of the tasks (semantic and syllabic) for the verb categories (hand-action, "*hand*"; non-hand action, "*non-hand*"; and non action, "*non-act*"). Vertical bars denote the Standard Error of the mean. In Experiment 1 **(A)** and 2 **(B),** both action-verb categories were processed faster than non-action verbs in the semantic task; RTs for the three categories did not differ in the syllabic task. In Experiment 3 **(C),** the pattern of performance was similar to that of Experiments 1-2, although the interaction did not approach significance.

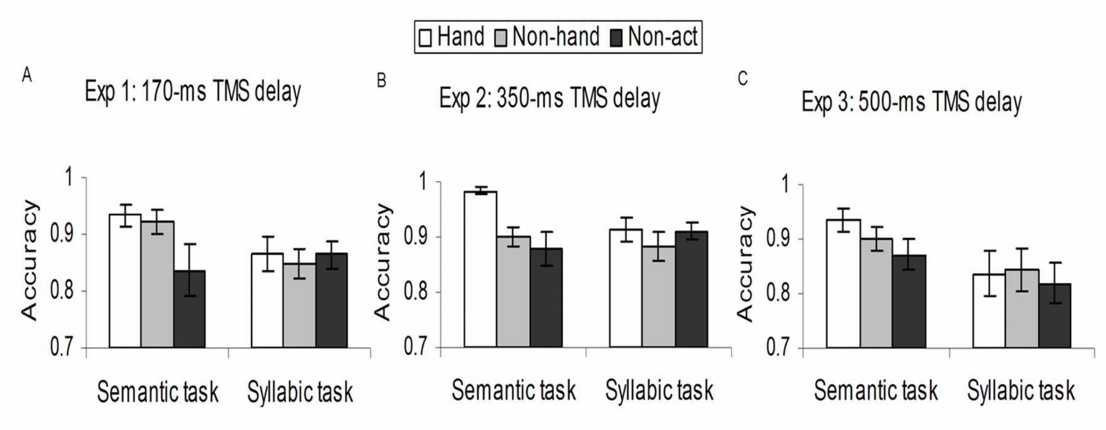


Figure 2. Experiment 2: Mean accuracy (proportion of correct responses) as a function of the tasks (semantic and syllabic) for the verb categories (hand-action, "*hand*"; non-hand action, "*non-hand*"; and non action, "*non-act*"). Vertical bars denote the Standard Error of the mean. **(A)** Experiment 1: in the semantic task, both the action-verb categories were processed more accurately than the non action verbs; accuracy did not differ for the three verb categories in the syllabic task. **(B)** Experiment 2: hand-action verbs were processed more accurately than the other verb categories in the semantic task; the three categories did not differ in the syllabic task. **(C)** Experiment 3: qualitative, the pattern of performance was consistent with that of Experiments 1-2, although the interaction did not approach significance.

Table 3. Means of normalized (sem) MEP peak-to-peak amplitudes in all experimental conditions of Experiments 1-3.

	Semantic task			Syllabic task		
	Hand-act	Non-hand act	Non-act	Hand-act	Non-hand act	Non-act
Experiment 1	-0.05 (0.05)	0.06 (0.08)	-0.02 (0.06)	0.03 (0.07)	-0.09 (0.06)	-0.003 (0.03)
Experiment 2	0.04 (0.05)	-0.17 (0.07)	0.06 (0.04)	-0.04 (0.08)	-0.09 (0.09)	0.06 (0.04)
Experiment 3	**0.12 (0.04)**	0.07 (0.08)	-0.07 (0.04)	**-0.19 (0.07)**	0.01 (0.07)	0.05 (0.05)

Tabled mean normalized MEP amplitude following the semantic and the syllabic processing of the hand-action (*Hand-act*), the non-hand action (*Non-hand act*) and the non action (*Non-act*) verbs in Experiments 1-3. The regions in bold type showed the facilitation in the semantic task and the inhibition in the syllabic task, for hand-action verbs only, as compared to non-action verbs (Experiment 3). A similar dissociation between tasks was not observed for the other verb categories in any of the three experiments.

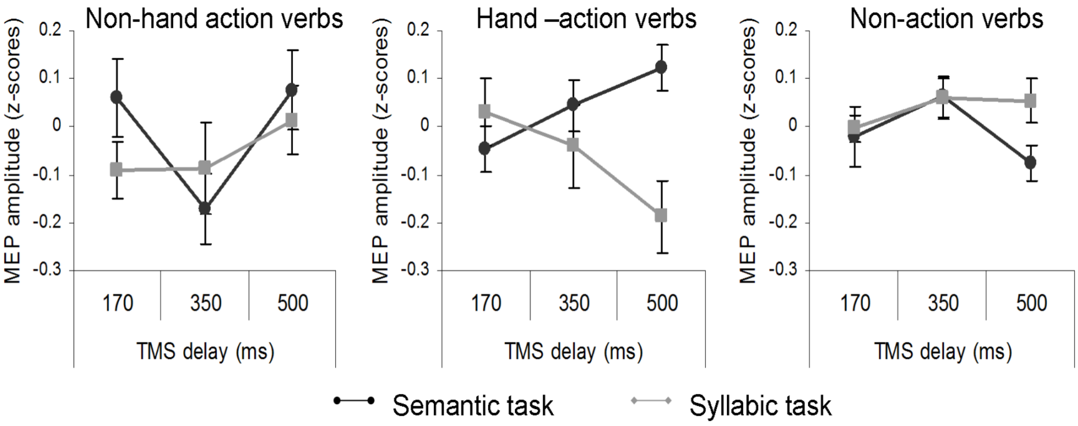


Figure 3. Analysis of normalized MEP peak-to-peak amplitude for the verb categories (hand-action, non-hand action and non action verbs) as a function of the tasks (semantic and syllabic) and the timing of TMS delivery (170, 350, 500 ms). At 500 ms post-stimulus, MEP amplitude increased when the participants performed the semantic task on hand-action verbs compared with non-action verbs. It decreased, relative to non-action verbs, when they performed the syllabic task on the hand-action verbs. The difference in MEP amplitude between the two task was significant for hand-action verbs. A similar dissociation was never observed for the non-hand action verbs. Vertical bars denote the Standard Error of the mean.

3.4.4. Between-subjects analysis

MEP data from all the three experiments were subjected to an ANOVA with factors, 2 task and 3 verb-category, manipulated within subjects, and 3 timing of TMS delivery as a between-subjects factor. This analysis was performed in order to investigate the time-course of M1 activity associated with each verb category during their semantic and syllabic processing. The three-way interaction between task, category and TMS timing approached significance, $F(4,66)=2,1656$, $p=0.08$ (see Figure 3). Post-hoc comparisons revealed a different pattern of M1-activity for hand- vs. non-hand action verbs, when compared with non-action verbs.

Hand-action verbs. At the first two timings of TMS delivery (i.e., 170 and 350 ms post-stimulus), MEP amplitude for hand-action verbs was not different from that for non-action verbs, in either task (all ps>0.3). Moreover, at these latencies, MEP amplitude following the semantic and the syllabic processing of hand-action verbs did not differ ($p>0.3$). When recorded at 500 ms post-stimulus, the difference between MEPs for hand-action verbs and non-action verbs approached significance in the semantic task ($p=0.07$), and reached significance in the syllabic task ($p=0.03$). Moreover, M1 activity for hand-action verbs resulted greater in the semantic than in the syllabic task ($p<0.01$). Confirming the results of the individual experiments, this analysis suggests that M1 activity is modulated by hand-action verb processing only during post-conceptual stages of word recognition (500 ms post-stimulus), with the direction of the modulation (increase or decrease) depending on the task-demand.

Non-hand action verbs. The pattern of M1-activity following non-hand action verbs proved to be different from that of hand-action verbs. At 350 ms, I observed a dramatic decrease of MEP amplitude for non-hand action verbs relative to the other two verb-categories, in the semantic task only (ps<0.05). However, besides this effect, the MEP amplitude associated with non-hand action verbs never differed from that of non-action verbs in either task condition, and at any time interval (all ps>0.2). No difference was found when the same verbs were subjected to the two tasks (p=0.5). In other words, the difference in MEP amplitude between semantic and syllabic tasks, I observed for hand-action verbs at 500 ms post-stimulus, never occurred for non-hand action verbs.

The results of the between-subject analysis confirmed those of the single experiments. The effect of action-verb processing on M1 activity was observed at 500 ms post-stimulus when hand-M1 activity for hand-action verbs increased during the semantic task, and decreased during the syllabic task. Motor activation associated with action verbs did not occur within 350 ms, i.e. in the time interval for lexical-semantic access. In other words, hand-M1 activity increased only after the lexical-semantic access to representations of hand-action verbs, and only when the task explicitly required processing the motor information associated with a word. At this latency, the syllabic segmentation of the same hand-related items led to an inhibition of motor activity. The fact that this pattern was observed only with hand-action verbs indicates that the phenomenon of language-induced motor activity occurs in a somatotopic fashion, reflecting the implied-language content.

The pattern of M1 activity associated with non-hand action verbs appears quite unclear. No conclusion can be drawn, also because it is not possible to establish whether any MEP effect for this verb-category actually resulted from hand-M1 activity, or from activity in other M1 sites (e.g., leg- or face-area) spreading to hand-M1, through horizontal cortico-cortical connections (Schieber, 2001). On the other hand, the different apttern of M1 activity associated with the processing of hand-action and non-hand action verb, suggests that the interaction between action-word meanings and motor system is sensitive to the somatotopic organization of M1 (Pulvermüller, Hauk, Nikulin & Ilmoniemi, 2005).

3.5. Discussion

In this chapter, TMS has been used to measure the excitability of the participants' left M1 while they processed action verbs. RTs and accuracy were analysed to assess whether action verb processing was significantly affected by TMS interference with M1 activity. The results challenge the view that motor activity is automatic in response to action-words, and crucially contributes to their processing.

Participants' performance showed that action verbs (both hand and non-hand related) were processed faster (and better) relative to non-action verbs, in the semantic but not in the syllabic task (Experiments 1-2). Relative to sham, TMS delayed the semantic judgments of non-action verbs and the syllabic segmentation of action verbs when applied 350 ms post-stimulus (Experiment 2). Although the semantic processing was sometimes faster and more accurate for hand-action than for non-hand action verbs (Experiments 2-3), these two categories interacted similarly with the other factors, and differently with respect to non-action verbs. MEP results showed no enhancement of hand-M1 activity within the response latency critical for lexical-semantic processing (Experiments 1-2). The hand-M1 activity was modulated by the word content only when measured at 500 ms post-stimulus. In particular, relative to non-action verbs, M1 activity increased when participants performed the semantic task on hand-action verbs, and decreased when they performed the syllabic task on the same items (Experiment 3). A similar pattern was not observed for non-hand action verbs: M1 activity associated with these stimuli did not differ from that associated with non-action verbs, both in the semantic and in the syllabic task. The MEP analysis, where the timing of TMS delivery was included as a between-subjects factor, confirmed the findings of the three individual experiments.

3.5.1. Verb processing with and without M1 TMS

The overall advantage of action verbs relative to non-action verbs is well established in the literature on lexical-semantic processing. Using ERP, Kellenbach *et al.* (2004) found that the earliest effect associated with the processing of semantic attributes was elicited by motor words at about 250 ms, compared with abstract and visual words. Notice, however, that while this study revealed a temporal precedence of cortical responses to motor attributes, it found no difference in the cortical networks involved in processing the different word categories. Accordingly, behavioral studies on healthy participants showed that the comprehension of language with associative-functional (motor) attributes is faster than the processing of items with non-motor (visual) attributes (Laws, Humber, Ramsey & McCarthy, 1995). Following these findings, Laws *et al.* (1995) proposed that the former category may be characterized by a more extensive and complex cortical representation than the other categories, possibly because the motor information “attached” to action-word representations provides a relational context - including path, manner, results and instruments - that instantiates and enriches their conceptualization. This possibility well matches the classical concreteness and imageability effects, whereby more concrete and imaginable words are processed faster, which characterizes word retrieval and recognition of both healthy and brain-damaged individuals (Berndt, Haendiges, Burton & Mitchum, 2002; Luzzatti, Raggi, Zonca et al., 2002; see Paivio, 1971).

In Experiment 2 two further effects were observed: compared with the sham condition, M1 TMS delayed RTs in (1) the semantic encoding of non-action verbs, and (2) the syllabic segmentation of action-verbs (both hand and non-hand related). These results, which were quite unexpected and only partial (i.e., no facilitation was found for action verbs in the semantic task), can be tentatively interpreted in the framework of *congruence effects* between stimulus and response or between concurrent stimuli (Kornblum et al., 1990). In general, when multisensory stimuli co-occur, the information they convey is combined to generate the response (Laurienti, Kraft, Maldjian et al., 2004). Thus, the former effect may be the consequence of accessing the semantics of words with non-motor content, while a concurrent motor stimulation was provided. By eliciting overt hand movements, TMS might have acted as an incongruent prime-*like* stimulus when participants processed non-action word content (see Pulvermüller et al., 2005; Tomasino et al., 2008)[2]. A similar mechanism possibly explains the latter effect. Here, the co-occurrence of motor stimulation (or the view of hand movement elicited by TMS) and an action verb, might have facilitated the automatic activation of the *task-irrelevant* motor information associated with the word, which had to be inhibited before responding, with a processing

---

[2] The reason why we failed in detecting a facilitation of the semantic processing of hand and non-hand action-verbs might be that, as these were the fastest of the experimental conditions, RTs could not be further shortened - with a statistically significant time period - by a congruent stimulation.

cost in terms of RTs (Eimer, Hommel & Prinz, 1995; Kornblum, Hasbroucq & Osman, 1990; Lu & Proctor, 1995). The assumption here is that, although syllabic segmentation primarily involved phonological computations, automatic access to semantics occurs whenever a word is read (MacLeod, 1991; Neely, 1977).

Congruence effects suggest that a stimulus-response or a stimulus-stimulus (as in our case) set overlap for any dimension, and the two underlying systems interact at some *unspecified* level (Kornblum et al., 1990). In the context of our study, these effects were observed just at the latency (350 ms) when word's motor or non-motor attributes are alleged to be processed, but were not accompanied by a specific M1 activation. Thus, while they may suggest an interaction between language and motor systems, such interaction seems to occur at the stage of processing when abstract, conceptual representations of words and actions are contacted, with no involvement of lower-level motor programs.

3.5.2. M1 activity in different stages of action and non-action verb processing

M1 activity increased when TMS was applied 500 ms post-stimulus, only when participants performed the semantic task with hand-action verbs, suggesting that language-induced motor activation depends upon the *explicit retrieval* of the motor content of the word. On the contrary, in the syllabic task, I detected a decrease of M1 activity following hand-action verbs, which may reflect the inhibition of motor processes not required by the task.

The increase and the decrease of corticospinal excitability have been previously associated with facilitation and inhibition of motor processes, respectively (Koch, Franca, Del Olmo et al., 2006; Reynolds & Ashby, 1999). In particular, Koch *et al.*'s (2006), in a paired-pulse TMS study on the functional connectivity between premotor cortex and M1, found that MEP amplitude increased when a response had to be performed, and decreased when a response was one of the possible alternatives, but not the correct one, and therefore, had to be suppressed. Interestingly, M1 activity was modulated, in a top-down manner, by the activity of higher-level motor areas selecting the response, among the alternatives, to satisfy the task demand (Koch et al., 2006). Similarly, in our study, the modulation (increase or decrease) of hand-M1 activity appears as strongly constrained by the demand of the task.

This chapter contains the first study in which M1 activity has been measured at different timings, during different linguistic tasks involving the very same stimuli, and in which the effects of its temporary disruption have been tested on participants' behavior. According withy previous studies, our results show that the motor system does activate in action word processing. However, relative to previous studies, ours *adds* that this activity depends on whether the task required explicitly processing the motor content of the word, or not. Moreover, the late *co*-occurrence of M1 activity, together with the lack of effect on participants' performance, when TMS interfered with M1 activity, suggests that this region is not part of network subserving the lexical-semantic encoding of action-words.

A previous TMS study, in which M1 activity was tested at different time intervals while participants were reading concrete nouns aloud, found enhancement at 600 ms post-stimulus and later, but not before (Meister, Boroojerdi& Foltys, 2003). To the best of our knowledge, this time interval falls far beyond that for lexical-semantic encoding, within post-conceptual stages. The existence of post-conceptual stages of language processing has been suggested by the activation of a fronto-temporal network, after the lexical-semantic access, which may sustain the supramodal contextual integration of different levels of information from different modalities (Marinkovic, Dhond, Dale et al., 2003). In the case of action verbs, the retrieval of conceptual representations may lead to the implicit activation – or generation - of motor images that, in turn, activate M1 (e.g., Kosslyn, Thompson, Wraga & Alpert, 2001). This form of imagery is known to be engaged automatically as a strategy to perform tasks with sensorimotor components that "cannot easily be inferred from […] verbal material" (Kosslyn, Behrmann & Jeannerod, 1995; p. 1337) or, I add, whose recall is more effective via simulation. The time at which language-related M1 activation (500 ms) was found in the present study, fell fairly within the lengthy interval for imagery processes (from 400 ms to 750 or more; Ganis, Keenan, Kosslyn & Pascual-Leone, 2000; Iwaki, Ueno, Imada & Tonoike, 1999). Finally, M1 is involved in motor imagery in a somatotopic fashion (e.g., Ehrsson et al., 2003), therefore, it is not surprising that the effect I reported was specific for hand-action verbs, when only hand-M1 was stimulated.

M1 activation would *result from* understanding action verbs rather than *contributing to* it: it may reflect post-conceptual operations resulting from the explicit retrieval of motor information associated with a word. Here, I suggest that the strategic function of motor imagery can provides an insight as to why language processing goes beyond the completion of lexical-semantic encoding and engages the motor system.

Chapter 4.

“She” is not like “I”: Agent-dependent motor activity in verb processing

4.1. Introduction

Embodied cognition holds that action understanding results from the automatic mapping of a perceived action onto the perceiver’s motor system (“self-other shared representation”), where a simulation of that action is carried out (Rizzolatti, Fogassi, & Gallese, 2001). This *mirror matching* may be accomplished by neurons in the motor circuits that “respond to the action itself, rather than to the body (or the person) who performs that action” (Jeannerod, 2004, p.423). As activations in left motor and premotor regions in humans have been reported not only when an action was observed (Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995), but also when a presented word implied an action (Hauk, Johnsrude, & Pulvermüller, 2004), mirror matching has been generalized to language. Lexical-semantic processing of action words, like the processing of any other action-stimulus, may depend upon the early (within 250 ms) and automatic activation of agent-neutral motor representations via motor simulation (Pulvermüller, 2005). Moreover, the idea of “self-other shared representation” grounding the mirror matching implies that the motor system responds equally to words with self- and other-related action meaning.

While the motor facilitation for self versus others’ action has been widely studied in action observation (Decety & Chaminade, 2003), only Tomasino, Werner, Weiss and Fink (2007) have explored this phenomenon using word as stimuli The authors reported no difference in BOLD signal in the primary motor cortex (M1), when participants imagined the content of action phrases adopting the first-person (1P) or the third-person (3P) perspective. However, as participants had to report whether the mental scene took place indoor or outdoor, it is possible that they failed to focus on the subject of the verb and used the egocentric perspective by default, as it is likely to occur during simulation (Willems, Hagoort & Casasanto, 2010).

Soliciting the integration of the subject with the meaning of an action verb can crucially contribute to establish how self and others’ actions modulate motor activity. In action observation, the diversity in stimulus orientation between 1P and 3P actions can produce, on its own, different effects on the motor system (Saxe, Jamal, & Powell, 2006), and it is not easy to isolate this visual effect from the effect of the agent on the system. In contrast, words enjoy the advantage of holding constant visual inputs associated with either action perspective.

In this chapter I report a study in which transcranial magnetic stimulation (TMS) was combined with a linguistic task to test word-related motor facilitation. Participants were requested to read and report the subject of action and nonaction verbs presented in 1P (*afferr-o*) or 3P (*afferr-a*). TMS was applied to the left hand-M1 to measure cortico-spinal excitability, defined by the amplitude of TMS-induced motor-evoked potentials (MEPs) in peripheral muscles responding to the stimulated area. This approach permitted the investigation of two hierarchical questions. First, are motor responses to action verbs automatic and independent of the subject of the action? A positive answer to this question would support the hypothesis that neurons with *mirror* properties contribute to action language processing. Alternatively, is motor activation greater for self-referential or for other-referential action verb meaning?

4.2. Materials and Methods

4.2.1. Participants

Sixteen native-Italian university graduates and undergraduates (8 female; 20-35 years) participated in the experiment. All were right-handed (laterality quotient: 80-100; Oldfield, 1971) with normal or corrected-to-normal vision. Before the experiment, they received information about TMS, compiled a questionnaire to ensure they were clear of contraindications (Wassermann, 1998), and confirmed their voluntary participation in writing. The study was approved by SISSA Ethics committee.

4.2.2. Stimuli

Sixty-four Italian verbs associated with hand-actions ("*mescolare", to stir*), and 64 nonaction verbs (state/psychological verbs; "*meditare", to wonder*) were used, each presented in both 1P and 3P of the present tense, yielding a total of 256 items. Verbs were chosen from a larger database used in a previous study (see Chapter 2), where 375 verbs were selected according to the criteria of linguistic tradition (e.g., Taylor, 1977), and then assessed by a panel of 10 judges for their semantic association with action and the body part involved. The selected experimental stimuli were divided in two equivalent lists, matched for length (number of graphemes) and written frequency (Laudanna, Thornton, Brown, Burani, & Marconi, 1995), in which each verb appeared only in one of the two possible forms (either 1P or 3P). The present tense inflectional morphology of all the verbs was regular.

4.2.3. Procedure

Participants sat on a height-adjustable chair at 1 meter from a LCD screen that displayed the stimuli (font: Arial 45); they had to read each verb and state whether the subject was the 1P or 3P. They were encouraged to read the verbs accurately in order to perform a successive recognition test. Each trial began with a 1500-Hz pure tone followed by a 100-ms blank screen, after which a central fixation was displayed for 1450 ms. The screen went blank again for 50 ms, then the verb appeared in the centre for 350 ms. Finally, three dots were displayed for 4075 ms, soliciting the participants’ response. On conclusion of this cycle, the next trial began. Each trial lasted 6025 ms, a time sufficient to prevent interaction between consecutive TMS-pulses (Robertson, Théoret & Pascual-Leone, 2003). Half of the participants were instructed to respond */ba/* when the subject was 1P, and */da/*, when the subject was 3P. The remaining participants were given opposite instructions. These syllables were preferred to the obvious “*I*” and “*s/he*” in order to avoid response bias due to phonological difference between the two responses. The voice-onset time was recorded as a measure of RTs, using a microphone connected to the external response box of an E-prime PC-controlled system (Psychology Software Tools Inc., Pittsburgh, PA). Response accuracy was recorded online by an experimenter pressing the right mouse-key for 1P-responses and the left one for 3P-responses. Each participant performed a 8-trials training phase and then 2 blocks, one with M1 TMS and one with sham stimulation, each comprising a list of 128 items (32 1P-action verbs, 32 3P-action verbs, 32 1P-nonaction verbs and 32 3P-nonaction verbs), for a total of 256 randomized trials. The mapping between the list in a block and the stimulation condition (TMS or sham) was counterbalanced across subjects. A pause was allowed every 32 trials. The experimental design was 2 x 2 x 2 with factors TMS (M1 TMS and sham), person (1P and 3P) and verb category (hand-action and nonaction), all manipulated within-subjects.

4.2.4. TMS protocol

Site and intensity. Single-pulse TMS was applied to the left M1, using a Magstim 200 stimulator (Magstim Company, Withland, UK) connected to a figure-of-eight coil, positioned over the cortical representation of the right-hand first dorsal interosseus muscle (FDI). This site was mapped starting from the Cz reference point of the international 10–20 EEG system (Jasper, 1958), and moving approximately 6 cm leftward, i.e. position C3/C4. The optimal scalp position for the induction of maximum MEP amplitude in the right FDI muscle was individuated for each participant and marked with a cosmetic pencil. The coil, tangential to the scalp surface, was maintained in position by an articulated arm. The TMS intensity was adjusted to 120% of the motor threshold at rest (mean threshold: 40±2.8% of the maximum stimulator output), defined as the minimum intensity to evoke MEPs with $\geq$50 μV peak-to-peak amplitude in the relaxed FDI, in at least 3 of 5 consecutive pulses. Participants were instructed to keep their right arm/hand and head motionless and were monitored throughout the experiment to control muscle relaxation and the presence of a muscle twitch, an abduction movement of the right forefinger, after each M1-TMS delivery.

The same magnetic pulse intensity was used for both TMS and sham stimulation. In sham, the coil was held perpendicularly to the scalp surface over the left M1. This condition provides a control for nonspecific effects of TMS, as it mimics the characteristic TMS noise and the mechanical vibration, without magnetic stimulation reaching the scalp (Robertson et al., 2003). The order of the two stimulation conditions was counterbalanced across the participants, who were not informed whether they were going to receive TMS or sham stimulation. TMS-induced MEPs were recorded by a pair of gold surface electrodes placed over the FDI (active electrode) and the metacarpophalangeal joint of index finger (reference electrode). The ground electrode was placed on the ventral surface of the right wrist. The electromyographic (EMG) signal was amplified and filtered (bandpass 20-2000 Hz) through a Grass amplifier (P122 Series), and recorded with the Biopac system (MP150 model) at a sampling rate of 5 kHz. EMG data were transferred to a personal computer for offline analyses with Matlab (The MathWorks, Natick, Massachusetts, USA).

TMS timing. In both stimulation conditions, TMS was delivered 250 ms after the stimulus-onset. This timing was set empirically, on the basis of pilot tests. In the first pilot, the approximate timing for the retrieval of referential information was estimated implementing the same experimental paradigm as in the main TMS experiment, except that TMS was not used and participants (9 right-handed native-Italians, 7 female, 20-35 years) had to respond */io/* for 1P verbs and */lui/* for 3P verbs. The mean RT for referential judgments across all conditions was 288 ms. This delay is consistent with both electrophysiological studies reporting a negative deflection before 300 ms after word-onset, associated with referential processes (Van Berkum, Koornneef, Otten, & Nieuwland, 2007) and electrophysiological responses in frontocentral regions associated with action-word processing (Pulvermüller, 2005). I also found that 1P verbs were processed faster than 3P verbs, $F_{(1,8)}=9.71$, $p=0.01$. As this result could be biased by phonological difference in vocal responses, a second pilot was run with 8 new participants (5 female, 20-31 years), who responded with the syllables */ba/* and */da/*, as in the TMS experiment. The mean RT was 406 ms, and 1P verbs were again processed faster than 3P verbs, $F_{(1,7)}=22.87$, $p<0.01$[1]. While the increase of mean RTs in the latter experiment probably reflected additional processing needed to map the intended responses to the appropriate label, the pattern of results confirmed the temporal advantage in processing 1P over 3P verbs.

4.2.5. Recognition test

Participants performed a recognition test after the TMS session, to test whether they had actually processed the whole verbs and not just its last part (i.e., the verb suffix) that is often sufficient in Italian for extracting information about the subject. The experimental setup was the same as before, except that TMS was removed from the participant’s head

---

[1] Mean RTs to the verbs in the two experiments were tightly correlated ($N=256$; $r=0.24$, $p>0.0001$).

and turned off. Eighty verbs were randomly presented, one at a time, on the computer screen in their infinitive form: 40 (20 action- and 20 nonaction-related) were selected from the experimental stimulus-set (“old” list); the remaining 40 were new action (N=20) and nonaction (N=20) verbs (“new” list). The old and new verb lists were matched for frequency and length. Each trial began with a fixation cross remaining on the screen for 400 ms and followed by the verb, shown up to 20 sec. Participants were instructed to read and decide whether the verb had been presented during the TMS section, by pressing the right mouse-key for yes-response and the left for no-responses. They were encouraged to favor response accuracy over speed, and received feedback about the correctness of response for each trial.

4.2.6. Analysis

The criterion for including a participant in the offline analysis was the successful performance on the recognition test. Therefore, a binomial test was performed on each individual performance (number of correct response), to check that it was significantly above the chance-level (50%). This led to the exclusion of 3 participants (*p*s>0.05).

The remaining 13 participants were all included in the following analysis. The all achieved at least 90% accuracy (*M*=97%) in the referential-judgment task administered during the TMS experiment. Mean accuracy and RTs were entered in a 2 x 2 x 2 repeated-measures analysis of variance (ANOVA), with factors TMS (M1 TMS vs. sham), person (1P vs. 3P) and verb category (hand-action vs. nonaction). In the RT analysis, trials in which participants provided an incorrect response (3%) and those with RTs 2 standard deviations (*SD*) above or below the individual condition mean (5% of correct responses), were excluded. Post-hoc comparisons were carried out using LSD Fisher's test ($\alpha \leq 0.05$).

In the MEP analysis, the peak-to-peak amplitude (mV) of each of the 128 MEPs obtained from each participant was computed with Matlab and then normalized. Trials in which participants provided an incorrect response were discarded (6%). Z-scores of the remaining MEPs were calculated using the individual condition mean and SD. Normalized values were then subjected to a 2 x 2 repeated-measures ANOVA with person (1P vs. 3P) and verb-category (hand-action vs. nonaction) as within-subject factors.

4.3. Results

MEP. The interaction between Person and Verb-category was significant $F_{(1,12)}=8.27$, $p=0.01$ (Fig. 1): motor facilitation was greater for 1P-action verbs than for 3P-action verbs ($p<0.03$), while no difference was found between 1P- and 3P-nonaction verbs ($p>0.1$). Motor facilitation for 1P-action verbs was also greater relative to 1P- and 3P-nonaction verbs (*p*s<0.05), while it did not differ for 3P-action verbs and 1P- and 3P-nonaction verbs (*p*s>0.1). Neither the main effect of Person nor the main effect of Category resulted significant (*p*s>0.1).

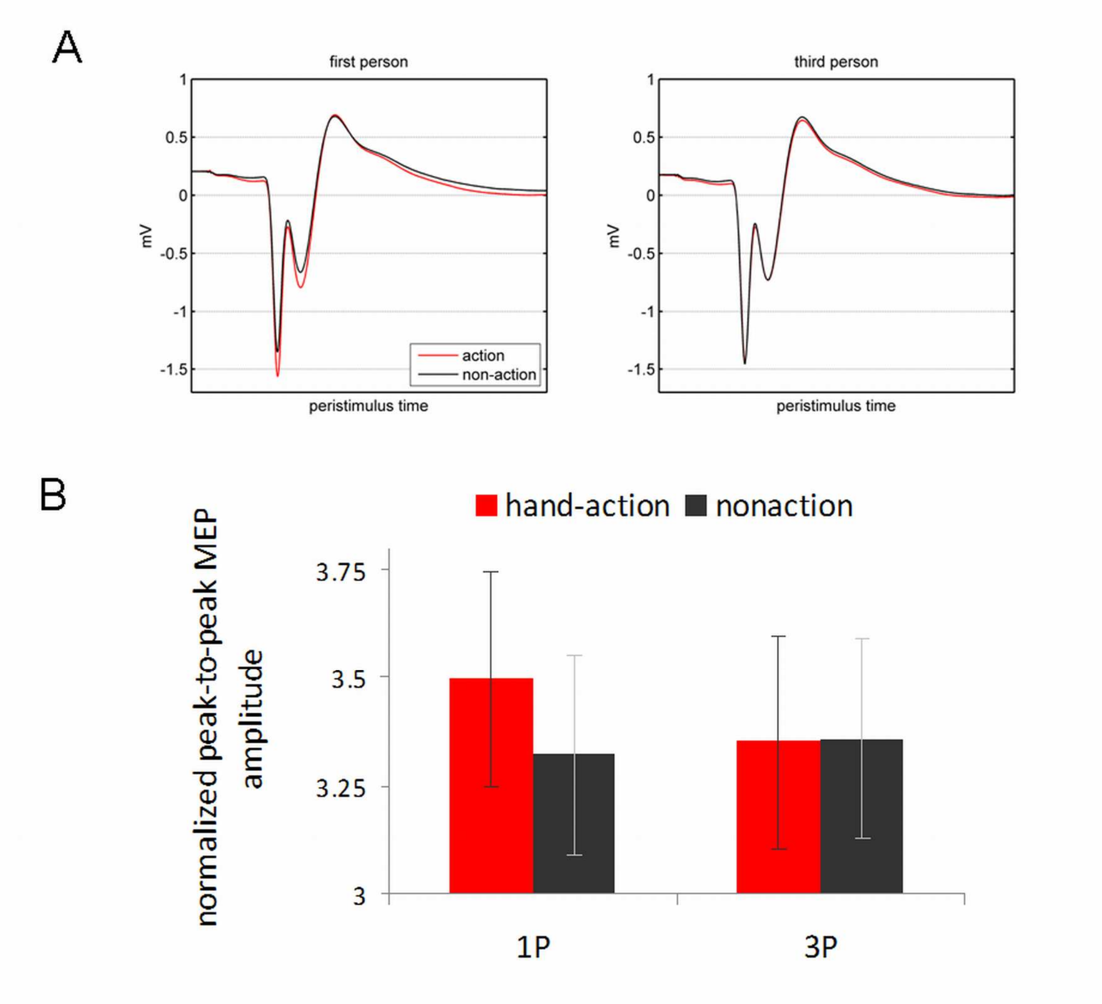


Figure 1. A) Sample MEPs (mV) for 1P and 3P hand-action and nonaction verbs. Data from one representative subject. B) Mean normalized peak-to-peak MEP amplitude for 1P and 3P as a function of the Verb category (hand-action and nonaction). 1P-action verbs enhanced cortico-spinal excitability to a greater extent than 3P-action verbs and (1P and 3P) nonaction verbs. Vertical bars denote SEM.

Accuracy. The analysis revealed significant effects of TMS, $F_{(1,12)}$=5.29, p=0.04, and Verb category, $F_{(1,12)}$=7.61, p=0.01. Accordingly, participants were more accurate during sham TMS than during M1-TMS delivery, and performed better on nonaction than on hand-action verbs. However, the two factors did not interact, $F_{(1,12)}$<1. The main effect of Person was not significant, $F_{(1,12)}$<1.

RTs. The effect of Person was significant, $F_{(1,12)}$=6.43, p=0.02: participants' responses were faster on 1P than on 3P verbs. The TMS x Person interaction approached significance, $F_{(1,12)}$=4.36, p=0.05 (Fig. 2): during sham, participants were faster when processing 1P verbs than 3P verbs (p<0.01); this advantage was abolished during M1-TMS delivery (p>0.1). Neither the main effect of TMS, nor the main effect or category resulted significant, $F_{(1,12)}$<1. Mean accuracy and RTs are summarized in Table 1.

Table 1. Mean RTs and accuracy (standard error of the mean, *SEM*) in each experimental condition.

		RTs (ms)		Accuracy*	
		1P	3P	1P	3P
TMS	hand-action	586 (66)	592 (64)	95 (1.3)	95 (0.9)
	Nonaction	568 (60)	574 (62)	97 (1.1)	97 (1.2)
Sham	hand-action	554 (69)	592 (78)	97 (1.1)	96 (1.2)
	Nonaction	561 (75)	612 (88)	98 (0.5)	98 (0.9)

* Percentage of correct responses

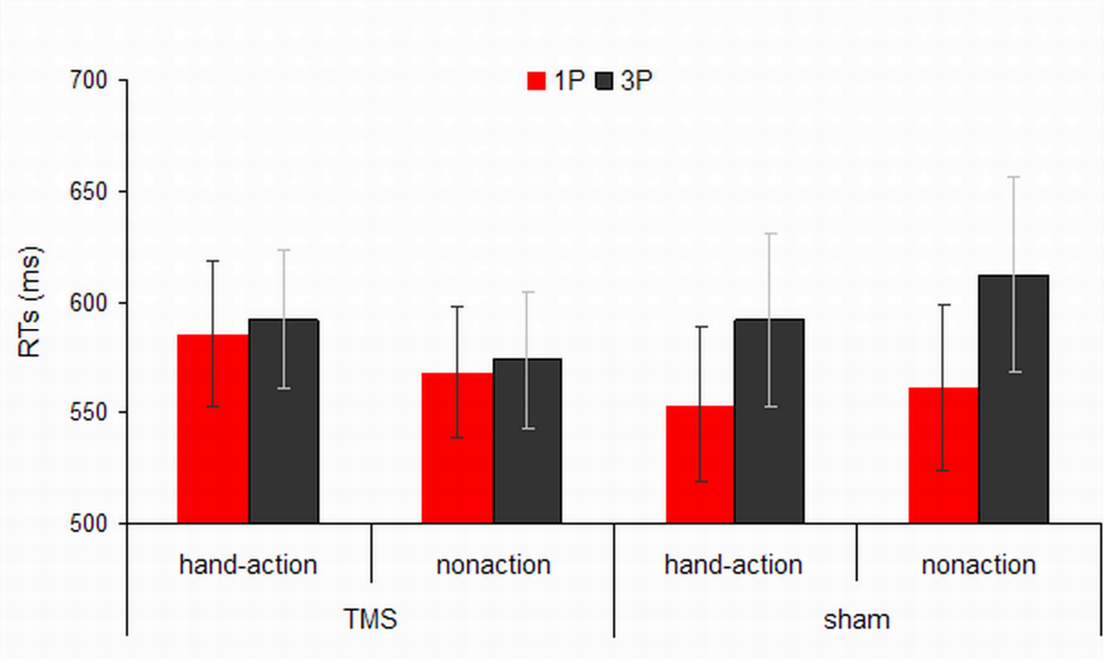


Figure 2. Mean RTs (ms) for 1P and 3P as a function of the Verb category (hand-action and nonaction) in each TMS condition (M1 TMS and sham). M1 TMS abolished the temporal difference in processing 1P and 3P verbs, observed during sham, independent of the verb category. Vertical bars denote *SEM*.

Additional analysis. The RT results showed that 1P verbs were processed overall faster than 3P verbs (in sham condition), consistently with what we found in the two pilot tests (see above). One possibility is that the (early) timing of TMS delivery, in our study, allowed detecting motor facilitation only for verbs that were processed faster. In other words, we might not have detected motor facilitation for 3P-action verbs because, on average, they were processed later than the average of 1P-action verbs.

To check this, we analyzed the MEPs corresponding to 3P verbs with the fastest RTs, i.e., with RTs falling within the first and the second percentile of the RT distribution of each participant. The mean RTs for the first quartile were 417 ms ± 49 (sem) and 419

±54 for 3P-action and nonaction verbs, respectively. The two-tail *t* test revealed no difference between 3P-action versus nonaction verbs, *t*(12)=-1.80, *p*>0.09, and, on average, the MEP amplitude was greater for 3P-nonaction verbs (3.3±0.44) than for 3P-action verbs (3±0.44). The same analysis was run considering the MEPs corresponding to 3P verbs with RTs belonging to the second quartile of each participant's distribution. The mean RTs were 532 ±52; 526 ±51 for 3P-action and 3P-nonaction verbs, respectively. Notice that these values approach closely the mean RTs for 1P-action (586 ±33) and nonaction (568 ±30) verbs. Again, the two-tail *t* test revealed no difference in MEPs between 3P-action and 3P-nonaction verbs, *t*(12)=-0.6, *p*>0.55, with MEP amplitude for 3P-nonaction verbs (3.5±0.54) being qualitatively greater than for 3P-action verbs (3.4±0.47).

To conclude, there was no difference between 3P-action and nonaction verbs, even when processing time for these items matched that for 1P verbs.

4.4. Discussion

In the present study, I compared TMS-induced MEPs when participants processed 1P or 3P hand-action and nonaction verbs. Our results provide novel demonstration about the specificity of motor facilitation during action verb processing: M1 activity increased for action (as opposed to nonaction) verbs, only when presented in 1P. Significant lower excitability was found when the same verbs were presented in 3P. In this case, no difference between action and nonaction verbs was found. Furthermore, I found that, during sham, participants were faster in processing 1P verbs relative to 3P verbs, but this temporal advantage dasappeared when TMS interfered with M1 activity. Our data have critical implications in relation to whether primary motor response to action verbs is automatic, and to what extend motor circuits house shared representation for self and others’ actions.

To the best of our knowledge, this is the first demonstration that motor system does not respond automatically to any action word but only to those implying self-referential action meaning. Since I compared motor facilitation on randomly interleaved trials, the effect appears immediate and not attributable to long-term contextual fluctuations of participants’ cortical states, which can threaten block designs. I can also exclude that task-related cognitive effort, which may cause increased cortical excitability (Scott, McGettigan, & Eisner, 2009), accounts for this interaction: during sham stimulation, participants were faster in responding to 1P than to 3P verbs and, although they were overall more accurate on nonaction compared to action verbs, there is no indication that processing 1P-hand action verbs was more difficult relative to 3P-hand action verbs.

The first implication of the non-automatic motor activity is that the motor system is not a necessary component of the lexical-semantic network, as proposed by some embodied accounts of language-induced motor activity (Pulvermüller, 2005). If the motor system directly encoded the motor attributes of a word, motor facilitation would have followed 1P- and 3P-action verbs to an equal extent, as the same attributes applied to both. On the contrary, the involvement of M1 in conceptual processing seems to depend on the word having an action meaning, as well as on the agent of the implied action.

The difference in motor facilitation between 1P- and 3P-action verbs also unhinges the core principle of the embodied hypothesis that action understanding results from a direct coupling between a perceived action and one’s own motor representation. In fact, the motor cortex seems *capable* of distinguishing between self and other, by representing action contents in a subject-specific (1P), rather than subject-neutral format. The hypothesis that self and other actions share the same representation has been already challenged in the domain of action observation. For instance, using TMS, Maeda, Kleiner-Fisman and Pascual-Leone (2002) found that action observation modulated the left M1 activity maximally when the observed action matched the observer’s orientation. Likewise, Jackson, Meltzoff and Decety (2006) reported greater BOLD responses in left motor system for 1P than for 3P views of actions. In our study, the role of the acting subject in modulating motor activity has been extended to language processing.

A more general role of M1 in self-other distinction is suggested by the abolition of the participants’ advantage in processing 1P over 3P verbs, when TMS disrupted M1 activity. This advantage found both in the pilots and the main experiment with sham stimulation, conforms to previous evidence of “self-reference” effect, whereby self-related words are easier (e.g., faster RTs) to process than other-related words (Markus, 1977). Notice that TMS slowed down participants’ performance but did not impede their ability to do the task (in the accuracy analysis, the TMS x Person interaction was not significant). This suggests that the self-other distinction is maintained by the joint activity of a constellation of brain regions forming the “self-other distinction network” that assigns an action to an agent (Jeannerod, 2004). Our data corroborate previous evidence that the left M1 belongs to this network (Ruby & Decety, 2003).

In summary, I have shown that processing action words modulate the motor system, depending on the agent to whom the implied action is attributed: processing 1P-action verbs does facilitate the motor system, whilst processing 3P-action verbs do not. It follows tha the motor system does not respond automatically to the word's action content itself, but it does only when the conceptual representation of a word integrates the action *with* the self as the agent of that action.

Intriguingly, these constraints parallel those that typically elicit kinaestethic motor imagery. Imagery, the internal rehearsal of motor acts, is accompanied by kinaesthetic sensations and motor activations similar to those of the corresponding execution, when people generate and transform images of body movements (Solodkin, Hlustik, Chen & Small, 2004). Moreover, activity in M1, premotor and somatosensory regions is greater when people represent actions in 1P perspective, than in 3P perspective (Jackson et al., 2006), and when they imagine to manipulate objects with their own hands rather than when they imagine objects rotating on their own (Kosslyn, Ganis, & Thompson, 2001), to the extent that a virtual identity has been established between kinaestethic motor imagery and first-person imagery.

The idea that language-induced motor activations would reflect *opportunistic* - rather than obligatory - implicit imagery (or simulation) triggered by the words' motor content, accommodates at best recent observations for motor activation during certain but not all conditions of action-word processing. In particular, TMS and imaging studies reported increased motor activity only during tasks that focused participants' attention on the motor attributes of words (Papeo et al., 2009; Tomasino et al., 2007), or when action words were presented in a context (i.e., a sentence) that emphasized the representation of body movements (Raposo, Moss, Stamatakis, & Tyler, 2009). However, none of those studies compared directly motor activation for action verbs with different subjects, or asked participants to process, or mentally represent, referential information. If people do not routinely attend to this information and use the egocentric perspective as default in mental simulation (Willems et al., 2010), the motor aspects of word meaning to which the 1P perspective is applied, could be themselves sufficient to elicit motor activity.

While no one denies that "*images play an important role in many cognitive processes*" (Fodor, 1975, p.184) and motor imagery can be implicitly triggered by virtually any stimulus or task with sensorimotor components (Kosslyn, Behrmann, & Jeannerod, 1995), only the classic embodied account of comprehension predicts that motor simulation is obligatorily engaged in processing action-related words. The study I reported in this chapter seriously challenges this interpretation of the relationship between language and motor system.

Chapter 5.

Human versus object motion: The stimulus-dependency of motor processes in language comprehension

5.1. Introduction

When people process the sentence "Close the drawer" implying an action away from the body, they are faster in performing a response movement in a congruent direction than in the opposite (toward the body) direction (Glenberg & Kaschak, 2002). These *congruence effects* suggest that language and motor system interact because "*the stimulus and response sets in the ensemble have properties in common, and elements in the stimulus set automatically activate corresponding elements in the response set*" (Kornblum et al., 1990, p. 253). That is, they prove that the comprehender activates a motor representation of the implied-language motion, which shares features with motor processes for response. The activation of motor representations in language comprehension is widely accepted to reflect motor simulation (Barsalou, 1999; Glenberg et al., 2008; Rizzolatti & Crighero, 2004), the mental rehearsal of a motor act that relies on motor neural substrates but is not accompanied by overt body movements (Jeannerod, 1995; Porro et al., 1996). Motor simulation is experienced implicitly (i.e., unconsciously), during action observation, understanding, planning or anticipation (Jeannerod & Decety, 1995). The term is often used as a synonym of motor imagery, which is considered its conscious counterpart, as both deal with motor representations and are associated with largely overlapping neural substrates in the motor areas (Grèzes & Decety, 2001). However, the two operations may differ with respect to some properties. For instance, imagery, being a conscious process, may require greater specification of the imagined movement, relative to motor representations implicitly triggered during simulation (Willems, Hagoort, & Casasanto, 2010).

The extent to which the simulation process involved in motion-language comprehension shares properties with imagery process it is still not clear. To address this question, in the current study, we tested whether the conditions triggering motor simulation in the case of language are the same as those triggering motor imagery for other cognitive operations (e.g., mental rotation), or whether a special relationship exists between motor simulation and language comprehension. The latter hypothesis has been forwarded in the embodied theories of language, according to which motor simulation *determines* the understanding of motion-language, because motor meanings are directly mapped into the comprehender’s motor representations (Rizzolatti Fogassi, & Gallese, 2001). This implies that motor simulation is necessarily recruited, whenever an action word is processed. On the other hand, studies on imagery have shown that perceiving a motion-stimulus is not sufficient to elicit motor processes or simulation (e.g., Solodkin, Hlustik, Chen, & Small, 2004). Establishing whether motor simulation is recruited in language comprehension, and motor imagery in other cognitive operations (e.g., mental rotation) following the same constrains, will help define the nature of the relationship between language and motor processes.

What do we know about the involvement of motor processes in imagery? A wealth of studies demonstrated that motor processes support imagery when individuals imagine the rotation of body parts and bodily or manual interactions with objects (Kosslyn, Thompson, Wraga, & Alpert, 2001). In other words, imagery recruits motor processes when a stimulus is transformed in an egocentric frame of reference, or in a “personal” perspective (Jackson, Meltzoff, & Decety, 2006), and its motion is associated with the kinesthetic feelings of moving one’s own body (Solodkin et al., 2004). In contrast, imagining stimuli moving in an object-centered visual space engages processes analogous to those recruited for visuospatial perception within the posterior parieto-occipital regions (see Zacks, 2008). Thus, imagery is not a unique, undifferentiated ability, but it relies on different sets of processes, or *strategies*, which can be independently employed or disrupted by brain injury (Tomasino & Rumiati, 2004).

Moreover, even in those cases when a motor strategy is triggered, the motor system *responds* differently, depending on the properties of the movement involved. The kinematic and kineasthetic features of a movement, indeed, determine the way that movement is represented. Movements conforming to postural bias are easily and frequently performed and, therefore, have more accurate, detailed representations owning the same features as the actual physical motion (Cooper & Shepard, 1975; Parsons, 1987). This isomorphism results in a linear relationship between the time for simulation and execution of those movements

(Parsons, 1994). In contrast, movements opposite to postural bias, which require reaching uncommon postures near the extremes of joint limits and are associated with more uncomfortable kinaesthetic sensations, have less detailed mental representations, resulting in a weaker, non-linear relationship between their mental simulation and actual execution (Parsons, 1994). This phenomenon, named *awkwardness effect* (Sekiyama, 1982), has typically been observed in the mental rotation of hands (Funk et al., 2005; Parsons, 1987; 1994). Recent imaging studies further support the role of the familiarity of a movement on motor activity: motor regions are more active when people perceive familiar movements (movements that they often perform), relative to less familiar ones (Calvo-Merino, Glaser, Grèzes, Passingham, Haggard., 2005; see also Cross, Kraemer, Hamilton, Kelley, Grafton, 2009).

In the current study, we selected sentences describing a manual action requiring either clockwise (CW) or counterclockwise (CCW) rotation performed by a human agent (e.g., *The worker is screwing the light bulb into the lamp*), and the CW or CCW rotation of a mechanical, non-manipulable object (e.g., *The video-tape is rewinding*). Although both human- and object-related sentences included similar motor words (i.e., verbs) and referred to motion, the sentential context was varied in order to elicit kineasthetic or visuospatial representations, respectively. Right-handed participants were asked to listen to motion sentences (and nonsensical sentences) and provide yes-or-no sensibility judgments by turning a knob either CW or CCW with the right hand/wrist (see Methods). The CCW wrist rotation is an awkward movement, as it has very limited degrees of freedom toward a posture close to the limits of the wrist's joint, and opposite to the bodily postural bias. In contrast, the CW manual rotation has more degrees of freedom and is far from biomechanical constraints; therefore, it is likely to be more comfortably and frequently performed than the CCW one.

If motor simulation *determines* the understanding of motion-related words, both human- and object-related motion sentences should affect the subsequent motor response, as they both include verbs with motor meaning. If, on the other hand, motor processes serve a motor strategy that supports the retrieval of kineasthetic information associated with a linguistic utterance, language should affect the subsequent motor response only when sentences elicit representations with kinaesthetic, *embodied,* motor components (i.e., human actions). If this is the case, we also expect that the interaction between motor simulation elicited by kineasthetic language and motor processes, is affected by the type of movement involved. In the case of common movements having presumably more accurate representation (CW rotations), the simulation elicited by a sentence should *fit* the motor representation for performing a similar movement (CW rotation), resulting in a congruence effect. When an awkward movement (CCW rotation) is involved, the interaction between the mental simulation of that movement and the motor representation activated for performing a similar movement is expected to be weaker, thus resulting a diminished or less stable congruence effect.

5.2. Experiment 1: congruence effect between implied-language and physical rotation

Participants were asked to make yes-or-no sensibility judgments (i.e., semantic-judgment task) on sensible and nonsensical sentences, including a selected subset (see Norming study) that described human-hand or mechanical-object CW and CCW rotations. Participants provided the response by turning a knob either CW or CCW. We tested whether motion-related words automatically elicit motor representations that interact with a subsequent motor response. Alternatively, and consistently with the mechanisms of mental imagery, motor simulation may be recruited only when participants process sentences where motion words are used to build kinaesthetic motor representations, such as bodily motion, but not external-object motion.

5.2.1. Materials and methods

5.2.1.1. Stimulus selection

Twelve Italians were asked to assess whether 72 sensible Italian sentences described motion. After judging a sentences as motion-related, participants had to specify the type of motion, choosing between "manual" (e.g., The worker is screwing the light bulb into the lamp), "mechanical" (e.g., The video-tape is rewinding) or "other", and its direction (CW, CCW or other). Fifty-six sensible sentences, 28 motion and 28 state items, judged consistently in each of the above dimensions by at least 85% of the panel, were thus selected. Of the 28 motor sentences (see Appendix C), 14 described human actions requiring CW (N=7) or CCW (N=7) manual rotation, and 14 described external objects rotating CW (N=7) or CCW (N=7) by a mechanical device. The 28 sensible state sentences, matched for length with motion sentences (number of phonemes, $p > .1$), described psychological or physical state of people (N=14) or objects (N=14; e.g. "Stars are shining in the night sky").

In all sentences, verbs had an imperfective aspect (e.g., is turning), as it activates event knowledge more strongly than the perfect aspect (e.g., had turned), and is most likely to elicit a mental image of the implied language context (Ferretti, Kuta, & McRae, 2007). The verb in each sentence was followed by 2-6 words that specified the context, the manner and the path (i.e., direction) of motion described by the verb. In Italian, very few verbs denote a rotation and the same verb can be used to describe different kinds of motion; the argument of the verb was therefore necessary to define motion (rotation) and its direction. For instance, in the sentence "The child is sharpening the colored pencil", the direct object (the pencil) is crucial to denote a rotating motion, whilst sharpening with a knife would change radically the manner and path of motion. In order to allow the semantic-judgment task, 56 nonsensical sentences with the same structure as the sensible ones (subject, verb and 2-6 words as complement) and comparable length ($p > .1$) were created.

5.2.1.2. Norming study

A Norming study was carried out with the objective to collect basic information about the selected sentences. Mean reaction times (RTs) to each sentence were obtained with a semantic-judgment task, where the above 56 sensible and 56 nonsensical sentences were presented acoustically to 29 right-handed Italians. They had to decide whether each sentence made sense by pressing a key (see Appendix D).

At the end of the experiment, the same volunteers completed a questionnaire to evaluate whether CW and CCW human sentences and CW and CCW object sentences were comparable for those attributes that might influence the relationship between language and motor processes. The familiarity tightly correlates with the processing time of an item, and the imageability of an utterance affects the ability to mentally represent its content (Connine, Mullennix, Shernoff, & Yelen, 1990). Moreover, features such as amplitude and continuity of implied-language motion need to be controlled as they might render the motion implied in some items, more perceptually salient and suitable to the interaction with motor processes, than others. The same features might modulate the processing times of sentences, because, if simulation is triggered, the time spent for mentally rotating a stimulus is proportional to the degrees of rotation (e.g., Shepard & Metzler, 1971; Shepard & Cooper, 1982). Thus, participants were asked to rate the familiarity, imageability, amplitude and continuity (i.e., whether the implied motion was continuous or part-way) of the motion implied by each sentences.

The results of the questionnaire showed that CW and CCW human sentences were matched for all the assessed dimensions. The same was true for CW and CCW object sentences. Therefore, besides length and structure complexity, CW and CCW sentences within each stimulus-type were comparable for familiarity, imageability, amplitude and continuity of implied motion. The RTs analysis revealed that participants processed CW and CCW human sentences equally fast, $t(28) = 0.88$, $p = .3$; for object sentences, they showed a temporal advantage in processing CW items over the CCW ones, $t(28) = 2.17$, $p = .03$, $t(28)_{item}=2.62$, $p=.01$ (Fig. 1). This preliminary study provided information on participants' performance in a response condition (i.e., keypress) that did not elicit congruence effect with the implied-language motion. In the following experiment, we investigated whether and to what extent the congruence between implied and actual motion affected participants' performance. Additional information on procedure, analysis and results of this norming study is given in the Appendix D.

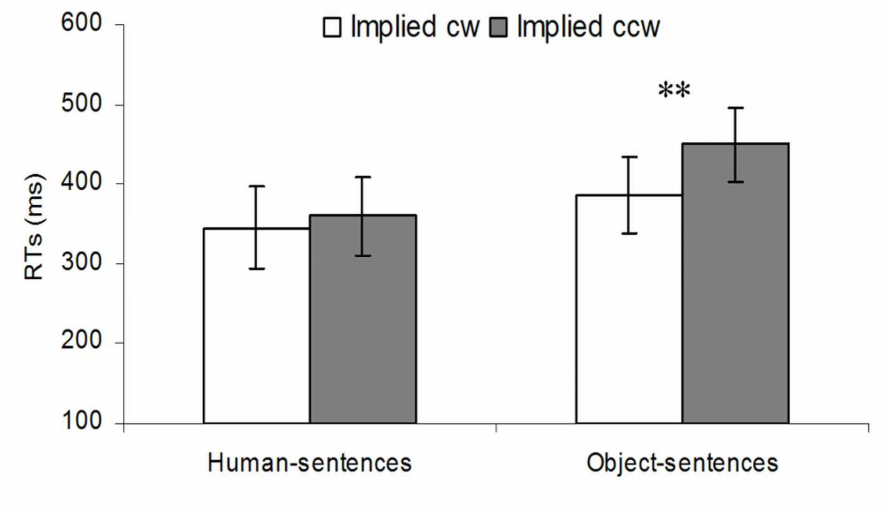


Figure 1. Norming study: mean RTs (ms) for the processing of human sentences and object sentences implying clockwise ("implied cw") or counterclockwise ("implied ccw") motion. Vertical bars denote the Standard Error of the mean.

5.2.1.3. Participants

Forty-four healthy, native Italian speakers (14 males; 18-36 years), all university graduates or undergraduates, participated in the study. They were all right-handed, according to the Edinburgh Handedness Inventory (EHI, Oldfield, 1971).

5.2.1.4. Procedure

The 56 rational sentences (28 motion-related and 28 state items) and 56 nonsensical sentences described above were presented to participants. All items had been previously read aloud and recorded (http://audacity.sourceforge.net/) by a female Italian speaker. They were transmitted through headphones, their length ranging from 2.066 to 3.995 ms. Participants made yes-or-no sensibility judgments by turning a knob (diameter 7 cm) requiring a power grip and wrist rotation in a CW or CCW direction from a central position. The knob was fixed to a panel, orthogonal to the table. Participants sat in front of the panel and handled the knob with their right hand. They were instructed to keep the right elbow motionless on the table, so that the knob could be rotated only by wrist. The knob triggered a metallic stick, hidden behind the panel, which stopped the rotation after 60° in either direction by touching a micro-switch. Left and right micro-switches, connected to the external response box of an E-prime PC-controlled system (Psychology Software Tools, Inc., Pittsburgh, PA), acted as key-presses. Responses were recorded from the onset of each sentence; RTs used in the analysis were calculated by subtracting the sentence length from this value.

Each sentence was presented twice for a total of 224 items. Participants were divided into two equal groups. Group 1 was instructed to turn the knob CW for yes-response and CCW for no-response, and Group 2 was instructed to do the opposite (i.e., CW rotation for no-response and CCW rotation for yes-response). Thus, in Group 1, responses to critical items (i.e., motion sentences) were congruent with sentences implying CW rotations and were incongruent with sentences implying CCW rotations; the opposite was true for Group 2. The manipulation of the relationship between implied and actual rotation was never mentioned and the critical sentences constituted only 25% of the whole stimulus-set; therefore, it was unlikely that participants became aware of the critical sensorimotor components of the task and generated expectations that could bias the performance (Frith & Dolan, 1997; Rees, Frith, & Lavie, 1997).

Prior to the experiment, participants were trained in handling the knob with an 8-trial familiarization phase. They were instructed to respond as quickly as possible, but not before they had listened to the whole sentence, as most nonsensical sentences could not be recognized as such, until the last word had been heard. After completing the experiment, participants were debriefed to assess whether they were aware of the critical task manipulations and how they felt during CW and CCW movements.

The experimental manipulations yielded a 2 x 2 x 2 design with factors: (i) Stimulus-type (human and object sentences), (ii) Congruence (congruence and incongruence between implied language and manual rotation), and (iii) Group (CW responses to critical items in Group 1 and CCW responses in Group 2) as the only between-subjects factor.

5.2.1.5. Analyses

Familiarization, state and nonsensical trials were discarded from the off-line analysis. All participants achieved at least 85% accuracy (M=97%) in sensibility judgments and were all included in the RT analysis. Incorrectly judged trials (3.2%) and those with response latencies 2 standard deviations (SDs) away from the individual condition mean (4.5% of correct responses) were discarded (Ratcliff, 1993). The remaining data were subjected to a 2 Stimulus-type x 2 Congruence x 2 Group repeated-measures ANOVA. Planned comparisons between critical conditions were run using two-tailed t-tests ($\alpha \leq .05$). To test for the generalizability of the effects over the items (Clark, 1973), the by-item analysis was performed with regressions of repeated measured data, according to the method proposed by Lorch and Myers (1990).

5.2.2. Results

Table 1 summarizes the results of the RT analyses for Experiment 1 (and for the following Experiments 2 and 3).

The main effect of Stimulus-type was significant: participants were faster in judging human than object sentences, F(1,42)= 34.74, p<.001, □p2=.45. The Congruence x Group interaction was significant, F(1,42)= 18.57, p<.001, □p2=.30. Participants in Group 1 (CW responses) were faster on congruent than on incongruent trials, p <.001; conversely, those in Group 2 (CCW responses) were slower when processing incongruent relative to congruent trials, p = .02. The three-way interaction between Stimulus-Type, Congruence and Group was also significant, F(1,42)= 4.08, p = .05, □p2=.09 (Figure 2A). Two-tailed t tests between critical conditions revealed that in Group 1, manual rotation was faster when it was congruent with the rotation implied by both human, t(21)= -2.44, p=.02, t(21)item= 4.33, p < .001, and object sentences, t(21)= -2.75, p = .01, t(21)item= 2.16, p = .01. In Group 2, this difference was no longer significant for human sentences, p > .1, whilst for object sentences, judgments of incongruent trials were faster than those of congruent trials, t(21)=2.24, p = .03, t(21)item=1.82, p = .08.

Importantly, incongruent trials in Group 2 involved the same CW object-related sentences that led to faster responses in Group 1. This suggests that there was always a temporal advantage for CW object sentences, irrespective of the direction of the manual response. This bias was already found in the norming study, where participants responded with a keypress. It is possible, however, that in Group 2 the congruence between CCW sentences and the motor response (CCW rotation) facilitated its execution, thus reducing the size of the bias (i.e. the RT difference between CCW and CW trials) in this group, relative to Group 1. In other words, a congruence effect might have taken place also for object sentences. To check this, we compared the size of the bias in the two groups, which was far from being significant, t(21)= 1.16, p >.1. This confirmed that CW sentences were always processed faster relative to the CCW ones, the size of this bias remaining unaffected by the status of congruence between implied and actual rotation. As expected, in the post-experimental debriefing, all participants reported greater discomfort associated with CCW than CW manual responses.

Table 1. Mean RTs (ms) in all experimental conditions of Experiments 1-3.

		Human sentences		Object-related sentences	
		Congruence	Incongruence	Congruence	Incongruence
Experiment 1	Group 1	**305**	**352**	**369**	**484**
	Group 2	387	373	**482**	**422**
Experiment 2	Group 1	**193**	**261**	**256**	**308**
	Group 2	294	262	**355**	**268**
Experiment 3	Group 1	**287**	**348**	**337**	**427**
	Group 2	355	330	**385**	**332**

Tabled mean RTs (ms) in Experiments 1-3, following the processing of human and object sentences in Group 1 (clockwise manual response) and Group 2 (counterclockwise manual response), when the implied language direction was congruent and incongruent with the manual response. The regions in bold type showed the significant differences between congruent and incongruent trails in the same condition of Sentence-type and Group.

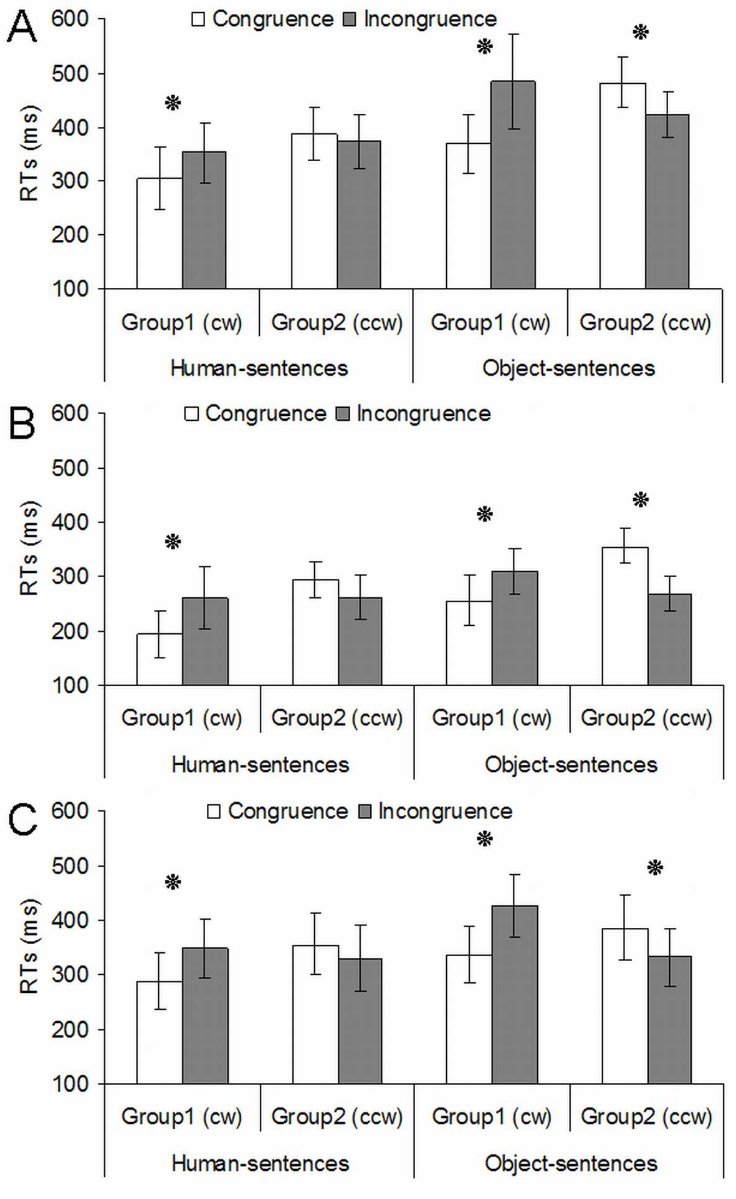


Figure 2. Mean RTs (ms) for the processing of human sentences and object sentences in Group 1 (“cw”, clockwise manual response) and Group 2 (“ccw”, counterclockwise manual response), when the implied language direction was congruent and incongruent with the manual response. The pattern of performance observed in Experiment 1 (A) was replicated both in Experiment 2 (B) and Experiment 3 (C). Vertical bars denote the Standard Error of the mean.

5.2.3. Discussion

We found that the congruence effect (faster response following a sentence implying congruent motion) took place when participants responded with CW rotation (Group 1), but not with CCW rotation (Group 2). However, the three-way interaction showed that these two factors interacted differently, depending on the Stimulus-type. For human-related sentences, physical responses congruent with implied-language direction were faster than incongruent responses when participants responded with CW rotation (Group 1), while no difference was found between congruent and incongruent trials when the motor response was CCW (Group 2). The performance difference in processing CW and CCW sentences in Group 1 reflects a congruence effect between the sentence content and the motor response, as the same sentences were processed equally fast in the Norming study, when participants responded with a keypress. Although the same sentences were presented, a congruence effect was not found in Group 2, suggesting a role of the type of involved motion (CW or CCW) in the interaction between stimulus and response.

The relationship between mental simulation elicited by sentences and motor processes for response gave rise to different effects, depending on the kinematic features and familiarity of the involved movement. In particular, when the stimulus-response interaction involved a manual rotation conforming to postural bias and associated with comfortable kinaesthetic sensations (i.e., CW in Group 1), motor simulation elicited by human sentences matched the motor representation for the execution of a congruent movement, resulting in the congruence effect (e.g., Glenberg & Kaschak, 2002). In Group 2, we found no congruence effect, but an overall qualitative increase of RTs, possibly reflecting the awkwardness effect, expected when the stimulus-response interaction involve awkward movements (CCW rotations) that have weaker, less accurate representations, relative to more comfortable and familiar movements (Parsons, 1994).

Using human-related sentences and a paradigm similar to the one employed by us, Zwaan and Taylor (2006) reported a congruence effect when participants responded with both CW and CCW manual rotation. In their study, however, the rotation required a precision grip that involved only finger movements, while we asked participants to respond by rotating their wrists. As aforementioned, the awkwardness effect has been demonstrated for hand rotations, but never for finger rotation. Hand/wrist and fingers clearly have different biomechanical constraints and discrete representations in the brain (Goldenberg, 1999; Haggard, Kitadono, Press, & Taylor-Clarke, 2006); hence, phenomena observed with hand-related tasks do not necessarily apply to finger-related tasks. More crucially, in the domain of mental rotation studies, different patterns of participants' performance have been reported in similar tasks, depending on the kind of movement involved in the task (see Sack, Lindner, & Linden, 2007). Thus, although most current explanations assume that the stimulus-response interaction takes place at a higher level of representation (Hommel, Müsseler, Aschersleben, & Prinz, 2001), it has been suggested that motor and premotor representations of different muscle groups are differently susceptible to interaction with mental simulation (Sack et al., 2007).

Our findings with human sentences do not contradict those of Zwaan and Taylor (2006), but the different responses employed in the two studies might have elicited the awkwardness effect in our but not in their study, or the congruence effect even with CCW rotation, in their but not in our study. This concern about the potential importance of specific muscle groups may pose a limit to the generalization of our findings. Overall, the congruence effect in Group 1 and the awkwardness effect in Group 2 suggest that human sentences evoked motor representations.

As for object-related sentences, participants in Group 1 were faster in responding to CW relative to CCW items. This pattern, however, did not reflect a congruence effect, as the same advantage was found in Group 2, even though, here, the response was congruent with CCW items. If the motor response interacted with representations elicited by object sentences, the CW bias should have been abolished or – at least - significantly diminished in Group 2, because the congruence between implied and actual CCW motion would have facilitated CCW responses. On the contrary, our findings suggest that participants' processing of object sentences did not elicit (motor) representations that could affect the motor processes for response.

The key result of Experiment 1 is that representations evoked by human sentences affected a subsequent motor response, while representations elicited by object sentences did not. In other words, only human sentences elicited representations owning kineasthetic motor components that trigger a motor modality of simulation. These findings mirror those observed in imagery studies, where stimulus-specific interactions between manual and mental rotation were reported, when mental rotation was applied to different visual stimuli. For instance, Sack, Lindner and Linden (2007) reported that the mental rotation of hands was facilitated by congruent and inhibited by incongruent manual rotation, whilst the mental rotation of cubes was unaffected by the congruence with manual rotation. Likewise, imaging studies reported motor and premotor activations only when participants mentally simulated movements associated with a kinesthetic feeling of the movement (Solodkin et al., 2004).

In the case of external-object motion, it is likely that our participants produced a visual representation of the moving object. Overall, a number of studies showed that this kind of stimuli activates visuospatial parieto-occipital regions (see Zacks, 2008 for a review). More crucially, the CW bias observed here, reminds of left-to-right directionality preference, ubiquitously found in visuospatial processes (Tversky, 1995). We will later return to this point of discussion.

5.3. Experiment 2: the effect of the angle of rotation

Experiment 1, we observed a congruence effect in Group 1, when participants responded to human sentences with a CW manual rotation, but not in Group 2, when they responded with a CCW rotation. We proposed that this difference in participants' performance resulted from CW and CCW movements involved in the stimulus-response interaction in Groups 1 and 2, respectively, having qualitatively different representations. In particular, CCW movements may be less accurately represented than the CW ones, because they are less frequently experienced. The reduced familiarity of CCW movements, relative to CW movements, is primarily due to the greater awkwardness for their execution, as they are opposite to the bodily postural bias. Thus, the difficulty of execution, in itself, might account for the lack of congruence effect, as this might have been precluded by generally slow reaction times.

The aim of Experiment 2 was to assess whether our results were due to the mere difficulty in executing CCW responses, or to the type and accuracy of mental representations that these motor responses rely on. Experimental design and procedure were the same as in Experiment 1, except that participants responded by rotating their wrist of

30° (rather than 60° as in Experiment 1) in either direction. This reduction of the angle of rotation was meant to facilitate the performance of CCW responses.

5.3.1. Materials and methods

5.3.1.1. Participants

Participants were forty university graduates or undergraduate students (14 male; 18-38 years), all healthy, right-handed (EHI, Oldfield, 1971), native Italian speakers.

5.3.1.2. Procedure

Stimuli and procedures were identical to those employed in Experiment 1, the only difference being that the knob was adjusted as to require a 30° rotation in either direction.

5.3.1.3. Analyses

Familiarization, state and nonsensical trials were discarded. All participants provided at least 85% of correct sensibility judgments (M=96%) on critical items. Incorrectly-judged trials (4.1%) and those with response latencies 2 SDs away from the individual condition mean (5% of correct responses) were discarded from the RT analysis. By-subjects and by-items analyses were performed as in Experiment 1.

5.3.2. Results

The results of Experiment 2 were qualitatively identical to those of Experiment 1. The effect of Stimulus-type was significant, F(1,38)= 6.08, p = .02, □p2=.14: motor responses were faster for human than for object sentences. There was a significant Congruence x Group interaction, F(1,38)= 28.06, p < .001, □p2=42: in Group 1, RTs were faster for congruent than for incongruent trials, t(19)=-3.87, p = .001; whilst incongruent trials were faster than congruent trials in Group 2, t(19)=3.63, p = .001. The three-way interaction was not significant, F(1,38)<1, n.s. (Figure 2B). However, planned comparisons between critical conditions revealed that participants of Group 1 were faster in congruent than incongruent trials, when processing both human, t(19)=-2.96, p < .01, t(19)item=5.17, p < .0001, and object sentences, t(19)=-2.63, p = .01, t(19)item=2.36, p = .02. No difference was found in Group 2 between congruent and incongruent trials for human sentences, p > .1. For object sentences, incongruent trials were processed faster than congruent trials, t(19)=3.28, p < .01, t(19)item=3.66, p = .001; in other words, CW object sentences were always processed faster than CCW sentences. As in Experiment 1, the size of this bias (i.e., the difference in RTs between CCW and CW sentences), did not differ in Groups 1 and 2, t(19)=-.94, p =.3, suggesting that RTs to object sentences were not affected by the relationship between the implied and the actual rotation.

Finally, that the 30° CCW rotation was equally difficult to perform, compared to the 30° CW rotation, was confirmed by the 92.5% of participants (N=37) in the post-experimental debriefing.

5.3.2. Discussion

As in Experiment 1, here we found that processing human sentences interacted with concomitant motor processes for responding, as revealed by congruence effects in Group 1, and awkwardness effects in Group 2. Importantly, in the current experiment, the decrease of the knob rotation from 60° to 30° made the CCW response less difficult to perform than in Experiment 1. As a result, participants' RTs decreased visibly in Experiment 2 (see Figure 2), even though the overall pattern of performance remained unchanged.

We obtained different results when participants responded to human sentences with CW and CCW rotation, even though both movements were equally-demanding. This demonstrates that the difference in performance between Groups 1 and 2 cannot be explained in terms of mere physical difficulty in the execution of either movement. In contrast, it seems that, in the two conditions, the stimulus-response interaction involves qualitatively different motor representations (Cooper & Shepard, 1975; Funk et al., 2005; Parsons, 1994). The temporal advantage in processing CW object sentences over the CCW ones occurred when participants responded with both CW and CCW rotation, and its size was unaffected by the response direction.

One might observe that the manual rotation of the knob mimicked better manual actions implied in human sentences, than the described trajectory of mechanical objects, to the extent that the stimulus-response interaction might have been promoted for human but not for the object items. Although the apparatus employed in the present study and the biomechanical constraints of human hand/wrist were not suitable to replicate some implied mechanical-object rotations (e.g., a continuous 360° rotation), consistent findings in Experiments 1-2 suggest that participants' performance was not constrained to a specific amplitude of the response. This issue has been further addressed in the following Experiment 3.

5.4. Experiment 3: the effect of the plane of rotation

anguage can convey very detailed features of the described context, which are used to construct imaginal representations during comprehension (Bergen & Chang, 2005; Jackendoff, 2002). The plane along which motion takes place (e.g., vertical or horizontal) was found to be encoded in language-evoked representations (Bergen, Lindsay, Matlock, & Narayanan, 2007; Richardson, Spivey, McRae, & Barsalou, 2003; see Anderson, Chiu, Huette, & Spivey, 2010, for a review). For instance, Bergen and colleagues (2007) reported that the processing of sentences implying up- (e.g., "The patient rose") or down-direction ("The glass fell") selectively interfered with visual processing in the same part of the visual field.

In Experiments 1-2, the plane of rotation in the manual response was fixed, whereas that implied by sentences was variable. Indeed, some of our sentences (e.g., "The boy is turning up the volume of the hi-fi") involved rotation on the same vertical plane as the manual rotation; other sentences, such as "the CD is turning in the CD-player", described motion that took place on a horizontal plane. The variable relationship (congruence or incongruence) between implied and actual plane of rotation, which was not experimentally controlled, might have promoted the interaction between language and motor processes in some cases, but not in others.

Experiment 3 was carried out to investigate whether the effects observed in Experiments 1-2 were constrained by the specific plane of manual rotation, or could be generalized to a condition differing for this dimension. The experimental paradigm was the same as in the previous experiments, except that the knob used for responding was adjusted as to require a manual rotation on a (almost) horizontal plane.

5.4.1. Materials and methods

5.4.1.1. Participants

Forty-six university graduates or undergraduates (19 males; 18-35 years) volunteered for this study. They were all healthy, right-handed (EHI, Oldfield, 1971), native Italian speakers.

5.4.1.2. Procedure

Stimuli and procedures were the same as in Experiment 1 except that the panel, to which the knob was fixed, was placed at an angle of 30° to the table, obliging the participants to rotate their wrists CW or CCW on an almost-horizontal plane.

5.4.1.3. Analysis

Familiarization, state and nonsensical trials were discarded. All participants achieved at least 85% accuracy on sensibility judgments (M=96%) and were all included in the following analysis. Incorrectly-judged trials (3.8%) and those with RTs 2 SDs away from the individual condition mean (4.8% of correct responses) were discarded. RT data entered a repeated-measures ANOVA with the same factors as in Experiments 1-2. Planned-comparisons between critical conditions and the by-item analysis were performed as above.

5.4.2. Results

The results of Experiment 3 were qualitatively similar to those of Experiments 1-2. The effect of Congruence was significant, F(1,44)=5.57, p = .02, □p2=.11: RTs were faster when implied language and manual rotations were congruent. The effect of Stimulus-type was also significant, F(1,44)=14.13, □p2=.24, p = .001, with responses to human sentences being faster than those to object sentences. The Stimulus-type x Group interaction was significant, F(1,44)=4.93, p = .03, □p2=.11, suggesting that that the above advantage in judging human sentences occurred when participants responded with a CW (Group 1, p = .0001), but not with a CCW rotation (Group 2, p > .1). The Congruence x Group interaction was also significant, F(1,44)=58.9, p < .0001, □p2=.57. Participants in Group 1 were faster in congruent trials, p < .0001; conversely, participants in Group 2 were significantly slower with congruent trials, p < .01. The Stimulus-type x Congruence x Group interaction was not significant, F(1,44)=1.30, n.s. However, planned comparisons between critical conditions revealed that, in Group 1, the congruence effect took place both for human and object sentences, as participants were faster in processing CW than CCW sentences (human sentences: t(22)=-2.74, p = .01, t(22)item=2.20, p = .03; object sentences: t(22)=-4.59, p= < .001, t(22)item=4.34, p < .001). In Group 2, this difference was no longer significant for human sentences, p >.1, whilst for object sentences, incongruent trials were faster than congruent trials, t(22)=2.51, p > .02, t(22)item=-5.58, p < .0001 (Fig. 2C). Once more, the size of the bias for CW object sentences over the CCW ones, was not significantly different in Group 1 and Group 2, t(22)=1.20, p = .2. This validated our argument that language did not affect participants’ motor responses when it concerned external-object motion.

5.4.3. Discussion

While the interaction between the processing of human sentences and the subsequent response resulted in the congruence (Group 1) and awkwardness effects (Group 2), for object sentences, the faster processing of CW items was not affected by the direction of the motor response. Thus, with the current experiment, we replicated the results of Experiments 1-2 and generalized them to a condition in which subjects' response was performed on a different plane of rotation, relative to the previous experiments. These results ruled out the possibility that the variable relationship (congruence or incongruence) between the plane of motion implied by sentences and the plane of manual rotation brought a confounding factor in our participants' performance.

5.5. General discussion

By comparing sentences implying human and external-object motion we have shown that motor simulation is a stimulus-specific mechanism in language comprehension, as it takes place when language content describes human bodily actions , but not when the implied motion refers to external, non-manipulable objects. The interaction between motor simulation evoked by human sentences and motor representations for responding was reflected in the congruence effect and its susceptibility to different types of motor representations involved in the response (i.e., awkwardness effect) (Experiment 1). Identical results were replicated when the angle and plane of rotation in the response were varied (Experiments 2-3). This suggests that the direction of rotation was the critical dimensional overlap between representations of stimulus and response, which, however, was effective only when the former referred to human motion. Our findings also add that the experience (or familiarity) with a given movement plays a role in the interaction of basic (motor) systems with high-level cognitive processes (language). In particular, the congruence effect takes place when a simulated movement matches the representation underlying its physical performance. This match occurs most likely when the involved movement conforms to the postural bias and, as such, is frequently experienced, resulting in a more accurate or detailed representation, relative to awkward (less comfortable and less familiar) movements.

The conditions that trigger motor processes (or simulation) in language comprehension mirror those that elicit the motor strategy, or kineasthetic motor imagery, in mental rotation of visual stimuli (Kosslyn et al., 2001; Solodkin et al., 2004; Tomasino, Borroni, Isaja, & Rumiati, 2005). This implies that motor simulation does not reflect the automatic and obligatory mapping of motor meanings into the comprehender’s motor system (Rizzolatti & Craighero, 2004). If it were the case, both human- and object-related motion sentences should have affected the subsequent motor response, as they both include words (verbs) with motor meaning. Motor simulation rather appears as one strategy to support the retrieval of kineasthetic motor information associated with a language meaning, as cued by the context (Rumiati, Papeo, Corradi-Dell’Acqua, 2010). This strategy-based interpretation accommodates a number of studies reporting increased motor activity when people were induced (explicitly or implicitly) to access the motor attributes of words, but not when their attention was driven to other aspects of the same verbal materials (Papeo, Vallesi, Isaja, & Rumiati, 2009; Tomasino, Werner, Weiss, & Fink, 2007; Willems, Hagoort, & Casasanto, 2010). In the same vein, linguistic accounts that attempted to explain the connection of language to “the rest of cognition” (i.e., modality-specific sensory or motor systems) pointed at imagery as the linkage between the two, but not the core attribute of comprehension (Jackendoff, 2007; Machery, 2007; Myachykov, Posner, Tomlinal, 2007).

These findings also highlight the importance of the sentential context in the activation of motor representations during comprehension (see also Raposo, Moss, Stamatakis, & Tyler, 2009). We showed that the association of a lexical unit with motion was not sufficient to elicit motor simulation, but it was the integration of all words' meanings in a sentence that yielded motor imagery effects. Even though the verb typically brings motion within the linguistic focus and can be crucial to trigger simulation (Taylor & Zwaan, 2008), this appears limited to those cases when the sentence, as a whole, describes bodily actions, thus activating kineasthetic motor attributes of a verb meaning. The influence of the sentential context on the engagement of a motor modality of language processing requires a higher-level cognitive mediation at that is not predicted by the proposal that a motor word is directly and automatically matched with the motor representation of the corresponding physical act (Rizzolatti et al., 2001).

Differently from human-sentences, mechanical-object sentences showed a consistent advantage (faster RTs) for CW items over CCW items, which remained irrespective of the direction of the motor response (Norming study and Experiments 1-3). Sentences describing the rotation of mechanical objects that do not afford interactions with human body, were selected on purpose, as imagery studies showed that this type of content evokes visuospatial representations with no kinaesthetic components that affect the motor system (Solodkin et al., 2004). On the other hand, visuospatial processing is characterized by a preference for left-to-right directionality (Tversky, 1995) that is in keeping with the advantage we observed for CW object sentences. This bias appears ubiquitously in the mental representation of visual scenes (Tversky, 1995), numbers (Dehaene et al., 1993) and time (Vallesi et al., 2008). Moreover, it influences the mental representation of sentential contexts: for instance, Italians spontaneously represent actions described in subject-verb-object sentences, as evolving with a left-to-right trajectory (Maas & Russo, 2003). The left-to-right bias seems modulated by cultural aspects, such as habits of writing and reading, as it is less strong or even reversed in Arabic and Hebrew speakers, relative to Western population (Maas & Russo, 2003). Thus, if our argument is correct, the pattern of performance we observed for object sentences may be abolished or reversed in participants belonging to a population with right-to-left writing and reading system.

As in imagery, in language domain, motor or visuospatial processes can go along with word processing depending on the kind of (concrete) information that is the most salient in a linguistic message. For instance, sensory-motor representations might be activated for making judgments about detailed sensory properties of named objects (see also Caramazza & Mahon, 2003; Machery, 2007; Martin & Caramazza, 2003; Oliver & Thomson-Schill, 2003; Tyler, Moss, 2001). However, the claim that semantics can also encode the physical aspects of a concept (see Louwerse, 2008), or that conceptual processes can sometimes (e.g., when cued by the context) rely on modality-specific systems is quite different than claiming that motor simulation is a core attribute of the understanding of motion language. We believe that, given the available evidence, the notion of "strategy" accounts at the best for the relationship between motor simulation and language (Papeo et al., 2009; Rumiati et al., 2010). This notion implies that different mechanisms, beyond motor simulation, can yield the same output or support the same task, depending on a given task context (Price & Friston, 2002).

The parallel between the conditions that trigger motor imagery in mental rotation tasks, and motor simulation in language, leaves still open a possibility that the two differ to some extent. For instance, if we assume the view of imagery as the conscious counterpart of simulation (Jeannerod & Decety, 1995), it might be that motor representations evoked by motion-related sentences are less detailed than those consciously generated and transformed during imagery tasks. Suggestively, in this study, we found that the effects of interaction between human sentences and motor response were quite independent of the detailed features of the involved motion (i.e., angle and plane of rotation), as if a general description of the implied-language action was created, lacking the kind of specification that would be needed if one imagined that action explicitly.

5.6. Conclusions

The stimulus-specific interaction between language and motor processing suggests that motor simulation is constrained by the context in which motion-related words are presented. What does this finding add to our understanding of the relationship between motor simulation and language comprehension?

Sentential contexts implying human (or biological) motion are most likely to evoke motor representations with kineasthetic components that affect the comprehender’s motor system. This suggests that motor simulation is a consequence of *embodiment*, reflecting the *sense of agency*, or *ownership* (“it is my body, it is me”; see Longo et al., 2008), and the influence of bodily experience (i.e., one’s own motor repertoire) in cognition, when one applies a “personal perspective” (Buccino et al., 2004) in processing language contents. The role of kinematics and kineasthetic sensations people experience when performing different movements (e.g., CW versus CCW rotation) on their mental representation, as shown here, brings support to this interpretation (see also Chatterjee, 2010). On the other hand, the relevance of the sentential context in eliciting motor simulation immediately implies that the motor system does not respond automatically to motion words: the lack of motor imagery effects when motor words (verbs) were presented in object-related sentences reveals the inadequacy of motor simulation as a general and necessary mechanism for encoding motor meanings. Our motor experience may influence how we understand actions to the extent that, under certain conditions, embodied representations can go along with – or even supersede - more abstract representations of meanings. Nothing in the evidence supporting this claim motivates the inference that motor simulation is the core of the understanding of motion-related words.

Chapter 6.

The implicit transfer of motor strategy in language processing: an fMRI study

6.1. Introduction

Mental simulation is a form of implicit imagery, whereby images of things or events are “visualized” and transformed in a three-dimensional mental space, when the physical stimulus is out of view (e.g., Jeannerod & Decety 1995; Kosslyn et al., 1995). Activations of primary motor (M1) and premotor (PM) cortices during imagery are triggered when individuals imagine the movements of their own body parts or bodily interactions with objects (motor strategy), but not whet they imagine, for instance, an object rotating on its own, in an object-centered reference frame (i.e., visual strategy; Kosslyn et al., 1998; 2001). Accordingly, several studies showed that the left M1 and PM are activated especially in tasks that drive participants’ attention toward the motor content of word-stimuli as opposed to their lexical-phonological features (e.g., Tomasino et al., 2007; Willems, Hagoort & Casasanto; 2010). In contrast with the *simulationist* view that motor simulation is automatically and necessarily involved in word processing (e.g., Rizzolatti et al., 2001; Rizzolatti & Craighero, 2004; Pulvermüller, 2005), it has recently been suggested that, just like in imagery, simulation in language is an opportunistic strategy to accomplish certain linguistic task (e.g., Rumiati et al., 2010).

Yet, the specific conditions that are found to activate motor system leave open one possibility that simulation is at least necessary for deep semantic analysis of action-related language. In breaking out of this impasse, we used a novel paradigm in the action related verb processing domain, whereby we assessed the effect of the *cognitive context* (motor and nonmotor) on the subsequent language-related processing (and activation), while keeping constant the stimuli (action and nonaction verbs) and the task requiring deep semantic analysis of those stimuli. We could thus investigate whether a *highest*-level factor could modulate the engagement of motor simulation, even under those stimulus- and task-conditions that typically elicit it.

Wraga et al. (2003) showed that individuals solved a mental rotation task using a motor strategy, when they had previously performed a motor rotation task, but not when the preceding task involved visual rotation. The transfer of a motor-modality of processing from one task to another that does not necessarily require motor processes is based on motor learning (Grafton et al., 1995; Grafton et al., 1998; Pascual-Leone et al., 1994), which takes place in the absence of participants' awareness and is tested indirectly via performance (Graf & Schacter, 1985). We exploited the mechanisms of motor learning and transfer to modulate the cognitive context in which participants processed language.

We asked participants to read action and nonaction verbs for delayed recognition, after either a motor task (motor context) or a visual task (nonmotor context). The instruction to read verbs for delayed recognition is thought to trigger deep levels of processing, whereby depth is intended in terms of the extent to which meaningfulness is extracted from the stimulus (Lockhart & Craik, 1990). Functional magnetic resonance imaging (fMRI) was used to assess M1 and PM activation in the two conditions that were identical, meaning that similar linguistic items were presented for the same task, except for the cognitive context elicited by the preceding task. We reasoned that, if motor simulation is necessary for understanding action words, M1 and PM activity should *burst* whenever an action-word is being deeply processed; if, on the contrary, it is one (unnecessary) strategy for encoding action meanings, the highest-level contextual variable might modulate motor activation, top-down, irrespective of the stimulus-content and task demand.

6.2. Materials and method

6.2.1. Participants

Since gender differences in handedness tasks have been reported in behavioral (Voyer et al., 1995) and neuroimaging (Jordan et al., 2002) studies, only healthy female university graduates or undergraduates (N = 18, right handed, aged 22-28 years) took part in the present experiment as paid participants. All of them were right-handed (on the Edinburgh Inventory test, Oldfield, 1971) native speakers of Italian, with normal or corrected-to-normal vision and no history of neurological illness, psychiatric disease, or drug abuse. They all gave written informed consent prior to the study. The study was conducted in accordance with the Declaration of Helsinki and approved by the local ethics committee.

6.2.2. Stimuli

Linguistic stimuli

In the linguistic task, 240 stimuli were presented, one at a time, on a white-background computer screen. Legal words (N=160) presented in their infinitive form (Verdana: 40), included 80 verbs associated with hand actions ("*mescolare*", *to stir*), and 80 nonaction verbs (state/psychological verbs; *"adorare", to adore*). In addition, a list of 80 meaningless illegal letter strings (*"csdawq"*), matched for length with the above verb list, $t(79) < 1$, was presented. Verbs were chosen from a stimulus-set selected with a Norming study and used in previous studies (see Papeo et al., 2009, and Chapter 3). The selected stimuli were divided in two equivalent lists, matched for the percentage of agreement on the category (action vs. nonaction), length (number of graphemes) and written frequency (Laudanna et al., 1995).

In the recognition task administered at the end of the fMRI scanning section, a subgroup of 40 verbs (20 action and 20 nonaction) was selected from the experimental list ("old" list), and presented, intermingled with 20 new action and 20 new nonaction verbs ("new" list). The old and new verb lists were matched for frequency and length.

Stimuli in the motor and nonmotor learning phase

Two types of stimuli were used one for each mental rotation task (MR) constituting the learning phase. Color photographs of a hand or a geometrical figure, appeared, one at a time, on a white-background computer screen, in the motor and in the visual leaning phase, respectively. In both conditions, stimuli were shown in one of six possible orientations in the picture plane, namely, at 45°, 90°, 135°, 225°, 270°, or 315° from their upright canonical orientation. Each figure appeared at each of the six angles of orientation 20 times, the total set of stimuli, in each learning phase, resulting in 120 photographs (Figure 1a). For both sets of stimuli, the photographe were 560x560 pixels.

In the motor task, the 120 photographs could depict either the right (50% of trials) or the left hand (50% of trials). In the visual condition, the 120 geometrical figures depicted three-dimensional armed cubes (Shepard & Metzler, 1971) created by using Blender (http://www.blender.it/). The figure, in its upright orientation, had approximately the shape of a "Z". A red marker was placed on either shorter arm of the figure. A black arrow heading either leftward (50% of the trials) or rightward (50% of the trials), was placed at the center of the vertical arm cueing the direction for mental rotation.

6.2.3. Experimental design and procedures

We used a 2 x 2 block experimental design in which we manipulated the cognitive context (motor versus nonmotor) of word processing, as defined by the preceding MR, and the word-stimulus (i.e., action verbs versus nonaction verbs). In addition to action and nonaction verbs, meaningful letter strings were presented.

Eight-trials blocks of action verbs, nonaction verbs or strings were randomly presented (2 sec per stimulus), after each block of either motor or nonmotor task (2 sec per stimulus), for a total of 60 blocks (30 silent reading, 15 motor and 15 nonmotor task), This yielded six experimental conditions: (1) action verb (act), (2) nonaction verb (nact), (3) letter strings (string), after the motor task (post_H), and, (4) action verb, (5) nonaction verb, (6) letter strings, after the visual task (post_C). A fixation cross (150 ms) separated each stimulus in a block. Each block was introduced by instructions (5000 ms) informing the participants about the upcoming task (silent reading or either MR), and followed by a resting baseline of 10000 ms.

The motor and the nomotor tasks corresponded to a hand-rotation (or handedness) task and a cube-figure rotation task, respectively. The former required participants to decide whether each presented photograph depicted a left or a right hand. Participants were explicitly instructed to perform the task using a motor strategy consisting in imaging to rotate their own hand until it reached the position of the hand-stimulus on the screen. These task instructions and stimuli have been reliably shown to elicit egocentric-perspective taking, motor cortical activations and processes (motor strategy) analogous to those for actual execution of hand movements (e.g., Kossyn et al., 1998; 2001; Parsons, 1998). In the cube-figure rotation task, participants were required to imagine the figure rotating leftward or rightward, according to the direction prompted by the central arrow, until it reached the canonical orientation with its longer arm aligned with the midsagittal line of the computer screen, and then decide whether, from that position, the red spot was at the left or at right of the screen. This type of stimuli and the instructions of imagining an external object rotating in an object-centered visual space engage a visual strategy that recruits cortical regions and processes analogous to those for actual visuospatial perception (Kosslyn et al., 1998; 2001).

Participants performed the three tasks (reading, motor and nonmotor task) in the MRI scanner. Before the scanning session, they were trained outside the scanner on the hand- and cube-rotation tasks. Training was protracted until participants felt confident that they understood the task and applied the correct strategy. During the scanning session, they laid supine with their head fixated by firm foam pads and their arms along the body with the palms parallel to the legs. They were asked to keep the head and the arms/hands motionless for the whole duration of the experiment. Stimuli were presented using Presentation 9.0 (Neurobehavioral Systems) and projected to a VisuaStim Goggles system (Resonance Technology). Behavioral responses in MR were provided by participants pressing the keys placed under the left toes, for “left” responses (left-hand or left-sided marker), or under the right toes, for “right” responses (right-hand or right-sided marker) of an MRI-compatible response device (Lumitouch, Lightwave Medical Industries, CST Coldswitch Technologies, Richmond, CA, USA) mounted on a custom-made feet support. Foot responses were chosen to minimize interference between response preparation and execution and the predicted task-related activity in M1 and PM hand areas. In the linguistic task (silent reading) no response was required.

Hand-area localizer. To individually locate the hand representation within M1 of both hemispheres, a functional localizer task (Grefkes et al., 2008; Tomasino et al., 2010) was performed within the scanner, immediately after the main experiment. Participants were instructed to perform right or left hand clenching movements in synchrony with the white-to-red color alternation (frequency: 55 Hz) of a circle appearing in the center of the white-background computer screen. Participants performed 9 blocks of active hand movements (15s each) alternated with 9 baseline resting periods (15s each), during which they performed no movement. Each "active" block was preceded by an instruction-screen (3 s) informing participants on whether they had to move the right or the left hand. The time between instruction and stimulation onset was jittered (1.5, 2.0, 2.5 ms).

Recognition task. The recognition task was administered at the end of the fMRI session and outside the scanner. Participants sat on a chair at 1 meter from a LCD screen that displayed each verb (Verdana: 45) for 2000 ms, followed by a blank that remained on the screen up to 10000 ms, to allow the response. They were instructed to decide whether the verb had been presented during the fMRI session by pressing the K-key of a keyboard for yes-response and the L-key for no-responses. As soon as they provided the response, the new trail started. In this task, they were encouraged to favor response accuracy over speed.

6.2.4. fMRI data acquisition

A Philips Achieva 3-T whole-body scanner was used to acquire both T1-weighted anatomical and functional images using a SENSE-Head-8 channle head coil and a custom-built head restrainer to minimize head movements. Each subject was scanned first for the main experiment and then again for the localizer task. Functional images were obtained using a single-shot gradient echo, echoplanar imaging (EPI) sequence. EPI volumes for the main experiment (N = 840) contained 30 axial slices (TR = 2500 ms, TE = 35 ms, FOV = 200.000 90.000 230.000 mm, matrix: 128 x 128; slice thickness of 3 mm with no gaps, 90°

flip angle, voxel size: 1.79×1.79×3.3 mm) and were preceded by 7 dummy images that allowed the MR scanner to reach a steady state. EPI volumes for the functional localizer (N = 265 images) were acquired with the same sequence characteristics as in the main experiment except for a shorter TR of 1600 s, fewer (21) axial slices, and 5 dummy images. Both experiments were obtained in the same fMRI session. The main experiment lasted 35.54 min and the localizer task 7.15 min. After functional neuroimaging, high-resolution anatomical images were acquired using a T1-weighted 3-D magnetization-prepared, rapid acquisition gradient fast filed echo (T1W 3D TFE SENSE) pulse sequence (TR = 8.227 ms, TE = 3.76 ms, FOV = 240.000 190.000 240.000 mm, 190 sagittal slices of 1 mm thickness, flip angle = 8°, voxel size: 1 x 1 x 1) lasting 8.8 min.

6.2.5. Behavioral data processing

Behavioral data were analyzed to ensure that participnats performed successfully on both MR tasks and on the recognition tasks.

Mental rotation tasks. A general indication that participants have been actually performed the mental rotation is provided by a gradient in RTs, which increase linearly with the increase of the angle of rotation (Kosslyn et al., 1998; Shepard & Metzler, 1971). In addition, to ascertain that participants rotated the stimuli according to either (motor or visual) strategy, we checked whether RTs reflect arm-hand biological constraints (Parsons, 1987; 1994). Performing the handedness task (motor-imagery based strategy), which involves a somatic or biomechanical space (Parsons, Gabrieli, Phelps & Gazzaniga, 1998), induces faster processing of stimuli oriented towards the body’s midsagittal plane (i.e., medial) compared to those oriented away from it (i.e., lateral). This “lateral-medial” effect, which holds that imagined movements are affected by biomechanical limitations that apply to real movements, is not expected when participants mentally rotate the stimulus in the visual space (i.e., visual-imagery based strategy).

Thus, consistently with previous experiments (Parsons, 1987; 1994), lateral orientations corresponded to 45°, 90° and 135° right-hand rotations, and to 225°, 270°, and 315° left-hand rotations, from the upright canonical orientation. For cubes, lateral orientations corresponded to the figure rotated at 45°, 90° and 135° from its upright orientation. “Medial” orientations corresponded to right hands rotated at 225°, 270° and 315°, left hands at 45°, 90° and 135°, to cube-figure at 225°, 270° and 315°, from the upright orientation.

First, for each individual, we performed a binomial test on the performance (number of correct response) in both MR tasks, to check that it was significantly above the chance-level (50%, $p<0.05$). Then, to assess the angle-gradient effect in both MR tasks, and the lateral-medial effect, which was expected for the handedness task but not for the cube-rotation task, a repeated-measures ANOVA was run on RT data, with factors stimulus (hands versus cubes), orientation (lateral versus medial) and angle (short versus middle versus long). Notice that we collapsed the handedness of hand-stimuli (right or left); as a result, short, middle and long angles for later orientations corresponded, respectively, to right-hands rotated at 45°, 90° and 135°, and left hands rotated at 315°, 270° and 225°; for medial they corresponded, respectively, to right hands rotated at 315°, 270° and 225°, and left hands rotated at 45°, 90° and 135°. For cube figures, lateral short, middle and long angles corresponded, respectively, to 45°, 90° and 135° ; medial short, middle, lateral orientations corresponded, respectively, to 315°, 270° and 225°.

Trials in which participants provided an incorrect response (12% for the motor and 18% for the nonmotor task) and those with RTs 2 *SD*s above or below the individual condition mean (6% of correct responses for the motor and 9% for the nonmotor task), were previously discarded from the analysis (Ratcliff, 1993). All post-doc comparisons were performed with the LSD Fisher's test ($\alpha \leq 0.05$).

Recognition task. A binomial test was performed on each individual performance (number of correct response), to check that it was significantly above the chance-level (50%). The successful performance on this task, as well as on both MR tasks, was the criterion for including a participant in the offline analysis of bahvioral and fMRI data. Moreover, mean accuracy rates of participants were submitted to a 2 x 2 repeated-measures ANOVA, with factors context (motor versus nonmotor) and word-stimulus (action versus nonaction). This ANOVA was performed in order to assess potential effects of the context (motor and nonmotor) on the delayed recognition of action and nonaction verbs.

6.2.6. fMRI data processing

Statistical analysis were performed on UNIX workstations (Ubuntu 8.04 LTS, i386, http://www.ubuntu.com/) using MATLAB r2007b (The Mathworks Inc., Natick, MA/USA) and SPM5 (Statistical Parametric Mapping software, SPM; Wellcome Department of Imaging Neuroscience, London, UK http://www.fil.ion.ucl.ac.uk/spm). Dummy images were discharged prior to further image processing. Pre-processing included: spatial realignment of the images to the reference volume of the time-series; segmentation producing the parameter file used for normalization of EPI data to a standard EPI template of the Montreal Neurological Institute template provided by SPM5; re-sampling to a voxel size of 2×2×2 mm; and spatial smoothing with a 8-mm FWHM Gaussian kernel to meet the statistical requirements of the General Linear Model and to compensate for residual macro-anatomical variations across subjects.

We modeled the alternating epochs by a simple boxcar reference vector. A general linear model for blocked designs was applied to each voxel of the data by modeling the activation and the baseline conditions for each subject and their temporal derivatives by means of reference waveforms which correspond to boxcar functions convolved with a hemodynamic response function (Friston et al., 1995a; Friston et al., 1995b). To correct for motion artifacts, we included 6 additional regressors of no interest, which modeled head movement parameters obtained from the subject-specific realignment parameters.

To delineate the network involved in the MR and in the silent reading tasks *per se*, we performed a whole brain random effects analysis. Low-frequency signal drifts were filtered using a cut-off period of 128 s. The presentation of MR blocks (hands and cubes) and of the silent reading blocks of each stimulus type (act, nact and strings) were modelled as the regressors of main interest (MR_hands, MR_cubes, act_ postH, act_ postH, string_postH, and act_postC, nact_postC, string_postC). All the regressors were convoluted with a canonical hemodynamic response function.

At the single subject level, specific effects were assessed by applying appropriate linear contrasts to the parameter estimates of the experimental conditions resulting in t-statistics for each voxel. First, we calculated the following contrast images for each subject:

the task-related network both for the mental rotation [MR(hands+cubes)–baseline], and for the silent reading collapsing the meaningful words [(act_postH + act_postC + nact_postH + nact_postC) – (string_postH + string_postC)] to check that participants were actually engaged in the mental rotation and the linguistic networks respectively. To ensure that the MR of hands (vs. MR of cubes) differentially activated the motor areas, we calculated the contrast images for the stimulus (hands – cubes and cubes -hands). We tested the following main effects: context (reading_postH > reading_postC) and (reading_postC > reading_postH), [(act_postH + act_postC) > (nact_postH + nact_postC)], and word-stimulus [(nact_postH + nact_postC) > (act_postH + act_postC)]. Finally, we calculated the interactions: context × stimuli [(act_postH - nact_postH) > (act_postC - nact_postC)] and stimuli x contest [(act_postC - nact_postC) > (act_postH - nact_postH)].

For the second-level random effects analyses, contrast images obtained from individual participants were entered into a one-sample *t*-test to create a SPM{T}, indicative of significant activations specific for this contrast at the group level. We used a threshold of $p<0.05$, corrected for multiple comparisons at the cluster level (using FWE), with a height threshold at the voxel level of $p < 0.001$, uncorrected.

The localization of the functional activations with respect to cytoarchitectonic areas was analyzed based on probabilistic cytoarchitectonic maps derived from the analysis of cortical areas in a sample of 10 human postmortem brains, which were subsequently normalized to the MNI reference space. The significant results of the random effects analysis were compared with the cytoarchitectonic maps using the SPM Anatomy toolbox (Eickhoff et al., 2005).

In the hand localizer task identical pre-processing and first-level analysis procedures were used as in the main experiment. Accordingly, a design matrix, which comprised contrasts modeling alternating intervals of “activation” (hand clenching) and “baseline” (no movement), was defined. Specific effects were assessed by applying appropriate linear contrasts to the parameter estimates of the experimental condition and the baselines resulting in t-statistics for each voxel. The hand representations within the left and right hemispheres were defined for each subject as the set of all contiguous voxels that were significantly more active for performing clenching hand movements vs. baseline at a threshold of $p < 0.05$, family-wise error (FWE) corrected. Thereafter, we considered only these voxels that were located within the cytoarchitectonically defined maximum probability maps (MPMs) of the primary motor cortex (Brodmann Area 4) provided by the SPM Anatomy toolbox (Eickhoff et al., 2005). This combined anatomical and functional approach was necessary since the (anatomical) cytoarchitectonically defined probability maps do not specify the (functional) hand representations within the motor areas.

6.3. Results

6.3.1. Behavioral results

Mental rotation tasks. Performance on both MR tasks was above the chance level (ps < 0.05) for all participants but three, of whom one failed the handedness task, another failed the cube-rotation task, and the last one failed both tasks (ps > 0.05). They were therefore discarded form the following analyses. The remaining 15 participants performed successfully on the recognition task (*p*s < 0.05), and were all included in the following analyses.

The ANOVA showed a significant effect of Stimulus, F(1,14)=14.97, p = 0.001, Orientation, F(1, 14)=20.16, p < 0.001, and Angle F(2,28)=78.95, p < 0.001. According to these main effects, hands were processed faster than cubes, medial orientations were processed faster than the lateral ones; and short angles were processed faster than middle angles (p < 0.001) and the latter, faster than long angles (p < 0.001). Importantly, the Stimulus x Orientation interaction was significant, F(1, 14)=12.32, p < 0.01 (Figure 1b): in rotating hands, participants were faster with medial than with lateral orientations (p < 0.001), while in rotating cubes, they showed no difference between the two orientations (p = 0.6). The interaction between Orientation and Angle was also significant, F(2,28)=25.60, p<0.0001 (Figure 1b). Accordingly, RTs were faster for short angle than for middle and long angles for both stimulus orientations, although this gradient was more pronounced for lateral than for medial orientation. In particular, for medial orientations, there was no difference between short and middle angles of rotation (p > 0.05), while RTs increased significantly from middle to long angles (*p* < 0.001). For lateral orientations, short angles were processed faster than the middle ones, and these were processed faster than the long ones (*p*s < 0.001). Lateral orientations were processed overall slower than the medial ones, but this difference was significant for middle and long angles (*p* < 0.001) but not for short angles (*p* > 01).

Thus, the main effect of angle (and the lack of interaction between angle and stimulus) revealed that the typical angle-gradient effect applied to both hand- and cube-rotation. Moreover, as predicted, participants' performance on the handedness task was characterized by the lateral-medial effect, providing a crucial indication that they have actually been rotating the hand according to the motor strategy[1]. This effect was not found, when participants rotated the cube-figures. Following these results, we could be confident that the two learning phases elicited a motor and nonmotor (visual) processing.

Recognition task. The ANOVA revealed no significant effect or interaction (all *p*s > 0.05). This suggests that action and nonaction verbs were processed and recognized equally well, regardless of the context in which they appeared during the fMRI session.

6.3.2. Neural activations

Network for mental rotation tasks

The neural network sustaining MR (i.e., all experimental trials including hand- and cube-rotation versus baseline) was assessed by a whole brain random effects analysis ($p < 0.05$, FWE corrected for multiple comparisons at the cluster level, with a height threshold at the voxel level of $p < 0.001$). This network included activation clusters bilaterally in the: i) precentral gyrus (Area 6); ii) superior frontal gyrus; iii) middle frontal gyrus; iv) superior parietal lobe; v) insula; vi) thalamus, and vii) occipital gyrus. Furthermore, the putamen was activated in the left hemisphere (see Table 1 and Figure 1c). These activations

---

[1] With a one-way ANOVA, we checked the lateral-medial effect, at individual level, defined as the temporal advantage in processing medial, over later orientations. It was significant in 10 out of 15 participants ($p<0.05$). The remaining 5 participants, qualitatively, showed a temporal advantage for medial orientations, although it did not approach significance ($p>0.05$).

encompass the classic network for MR (e.g., Kosslyn et al., 1998; 2001; Vingerhoets, de Lange, Vandemaele, Deblaere et al., 2002; Wraga, Shephard, Churcha, et al., 2005).

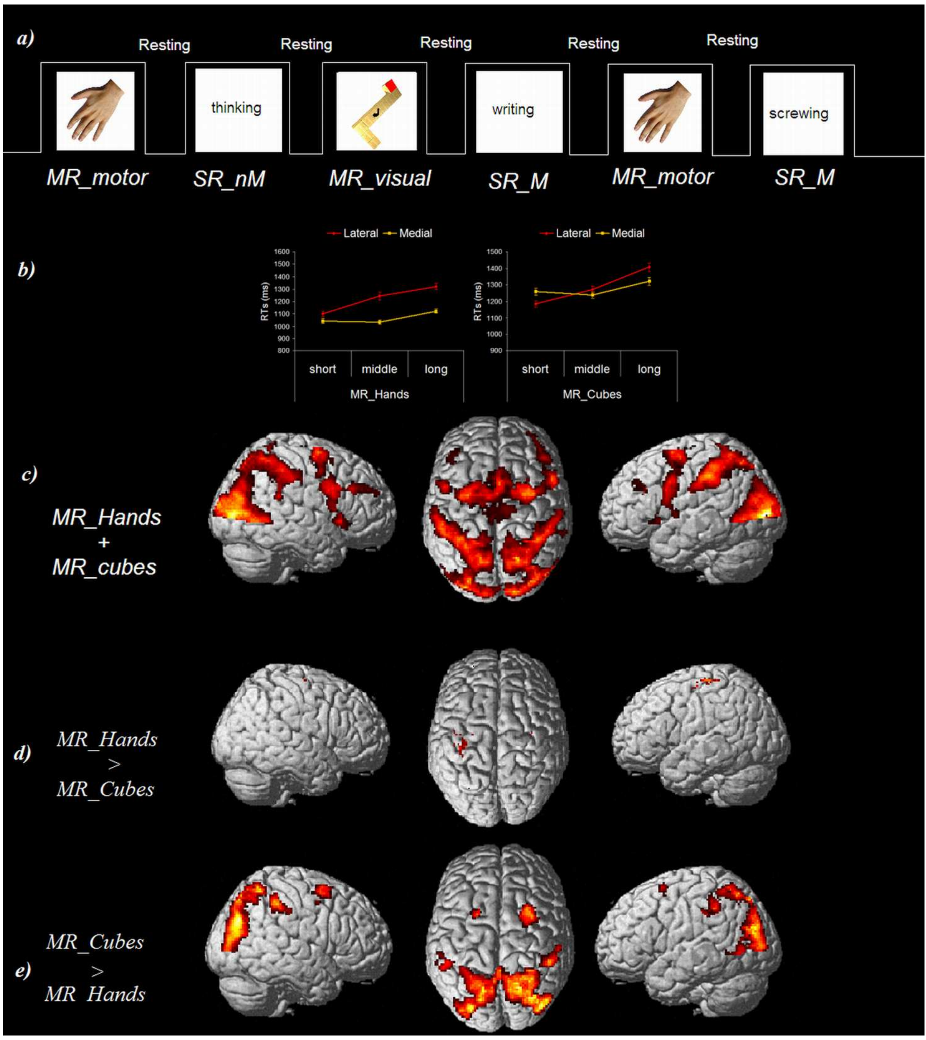
The motor task (MR of hands versus MR of cubes, Figure 1d) activated clusters in the: i) right superior frontal gyrus extending to the middle frontal gyrus; ii) left inferior frontal gyrus (pars Orbitalis); iii) left superior occipital gyrus extending to cuneus. Additionally, a small volume correction was employed to allow for a hypothesis-driven region-of-interest (ROI)-based approach (Friston, 1997). The small volume correction was performed on the M1 hand representation, to assess whether this region was activated during hand rotation. The *x*-, *y*- and *z*-coordinates for the position of M1 hand area were derived from the localizer task, averaging across participants, and were used to center the ROI for the current analysis. The resulting coordinates were: $x = -38$, $y = -24$ and $z = 60$ (left hand area of M1). The extent of the spherical ROI was set to 8 mm (corresponding to the smoothing kernel used in single subject analysis). Individual and group-mean coordinates (in MNI space) of the maximally activated voxel within the anatomically-constrained functional ROIs comprising the hand representation in the left and right primary motor (M1) cortices, obtained by the functional localizer task and the maximum probability maps (MPMs) are presented in the Appendix E (Table S1) and in Figure 2a. Using a threshold of $p<0.05$, FWE corrected for the ROI, we found a significant activation at x = -38, y = -26 and z = 66 in the left postcentral gyrus (Area 4a and Area 1).

The visual task (MR of cubes versus MR of hands, Figure 1e) activated clusters in the: i) middle frontal gyrus bilaterally; ii) right superior parietal lobule; iii) left inferior parietal lobule; and iv) thalamus bilaterally.

Table 1: Whole brain analysis: brain regions showing significant relative increases of BOLD response associated with *Mental Rotation* tasks.

			MNI		Z	Cluster size
Region	**Side**	**x**	**y**	**z**		**Voxel**
MR task (Hands + Cubes) >Baseline						
Precentral gyrus (Area 6)	L	-30	-4	62	5.87	4811
Superior Frontal gyrus	L	-22	-4	50	5.70	
Middle Frontal gyrus	R	28	2	48	5.62	
Inferior Frontal gyrus (P.Opercularis)	R	54	8	28	5.18	979
Precentral gyrus	R	44	4	32	4.97	
Middle Frontal gyrus	R	38	48	28	4.46	
Middle Frontal gyrus	L	-42	36	34	3.77	70
Inferior Frontal gyrus (P.Triangularis)	L	-40	28	26	3.62	
Insula	R	30	20	4	5.19	540
Insula	L	-34	16	4	5.15	290
Thalamus	L	-18	-24	10	5.95	3381
Thalamus	R	18	-24	10	5.52	
Putamen	L	-24	10	4	3.98	70
Middle Occipital gyrus	L	-32	-92	6	6.98	15495
Cuneus	R	18	-98	14	6.27	
Parietal lobule	L	-24	-64	-52	6,07	
Parietal lobule	R	12	-70	-50	6,07	
MR_Hands > MR_cubes						
Superior Frontal gyrus	R	18	60	18	4,51	82
Middle Frontal gyrus	R	24	54	22	3,87	
Inferior Frontal gyrus (P.Orbitalis)	L	-42	36	-6	4,06	99
Primary motor cortex, hand area	L	-38	-30	66	3,58**	15
Superior Occipital gyrus	L	-14	-96	20	4,43	761
Cuneus	R	4	-92	14	4,26	
MR_cubes > MR_Hands						
Middle Frontal gyrus	R	30	4	56	4,56	531
Middle Frontal gyrus	L	-20	2	44	3,95	135
Superior Parietal lobule	R	18	-60	56	5,92	8273
Inferior Parieltal lobule	L	-52	-42	46	4,25	221
Thalamus	R	18	-30	14	6,04	150
Thalamus	L	-20	-34	14	4,30	70

For each region of activation, the coordinates in MNI space are given in reference to the maximally activated voxel within an area of activation, as indicated by the highest Z-value ($p<0.05$, corrected for multiple comparisons at the cluster level, height threshold $p<0.001$, uncorrected). L/R = left/right hemisphere.
**$P_{\mathrm{svc}}<0.05$, [corrected for region of interest, ROI, i.e. left hand motor area of the M1 cortex, coordinates derived from the localizer task ($x=-38$, $y=-26$, and $z=60$)].



7

Figure 1. ***A)*** Experimental Design: in each block of silent reading (SR), 8 trails of action verbs (SR_M), nonaction verbs (SR_nM) or strings were presented. Each SR block was followed by one block of either hand- (MR_motor) or cube-rotation (MR_visual). ***B)*** Behavioral data: RTs increased linearly with the angle of rotation (short, middle, long) in both MR of hands and cubes; only in the former case Rts were consistently faster for medial vs. lateral orientations. Vertical bars denote the standard error of the mean. ***C)*** Common network underlying the mental rotation tasks as revealed by the whole brain analysis. Relative increases in neural activity associated with the hands and cubes mental rotation tasks ($p<0.05$, FWE corrected at the cluster level; see Table 1) are displayed on a rendered template brain provided by spm5. MR=Mental Rotation. ***D)*** Differential activation of M1 revealed by the main effect of task (MR_Hands > MR_Cubes). The activation cluster in left M1, centered in the central sulcus during MR_hands (vs. MR_cubes) is shown. E) Differential activation of M1 revealed by the main effect of task (MR_Cubes > MR_Hands).

Network for silent reading

The neural network underlying the silent reading task of all meaningful verbs (i.e., action and nonaction verbs following either MR task versus strings) included activation clusters in the left: i) inferior frontal gyrus (pars triangularis); ii) supplementary motor area; iii) precentral gyrus (Area 4p extending to Areas 4a and 6). The postcentral gyrus (Area 4p extending to Areas 1 and 3b) was activated in the right hemisphere. Finally, significant activation was found, bilaterally, in the middle temporal gyrus (see Figure 2a and Table 2).

This pattern of activity corresponds to the classic network involved in visual word processing and semantic analysis (e.g., Chee, O'Craven, Bergida et al., 1999; Fiez & Petersen, 1998; Friederici, Optiz & von Cramon, 2000).

Main effect of context

Figure 2b and Table 2 shows that the areas differentially recruited by reading action and nonaction verbs following the motor task (versus silent reading following the nonmotor task) involved clusters of activity in the: i) left precentral gyrus (Area 6, 4a) extending to Poscentral gyrus (Areas 3b, 2), and in the ii) right precentral gyrus (Area 6).

No differential activation was found for silent reading following the visual task, as compared with silent reading following the motor task.

Main effect of stimuli

Irrespective of the context (motor and nonmotor), action verbs relative to nonaction verbs activated the: i) right middle frontal gyrus; ii) left postcentral and precentral gyrus bilaterally (Area 6 and Area 1); iii) right anterior cingulate cortex; iv) superior medial gyrus bilaterally; v) middle orbital gyrus extending to the inferior frontal gyrus, bilaterally; vi) middle temporal gyrus bilaterally; vii) middle occipital gyrus bilaterally; viii) right paracentral lobule; ix) angular gyrus; and x) left superior parietal lobule (see Table 1). The reverse contrast (nonaction versus action verbs) included a cluster of activation in the left middle frontal gyrus.

Context x Stimuli interaction

The Context x Stimulus interaction [(act-nact)_postH > (act-nact)_postC] revealed no significant activation at the predefined statistical threshold. The reverse contrast [(act-nact)_postC > (act-nact)_postH] differentially activated regions within the left precentral gyrus (Areas 6) and within the right postcentral gyrus (Areas 3a). Precentral activity was modulated, as follows: while the activation was greater for action than for nonaction verbs, when reading in the nonmotor context, $t(14)=2,671$, $p =0.01$, comparable PM activation was found for both verb categories, when read in the motor context $t(14)=-1,470$, $p = 0,1$. The modulation of activity in the right postcentral gyrus was modulated as follows: activation was greater when reading action versus nonaction verbs, in the nonmotor context, $t(14)=3,68$, $p<0.01$, and when reading nonaction versus action verbs, in the motor context, $t(14)=-3,24$, $p < 0.01$.

Table 2. Whole brain analysis: brain regions showing significant relative increases of BOLD response associated with *Silent Reading* task.

Region	Side	MNI			Z	Cluster size
		x	y	z		Vox
Silent Reading: (action+nonaction) > string						
Inferior Frontal gyrus (P.Triangularis)	L	-48	14	26	4.97	1842
Supplementary Motor Area	L	-4	8	58	4.65	427
Precentral gyrus (Area 4p)	L	-34	-24	54	5.24	248
Precentral gyrus (Area 4a)	L	-36	-30	62	4.30	
Precentral gyrus (Area 6)	L	-30	-20	68	3.52	
Postcentral gyrus (Area 4p)	R	32	-22	44	3.92	72
Precentral gyrus (Area 1)	R	44	-24	56	3.64	
Precentral gyrus (Area 3b)	R	42	-24	44	3.60	
Middle Temporal gyrus	L	-66	-44	2	5.16	833
Middle Temporal gyrus	R	52	-30	-2	4.53	115
CONTEXT: (action+nonaction) post_ Hands > (action+nonaction) post_ cubes						
Precentral gyrus (Areas 6, 4a)	L	-30	-24	62	4,65	88
Poscentral gyrus (Area 6)	L	-30	-34	62	4,07	
Precentral gyrus (Areas 6)	R	26	-16	66	4,02	52
CONTEXT: (action+nonaction) post_ cubes > (action+nonaction) post_ Hand						
-	-		-		-	-
STIMULI: action (post_ Hands + post_ cubes) > nonaction (post_ Hands + post _cubes)						
Middle Frontal gyrus	R	44	12	52	5,44	175
Postcentral gyrus (Area 1)	L	-52	-16	48	5,05	1594
Precentral gyrus (Area 6)	L	-46	0	44	5,05	
Precentral gyrus (Area 6)	L	-32	-24	64	4,91	
Postcentral gyrus (Area 1)	R	50	-22	52	4,57	569
Precentral gyrus (Area 6)	R	36	-16	64	4,23	
Postcentral gyrus (Area 1)	R	62	-8	36	4,06	
Anterior cingulate cortex	R	10	48	18	4,97	613
Superior Medial gyrus	R	12	58	18	4,69	
Superior Medial gyrus	L	-6	40	36	4,84	1189
Middle Orbital gyrus	L	-36	52	-10	4,12	180
Inferior Frontal gyrus (P.Orbitalis)	L	-42	42	-14	3,95	
Middle Orbital gyrus	R	38	44	-10	4,11	168
Inferior Frontal gyrus (P.Orbitalis)	R	50	40	-8	4,09	
Middle Temporal gyrus	R	50	-34	-2	4,79	75
Middle Occipital gyrus	L	-32	-94	4	4,65	201
Middle Temporal gyrus	L	-46	-54	-2	4,47	166
Middle Occipital gyrus	L	-46	-74	0	3,97	
Middle Occipital gyrus	R	40	-64	-2	4,43	100
Middle Temporal gyrus	R	48	-60	4	3,45	
Middle Temporal gyrus	L	-64	-30	-4	4,13	66
Middle Occipital gyrus	R	24	-98	4	3,75	125
Paracentral lobule	R	6	-24	66	4,29	108
Angular gyrus	R	58	-56	30	3,66	64
Superior Parietal lobule	L	-28	-58	50	3,48	60

Table 2 continued

STIMULI: nonaction (post_Hands + post_cubes) > action (post_Hands + post_cubes)						
Middle Frontal gyrus	L	-30	-8	54	4,24	64
CONTEXT x STIMULI (action>nonaction)_post_Hands > (action>nonaction) post_cubes						
-	-	-	-	-	-	-
CONTEXT x STIMULI (action>nonaction) post_cubes > (action>nonaction) post_hands						
Postcentral gyrus (Area 3a)	R	40	-20	38	4,28	212
Precentral gyrus (Area 6)	L	-52	4	34	3,93	52

For each region of activation, the coordinates in MNI space are given in reference to the maximally activated voxel within an area of activation, as indicated by the highest Z-value ($p<0.05$, corrected for multiple comparisons at the cluster level, height threshold $p<0.001$, uncorrected). L/R = left/right hemisphere

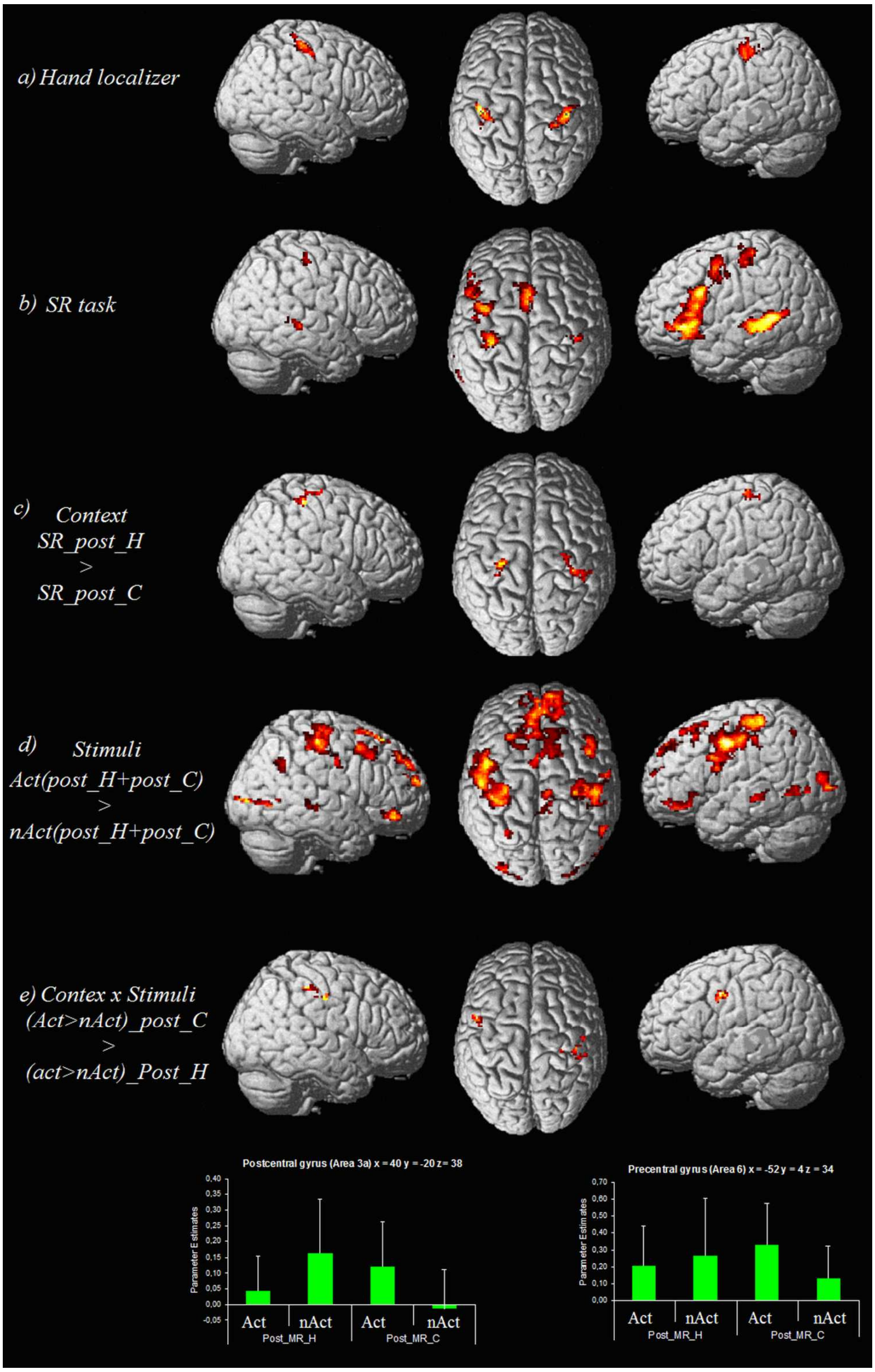


Figure 1. *(Caption on the next page)*

Figure 1. ***A)*** Group mean coordinates (*x*= − 38, *y* = −24 and *z*= 60 in MNI space) of the maximally activated voxel within the (anatomically-constrained functional) ROIs comprising the hand representation of the left and the right primary motor cortices obtained by the functional localizer task and the maximum probability maps (MPMs). ***B)*** Common network underlying the silent reading task as revealed by the whole brain analysis. Relative increases in neural activity associated with the silent reading (action + nonaction verbs vs. strings; p<0.05, FWE corrected at the cluster level; see Table 2) are displayed on a rendered template brain provided by spm5. ***C)*** Main effect of context (post_H = motor; post_C = nonmotor) on silent reading (SR), irrespective of the verb category (action and nonaction). ***d)*** Main effect of Stimuli (Act = action verbs; nAct = nonaction verbs) independent of the context**.** ***D)*** Context x Stimulus interaction and the plots of relative BOLD signal changes in the left precentral and right postcentral gyri.

6.4. Discussion

6.4.1. Implicit transfer of motor strategy to the processing action and nonaction verbs

We have combined the paradigm for implicit transfer of motor strategies and fMRI technique to manipulate the cognitive context (motor versus nonmotor) in which participants processed action and nonaction verbs, and investigate the nature of motor activation in word understanding.

Behavioral performance together with M1 and somatosensory activations specifically associated with the hand rotation (versus cube rotation) confirmed that participants carried out this task according to the motor strategy. The main effect of context showed that the same modality of processing was *implicitly transferred* from the motor (hand) rotation to the encoding of the subsequent words, despite the fact that participants were given no instruction to relate hand rotation to word-stimuli. Indeed, silent reading after the motor task (versus the nonmotor task) specifically activated M1 and primary somatosensory cortex, which are expected correlates of motor imagery (Decety et al., 1990; Kosslyn et al., 2001; Parsons et al., 1995; Porro et al., 1996; Sirigu et al., 1995; Tomasino et al., 2005). The cluster of activation in the left M1 included the hand-area activated in both hand rotation and hand-localizer tasks. Importantly, the motor strategy was extended to both action and nonaction verbs. A similar effect was not found when the linguistic task was preceded by the nonmotor (cube rotation) task. The present results provide novel demonstration that motor activations reflect the strategy of relating the word content to an embodied meaning, which can, or cannot, be engaged depending of implicit learning and regardless of the word category.

Why did the nonmotor (visual) context not have a clear effect on word-related activation? In motor simulation, people also produce a visual representation of their moving limb or the simulated scene; thus, while the motor processes (and the associated kinesthetic feelings) are specific for the motor strategy, visual processes are likely to apply to both the visual and the motor strategy (Solodkin et al., 2004). The observed activationof body-related sensory areas (precentral gyrus), together with M1 and PM, during reading in motor context, supports this argument.

6.4.2. Action verbs and sensorimotor representations

Relative to nonaction verbs, action verbs specifically activated a widespread neural network, distributed across the two hemispheres. Differential activation for action and nonaction verbs is in keeping with previous evidence that concrete and abstract concepts rely on partly distinct neural systems (Fiebach & Friederici, 2003; Jessen et al., 2000; Noppeney & Price, 2004). In particular, the former are characterized by a more extensive and complex, bilaterally distributed, cortical representation, while the latter are strongly left-lateralized (e.g., Laws et al., 1995; Binder et al., 2005). In the following discussion, I focus on sensorimotor activations associated with word processing. Other activations will not be dealt with here, as our *a priori* hypothesis focused on potential changes of brain activity in sensorimotor areas.

Relative to nonaction verbs, action-verb processing activated sensorimotor regions centred in the bilateral ventral premotor (vPM) and precentral gyrus. Our findings are consistent with a wealth of studies reporting the involvement of extrasylvian frontal and temporal regions in word processing (Damasio, Grabowski, Tranel, et al., 1996; Tranel, Damasio & Damasio, 1997). Among these ‘‘nonclassical’’ language areas, vPM and, sometimes, parietal regions (including the precentral gyrus) are activated during reading action words (Hauk et al., 2004; Rueschemeyer, van Rooij, Lindemann et al., 2009), verb generation (Grabowsky, Damasio, Frank et al., 1995; Petersen, Fox, Posner et al., 1988) and tool naming (Grabowsky, Damasio & Damasio, 1998; Grafton, Fadiga, Arbib & Rizzolatti, 1997; Martin et al., 1995; 1996). While these activations are typically left-lateralized, clinical studies suggested that sensorimotor regions in the right hemisphere may contribute to action-word processing, particularly for attention-demanding tasks (Cappa, Binetti, Pezzini et al., 1998; Neininger & Pulvermüller, 2001; 2003).

Premotor activity is especially triggered in tasks requiring the retrieval of action knowledge related to stimuli (Grabowsky, Damasio & Damasio, 1998; Martin et al., 1996). Thus, this region has been suggested to mediate the conscious processing of action concepts, by promoting the explicit and *efficient* retrieval of sensorimotor representations associated with a word or concept (Mahon & Caramazza, 2009; Martin & Chao, 2001; Tranel, Damasio & Damasio, 1997). On the other, it is unlikely that PM regions host the representations of action concepts or the lexical definition of those categories. Clinical studies have indeed shown that the retrieval of action concepts, although defective, is not entirely precluded by damage to sensorimotor areas, suggesting that other mechanisms can sustain it (Tranel et al., 1997). Likewise, patients with impaired action performance can preserve the ability to recognize objects and actions (Negri et al., 2007; see Mahon & Caramazza, 2005, for a review) and comprehend action words (refer to Chapter 1).

6.4.3. Verbs and sensorimotor representations

The interaction between context and word-stimulus showed two clusters of activation centered in left vPM and right postcentral gyrus. The modulation of vPM activity revealed that in a context that did not cue a motor-modality of processing, this region was more activated for action than for nonaction verbs. This is as expected, according to the above discussed findings (e.g., Grabowski et al., 1998; Martin et al., 1996). When a motor-modality of processing was cued, vPM was equally activated for action and nonaction verbs, suggesting that the cognitive context elicited the retrieval of sensorimotor representations, irrespective of the word category. This finding further support the abovementioned view that sensorimotor areas are not essential components of the lexical-semantic network; instead, their involvement is strongly constrained by the task-context eliciting the conscious, explicit processing of concrete, *embodied* information associated with a stimulus (e.g., Tranel et al., 1997). Importantly, a similar modulation was not observed for M1 activity. Activity in this region was only modulated by the context, in that it was triggered when participants processed verbs in the motor context, irrespective of their category.

Right postecentral activity resulted greater for action verbs in the nonmotor context, and for nonaction verbs in the motor context. Postcentral activity have been repeatedly observed in motor imagery (Corradi-Dell'Acqua et al., 2009; Hodge et al., 1996; Porro et al., 1996; Ruby & Decety, 2001; 2003). In particular, right-lateralized activation has been related to visuospatial processing of body-related stimuli (Goldenberg, 1999; Goldenberg & Hagmann, 1997; Tanaka & Inui, 2002). Thus, it is possible that the nonmotor (visual) context highlighted the visuospatial component of concrete sensorimotor representations, which were activated for action, but not for nonaction verbs. The increased postcentral activity for nonaction verbs confirmed that, in the motor context, concrete representations were elicited and simulated for these items. It is not clear why, in the same context, postcentral activation was lower for action than for nonaction verbs. As a tentative explanation, this may reflect the phenomenon of suppression of the somatosensory activity, ipsilateral to the (right-hand) task-relevant sensorimotor information (Staines, Graham, Black & McIlroy, 2002). In fact, in the motor task, the simulation associated with action verbs (all denoting hand-actions) might be strongly centered on right-hand movements, all participants being right handed (see Willems et al., 2010).

6.4.4. Motor simulation is one strategy for language comprehension

These results support a twofold role of the motor system in word processing and help clarify the nature of motor simulation in word understanding. We suggest that the activity in the vPM can be reliably linked to its *representational function* for concrete concepts; M1 activity reflects the motor-based *strategy* of referring a given stimulus to one’s own bodily movement, via simulation. The activation of sensorimotor representations and the motor simulation of their implied content do necessarily not co-occur.

As discussed above, when the task, or the cognitive context, require relating stimuli to action knowledge, the distributed semantic system can recruit PM regions, which promote the explicit sensorimotor representation of that knowledge. This recruitment can be preferential and possibly automatic in *normal* retrieval, when stimuli saliently refer to actions, because the modality in which individuals typically interact with entities may constrain conceptual organization (Pulvermüller, 2002; Tranel et al., 1997; Warrington & McCarthy, 1987; Warrington & Shallice, 1984).

There is reason to believe that, under certain task conditions, sensorimotor representations can be elicited also for nonaction verbs. Overall, the class of "verbs" owns *in se* the idea of action (Bates & MacWhinney, 1982; Langacker, 1987). Moreover, the polysemy, i.e., the capacity to covey multiple meanings and subsume novel usage, depending on the context, applies to concrete as well as to abstract words (Lee, 1990). Extensive behavioral priming studies documented the effects of context on the activation of specific meaning attributes of a word (Tabossi, 1988; Tabossi, Colombo & Job, 1987), and tasks involving explicit motor skills (specific movements for responding), such as the one presented in Chapter 4, may cue motor processes also when processing of abstract utterances (see Glenberg & Kashak, 2002; see Louwerse & Jeuniaux, 2008 for a discussion). Finally, imaging studies found that other dimensions, such as the imageability, can activate premotor areas in processing nonaction word (D'Esposito et al., 1997; Mellet et al., 1998; Postle et al., 2008; Pulvermüller & Hauk, 2006). These and our findigs strongly support the view of human brain as a distributed flexible architecture (Friston, 1998; McIntosh, 2000), whereby learning can immediately promote a cognitive or neural context that affects structure and operations.

Our results also contribute to depict motor simulation as a strategy or a *procedure*, which is defined by the reliance on the context, rather than stimulus-driven, to the extent that it can be applied to the processing of action verbs in a given (motor) context but not in another (nonmotor), and can be "learnt" and immediately extended to the processing of nonaction verbs. This explains why M1 activity is so inconsistently found in imaging study on action-word processing (see Hickok et al., 2009; Turella et al., 2009). By this, it is not meant that motor simulation cannot be engaged spontaneously in action-word understanding. It may provide one (the most) efficient strategy that individuals acquire early and adopt in performing task with critical sensorimotor components. Yet, it is not the sole strategy to encode action meanings. In fact, when another (nonmotor) modality of processing was cued, identical task instructions for action-verb processing were not accompanied by M1 activity. Despite so, participants' performance was as successful as in the motor context (see Recognition results).

The proposal that different networks can support the same cognitive operation is framed within the same aforementioned conception of brain as a flexible, distributed architecture (Price & Friston, 2002). The ability of structurally different mechanisms to yield the same output is well acknowledged in cognitive neuroscience, whereby multiple routes, associated with segregated brain networks, have been described for action imitation (Cubelli et al., 2000; Tessari & Rumiati, 2004), object recognition (Hmphreys & Riddoch, 1984), or word reading (Marshall & Newcomb, 1973). Particularly, a cognitive counterpart of our results can be found in the different kinds of representations (propositional/symbolic or situational/analogue) of the same linguistic materials (texts), which can be activated for comprehension (Kaup & Zwaan, 2003; Perring & Kintsch, 1985).

We have so far assumed a virtual identity between motor simulation and M1 activity, claiming that the latter implicates the former. One might argue that vPM can also reflect simulation, so that this operation applies to the processing of action verbs also in the nonmotor context. We find this explanation implausible. First, imaging studies have shown that mental simulation engages more often the dorsal, than the ventral aspect of PM region

(Kosslyn et al., 1998; Solodkin et al., 2004; Vingerhoets, de Lange, Vandemaele et al., 2002), which is massively connected to M1 (Baumer et al., 2006; Koch et al., 2006; Kosslyn et al., 1998; Xiong, Parsons, Gao, and Fox, 1999). Moreover, high-resolution fMRI and a number of other techniques have demonstrated that M1, particularly in the left hemisphere, is an essential correlate of motor simulation, to the extent that this cognitive ability is defined as a *true motor behavior* sharing important features (including brain network, kineasthetic sensations and autonomic activation) with overt motor execution (Decety, Jeannerod, Durozard & Baverel; 1993; Jackson et al., 2006; Jeannerod, 2001; Kosslyn et al., 1998; Porro et al., 1996; Solodkin et al., 2004; Tomasino et al., 2005).

The idea underlying this study was challenging in that the experimental paradigm, which has been typically implemented across tasks of the same domain (e.g., sequence learning or mental rotation in both learning and testing phases; Fletcher et al., 2004; Wraga et al., 2003), here, was used to transfer strategies across domains (motor/visual rotation and language). Our results, therefore, provide insight to the long-lasting issue concerning the degree of specificity of implicit transfer. In contrast with the proposal that implicit transfer is strictly limited to tasks that are based on the same underlying structure and tap in the same domain (Dienes & Berry, 1997), we have shown that it is a flexible mechanism, not bounded to a specific type of learning material or domain (Willingham, 1999).

This study provides strong evidence that simulation in language is one strategy or procedure that can be prevented by top-down context-dependent factors, even for tasks and stimuli with salient sensorimotor components. And it is so truly a strategy that it can be *imposed* top-down to the processing of stimuli (nonmotor verbs) that do not *normally* elicit it.

Chapter 7.

General Discussion

7.1. The tie between action and language is in our imagination

In this thesis I described a number of conditions, at stimulus- and task-level, that make the cross/talk between language and motor system possible. These conditions are compatible with the kind of circumstances that *strategically* elicit a motor modality of processing, based on imagery ability. On the other hand, the definition of conditions that *do not* elicit simulation implies, *per se*, that motor simulation is not the general mechanism for understanding action language.

In chapter 2, I have reproted neuropsychological double dissociations between language and praxis, even when the two abilities were tested under conditions (i.e., equally early-acquired verbal and motor tasks involving perceptually and conceptually identical stimuli) that may increase the degree of overlap between the two systems (e.g., Bates & Dick, 2002). In the same study, there was no indication that the deficit in action-word understanding could specifically relate to lesions in frontocentral (motor and premotor) regions that are held to encode action meanings. These findings brought support to the hypothesis that motor areas are not essential for action-word understanding (see also Hickok, 2010). Starting from here, I attempted to define the nature of motor simulation in *normal* language processing.

In chapter 3, using TMS, I found that motor simulation, as reflected in primary motor (M1) activity, mediates language processing only when the task required the explicit retrieval of action knowledge associated with a word (versus other tasks). Importantly, M1 activity enhanced beyond the time interval for lexical-semantic encoding (before 400 ms; e.g., Sereno et al., 1998), and within that for imagery (after 400 ms; e.g., Iwaki et al., 1999). Moreover, in chapter 5, I provided evidence that language affected a subsequent motor response when the sentential context described human action versus not non-biological mechanical motion. Not only is the motor system capable of *distinguishing* humans from non-humans actions, but it can also differentiate the self from others. Indeed, in a second TMS study (Chapter 4), I found that motor activity increased selectively for actions attributed to the self versus a third subject/agent. The fMRI study reported in Chapter 6 provides, in my view, the ultimate evidence that simulation in language is one strategy that can be prevented by context-dependent factors, even for tasks and stimuli with salient sensorimotor components, and readily learnt and *imposed* top-down to the processing of (nonmotor) words that do not normally elicit it.

This set of results suggests that the exposure to action-related words, on its own, is not sufficient to elicit simulation. In other words, motor simulation, in language understanding, is not completely stimulus-driven, but is defined by the reliance on *top-down* higher-level factors, such as the individuals' attention to some aspects of the stimuli, the representation of self as distinct from others, the sentential and the cognitive (neural) context. The engagement of this modality of processing requires a *cognitive mediation* that is not predicted by the *direct* matching between a perceived stimulus and the corresponding motor representation, as the embodied hypothesis suggests.

Motor imagery provides the interface between language and action, by mediating the information transfer of across the two domains. Adding a third component to the relationship between action and language, immediately implies that action understanding and motor simulation are not identical processes and language and action are independent, although highly interactive, domains. The view of strategic, rather than obligatory, motor simulation (or imagery) can explain why motor activation is so inconsistently found in imaging studies on language and action understanding (Hickok et al., 2009; Turella et al., 2009).

It is conceivable that motor simulation is the preferential, most effective modality to achieve comprehension, for normally-able individuals who are typically tested in studies involving daily actions that can be easily "visualized" or simulated. The familiarity with an action has been already shown to affect motor activation during action observation (Calvo-Merino et al., 2005; see also Chatterjee, 2010). No theory denies "(…) *that images exist or images play an important role in many cognitive processes*" (Fodor, 1975, p. 184), or that *"all higher mental capacities including language make use of some sort of basic machinery"* (Jackendoff, 2007, p. 389). However, the claim that our complex ability to comprehend can take advantage of sensorimotor experience and modality-specific systems, which are the link to senses and environment, is quite different from the claim that motor simulation is the “core attribute” of our understanding of actions.

7.2. Brain functioning and flexibility

The interpretation, proposed here, of a strategic interplay between action and language relates to a vision of the brain as a flexible distributed architecture, owning the faculty to cross the boundaries of traditionally distinct cognitive domains when needed by the task (see Rumiati, Papeo, & Corradi-Dell’Acqua, 2010; Willems & Hagoort, 2007). In this view, every cognitive task can, in principle, be mediated by context-dependent interactivity of different neural elements, so that every brain area can be part of different networks depending on a given task (McIntosh, 2000), and different networks can support the same function (Friston & Price, 2003).

The cross-talk between action-related language and motor processes may represent one paradigmatic example of the brain flexibility for making sense of task-relevant sensorimotor information in a verbal message, without implying an exclusive relationship between action and language. Instead, language comprehension can rely on different networks that can or cannot involve simulation. In chapter 5, for instance, I have suggested that visuospatial, rather than motor processes can be involved in linguistic tasks, when the sentential context cues perceptual/spatial, rather than motor representations (see also Bergen et al., 2007; Landau & Jackendoff, 1993; Talmy, 2000). The notion of strategic (context-dependent) brain functioning is well acknowledged in cognitive science, where multiple-route models have been conceived to account for empirical results in different domains of cognition. For instance, dual-route models have been proposed for word reading (Marshall & Newcombe, 1973), action imitation (Cubelli et al., 2000; Rothi et al., 1991; Tessari & Rumiati, 2004), and object recognition (Humphreys & Riddoch, 1984). Likewise, psycholiguistic research have suggested that comprehenders can construct either propositional (i.e., a symbolic description of the event) or situational representation (i.e., an analogue description to mimic structural relations between entities in the described scene) of the same text (e.g., Kaup & Zwaan, 2003; Perring & Kintsch, 1985).

In the case of language comprehension, we have so far assumed that simulation serves for conveying concrete information to conceptual representations. In the following section I will sketch alternative answers to the question why motor simulation should be engaged, if comprehension can be achieved without it.

7.3. The role(s) of motor simulation in language: a question for future research

In discussing the involvement of motor simulation in language, we have been emphasizing the relevance of rehearsing previous sensorimotor experience, through imagery, to access the concrete attributes of a word meanings (see also Rumiati et al., 2010). This idea has been well articulated in Machery's reasoning about the role of visual imagery in cognition: "*to decide whether something is a part of something else, a reliable strategy is to visualize it. Relying on imagery is a reliable strategy to solve the part-whole property verification task because in visual imagery, we access some information about the physical structure of objects*" (Machery, 2007, p. 35). Likewise, to decide whether a word is related to an action (e.g., Chapter 3), or whether an implied action is carried out outdoor or indoor (Tomasino et al., 2007), motor simulation appears as an effective way to infer the response.

Compatibly with this view, it has been suggested that the information flow from the motor to the conceptual domain is functional to language understanding in itself, by providing concepts with a physical instantiation that enriches comprehension (Mahon & Caramazza, 2008; Tranel et al., 1997). On this view, language exploits the motor system as a device providing abstract representations with concrete, contextual information to sustain semantic encoding. Thus, the role of motor system in conceptual processing may provide a measure of individual difference in conceptual processes, depending of individual motor experience (Chatterjee, 2010). In the same vein, it may be expected that, patients with impaired motor function, while they can comprehend the core meaning of an action-concept, actually lose some aspects of that concept. Moreover, the phenomena of language-induced motor activity are typically observed in normal participants during the processing of words implying actions, which every able-bodied person can perform and frequently experience. The investigation of individuals with congenital deprivation of sensorimotor experience, due, for instance, to the congenital absence of upper-limbs, can represent a test-bed to establish the extent to which motor simulation actually reflects sensorimotor experience, and what, if anything, sensorimotor experience adds to conceptual knowledge.

It is equally possible that motor activity does not serve language (conceptual) processing or categorization *per se*, but underlies functions that are triggered by, but are different from, the encoding of action meanings. In Chapter 3, I provided evidence that motor activity results from (i.e., comes after), rather than contributing to action understanding. This observation is consistent with the idea that motor simulation in action understanding, serves action anticipation (Csibra; 2004; 2008). "*The motor activation in the observer may not mirror but anticipate, may not shadow but foreshadow, what the other is doing. The perception of dynamic events, whether or not they involve social stimuli, is always predictive in nature*" (Csibra, 2008, p.451). According to this view, action stimuli may elicit motor planning to anticipate the further course of an action. This hypothesis is particularly appealing because it does not deny "mirror" activity of the brain, but reverses its function from *replication* of a perceived action, as originally argued (Rizzolatti et al., 2001), to *anticipation*. The existence of the so-called "logically-related mirror neurons" in humans may constitute the neural foundation of this hypothesis. Imaging studies have showed that premotor "mirror" areas activates in response to an observed action, but discharge during the execution of another one that is the obvious consequence of the former (Iacoboni et al., 2005). Analogously, the activity in the frontoparietal "mirror" circuitry was found to increases massively to prepare an action complementary to the observed one (Newman-Norlund et al., 2007).

These observations raised in the domain of action observation, where the benefits of being able to anticipate the immediate future of another's action appear obvious (Csibra, 2008). In language comprehension, the comprehender's motor system may subserve a similar anticipatory function by implementing the commands implied in the sender's linguistic message. This may help coordinate behaviour for social communication and interaction, which is accomplished only when the comprehender understands the intentions underlying speech and reacts properly to them (Clark & Bly, 1995; Levinson, 1983; see also Scott et al., 2009). The associated enhancement of motor activity can have the adaptive value of bringing the system close to threshold for actual execution, when the sensorimotor meaning is the focus of a message, or words are intended as motor commands (see also Postle et al., 2008).

The involvement of motor system in language may imply a mechanism of word-response association that is not extraneous to some embodied accounts of language (e.g., Pulvermüller, 2002) or can be the result of evolutionary constraints to the functional connectivity within the brain (see Mahon & Caramazza, 2009; Riesenhuber, 2007; see Mahon et al., 2009 for related questions in visual domain). In this latter view, the motor system can be part of the brain network, innately disposed to handle motor information. Then, how much of motor activation depends on previous sensorimotor experience and, as such, is learned, and how much of it depends on *a priori* principles of cortical organization? Another question for future research!

To recap, we have discussed two alternative, though not mutually exclusive, functions of motor simulation in language and conceptual processing. Simulation may serve language understanding by enriching a word representation with details concerning concrete aspects of its meaning. Alternatively, it can reflect action anticipation to coordinate behavior for social communication and interaction. Either function (categorization or anticipation) would be compatible with our account based on strategic motor imagery. In fact, while imagery allows the rehearsal of motor images or acts, which may help comprehension of perceptual stimuli, its ultimate function is to continuously update mental representations in order to predict the consequences of our own and others' actions and prepare the appropriate response (e.g., Jeannerod, 2001).

What function is actually reflected in motor activation, how much of it depends on previous individual experience, and how much on our evolutionary history, what sensorimotor information adds to our conceptual abilities and how much flexible our innate conceptual structure is, are all questions for future research. Beneficiating of the apparent anatomical and functional *transparency* of the motor system, this investigation can reveal the neural mechanisms of brain flexibility, by explaining how information from *any* modality-specific system can be transferred and integrated in higher-level cognition.

7.4. Concluding remarks

It is hard to "imagine" how extreme versions of embodied (but also disembodied) cognition could account for the complex relationship between language and motor system. While the recruitment of motor simulation in language poses a challenge to traditional, strictly modular views of cognition, it cannot be explained by *collapsing* conceptual, language and sensorimotor systems in a unique substrate, ruled by a unique mechanism (i.e., the mirror matching). This proposal has been under examination here (and elsewhere), but have failed dramatically on empirical investigation. On the one hand, neuropsychological investigation does not allow to assume an identity between conceptual and sensorimotor representations and processes; on the other hand, behavioral, imaging and TMS studies, presented here, have significantly restricted, from *all* to *certain,* the conditions for action-language interaction. The combination of these imaging and neuropsychological findings defines the role of motor system as (sometimes) sufficient, but not necessary for language comprehension.

Strategic motor imagery seems to provide the most parsimonious explanation and the most plausible interface between basic (motor) and specific (linguistic) processing. This very powerful mental operation, in language comprehension, can mediate the information flow across domains, in order to enrich symbolic representations with embodied meaning, and/or extract crucial information for planning actions. In my view, there is nothing special about the relationship between action and language. Whole cognition may take advantage of information represented in distinct systems, which can be creatively connected to subsume novel usage. However, in any situation requiring *arbitrary* combinations of information from diverse sources, is there any combinatorial system as good as language?

APPENDIX A.

List of the 15 action-verbs and 15 tool-nouns (in alphabetical order) used as experimental stimuli for the linguistic tasks in the neuropsychological study reported in Chapter 1.

	Actions (verbs)	Tools (nouns)
1	Accendere (to light up)	Accendino (cigarette lighter)
2	Bere (to drink)	Bicchiere (glass)
3	Cancellare (to rub out)	Gomma (eraser)
4	Chiudere (to lock)	Chiave (key)
5	Cucire (to sew)	Ago (needle)
6	Fumare (to smoke)	Sigaretta (cigarette)
7	Lavare (to brush the teeth)	Spazzolino (toothbrush)
8	Mangiare (to eat)	Cucchiaio (spoon)
9	Pettinare (to comb)	Pettine (comb)
10	Scopare (to sweep)	Scopa (broom)
11	Scrivere (to write)	Penna (pen)
12	Suonare (to play the flute)	Flauto (flute)
13	Telefonare (to phone)	Telefono a rotella (telephone)
14	Timbrare (to stamp)	Timbro (stamp)
15	Versare (to pour)	Bottiglia (bottle)

Appendix B

Action-related and non-action related lexical items used in Experiments 1-3.

Hand-action verbs		*Non-hand action verbs*	
abbottono, I button up	*maneggio, I handle*	*accavallo, I cross*	*nuoto, I swim*
abbraccio, I embrace	*manipolo, I manipulate*	*accelero, I accelerate*	*oltrepasso, I outstrip*
accarezzo, I caress	*manometto, I tamper*	*addento, I bite*	*ondeggio, I stagger*
acchiappo, I catch	*martello, I hammer*	*ammicco, I wink*	*palleggio, I bounce*
acconcio, I comb	*mescolo, I steer*	*annuisco, I nod*	*passeggio, I stroll*
afferro, I grasp	*mitraglio, I shoot*	*annuso, I sniff*	*pedalo, I pedal*
agguanto, I grab	*mungo, I milk*	*arretro, I move back*	*percorro, I walk*
allaccio, I fasten	*palpeggio, I feel*	*avanzo, I move forward*	*peregrinare, I stroll*
amalgamo, I mix	*perquisisco, I frisk*	*ballo, I dance*	*pesto, I stamp on*
ammanetto, I arrest	*poto, I prune*	*bevo, I drink*	*piantono, I guard*
annodo, I tie	*prendo, I take*	*bighellono, I stroll about*	*piroetto, I twist*
applaudo, I clap	*pugnalo, I stab*	*calpesto, I stomp*	*proferisco, I utter*
arrostisco, I roast	*remo, I row*	*cammino, I walk*	*retrocedo, I demote*
autografo, I sign	*rimescolo, I reshuffle*	*cavalco, I ride*	*ridacchio, I chortle*
avvito, I screw	*riparo, I fix*	*circondo, I encircle*	*rido, I laugh*
bastono, I thrash	*saluto, I salute*	*corro, I run*	*rincorro, I run after*
cesello, I carve	*sbottono, I unbutton*	*danzo, I dance*	*salgo, I rise*
clicco, I click	*scaravento, I hurl*	*decelero, I slow down*	*saltello, I jig*
coloro, I color	*scavo, I dig*	*deglutisco, I swallow*	*salto, I jump*
condisco, I dress	*scrivo, I write*	*dondolo, I swing*	*sbuffo, I fume*
cucio, I sew	*sfoglio, I leaf through*	*espiro, I breathe out*	*scappo, I rush off*
decoro, I decorate	*sminuzzo, I chop*	*gareggio, I race*	*scavalco, I leap over*
digito, I press	*smonto, I dismantle*	*gattono, I crawl*	*scivolo, I slip*
dipingo, I paint	*soffriggo, I fry*	*gironzolo, I loiter*	*sgambetto, I trot*
firmo, I sign	*solletico, I tickle*	*girovago, I bum around*	*sgranocchio, I crunch*
imbottisco, I pad	*sparo, I shoot*	*imprigiono, I imprison*	*soffio, I blow*
impugno, I clasp	*spremo, I squeeze*	*inchino, I bow*	*sogghigno, I sneer*
incateno, I chain	*stappo, I uncork*	*indietreggio, I back off*	*striscio, I crawl*
indico, I point	*stiro, I iron*	*inseguo, I pursue*	*vagabondo, I rove*
inscatolo, I pack in tins	*stringo, I hold*	*marcio, I march*	*veleggio, I sail*
intarsio, I sculpt	*strofino, I rub*	*mastico, I chew*	*volteggio, I vault*

Non-action Verbs			
addoloro, I distress	*elimino, I eliminate*	*manco, I miss*	*rinnego, I disown*
adoro, I adore	*eredito, I inherit*	*medito, I wonder*	*rinuncio, I give up*
ambisco, I hanker	*esagero, I exaggerate*	*memorizzo, I memorize*	*riprovo, I retry*
analizzo, I analyze	*esamino, I examine*	*miglioro, I improve*	*rispetto, I respect*
angoscio, I am worried	*esigo, I demand*	*moltiplico, I multiply*	*sbaglio, I mistake*
annoio, I bore	*esordisco, I debut*	*nego, I deny*	*sboccio, I blossom*
annullo, I nullify	*evito, I avoid*	*obbedisco, I obey*	*scado, I decrease in value*
apprezzo, I appreciate	*evolvo, I evolve*	*odio, I hate*	*scelgo, I choose*
assumo, I assume	*fallisco, I fail*	*offendo, I offend*	*scoccio, I annoy*
attendo, I wait	*favorisco, I promote*	*omologo, I approve*	*scommetto, I bet*
auspico, I wish	*formulo, I formulate*	*ostento, I boast*	*sconto, I discount*
autorizzo, I authorize	*fuorvio, I mislead*	*perdo, I lose*	*sconvolgo, I distress*
bado, I take care of	*garantisco, I guarantee*	*placo, I calm*	*soffro, I suffer*
boccio, I flunk	*gioisco, I rejoice*	*plagio, I crib*	*sogno, I dream*
brillo, I shine	*gradisco, I enjoy*	*poltrisco, I lounge*	*somiglio, I resemble*
decido, I decide	*gravo, I bear upon*	*possiedo, I own*	*sopporto, I tolerate*
comincio, I begin	*idolatro, I idolize*	*preferisco, I prefer*	*sospendo, I suspend*
condivido, I share	*ignoro, I ignore*	*preoccupo, I worry*	*stanzio, I allocate*
condiziono, I influence	*illudo, I deceive*	*prevedo, I predict*	*stimo, I estimate*
conosco, I know	*imparo, I learn*	*proibisco, I prohibit*	*stupisco, I astonish*
consisto, I consist	*influenzo, I influence*	*promuovo, I promote*	*sublimo, I subliminate*
deludo, I disappoint	*interesso, I interest*	*provo, I feel*	*subordino, I subdue*
deplore, I deplore	*interpreto, I interpret*	*provoco, I provoke*	*sudo, I sweat*
deprimo, I depress	*intristisco, I get sad*	*ragiono, I reason*	*sussisto, I subsist*
desidero, I desire	*invecchio, I grow old*	*rallegro, I am happy*	*taccio, I shut up*
detesto, I detest	*invidio, I envy*	*rappresento, I represent*	*tasso, I tax*
dimentico, I forget	*ipotizzo, I hypothesize*	*rendo, I convey*	*temo, I fear*
distinguo, I distinguish	*istruisco, I teach*	*resisto, I resist*	*tollero, I tolerate*
divento, I become	*lamento, I complain*	*ricevo, I receive*	*trascuro, I abandon*
doto, I provide	*legalizzo, I legalize*	*riconosco, I acknowledge*	*turbo, I trouble*
dubito, I doubt	*limito, I limit*	*rifletto, I think overt*	*vario, I change*
elaboro, I elaborate	*lucro, I earn*	*rimpiango, I regret*	*vinco, I win*

Appendix C.

Sentences used as experimental stimuli in Experiments 1-3 reported in Chapter 5.

Clockwise human-related sentences

Il bambino sta temperando la matita colorata (*The child is sharpening the colored pencil*).
L'operaio sta avvitando la lampadina al lampadario (*The worker is screwing the light bulb into the lamp*).
L'autista sta sterzando velocemente a destra (*The driver is rapidly veering to the right*).
La signora sta componendo il numero sul telefono a rotella (*The lady is composing the phone number on the dial phone*).
Il ragazzo sta alzando il volume dello stereo con la manopola (*The boy is turning up the volume of the hi-fi with the knob*).
Il falegname sta stringendo la vite del tavolo (*The carpenter is tightening the screw of the table*).
Il ragazzo sta azionando il motore della macchina (*The boy is turning on the car engine*).

Counterclockwise human-related sentences

L'autista sta sterzando velocemente a sinistra (*The driver is rapidly veering to the left*).
La signora sta abbassando la fiamma del fornello (*The lady is turning down the gas on the hob*)
Il ragazzo sta abbassando il volume dello stereo con la manopola (*The boy is turning down the volume of the hi-fi with the knob*).
Il farmacista sta svitando il barattolo di vetro (*The pharmacist is opening the glass-jar*).
L'operaio sta svitando la lampadina dal lampadario (*The worker is removing the light bulb from the lamp*).
Il falegname sta estraendo la vite dal muro (*The carpenter is removing the screw from the wall*)
Il ragazzo sta spegnendo il motore della macchina (*The boy is turning off the car engine*).

Clockwise object-related sentences

Il CD sta girando nel lettore (*The CD is turning in the CD-player*).
Il disco sta girando sul grammofono (*The record is turning on the gramophone*).
La lavatrice sta centrifugando il bucato colorato (*The washing machine is spinning the colored laundry*).
La lancetta sta segnando lo scorrere dei secondi (*The second-hand is turning*).
La trottola colorata sta girando sul pavimento (*The spinning top is turning on the floor*).
La lancetta della bilancia sta segnando l'aumento di peso (*The scales are indicating the increase in weight*).
Il tachimetro sta avvertendo l'aumento di velocita' (*The speedometer is indicating the speed increase*).

Counterclockwise object-related sentences

Il mangianastri sta riavvolgendo la cassetta (*The cassette-player is rewinding*).
La videocassetta sta tornando indietro (*The video-tape is rewinding*).
La lancetta sta segnando un abbassamento di pressione (*The barometer is signalling a drop in pressure*).
La punta del trapano sta estraendo la vite dal muro (*The point of the screwdriver is removing the screw from the wall*).
Il carillon si sta muovendo in senso antiorario (*The mobile is moving counterclockwise*).
La lancetta della bilancia sta tornando sullo zero (*The scales are returning to zero*).
La lancetta del tachimetro sta registrando la riduzione di velocita’ (*The speedometer is signalling a decrease in speed*).

Appendix D

Norming study for the assessment of sentences used as experimental stimuli in Experiments 1-3 reported in Chapter 5.

A Norming study was carried out with the objective to collect basic information about the selected stimulus-sentences. Thirty-one participants were asked to complete a questionnaire to evaluate those motor dimensions implied by language that might influence the relationship between language and motor processes. Particularly, the familiarity tightly correlates with the time for item processing (e.g. Connine et al. 1990), and the imageability of an utterance determines the ability to mentally represent its content. Moreover, language can convey very detailed features of the described context that are used to construct situation models during comprehension (see Jackendoff 1987). Therefore, features like amplitude and continuity might render the motion implied in some items, more perceptually salient or suitable to interact with motor processes, than others. On the other hand, the time for mentally representing rotation is typically proportional to the degrees of rotation (Shepard and Cooper 1982). Thus, participants rated: 1) familiarity (how familiar they were with the scene described in the sentence); 2) imageability (how difficult/easy it was to elicit a mental image of the described scene); 3) amplitude of the implied motion; and 4) whether it was part-way or continuous. The first three dimensions were rated on 1-7 Likert-type scales, whereas a binary score (0-1) was required to judge whether the implied motion was part-way (0) or continuous (1).

We also collected simple RTs for each sentence, with the objective to test whether and to what extent any of the assessed dimensions influenced sentences comprehension. In other words, we wanted to ensure that implied motor dimensions, other than type (manual or mechanical) and direction, were balanced across sentences or, at least, did not crucially affected or biased sentence processing. In this manner, should any difference occur in the following experiments between CW and CCW human and objects sentences, it could be attributed to the interaction between type and direction of implied motion and motor process for responding. Therefore, before filling in the questionnaire, participants performed a semantic-judgment task, where they judged the sensibility of the selected sensible and nonsensical sentences by pressing a key, a response that did not elicit any congruence effect with the implied-language motion.

Materials and methods

Participants

Thirty-one healthy, right-handed native Italian speakers (11 males, 18-31 years), all university graduates or undergraduate students, participated in this preliminary study.

Materials and procedure

Participants were presented with the above 56 motion and state sentences and 56 nonsensical sentences for a semantic-judgment task. All items had been previously read aloud and recorded (http://audacity.sourceforge.net/) by a female Italian speaker. They were transmitted to participants through headphones, their length ranging from 2.066 to 3.995 ms. Participants were instructed to press the spacebar on a keyboard when the sentence made sense, while no response was required for nonsensical sentences. They were told to respond as quickly as possible, but not before they had listened to the whole sentence, as many nonsensical sentences could not be recognized as such until the last word was heard. Each sentence was randomly presented twice for a total of 224 trials. All factors were manipulated within-subjects; this yielded a 2 Stimulus-type (human-related and object-related sentences) X 2 implied-language rotation (clockwise and counterclockwise) experimental design. At the end of the experiment, the ratings for the several dimensions of the motion implied by the sentences were collected with a questionnaire.

Analyses

Familiarization, state and nonsensical trials were discarded. All participants achieved at least 85% accuracy in judging critical trials (*M*=97%), except two, who failed in 19% and 22% of trials respectively and were therefore excluded from subsequent analyses. Incorrectly-judged trials (2.6%) and those with response latencies 2 *SDs* away from the individual condition mean (7.5% of correct responses) were discarded. A repeated-measures ANOVA with factors Stimulus-type and Implied-language rotation was run on RTs. All planned comparisons between critical conditions were performed using two-tailed *t*-tests ($\alpha \leq .05$) and the by-item analysis was performed with regressions of repeated measured data (Lorch and Myers 1990).

Results

All participants achieved at least 85% accuracy in judging critical trials (*M*=97%), except for two, who failed in 19% and 22% of trials respectively and were therefore excluded from the analyses. RTs to state and nonsensical sentences, incorrectly-judged trials (2.6%) and those with response latencies 2 *SDs* away from the individual condition mean (7.5% of correct responses) were discarded (Ratcliff 1993). Responses to human-related sentences resulted overall faster than responses to object-related sentences $F(1,28)=10.47$, $p<.01$, $\eta_p^2=.27$, and CW sentences were overall faster than the CCW ones, $F(1,28)=5.70$, $p=.02$, $\eta_p^2=.17$. The interaction between the two factors was not significant , $F(1,28)=1.97$, *n.s.* No significant difference was found between CW and CCW human sentences, $p>.1$, while judgments on CW object sentences were faster than those on CCW sentences, $t(28)=2.17$, $p=.03$, $t(28)_{\text{item}}=2.62$, $p=.01$ (Fig. 1). That is, participants processed CW and CCW human sentences equally fast, whilst they showed a temporal advantage in processing CW over CCW object sentences. These comparisons provided us with information on participants' performance in a response condition (i.e. keypress) that did not elicit any congruence effect. In the following experiment, we investigated whether and how the congruence between implied and actual motion (i.e. manual rotation) altered such pattern of performance on human and object sentences.

Post-experimental questionnaire

The results of the questionnaire revealed no difference in familiarity and imageability between CW and CCW human- and object-sentences (*p*s>.1). The amplitude of motion was judged to be overall greater for object than human motion, $t(13)=4.73$, $p<.001$, but CW and CCW sentences within each type resulted matched for this dimension, *p*s>.1. Likewise, object motion was judged as having higher continuity than human motion, $t(13)=3.98$, $p=.001$, although this dimension was matched between CW and CCW human-related sentences and between CW and CCW object-related sentences, *p*s>.1. Then, a regression model was created using the participants' ratings of familiarity, imageability, amplitude and continuity, entered in a stepwise fashion, as predictors of the mean RT for each sentence[1]. This resulted in an effect size with $R^2(23)=.34$, and significant beta weight obtained for the familiarity factor only ($\beta=-.96$; $t(23)=-3.22$, $p=.003$). Thus, the only predictor of RTs was the familiarity that, however, could not constitute a bias in sentence comprehension because it was matched for all the critical types of sentences. Human and object sentences differed for amplitude and continuity of implied motion, both being higher for the latter type of stimuli. This is not surprising, because manual rotations described in human sentences involved the wrist (e.g. to open a glass jar) which has limited degrees of rotation, compared with many mechanical objects (e.g. a record rotating on a gramophone). Likewise, motion implied in object sentences was often a continuous rotation, whereas biomechanical joint-constraints of the wrist only allow part-way rotation. However, neither dimension predicted RTs, thus ensuring that these differences could not weight on participants’ performance. More importantly, the Norming study showed that CW and CCW sentences within each stimulus-type (which were the critical conditions for comparisons), besides length, structure and complexity, were fully comparable for familiarity, imageability, amplitude and continuity of implied motion.

---

[1] Mean RTs for each sentence were computed taking into account the response latencies of the first presentation of each sentence. The correlation between RTs for the first presentation of the item and the mean RTs of both presentations was highly significant ($r(27)=.94$, $p<.0001$)

Appendix E

Table S1. (*Relative to Chapter 6)* List of the individual and group mean coordinates (in MNI space) of the maximally activated voxel within the (anatomically-constrained functional) ROIs comprising the hand representation of the left and the right primary motor (M1) cortices obtained by the functional localizer task and the maximum probability maps (MPMs).

Left M1			***Right M1***		
x	***y***	***z***	***x***	***y***	***z***
-42	-24	60	38	-28	52
-38	-24	62	36	-24	58
-38	-24	56	36	-24	58
-42	-24	60	42	-22	50
-38	-26	62	42	-20	56
-32	-24	56	36	-22	58
-34	-24	58	38	-24	52
-38	-28	60	38	-24	50
-34	-28	60	40	-22	60
-42	-28	58	42	-20	56
-38	-28	60	36	-22	58
-38	-24	60	40	-26	62
-38	-22	62	42	-22	52
-38	-28	62	36	-24	60
-42	-22	56	42	-18	54
-38	***-26***	***60***	***39***	***-23***	***56***
3,07	*2,1*	*2,2*	*2,6*	*2.5*	*3,8*

The group mean coordinates are indicated in **bold** and the respective standard deviations in *italics*.

References

Ajuriaguerra J de, Hécaen H, Angelergues R (1960) Les apraxies: variétés cliniques et latéralisation lésionelle. Rev Neurol (Paris), 102, 566-94.

Allport DA. (1985) Distributed memory, modular subsystems and dysphasia. In Current Perspectives in Dysphasia, ed. SK Newman, R Epstein, 32–60. Edinburgh: Churchill Livingstone.

Augustine J (1996) Circuitry and functional aspects of the insular lobe in primates including humans. Brain Research Reviewws, 22, 229-44.

Aziz-Zadeh L, Wilson SM, Rizzolatti G, Iacoboni M (2006) Congruent embodied representations for visually presented actions and linguistic phrases describing actions. Current Biology, 16, 1818–1823.

Bak TH, O'Donovan DG, Xuereb JH, Boniface S, Hodges JR (2001) Selective impairment of verb processing associated with phonological changes in Brodmann areas 44 and 45 in the motor neurone disease-dementia-aphasia syndrome. Brain, 124, 103–120.

Bak, T.H., Yancopoulou D, Nestor PJ, Xuereb JH, Spillantini MG, Pulvermüller F, et al. Clinical, imaging and pathological correlates of a hereditary deficit in verb and action processing. Brain 2006; 129:321-32.

Barsalou LW (1999) Perceptual symbol systems. Behavioral and Brain Sciences, 22, 577–660.

Barsalou LW (2009) Simulation, situated conceptualization, and prediction. Philosophical Transactions of the Royal Society B. 364, 1281–1289.

Bates E, Dick F (2002) Language, gestures, and the developing brain. Developmental Psychobiology, 40, 293-310.

Bates E, MacWhinney B (1989). Functionalism and the Competition Model. In: B. MacWhinney, & E. Bates (Eds), The Crosslinguistic Study of Sentence Processing. (p. 1-73). Cambridge: Cambridge University Press.

Bäumer T, Bock F., Koch G., Lange R., et al. (2006) Magnetic stimulation of human premotor or motor cortex produces interhemispheric facilitation through distinct pathways. The Journal of Physiology, 572, 857-868.

Bell BD (1994) Pantomime recognition impairment in aphasia: an analysis of error types. Brain and Language, 47, 269–278.

Bergen B, Chang N (2005) Embodied construction grammar in simulation-based language understanding. In J.O. Ostman & M. Fried (Eds.), Construction grammars: Cognitive grounding and theoretical extensions (pp. 147–190). Amsterdam: Benjamins.

Bergen BK, Lindsay S, Matlock T, Narayanan S (2007) Spatial and Linguistic Aspects of Visual Imagery in Sentence Comprehension. Cognitive Science 31, 733-764

Berndt RS, Haendiges A, Burton M, Mitchum C (2002) Grammatical class and imageability in aphasic word production: their effects are independent. The Journal of Neurolinguistics 15: 353-371.

Berndt RS, Mitchum CC, Haendiges AN, Sandson J (1997) Verb retrieval in aphasia1. 1. Characterizing single word impairments. Brain and Language, 56, 68–106.

Binder JR, Medler DA, Desai R, Conant LL, Liebenthal E (2005). Some neurophysiological constraints on models of word naming. NeuroImage, 27, 677–693.

Binder JR, Westbury CF, McKiernan KA, Possing ET, Medler DA (2010). Distinct Brain Systems for Processing Concrete and Abstract Concepts. Journal of Cognitive Neuroscience, 17, 905–917.

Binkofski F, Buccino G, Posse S Seitz RJ, Rizzolatti G, Freund H (1999) A fronto-parietal circuit for object manipulation in man: evidence from an fMRI-study. European Journal of Neuroscience, 11, 3276-86.

Bookheimer S (2003) Functional MRI of language: New approaches to understanding the cortical organization of semantic processing. Annual Review, 25, 151-88.

Boroditsky L (2000) Metaphoric structuring: understanding time through spatial metaphors. Cognition, 75, 1–28.

Botvinick MM, Plaut DC (2006) Short-term memory for serial order: a recurrent neural network model. Psychological Reviews, 113, 201-33.

Boulenger V, Décoppet N, Roy A, Paulignan Y, Nazir TA (2007) Differential effects of Age-of-Acquisition for concrete nouns and action verbs: Evidence for partly distinct representations? Cognition, 103, 131-46.

Braitenberg V, Schüz A (1998) Cortex: Statistic and Geometry of Neuronal Connectivity (2nd ed.). Springer-Verlag, New York. (revised edition of Anatomy of the Cortex: Statistics and Geometry, Springer-Verlag, 1991).

Bub DN, Masson MEJ, Cree GS (2008) Evocation of functional and volumetric gestural knowledge by objects and words. Cognition, 106, 27–58.

Buccino G, Binkofski F, Fink GR, Fadiga L, Fogassi L, Gallese V, et al. (2001) Action observation activates premotor and parietal areas in a somatotopic manner: An fMRI study. European Journal of Neuroscience, 13, 400–404.

Buccino G, Raggio L, Melli G, Binkofski F, Gallese V, Rizzolatti G (2005) Listening to action-related sentences modulates the activity of the motor system: A combined TMS and behavioral study. Cognitive Brain Research, 24, 355-363.

Burgess C (1998). From simple associations to the building blocks of language: Modeling meaning in memory with the HAL model. Behavior Research Methods, Instruments, and Computers, 30, 188–98.

Buxbaum LJ, Kyle KM, Menon R (2005) On beyond mirror neurons: Internal representations subserving imitation and recognition of skilled object related actions in humans. Cognitive Brain Research, 25, 226–239.

Calvo-Merino B, Glaser DE, Grèzes J, Passingham RE, Haggard P (2005) Action Observation and Acquired Motor Skills: An fMRI Study with Expert Dancers. Cerebral Cortex, 15, 1243—1249.

Calvo-Merino B, Grèzes J, Glaser DE, Passingham RE, Haggard P (2006) Seeing or doing? Influence of visual and motor familiarity in action observation. Current Biology, 16, 1905–1910.

Cappa SF, Binetti G, Pezzini A, Padovani A, Rozzini L, Trabucchi M (1998) Object and action naming in Alzheimer’s disease and frontotemporal dementia. Neurology, 50, 351–355.

Caramazza A, Mahon BZ (2003) The organization of conceptual knowledge: The evidence from category-specific semantic deficits. Trends in Cognitive Science, 7, 354-361.

Caramazza A, Shelton JR. 1998. Domain specific knowledge systems in the brain: The animate-inanimate distinction. Journal of Cognitive Neuroscience, 10, 1-34.

Caramazza A (1986) On drawing inferences about the structure of normal cognitive systems from the analysis of patterns of impaired performance: the case for single-patient studies. Brain and Cognition, 5, 41-66.

Caramazza A (1997) How Many Levels of Processing Are There in Lexical Access? Cognitive Neuropsychology, 14, 177–208.

Caramazza A, Hillis AE, Rapp BC, Romani C (1990) The multiple semantics hypothesis: Multiple confusions? Cognitive Neuropsychology, 7, 161-189.

Caramazza A, Hillis AE (1991) Lexical organization of nouns and verbs in the brain. Nature, 349, 788–790.

Carey S (2009) The Origin of Concepts. New York: Oxford University Press.

Carey S, Spelke ES (1994) Domain specific knowledge and conceptual change. In Mapping the Mind: Domain Specificity in Cognition and Culture, ed. L Hirschfeld, S Gelman, (pp. 169-200). Cambridge: Cambridge University Press.

Carr L, Iacoboni M, Dubeau MS, Mazziotta JC, Lenzi GL (2003) Neural mechanisms of empathy in humans: A relay from neural systems for imitation to limbic areas. Proceedings of the National Academy of Science USA, 100, 5497-5502.

Carreiras M, Vergara M, Barber H (2005). Early Event-related Potential Effects of syllabic processing during visual word recognition. Journal of Cognitive Neuroscience, 17, 1803–1817.

Chao LL, Martin A. 2000. Representation of Manipulable Man-Made Objects in the Dorsal Stream. NeuroImage, 12, 478-484.

Chao LL, Haxby JV, Martin A (1999) Attribute-based neural substrates in posterior temporal cortex for perceiving and knowing about objects. Nature Neuroscience, 2, 913–919.

Chatterjee A (2010) Disembodying Cognition. Language and Cognition, 2, 79–116.

Chatterjee A, Southwood MH, Basilico D (1999) Verbs, events and spatial representations. Neuropsychologia, 37, 395–402

Chee MWL, O’Craven KM, Bergida R, Rosen BR, Savoy RL (1999). Auditory and Visual Word Processing Studied With fMRI. Human Brain Mapping, 7, 15–28

Chrisley R, Ziemke T (2002) Embodiment. In Encyclopedia of Cognitive Science. Macmillan.

Clark H (1973) The language-as-a-fixed-effect fallacy: critique of language statistics in psychological research. Journal of Verbal Learnning and Verbal Behavior, 12, 335–359

Clark HH, Bly B (1995) Pragmatics and discourse. In: Miller JL, Eimas PD, editors. Speech, language and communication (pp. 371-410). New York: Academic Press.

Colombo L, Burani C (2002) The influence of age of acquisition, root frequency and context availability in processing nouns and verbs. Brain and Language, 81, 398-411.

Connine CM, Mullennix J, Shernoff E, Yelen J (1990) Word familiarity and frequency in visual and auditory word recognition. Journal of Experimenatl Psychology Learnning Memory and Cognition, 16, 1084-1096.

Cooper LA, Shepard RN (1975) Mental transformations in the identification of left and right hands. Journal of Experimental Psychology Human Perception and Performance, 1, 48–56.

Corina DP, Gibson EK, Martin R, Poliakov A, Brinkley J, Ojemann GA (2005) Dissociation of action and object naming: Evidence from cortical stimulation mapping, Human Brain Mapping, 24, 1–10.

Corradi-Dell'Acqua C, Tomasino B, Fink G (2009) What is the position of an arm relative to the body? Neural correlates of egocentric and allocentric body reference frames Journal of Neuroscience, 29, 4162-4171.

Crawford JR, Garthwaite PH (2002). Investigation of the single case in neuropsychology: Confidence limits on the abnormality of test scores and test score differences. Neuropsychologia, 40, 1196–1208.

Crawford JR, Garthwaite PH (2005) Testing for suspected impairments and dissociations in single-case studies in neuropsychology: Evaluation of alternatives using Monte Carlo simulations and revised tests for dissociations. Neuropsychology, 19, 318–331.

Crawford JR, Garthwaite PH, Gray CD (2003). Wanted: Fully operational definitions of dissociations in single-case studies. Cortex, 39, 357–370.

Crepaldi D, Aggujaro S, Arduino LS, Zonca G, Ghirardi G, Inzaghi MG et al. (2006). Noun–verb dissociation in aphasia: The role of imageability and functional locus of the lesion. Neuropsychologia, 44, 73–89.

Cross ES, Kraemer DJM, Hamilton AFC, Kelley WM, Grafton ST (2009). Sensitivity of the Action Observation Network to Physical and Observational Learning. Cerebral Cortex, 19, 315--326

Csibra G (2004). Mirror neurons and action observation. Is simulation involved? Publication of the European Science Foundation. Available from: http://www.interdisciplines.org/mirror/papers/4.

Csibra G (2008) Action mirroring and action understanding: An alternative account. In P Haggard, Y Rossetti, M Kawato (Eds) Sensorimotor foundations of higher cognition. Attention and Performance XXII. Oxford: Oxford UP.

Cubelli R, Marchetti C, Boscolo G, Della Sala S (2000) Cognition in action: testing a model of limb apraxia. Brain and Cognition, 44, 144–165.

Dejerine J (1892). Contribution a l’etude anatomoclinique et clinique des differentes varietes de cecite verbal. CR Hebdomadaire Sceances Memories. Social Biology, 4, 61–90.

Damasio H, Tranel D, Grabowski T, Adolphs R, Damasio A. (2004), Neural systems behind word and concept retrieval. Cognition, 92, 179-229.

Damasio H, Grabowski TJ, Tranel D, Hichwa RD, Damasio AR (1996). A neural basis for lexical retrieval. Nature, 380, 499-505.

Damasio A, Tranel D (1993) Nouns and verbs are retrieved with differentially distributed neural systems. Proceedings of the National Academy of Science USA, 90, 4957–60.

Daniele A, Giustolisi L, Silveri MC, Colosimo C, Gainotti G (1994) Evidence for a possible neuroanatomical basis for lexical processing of nouns and verbs. Neuropsychologia, 32, 1325–41.

Daniloff JK, Noll JD, Fristoe M, Lloyd LL. (1982). Gesture recognition in patients with aphasia. Journal of Speech and Hearing Disorders, 47, 43-49.

D'Esposito M, Detre JA, Aguirre GK, Stallcup M, Alsop DC, Tippet LJ, Farah MJ (1997). A functional MRI study of mental image generation, Neuropsychologia 35, 725–730.

De Bleser R, Kauschkeb C (2003) Acquisition and loss of nouns and verbs: parallel or divergent patterns? Journal of Neurolinguistics, 16, 213–229.

De Renzi E, Faglioni P (1999) Apraxia. In: G. Denes, L. Pizzamiglio (Eds), Handbook of clinical and experimental neuropsychology (pp. 421–440). Hove, UK: Psychology Press.

De Renzi E, Lucchelli F (1988) Ideational apraxia. Brain, 111, 1173-1185.

De Renzi E, Motti F, Nichelli P (1980) Imitating gestures: a quantitative approach to ideomotor apraxia. Archives of Neurology, 37, 6-10.

De Renzi E, Pieczuro A, Vignolo LA (1968) Ideational apraxia: a quantitative study. Neuropsychologia, 6, 41-52.

Decety J, Chaminade T (2003) When the self represents the other: a new cognitive neuroscience view on psychological identification. Consciousness and Cognition, 12, 577-596.

Decety J, Grèzes J (1999) Neural mechanisms subserving the perception of human actions. Trends in Cognitive Science, 3, 172-178.

Decety J, Sjöholm H, Ryding E, Stenberg G, Ingvar DH. (1990). The cerebellum participates in mental activity: tomographic measurements of regional cerebral blood flow. Brain Research, 535, 313-317.

Decety J, Jeannerod M, Durozard D, Baverel G (1993). Central activation of autonomic effectors during mental simulation of motor actions in man. Journal of Physiology, 461, 549-63.

Dee HL, Benton AL, Van Allen MW (1970). Apraxia in relation to hemispheric locus of lesion and aphasia. Transactions of the American Neurological Association, 95, 147-150.

Dehaene S, Bossini S, Giraux P (1993) The mental representation of parity and number magnitude. Journal of Experimental Psychology General, 122, 371-396.

Devlin J, Gonnerman L, Andersen E, Seidenberg M (1998). Category-specific semantic deficits in focal and widespread brain damage: A computational account. Journal of Cognitive Neuroscience, 10, 77-94.

Di Pellegrino G, Fadiga L, Fogassi L, Gallese V, Rizzolatti G (1992). Understanding motor events: A neurophysiological study. Experimental Brain Research, 91, 176–180.

Dienes Z, Berry D (1997). Implicit learning: Below the subjective threshold. Psychonomic Bulletin and Review, 4, 3–23

Dinstein I, Hasson U, Rubin N, Heeger DJ (2007) Brain areas selective for both observed and executed movements. Journal of Neurophysiology, 98, 1415-27

Dinstein I, Thomas C, Behrmann M, Heeger DJ (2008) A mirror up to nature. Current Biology, 18, R13-18.

Dinstein I (2008) Human cortex: reflections of mirror neurons. Current Biology, 18, R956

Dronkers NF (1996). A new brain region for coordinating speech articulation. Nature, 384, 159–161.

Duffy RJ Duffy JR (1981) Three studies of deficits in pantomimic expression and pantomime recognition in aphasia. Journal of Speech and Hearing Research 46, 70–84.

Duffy RJ, Duffy JR, Pearson KL (1975) Pantomime Recognition in Aphasics. Journal of Speech and Hearing Research, 18, 115-132.

Duvernoy HM (1991) The human brain: surface, blood supply and three-dimensional sectional anatomy. Wien: Springer-Verlag.

Ehrsson HH, Geyer S, Naito E (2003) Imagery of voluntary movement of fingers, toes and tongue activates corresponding body-part specific motor representations. Journal of Neurophysiology, 90, 3304-3316.

Eickhoff SB, Stephan KE, Mohlberg H, Grefkes C, Fink GR, Amunts K, Zilles (2005) A new SPM toolbox for combining probabilistic cytoarchitectonic aps and functional imaging data. Neuroimage, 25, 1325–1335.

Eickhoff SB, Amunts K, Mohlberg H, Zilles K (2006) The human parietal operculum. ii. Stereotaxic maps and correlation with functional imaging results. Cerebral Cortex, 16, 268 –279.

Eickhoff SB, Grefkes C, Zilles K, Fink GR (2007) The somatotopic organization of cytoarchitectonic areas on the human parietal operculum. Cerebra Cortex, 17, 1800 –1811.

Eimer M, Hommel B, Prin W (1995). S-R compatibility and response selection. Acta Psychologica, 90, 301-313.

Fadiga L, Fogassi L, Gallese V, Rizzolatti G. (2000) Visuomotor neurons: ambiguity of the discharge or ‘motor’ perception? International Journal of Psychophysiology, 35, 165–177.

Fadiga L, Craighero L, D’Ausilio A (2009) Broca’s area in language, action, and music. Annals of the New York Academy of Science, 1169, 448–458.

Fadiga L, Fogassi L, Pavesi G, Rizzolatti G (1995) Motor facilitation during action observation: a magnetic stimulation study. Journal of Neurophysiology, 73, 2608-2611.

Ferretti TR, Kuta M McRae JK (2007) Verb Aspect and the Activation of Event Knowledge. Journal of Experimental Psychology Learnning Memory and Cognition, 33, 182–196.

Ferro JM, Santos ME, Castro-caldas A, Mariano G (1980) Gesture recognition in aphasia. Journal of Clinical and Experimental Psychology, 2, 277-292.

Fiebach CJ, Friederici AD (2003) Processing concrete words: fMRI evidence against a specific right-hemisphere involvement. Neuropsychologia, 42, 62-70.

Fiez JA, Balota DA, Raichle ME, Petersen SE (1999) Effects of Lexicality, Frequency, and Spelling-to-Sound Consistency on the Functional Anatomy of Reading. Neuron, 24, 205-218.

Fiez JA, Petersen SE. (1998) Neuroimaging studies of word reading. Proceedings of the National Academy of Science USA, 95, 914-21.

Fink GR, Manjaly ZM, Stephan KE, Gurd JM, Zilles K, et al. (2006) A role for Broca’s area beyond language processing: evidence from neuropsychology and fMRI. In: K. Amunts, Y. Grodzinsky (Eds), Broca’s area. Oxford US: University Press.

Finkelnburg DC (1870) [Niederrheinische Gesellschaft in Bonn, Sitzung vom 21. März 1870.] Berliner Klinische Wochenschrift, 7, 449–450, 460–462.

Fischer MH, Zwaan RA. (2008). Embodied language: a review of the role of the motor system in language comprehension. Quarterly Journal of Experimental Psychology, 61, 825-850.

Fletcher PC, Zafiris O, Frith CD, Honey RA, Corlett PR, Zilles K, Fink GR. (2005) On the benefits of not trying: brain activity and connectivity reflecting the interactions of explicit and implicit sequence learning. Cerebral Cortex, 15, 1002-1015.

Fodor JA (1975) The language of thought. Cambridge, MA: Harvard University Press.

Fodor JA (1983) The modularity of mind. Cambridge, MA: MIT Press.

Fogassi L, Ferrari PF (2007) Mirror neurons and the evolution of embodied language. Current Directions in Psychological Science, 16, 136-141.

Folstein MF, Folstein SE, McHugh PR (1975) 'Mini-Mental State': a practical method for grading the cognitive state of patients for the clinician. Journal of Psychiatric Research, 12, 189-198.

Frey SH, Vinton D, Norlund R, Grafton ST (2005) Cortical topography of human anterior intraparietal cortex active during visually guided grasping. Cognitive Brain Research, 23, 397-405.

Friederici AD (2002) Towards a neural basis of auditory sentence processing. Trends in Cognitive Science, 6, 78-84.

Friederici AD, Opitz B, von Cramon DY (2000) Segregating semantic and syntactic aspects of processing in the human brain: an fMRI investigation of different word types. Cerebral Cortex, 10, 698-705.

Friederici AD, Rüschemeyer S-A, Hahne A, Fiebach CJ (2003) The role of left inferior frontal gyrus and superior temporal cortex in sentence comprehension: localizing syntactic and semantic processes. Cereb Cortex, 13, 170-177.

Friston KJ, Price CJ (2003) Degeneracy and redundancy in cognitive anatomy. Trends in Cognitive Sciences, 7, 151–152.

Frith C, Dolan RJ (1997) Brain mechanisms associated with topdown processes in perception. Philosophical Transactions of the Royal Society London B Biological Science, 352, 1221–1230.

Friston KJ, Frith CD, Turner R, Frackowiak RS (1995a) Characterizing evoked hemodynamics with fMRI. Neuroimage, 2, 157–165.

Friston KJ, Holmes AP, Worsley KJ, Poline JB, Frackowiak RSJ (1995b) Statistical parametric maps in functional imaging: a general linear approach. Human Brain Mapping, 2, 189–210.

Friston KJ (1998) Imaging neuroscience: Principles or maps? Proceedings of the National Academy of Sciences USA, 95, 796–802.

Funk M, Brugger P, Wilkening F (2005) Motor processes in children's imagery: the case of mental rotation of hands. Developmental Science, 8, 402–408

Gainotti G, Ibbia R (1972) La comprensione del significato dei gesti simbolici negli afasici. Minerva Psichiatria e Psicologica. 13, 1-9.

Gainotti G, Lemmo MS (1976) Comprehension of symbolic gestures in aphasia. Brain and Language, 3, 451-460.

Galantucci B, Fowler CA, Turvey MT (2005) The motor theory of speech perception reviewed. Psychonomic Bulletin and Review, 13, 361–377.

Galantucci B (2005) An experimental study of the emergence of human communication systems. Cognitive Science, 29, 737–767.

Gallagher S (2007) Logical and phenomenological arguments against simulation theory. In D Hutto, M Ratcliffe (Eds) Folk Psychology Re-assessed. Berlin: Springer Publishers.

Gallese V, Fadiga L, Fogassi L, Rizzolatti G (1996) Action recognition in the premotor cortex. Brain 119, 593-609.

Gallese V, Lakoff G (2005) The brain's concepts: the role of the sensorymotor system in reason and language. Cognitive Neuropsychology, 22, 455-79.

Ganis G, Keenan JP, Kosslyn SM, Pascual-Leone A (2000) Trancranial magnetic stimulation of primary motor cortex affects mental rotation. Cerebral Cortex, 10, 175-180.

Gentilucci M, Gangitano M (1998) Influence of automatic word reading on motor control. European Journal of Neuroscience, 10, 752-756,

Geschwind N (1965) Disconnexion syndromes in animals and man. I. Brain, 88, 237-294.

Ghyselinck M, Lewis MB, Brysbaert M (2004). Age of acquisition and the cumulative frequency hypothesis: a review of the literature and a new multi-task investigation. Acta Psychologica, 115, 43-67.

Glenberg AM, Sato M, Cattaneo L, Riggio L, Palumbo D, Buccino G (2008) Processing abstract language modulates motor system activity. Quarterly Journal of Experimental Psychology, 61, 905-919.

Glenberg AM, Kaschak MP (2002) Grounding language in action. Psychonomic Bulletin and Review, 9, 558–565.

Goldenberg G (1999) Matching and imitation of hand and finger postures in patients with damage in the left or right hemisphere. Neuropsychologia, 37, 559-566

Goldenberg G, Hagmann S (1997) The meaning of meaningless gestures: a study of visuo-imitative apraxia. Neuropsychologia, 35, 333-41.

Goldenberg G, Hartmann K, Schlott I (2003) Defective pantomime of object use in left brain damage: apraxia or asymbolia? Neuropsychologia, 41, 1565–1573.

Graf P, Schacter DL (1985) Implicit and explicit memory for new associations in normal and amnesic subjects. Journal of Experimental Psychology Learning Memory and Cognition, 11, 501-518.

Grafton ST, Hazeltine E, Ivry RB (1995) Localization of independent cortical systems in human motor learning. Journal of Cognitive Neuroscience, 7, 497–510.

Grafton ST, Fadiga L, Arbib MA, Rizzolatti G (1997) Premotor cortex activation during observation and naming of familiar tools. Neuroimage, 6, 231-236.

Grafton ST, Hazeltine E, Ivry RB (1998) Abstract and effector-specific representations of motor sequences identified with PET. Journal of Neuroscience, 18, 9420–9428.

Grèzes J, Decety J (2001) Functional anatomy of execution, mental simulation, observation and verb generation of actions: A meta-analysis. Human Brain Mapping, 12, 1-19.

Hecaen H (1962). The clinical symptomatology of right and left hemispheric lesions. Cah Coll Med Hop Paris, 3, 259-70.

Hachinski V (2002) Stroke: the next 30 years. Stroke, 33, 1-4.

Haggard P, Kitadono K, Press C, Taylor-Clarke M (2006) The brain’s fingers and hands. Experimental Brain Research, 172, 94–102.

Hagoort P (2005) On Broca, brain, and binding: a new framework. Trends in Cognitive Science, 9, 416-423.

Harris JA, Clifford CWG, Miniussi C (2008) The functional effect of transcranial magnetic stimulation: signal suppression or neural noise generation? Journal of Cognitive Neuroscience, 20, 734-740.

Hart J, Gordon B (1990) Early-onset dementia and extrapyramidal disease: clinicopathological variant of Gerstmann-Straussler-Scheinker or Alzheimer's disease? Journal of Neurology Neurosurgery and Psychiatry, 53, 932-934.

Hartmann K, Goldenberg G, Daumüller M, Hermsdörfer J (2005) It takes the whole brain to make a cup of coffee: the neuropsychology of naturalistic actions involving technical devices. Neuropsychologia, 43, 625–637.

Hauk O, Davis MH, Pulvermüller F, Marslen-Wilson WD (2006) The time course of visual word recognition as revealed by linear regression analysis of ERP data. NeuroImage, 30, 1383–1400.

Hauk O, Johnsrude I, Pulvermüller. F (2004) Somatotopic representation of action words in human motor premotor cortex. Neuron, 41, 301–307.

Heilman KM, Rothi LJ, Valenstein E (1982) Two forms of ideomotor apraxia. Neurology, 32, 342-346.

Hermsdörfer J, Goldenberg G, Wachsmuth C, Conrad B, et al. (2001) Cortical correlates of gesture processing: clues to the cerebral mechanisms underlying apraxia during the imitation of meaningless gestures. Neuroimage 14, 149–161.

Hickok G. 2009. Eight Problems for the Mirror Neuron Theory of Action Understanding in Monkeys and Humans. Journal of Cognitive Neuroscience, 21, 1229-43.

Hickok G (2010). The role of mirror neurons in speech perception and action word semantics. Language and Cognitive Processes, 25, 749 – 776.

Hickok G, Poeppel D (2000) Towards a functional neuroanatomy of speech perception. Trends in Cognitive Science, 4, 131-138.

Hickok G, Poeppel D (2007) The cortical organization of speech processing. Nature Reviews Neuroscience, 8, 393-402.

Hillis AE, Work M, Barker PB, Jacobs MA, Breese EL, Maurer K (2004) Re-examining the brain regions crucial for orchestrating speech articulation. Brain, 127, 1479-1487.

Hodge C, Dubroff J, Huckins S, Szeverenyi N (1996) Somatosensory imagery activates primary sensory cortex in human: a functional MRI study. Neuroimage, 3, S209.

Howard MW, Kahanna MJ (2002) When does semantic similarity help episodic retrieval? Journal of Memory and Language, 46, 85–98.

Humphreys GW, Riddoch MJ (1984) Routes to object constancy: implications from neurological impairments of object constancy. Quarterly Journal of Experimental Psychology, 36, 385-415.

Iacoboni M, Molnar-Szakacs I, Gallese V, Buccino G, Mazziotta JC, Rizzolatti G (2005) Grasping the intentions of others with one's own mirror neuron system. PLoS Biology, 3, e79.

Iwaki S, Ueno S, Imada T, Tonoike M (1999) Dynamic cortical activation in mental image processing revealed by biomagnetic measurement. Neuroreport 10: 1793-1797.

Jackendoff R (1987) On beyond zebra: the relation of linguistic and visual information. Cognition, 26, 89–114.

Jackendoff R (2002) Foundation of language: brain, meaning, grammar, evolution. Oxford University Press, New York.

Jackendoff R (2007) Linguistics in cognitive science: the state of art. The Linguistic Review, 24, 347-401.

Jackson PL, Meltzoff AN, Decety J (2006) Neural circuits involved in imitation and perspective-taking. NeuroImage, 31, 429-439.

Jasper H (1958) The 10-20 electrode system of the international federation. Electroencephalography and Clinical Neurophysiology, 10, 371-375.

Jeannerod M (2001) Neural simulation of action: a unifying mechanism for motor cognition. Neuroimage, 14, S103-S109.

Jeannerod M, Decety J (1995) Mental motor imagery: a window into the representational stages of action. Current Opinions in Neurobiology, 5, 727-732.

Jeannerod M (2004) Visual and action cues contribute to the self-other distinction. Nature Neuroscience, 7, 422-423.

Jeffries E, Lambon Ralph MA (2006) Semantic impairment in stroke aphasia vs. semantic dementia: A case-series comparison, Brain, 129, 2132-2147.

Johnson-Frey SH, Newman-Norlund R, Grafton ST (2005) A distributed left hemisphere network active during planning of everyday tool use skills. Cerebral Cortex, 15, 681-695.

Johnson-Frey SH (2004) The neural bases of complex tool use in humans. Trends in Cognitive Science, 8, 71-78.

Kaup B, Zwaan RA (2003) Effects of negation and situational presence on the accessibility of text information. Journal of Experimental Psychology Learning Memory and Cognition, 29, 439-446.

Kellenbach ML, Wijers AA, Hovius M, Mulder J, Mulder G (2002) Neural differentiation of lexico-syntactic categories or semantic features? Event-related potential evidence for both, Journal of Cognitive Neuroscience, 14, 561–577.

Kellenbach ML, Brett M, Patterson K (2003) Actions Speak Louder Than Functions: The Importance of Manipulability and Action in Tool Representation. Journal of Cognitive Neuroscience, 15, 30-46.

Kertesz A, Hooper P (1982) Praxis and language: the extent and variety of apraxia in aphasia. Neuropsychologia, 20, 275-286.

Kertesz A, Ferro JM, Shewan CM. (1984) Apraxia and aphasia: the functional-anatomical basis for their dissociation. Neurology, 34, 40-47.

Kimberg DY, Coslett HB, Schwartz MF (2007) Power in Voxel-based lesion-symptom mapping. Journal of Cognitive Neuroscience, 19, 1067-1080.

Kintsch W (1998) The representation of knowledge in minds and machines. International Journal of Psychology, 33, 411–420.

Klatzky RL, Pellegrino JW,McCloskey DP, Doherty S (1989) Can you squeeze a tomato? The role of motor representations in semantic sensibility judgements. Journal of Memory and Language, 28, 56–77.

Koch G, Franca M, Del Olmo MF, Cheeran B, Milton R, et al. (2006) Time course of functional connectivity between dorsal premotor and contralateral motor cortex during movement selection. Journal of Neuroscience, 26, 7452-7459.

Kohler E, Keysers C, Umiltà MA, Fogassi L, Gallese V, Rizzolatti G (2002) Hearing sounds, understanding actions: action representation in mirror neurons. Science 297: 846-848.

Kornblum S, Hasbroucq T, Osman A (1990) Dimensional Overlap: Cognitive Basis for Stimulus-Response Compatibility - A Model and Taxonomy. Psychological Review, 97, 253-270

Kosslyn SM, Behrmann M, Jeannerod M (1995) The cognitive neuroscience of mental imagery. Neuropsychologia, 33, 1335-1344

Kosslyn SM, DiGirolamo GJ, Thompson WL, Alpert NM (1998) Mental rotation of objects versus hands: Neural mechanisms revealed by positron emission tomography. Psychophysiology, 35, 151-161.

Kosslyn SM, Ganis G, Thompson WL (2001) Neural foundations of imagery. Nature Reviews Neuroscience, 2, 635-642.

Kosslyn SM, Thompson WL, Wraga M, Alpert NM (2001) Imagining rotation by endogenous forces: distinct neural mechanisms. Neuroreport, 2, 2519-2525.

Lakoff G, Johnson M (1999) Philosophy in the flesh: The embodied mind and its challenge to western thought. New York: Basic Books.

Lakoff G, Johnson M (1980) Metaphors we live by. Chicago: University of Chicago Press.

Lakoff G (1987) Women, fire, and dangerous things:What categories reveal about the mind. Chicago: University of Chicago Press.

Lambon Ralph MA, Powell J, Howard D, Whitworth AB, Garrard P, Hodges JR (2001) Semantic memory is impaired in both dementia with Lewy bodies and dementia of Alzheimer's type: a comparative neuropsychological study and literature review. Journal of Neurology Neurosurgery and Psychiatry, 70, 149-156.

Lambon Ralph MA, Pobric G, Jefferies E (2009) Conceptual knowledge is underpinned by the temporal pole bilaterally: convergent evidence from rTMS. Cerebral Cortex, 19, 832-838.

Landau B, Jackendoff R (1993) “What” and “where” in spatial language and spatial cognition. Behavioral and Brain Sciences, 16, 217-238.

Landauer TK, Dumais ST (1997) A solution to Plato’s problem: the latent semantic analysis theory of acquisition, induction, and representation of knowledge. Psychological Review, 104, 211–40.

Landauer TK (2002) On the computational basis of learning and cognition: arguments from LSA. In N Ross, Ed. The Psychology of Learning and Motivation, 41, 43–84.

Langacker RW (1987) Foundations of Cognitive Grammar (Vol. 1). Stanford: Stanford University Press.

Laudanna A, Thornton AM, Brown G, Burani C, Marconi L (1995) Un corpus dell’italiano scritto contemporaneo dalla parte del ricevente. In S. Bolasco, L. Lebart, & A. Salem (Eds.), III Giornate internazionali di Analisi Statistica dei Dati Testuali (Vol. 1, pp. 103–109). Roma: Cisu.

Laurienti PJ, Kraft RA, Maldjian JA, Burdette JH, Wallace MT (2004) Semantic congruence is a critical factor in multisensory behavioral performance. Experimental Brain Research, 158, 405-414.

Laws KR, Humber SA, Ramsey DJC, McCarthy A (1995) Probing sensory and associative semantics for animals and objects in normal subjects. Memory, 3, 397-408.

Laws KR, Gale TM, Leeson VC, Crawford JR (2005) When is category specific in Alzheimer's disease? Cortex, 41, 452-463.

Lehmkuhl G, Poeck K (1981) A disturbance in the conceptualorganization of actions in patients with ideational apraxia.Cortex, 17, 153–158.

Lenneberg EH (1967) Biological foundations of language. New York: Wiley.

Levelt WJM, Roelofs A, Meyer AS (1999) A theory of lexical access in speech production. Behavioral and Brain Science, 22, 1–75.

Liberman AM, Cooper FS, Shankweiler DP, Studdert-Kennedy M (1967) Perception of the speech code. Psychological Reviews, 74, 431–461.

Liepmann H (1905) Die linke Hemisphere und das Handeln. Munch. Med. Wochenschr. 49: 2322–2326, 2375–78

Lingnau A, Gesierich B, Caramazza A (2009) Asymmetric fMRI adaptation reveals no evidence for mirror neurons in humans. Proceedings of the National Academy of Science USA, 106, 9925-9930.

Lockhart RS, Craik FIM (1990) Levels of processing: A retrospective commentary on a framework for memory research. Canadian Journal of Psychology, 44, 87-112.

Lorch RF, Myers JL (1990) Regression analyses of repeated measures data in cognitive research. Journal of Experimental Psychology Learning Memory Cognition, 16, 149-157.

Louwerse MM (2008) Embodied relations are encoded in language. Psychonomic Bulletin and Review, 15, 838-844.

Louwerse MM, Jeuniaux P (2008) Language comprehension is both embodied and symbolic. In M. de Vega, A. Glenberg, & A. C. Graesser (Eds.), Symbols, embodiment, and meaning (pp. 309–326). Oxford: Oxford University Press.

Lu CH, Proctor RW (1995) The influence of irrelevant location information on performance: A review of the Simon and spatial Stroop effects. Psychonomic Bulletin & Review, 2, 174-207.

Luzzatti C, Willmes K, De Bleser R. 1996. Aachener Aphasie Test (AAT), Italian version. Firenze, Italy: Organizzazioni Speciali.

Luzzatti C, Raggi R, Zonca G, Pistarini C, Contardi A, et al. (2002) Verb–noun double dissociation in aphasic lexical impairments: The role of word frequency and imageability. Brain and language, 81, 432–444.

Maas A, Russo A (2003) Directional bias in the mental representation of spatial events. Psychological Science, 14, 296-301.

Machery E (2007) Concept empiricism: a methodological critique. Cognition, 104, 19–46.

Maeda F, Kleiner-Fisman G, Pascual-Leone A (2002) Motor facilitation while observing hand actions: specificity of the effect and role of observer's orientation. Journal of Neurophysiology, 87, 1329-1335.

Mahon BZ, Caramazza A (2005) The orchestration of the sensory-motor systems: clues from neuropsychology. Cognitive Neurospychology, 22, 480-494.

Mahon BZ, Caramazza A (2008) A Critical Look at the Embodied Cognition Hypothesis and a New Proposal for Grounding Conceptual Content. Journal of Physiology - Paris

Mahon BZ, Caramazza A (2009) Concepts and categories: a cognitive neuropsychological perspective. Annual Review of Psychology, 60, 27-51.

Mahon BZ, Milleville SC, Negri GAL, Rumiati RI, Caramazza A, Martin A (2007) Action-related properties of objects shape object representations in the ventral stream. Neuron, 55, 507–520.

Mahon BZ, Anzellotti S, Schwarzbach J, Zampini M, Caramazza A (2009) Category-specific organization in the human brain does not require visual experience. Neuron, 13, 397-405.

Marinkovic K, Dhond RP, Dale AM, Glessner M, Carr V, Halgren E (2003) Spatiotemporal dynamics of modality-specific and supramodal word processing. Neuron, 38, 487-497.

Markus H (1977) Self-schemata and processing information about the self. Journal of personality and social psychology, 35, 63–78.

Marshall JC, Newcombe F (1973) Patterns of paralexia: a psycholinguistic approach. Journal of Psycholinguistic Research, 2, 175-199.

Martin A, Caramazza A (2003) Neurophysiological and neuroimaging perspectives on conceptual knowledge: an introduction. Cognitive Neuropsychology, 20, 95-212.

Martin A, Chao LL (2001) Semantic memory and the brain: structure and processes, Current Opinions in Neurobiology 11, 194–201.

Martin A, Haxby JV, Lalonde FM, Wiggs CL, Ungerleider LG (1995) Discrete cortical regions associated with knowledge of color and knowledge of action. Science, 270, 102–105.

Martin A, Wiggs, CL, Ungerleider LG, Haxby JV (1996) Neural correlates of category-specific knowledge. Nature, 379, 649–652.

Martin A, Caramazza A (2003) Neuropsychological and neuroimaging perspectives on conceptual knowledge: an introduction. Cognitive Neuropsychology, 20, 195–212.

McCarthy R, Warrington EK (1985) Category specificity in an agrammatic patient: the relative impairment of verb retrieval and comprehension. Neuropsychologia, 23, 709–727.

McClelland JL, Rogers TT (2003) The Parallel Distributed Processing Approach to Semantic Cognition. Nature Reviews Neuroscience, 4, 310-22.

McIntosh AR (2000) Towards a network theory of cognition. Neural Networks, 13, 861–870.

MacLeod CM (1991) Half a century of research on the Stroop effect: An integrative review. Psychological Bulletin, 109, 163-203.

Meister IG, Boroojerdi B, Foltys H, Sparing R, Huber W, Topper R (2003) Motor cortex hand area and speech: Implications for the development of language. Neuropsychologia, 41, 401-406.

Mellet E, Tzourio N, Denis M, Mazoyer B (1998) Corticcal anatomy of mental imagery of concrete nouns based on their dictionary definition, Neuroreport, 9, 803–808.

Mesulam M (2008) Representation, inference, and transcendent encoding in neurocognitive networks of the human brain. Annals of Neurology, 64, 367-378.

Miceli G, Silveri MC, Nocentini U, Caramazza A (1988) Patterns of dissociation in comprehension and production of nouns and verbs. Aphasiology, 2, 251–258.

Morrison CM, Ellis AW, Quinlan PT (1992) Age of acquisition, not word frequency, affect object naming, not object recognition. Memory and Cognition, 20, 705-714.

Morrison CM, Hirsh W, Duggan GB (2003) Age of acquisition, ageing, and verb production: Normative and experimental data. Quarterly Journal of Experimental Psychology, 56, 705-730.

Morton J, Patterson K (1980) A new attempt at an interpretation, or, an attempt at a new interpretation. In: M. Coltheart, K.E. Patterson, J. Marshall (Eds), Deep dyslexia (p. 91-118). New York: Routledge, Chapman & Hall.

Mozaz M, Rothi LJ, Anderson JM, Crucian GP, Heilman KM (2002) Postural knowledge of transitive pantomimes and intransitive gestures. Journal of the International Neuropsychological Society, 8, 958-962.

Mummery CJ, Ashburner J, Scott SK, Wise RJ (1999) Functional neuroimaging of speech perception in six normal and two aphasic subjects. Journal of the Acoustical Society of America, 106, 449-57.

Mummery CJ, Patterson K, Wise RJ, Vandenbergh R, Price CJ, Hodges JR (1999) Disrupted temporal lobe connections in semantic dementia. Brain, 122, 61-73.

Myachykov A, Posner MI, Tomlin RS (2007) A parallel interface for language and cognition in sentence production: theory, method and experimental evidence. The Linguistic Review, 24, 457-474

Naito E, Ehrsson HH (2006) Somatic sensation of hand-object interactive movement is associated with activity in the left inferior parietal cortex. Journal of Neuroscience, 26, 3783-3790.

Neely JH (1977) Semantic priming and retrieval from lexical memory: roles of inhitionless spreading activation and limited-capacity attention. Journal of Experimantal Psychology General, 106, 226-254.

Negri GAL, Lunardelli A, Gigli G, Rumiati RI (2007) Degraded semantic knowlegde and accurate object use. Cortex, 43, 376-388.

Negri GAL, Rumiati RI, Zadini A, Ukmar M, Mahon BZ, Caramazza A (2007) What is the Role of Motor Simulation in Action and Object Recognition? Evidence from Apraxia. Cognitive Neuropsychology, 24, 795-816.

Neininger B, Pulvermüller F (2001) The right hemisphere's role in action word processing: a double case study. Neurocase, 7, 303–17.

Neininger B, Pulvermüller F (2003) Word-category specific deficits after lesions in the right hemisphere. Neuropsychologia, 41, 53–70.

Newman-Norlund RD, van Schie HT, van Zuijlen AMJ, Bekkering H (2007) The mirror neuron system is more active during complementary compared with imitative action. Nature Neuroscience, 10, 817-818.

Nishitani N, Hari R (2002) Viewing lip forms: Cortical dynamics. Neuron, 36, 1211–1220.

Noppeney U, Price CJ (2004) Retrieval of abstract semantics. Neuroimage, 22, 164-170.

Ochipa C, Rothi LJ, Heilman KM (1989) Ideational apraxia: a deficit in tool selection and use. Annals of Neurology, 25, 190–193.

Oldfield RC (1971) The assessment and analysis of handedness: The Edinburgh inventory. Neuropsychologia, 9, 97–113

Oliver RT, Thompson-Schill SL (2003) Dorsal stream activation during retrieval of object size and shape. Cognitive Affective and Behavioral Neuroscience, 3, 309–322.

Oliveri M, Finocchiaro C, Shapiro K, Gangitano M, Caramazza A, Pascual-Leone A (2004) All talk and no action: A transcranial magnetic stimulation study of motor cortex activation during action word production. Journal of Cognitive Neuroscience, 16, 347-381.

Paivio A (1971) Imagery and verbal processes. New York: Holt, Rinehart Winston.

Papagno C, Della Sala S, Basso A (1993) Ideomotor apraxia without aphasia and aphasia without apraxia: the anatomical support for a double dissociation. Journal of Neurology Neurosurgery and Psychiatry, 56, 286-9.

Papeo L, Vallesi A, Isaja A, Rumiati RI (2009) Effects of TMS on different stages of motor and non-motor verb processing in the primary motor cortex. PLoS ONE, 4:e4508.

Parsons LM (1987) Imagined transformation of one's hands and feet. Cognitive Psychology, 19, 178-241.

Parsons LM (1994) Temporal and kinematic properties of motor behavior reflected in mentally simulated action. Journal of Experimental Psychology Humamn Perception and Performance, 20, 709-730.

Parsons LM, Gabrieli JD, Phelps EA, Gazzaniga MS (1998) Cerebrally lateralized mental representations of hand shape and movement. Journal of Neuroscience, 18, 6539-48.

Parsons LM, Fox PT, Downs JH, Glass T, Hirsch TB, Martin CC, Jerabek PA, Lancaster JL (1995) Use of implicit motor imagery for visual shape discrimination as revealed by PET. Nature, 375, 54–58

Pascual-Leone A, Grafman J, Hallett M (1994) Modulation of cortical motor output maps during development of implicit and explicit knowledge. Science, 263, 1287–1289.

Penolazzi B, Hauk O, Pulvermüller F (2007) Early semantic context integration and lexical access as revealed by event-related potentials. Biological Psychology, 74, 374-388.

Perani D, Cappa SF, Schnur T, Tettamanti M, Collina S, et al. (1999) The neural correlates of verb and noun processing. Brain, 122, 2337-2344.

Pérez MA (2007) Age of acquisition persists as the main factor in picture naming when cumulative word frequency and frequency trajectory are controlled. Quarterly Journal of Experimental Psychology, 60, 32-42.

Petersen SE, Fox PT, Posner MI, Mintun M, Raichle ME (1988) Positron emission tomographic studies of the cortical anatomy of single-word processing. Nature, 331, 585-9.

Petrides M, Pandya DN (1994) Comparative architectonic analysis of the human and the macaque frontal cortex. In Boller, F. & Grafman, J. (eds), Handbook of Neuropsychology, Vol. 9. Elsevier, Amsterdam, pp. 17-58.

Pfeifer R, Scheier C (1999) Understanding Intelligence. Cambridge, MA: MIT Press.

Pickett LW (1974) An assessment of gestural and pantomimic deficit in aphasic patients. Acta Symbolica, 5, 69–86.

Pillsbury WB (1911) The place of movement in consciousness. Psychological Review, 18, 83–99.

Porro CA, Francescato MP, Cettolo V, Diamond ME et al. (1996). Primary Motor and Sensory Cortex Activation during Motor Performance and Motor Imagery: A Functional Magnetic Resonance Imaging Study. Journal of Neuroscience, 16, 7688-7698.

Postle N, McMahon KL, Ashton R, Meredith M, de Zubicaray GI (2008) Action word meaning representations in cytoarchitectonically defined primary and premotor cortices. Neuroimage, 43, 634–644

Pramstaller PP, Marsden CD (1996) The basal ganglia and apraxia. Brain, 119, 319–340.

Price C (1998) The functional anatomy of word comprehension and production Trends in Cognitive Science, 2, 281-288.

Price CJ, Friston KJ (2002) Degeneracy and cognitive anatomy. Trends in Cognitive Sciences, 6, 416–421.

Prinz W (1997) Perception and action planning. European Journal of Cognitive Psychology, 9, 129–154.

Pulvermüller F (2002) A brain perspective on language mechanisms: from discrete neuronal ensambles to serial order. Progress in Neurobiology, 67, 85-111.

Pulvermüller F (2005) Brain mechanisms linking language and action. Nature Reviews Neuroscience, 6, 576-582.

Pulvermüller F, Fadiga L (2010) Active perception: sensorimotor circuits as a cortical basis for language. Nature Reviews Neuroscience, 11, 351-360

Pulvermüller F, Hauk O (2006) Category-specific conceptual processing of color and form in left fronto-temporal cortex. Cerebral Cortex 16, 1193–1201.

Pulvermüller F, Harle, M., Hummel, F (2001) Walking or talking: behavioural and neurophysiological correlates of action verb processing. Brain and Language, 78, 143-168.

Pulvermüller F, Hauk O, Nikulin VV, Illmoniemi RJ (2005) Functional links between motor and language systems. European Journal of Neuroscience, 21, 793-797.

Pulvermüller F, Shtyrov Y, Ilmoniemi R (2005) Brain signature of meaning access in action word recognition. Journal of Cognitive Neuroscience, 17, 884-892.

Pulvermüller F (2005) Brain mechanisms linking language and action. Nature Reviews Neuroscience, 6, 576-582.

Pylyshyn ZW (1984) Computation and cognition: toward a foundation for cognitive science. Cambridge MA: MIT/Bradford.

Rapcsak SZ, Ochipa C, Anderson KC, Poizner H (1995) Progressive ideomotor apraxia: Evidence for a selective impairment in the action production system. Brain and Cognition, 27, 213-236.

Raposo A, Moss HE, Stamatakis EA, Tyler LK (2009) Modulation of motor and premotor cortices by actions, action words and action sentences. Neuropsychologia, 47, 388–396.

Ratcliff R (1993) Methods for Dealing With Reaction Time Outliers. Psychological Bulletin, 114, 510-532

Rees G, Frith CD, Lavie N (1997) Modulating irrelevant motion perception by varying attentional load in an unrelated task. Science, 278, 1616–1619.

Reynolds C, Ashby P (1999) Inhibition in the human motor cortex is reduced just before a voluntary contraction. Neurology, 53, 730-735.

Richardson DC, Spivey MJ, McRae K, Barsalou LW (2003) Spatial representations activated during real-time comprehension of verbs. Cognitive Science, 27, 767–780.

Riesenhuber M (2007) Appearance Isn't Everything: News on Object Representation in Cortex. Neuron, 55, 341-344.

Rizzolatti G, Arbib MA (1998) Language within our grasp. Trends in Neuroscience, 21, 188-194.

Rizzolatti G, Craighero L (2004) The mirror-neuron system. Annual Review of Neuroscience, 27, 169-192.

Rizzolatti G, Fadiga L, Matelli M, Bettinardi V, Paulesu E, et al. (1996) Localization of grasp representations in humans by PET: 1. Observation versus execution. Experimental Brain Research, 111, 246-252.

Rizzolatti G, Fogassi L, Gallese V (2001) Neurophysiological mechanisms underlying the understanding and imitation of action. Nature Reviews of Neuroscience, 2, 661-670.

Rizzolatti G, Craighero L (2004) The mirror-neuron system. Annual Reviews of Neuroscience, 27, 169-192.

Robertson EM, Théoret H, Pascual-Leone A (2003) Studies in cognition: the problems solved and created by transcranial magnetic stimulation. Journal of Cognitive Neuroscience, 15, 948-960.

Rorden C, Brett M (2000) Stereotaxic display of brain lesions. Behavioural Neurology, 12, 191-200.

Rorden C, Karnath HO (2004) Using human brain lesions to infer function: a relic from a past era in the fMRI age? Nature Reviews Neuroscience, 5, 813–819.

Rosci C, Valentina C, Laiacona M, Capitani E (2003) Apraxia is not associated to a disproportionate naming impairment for manipulable objects. Brain and Cognition, 53, 412–415.

Rossini PM, Barker AT, Berardelli A, Caramia MD, Caruso G, et al. (1994) Non-invasive electrical and magnetic stimulation of the brain, spinal cord and roots: basic principles and procedures for routine clinical application. Report on an IFCN commettee. Electroencephalography and Clinical Neurophysiology, 91, 79-92.

Rothi LJG, Ochipa C, Heilman KM (1991) A cognitive neuropsychological model of limb praxis. Cognitive Neuropsychology, 8, 443-458.

Ruby P, Decety J (2001) Effect of subjective perspective taking during simulation of action: a PET investigation of agency. Nature Neuroscience, 4, 546-550.

Ruby P, Decety J (2003) What you believe versus what you think they believe: a neuroimaging study of conceptual perspective-taking. The European Journal of Neuroscience, 17, 2475-2480.

Rueschemeyer SA, van Rooij D, Lindemann O, Willems RM, Bekkering H (2010) The function of words: distinct neural correlates for words denoting differently manipulable objects. Journal of Cognitive Neuroscience, 22, 1844-1851.

Rumiati RI, Tessari A (2007) Automatic and strategic effects in human imitation. In Sensorimotor foundations of human cognition: Attention and Performance, Vol. XXII, ed. P Haggard, Y Rossetti, M Kawato. Oxford: Oxford University Press.

Rumiati RI, Weiss PH, Shallice T, Ottoboni G, Noth J, Zilles K, Fink GR (2004) Neural basis of pantomiming the use of visually presented objects. Neuroimage, 21, 1224-1231.

Rumiati RI, Zanini S, Vorano L, Shallice T (2001) A form of Ideational Apraxia as a deficit of contention scheduling. Cognitive Neuropsychology, 18, 617-642.

Rumiati RI, Papeo L, Corradi-Dell'Acqua C (2010) Higher-level motor processes. Annals of the New York Academy of Science, 1191, 219–241.

Sack AT, Lindner M, Linden DEJ (2007) Object- and direction-specific interference between manual and mental rotation. Perception and Psychophysics, 69, 1435-1449.

Saffran EM (1982) Neuropsychological approach to the study of language. British Journal of Psychology, 73, 317–337.

Saxe R, Jamal N, Powell L (2006) My body or yours? The effect of visual perspective on cortical body representations. Cerebral Cortex, 16, 178-182.

Saygin AP, Wilson SM, Dronkers NF, Bates E (2004) Action comprehension in aphasia: linguistic and non-linguistic deficits and their lesion correlates. Neuropsychologia, 42, 1788-1804.

Scheerer E (1984) Motor theories of cognitive structure: A historical review. In W. Prinz & A. F. Sanders (Eds.), Cognition and motor processes (pp. 77–98). Berlin: Springer-Verlag.

Scott SK, Johnsrude IS (2003) The neuroanatomical and functional organization of speech perception. Trends in Neuroscience, 26, 100-107.

Scott SK, McGettigan C, Eisner F (2009) A little more conversation, a little less action — candidate roles for the motor cortex in speech perception. Nature Reviews Neuroscience, 10, 295-302.

Seidenberg M, McClelland J (1989) A distributed model of word recognition and naming. Psychological Reviews, 96, 523-568.

Sekiyama K (1982) Kinesthetic aspects of mental representation in the identification of left and right hands. Perception and Psychophysics, 32, 89-95.

Sereno SC, Rayner K, Posner MI (1998) Establishing a time-line of word recognition: evidence from eye movements and event-related potentials. NeuroReport, 9, 2195-2200.

Seron X, van der Kaa MA, Remitz A, van der Linden M (1979) Pantomime interpretation and aphasia. Neuropsychologia, 17, 661–668.

Shallice T (1988) From Neuropsychology to Mental Structure. Cambridge University Press, New York.

Shapiro K, Caramazza A (2003) The representation of grammatical categories in the brain. Trends in Cognitive Science, 7, 201–206.

Shapiro KA, Mottaghy FM, Schiller NO, Poeppel TD, Fluss MO, et al. (2005) Dissociating neural correlates for nouns and verbs. Neuroimage, 24, 1058–1067.

Shapiro KA, Shelton J, Caramazza A (2000) Grammatical class in lexical production and morphological processing: Evidence from a case of fluent aphasia. Cognitive Neuropsychology, 17, 665–682.

Shuren J (1993) Insula and aphasia. Journal of Neurology, 240, 216-218.

Siegel LS (1981) Infant tests as predictors of cognitive and language development at two years. Child Development, 52, 545-557.

Sirigu A, Cohen L, Duhamel JR, Pillon B, Dubois B, Agid Y, Pierrot-Deseilligny C (1995) Congruent unilateral impairments for real and imagined hand movements. NeuroReport, 6, 997-1001.

Solodkin A, Hlustik P, Chen EE, Small SL (2004) Fine Modulation in Network Activation during Motor Execution and Motor Imagery. Cerebral Cortex, 14, 1246–1255.

Spinnler H, Tognoni G (1987) Standardizzazione e taratura italiana di test neuropsicologici. [Italian standardization and validation neuropsychological tests.] Italian Journal of Neurological Sciences, 6, 1–20.

Staines WR, Graham SJ, Black SE, McIlroy WE (2002) Task-Relevant Modulation of Contralateral and Ipsilateral Primary Somatosensory Cortex and the Role of a Prefrontal-Cortical Sensory Gating System. NeuroImage, 1, 190-199

Steyvers M, Shiffrin RM, Nelson DL (2004).Word association spaces for predicting semantic similarity effects in episodic memory. In A Healy, Ed. Experimental Cognitive Psychology and its Applications (pp. 237–49).Washington, DC: American Psychological Association.

Tabossi P (1988) Effects of context ontheimmediate interpretation of unambiguous words. Journal of Experimental Psychology: Learning, Memory and Cognition, 14, 153–162.

Tabossi P, Colombo L, Job R (1987) Accessing lexical ambiguity: effects of context and dominance. Psychological Research, 49, 161-167.

Talbot PR, Goulding PJ, Lloyd JJ, et al. (1995) Inter-relation between "classic" motor neuron disease and frontotemporal dementia: neuropsychological and single photon emission computed tomography study. Journal of Neurology Neurosurgery and Psychiatry, 58, 541-547.

Talmy L (2000) In Toward a cognitive semantics. Concept structuring systems (Vol. 1). Cambridge, MA, USA: The MIT Press.

Tanaka S, Inui T (2002) Cortical involvement for action imitation of hand/arm postures versus finger configurations: an fMRI study. NeuroReport, 13, 1599-1602.

Taylor B (1977) Tense and continuity. Linguistics and Philosophy, 1, 199–220.

Taylor LJ, Zwaan RA (2008) Motor resonance and linguistic focus. Quarterly Journal of Experimental Psychology, 61, 896-904.

Tessari A, Canessa N, Ukmar M., Rumiati RI (2007) Neuropsychological evidence for a strategic control of multiple routes in imitation. Brain, 130, 1111-1126.

Tessari A, Rumiati RI (2004) The strategic control of multiple routes in imitation of actions. Journal of Experimental Psychology: Human Perception and Performance, 30, 1107-1116.

Tettamanti M, Buccino G, Saccuman MC, Gallese V., Dann M, et al. (2005) Listening to action related sentences activates fronto-parietal motor circuits. Journal of Cognitive Neuroscience, 17, 273–81.

Tkach D, Reimer J, Hatsopoulos NG (2007) Congruent activity during action and action observation in motor cortex. Journal of Neuroscience, 27, 13241–13250.

Thompson-Schill SL, D’Esposito M, Aguirre GK, Farah MJ (1997) Role of left inferior prefrontal cortex in retrieval of semantic knowledge: A reevaluation. Proceedings of the National Academy of Science USA, 94, 14792–14797.

Tomasino B, Rumiati RI (2004) Effects of strategies on mental rotation and hemispheric lateralization: neuropsychological evidence. Journal of Cognitive Neuroscience, 16, 878-888.

Tomasino B, Skrap M, Rumiati RI (2010) Causal Role of the Sensorimotor Cortex in Action Simulation: Neuropsychological Evidence. Journal of Cognitive Neuroscience, in press.

Tomasino B, Borroni P, Isaja A, Rumiati RI (2005) The role of the primary motor cortex in mental rotation: a TMS study. Cognitive Neuropsychology, 22, 348-363.

Tomasino B, Werner CJ, Weiss PH, Fink GR (2007) Stimulus properties matter more than perspective: An fMRI study of mental imagery and silent reading of action phrases. Neuroimage, 36, 128–141.

Tomasino B, Fink GR, Sparing R, Dafotakis M, Weiss PH (2008) Action verbs and the primary motor cortex: a comparative TMS study of silent reading, frequency judgments, and motor imagery. Neuropsychologia, 46, 1915-1926.

Tomasino B, Weiss P, Fink GR (2010) To move or not to move: imperatives modulate action-related verb processing in the motor system. Neuroscience, 169, 246–258.

Toraldo A, Cattani B, Zonca G, Saletta P, Luzzatti C (2006) Reading disorders in a language with shallow orthography: A multiple single-case study in Italian. Aphasiology, 20, 823–850.

Tranel D, Damasio H, Damasio AR (1997) A neural basis for the retrieval of conceptual knowledge, Neuropsychologia, 35, 1319–1327.

Tranel D, Adolphs R, Damasio H, Damasio AR (2001) A neural basis for the retrieval of words for actions. Cognitive Neuropsychology, 18, 655–670.

Tucker M, Ellis R (2004) Action priming by briefly presented objects. Acta Psychologica, 116, 185-203.

Turella L, Pierno AC, Tubaldi F, Castiello U (2009) Mirror neurons in humans: consisting or confounding evidence? Brain and Language, 108, 10-21.

Tversky B (1995) Cognitive origins of graphic conventions. In F.T. Marchese (ed) Understanding images (pp 29-53). New York, Springer.

Tyler LK, Moss HE (2001) Towards a distributed account of conceptual knowledge. . Trends in Cognitive Science, 5, 244–52.

Tyler LK, Russell R, Fadili J, Moss HE (2001) The neural representation of nouns and verbs: PET studies. Brain, 124, 1619–1634.

Tzourio-Mazoyer N, Landeau B, Papathanassiou D, Crivello F, Etard O, et al. (2002) Automated anatomical labelling of activations in SPM using a macroscopic anatomical parcellation of the MNI MRI single-subject brain. Neuroimage, 15, 273–289.

Vallesi A, Binns MA, Shallice T (2008) An effect of spatial-temporal association of response codes: understanding the cognitive represetations of time. Cognition, 107, 501-527.

Van Berkum JJA, Koornneef AW, Otten M, Nieuwland MS (2007) Establishing reference in language comprehension: an electrophysiological perspective. Brain Research, 1146, 158-171.

Vandenberghe R, Price C, Wise R, Josephs O, Frackowiak RS (1996) Functional anatomy of a common semantic system for words and pictures. Nature, 383, 254-256.

Varney NR (1978) Linguistic correlates of pantomime recognition in aphasic patients. Journal of Neurology Neurosurgery and Psychiatry, 41, 564-568.

Varney NR (1982) Pantomime recognition defect in aphasia: implications for the concept of asymbolia. Brain and Language, 15, 32–39.

Vendler Z (1957) Verbs and times. Phylosophical Review, 66, 143-160.

Vingerhoets G, de Lange FP, Vandemaele P, Deblaere K, Achten E (2002) Motor imagery in mental rotation: an fMRI study. Neuroimage, 17, 1623-1633.

Voyer D, Voyer S, BrydenMP (1995) Magnitude of sex differences in spatial abilities: a meta-analysis and consideration of critical variables. Psychologucal Bulletin, 117, 250 –270.

Xiong J, Parsons LM, Gao JH, Fox PT (1999) Interregional connectivity to primary motor cortex revealed using MRI resting state images. Human Brain Mapping, 8, 151-156.

Washburn FL (1914) Heads of departments: a commentary upon dr. johnston's article. Science, 39, 646-648.

Walsh V, Rushworth M (1999) A primer of magnetic stimulation as a tool for neuropsychology. Neuropsychologia, 37, 125-135.

Warburton E, Wise RS, Price CJ, Weiller C, Hadar U, et al. (1996) Noun and verb retrieval by normal subjects. Studies with PET. Brain, 119, 159-179.

Wang L, Goodglass H (1992) Pantomime, praxis, and aphasia. Brain and Language, 42, 402–418.

Warrington EK, McCarthy R (1983) Category specific access dysphasia. Brain, 106, 859–78.

Warrington EK, McCarthy RA (1987) Categories of knowledge: further fractionations and an attempted integration. Brain, 110, 1273-1296.

Warrington EK, Shallice T (1984) Category specific semantic impairment. Brain, 107, 829–854.

Warrington EK (1996) The Camden memory test. Hove, UK: Psychology Press.

Wassermann EM (1998) Risk and safety of repetitive transcranial magnetic stimulation: report and suggested guidelines from the International Workshop on the Safety of Repetitive Transcranial Magnetic Stimulation, June 5-7, 1996. Electroencephalography and Clinical Neurophysiology, 108, 1-16.

Watson JB (1913) Psychology as the behaviorist views it. Psychological Review, 20, 158–177.

Willems RM, Hagoort P (2007) Neural evidence for the interplay between language, gesture, and action: a review. Brain and Language, 101, 278–289.

Willems RM, Hagoort P, Casasanto D (2010) Body-specific representations of action verbs: neural evidence from right- and left-handers. Psychological Science, 21, 67-74.

Willingham DB (1999) Implicit motor sequence learning is not purely perceptual. Memory and Cognition, 27, 561–572.

Wilson M (2002) Six views of embodied cognition. Psychonomic Bullettin & Review, 9, 625-636.

Wilson SM, Saygin AP, Sereno MI, Iacoboni M (2004) Listening to speech activates motor areas involved in speech production. Nature Neuroscience, 7, 701-702.

Wohlschläger A, Wohlschläger A (1998) Mental and manual rotation. Journal of Experimental Psychology: Humamn Perception and Performance, 24, 397-412.

Wraga M, Thompson WL, Alpert NM, Kosslyn SM (2003) Implicit transfer of motor strategies in mental rotation. Brain and Cognition 52, 135–143.

Zacks JM (2008) Neuroimaging studies of mental rotation: a meta-analysis and review. J Cognitive Neuroscience, 20, 1-19.

Zwaan RA (2004) The immersed experiencer: Toward an embodied theory of language comprehension. In BH Ross (Ed) The psychology of learning and motivation Vol. 44 (pp 35–62). Academic Press: New York.

Zwaan RA, Stanfield RA, Yaxley RH (2002) Language comprehenders mentally represent the shapes of objects. Psychological Science, 13, 168-171.

Zwaan RA, Taylor LJ (2006) Seeing, acting, understanding: motor resonance in language comprehension. Journal of Experimental Psychology General, 135, 1-11.