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Higher-level motor processes

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Traditionally the motor system was thought of as a movement output device that, after brain damage, can impede patients from correctly planning and executing an action. In the last 20 years neuropsychological observations have contributed to the development of a new view that attributes higher-level functions to this system. Rapidly, this area of investigation has grown very popular, with motor representations being considered critical for action and object recognition, imagery and even language understanding. At present, we can distinguish between embodied and disembodied theories. The former predominantly are built on associations of deficits in these abilities whereas the latter rely on dissociations between deficits. Neuroimaging research has also showed that different action-related functions activate either overlapping or discrete regions, thus sustaining either association-based or dissociation-based models. Although no convincing theory is, to date, available to explain both sets of observations, cognitive neuroscientists have begun to explore this intermediate hypothesis space. Here we suggest that concepts like strategy and simulation seem promising in explaining how the cognitive system alternates between action-related functions.

Keywords: apraxia; tool use; imitation; body representation; dual route

Introduction

Up to 20 years ago, research on the motor system was traditionally seen as movement output device.[1–3] As patients' observations cumulated, however, it became clear that motor processes do not exhaust themselves in a motor output. In 1991, Rothi and colleagues published the first cognitive model that promoted a new way of conceiving higher level motor processes, a view that had already proven its worth in the domains of language and vision.[4] As such, this and analogous models aimed to explain not only how a gesture is produced but also how it is recognized, named, and so forth.

In more recent years, the many observations of the motor system being involved in tasks that *prima facie* do not seem to require its involvement, have reinforced the idea that the same processes that mediate the production of actions might also be critically involved in perceptual, conceptual, and lexical processing. These formulations are known as sensorimotor or embodied theories of cognition, for they generally see cognitive operations as grounded in sensorimotor cortices. These theories vary in the extent to which they hold the motor processes as constitutive of all cognitive operations.

Scope of the review

In the present review we aim to accomplish the following tasks. We will first introduce the main assumptions and predictions based on models of higher-level motor processes. We will then examine how classic and modern theorizations coped with neuropsychological observations. We will also discuss neuropsychological, neurophysiological, and imaging evidence that, whereas supporting the existence of interaction between lower-level motor processes and higher-level conceptual processes, allow us to reject extreme formulations of contemporary sensorimotor views. We will conclude with an argument that neither the theories holding for complete separation between action production and action recognition or action-related language

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processes, nor those sustaining a total overlap between them, can satisfactorily accommodate the available observations. We will also suggest that concepts like *simulation* or *strategy* may be useful in beginning to understand the interactions between these different processes. This means that, even in the absence of neurological damage, one function of the motor system might be switched on or off depending on several factors such as stimuli, tasks, or cognitive resources.

Classical neuropsychological models

More than a century ago, Hugo Liepmann first proposed a theory of gesture production, based on observations of brain damaged patients, that distinguished between formulating of the idea of a movement (or movement formula) and its implementation in the corresponding innervations.[1] Accordingly, a deficit in formulating the idea of a movement would lead to ideational apraxia (IA), whereas a deficit of its execution would give rise to ideomotor apraxia (IMA). Patients with IA present a selective deficit in using objects and tools, but they are still capable of executing the same gestures by imitation. In contrast, patients with IMA show a deficit in imitating actions and/or performing them on verbal command. Liepmann's original dichotomy between conceptual and production levels of motor processing has been maintained in subsequent conceptualizations.[2,3,5,6]

A two-stage model of this sort regarded the motor system only for its fundamental characteristic in producing (or failing to produce) a motor output. What it could not explain was how, after brain damage, patients might show a selective deficit when imitating meaningless gestures, or how patients fail to understand visually presented gestures while preserving their ability to imitate and produce gestures prompted verbally, a pattern that Rothi and colleagues also called "pantomime agnosia."[7,8]

Cognitive neuropsychological models

The encounter between classic neuropsychology and the human information processing approach gave rise to the model of Rothi and colleagues.[4] The model distinguishes different inputs, a visual object, a visual gesture, or their names, each of which is analyzed perceptually. The model also comprises systems that are tied to these early perceptual operations: the structural description system (SDS) for objects and the input praxicon for actions (or axemes as they are called in Negri *et al.*[9]). The semantic system stores conceptual knowledge about objects and actions already known to the individual. The output praxicon involves processes that support implementation of object-related and object-unrelated actions. The input praxicon can be directly linked to the output praxicon, bypassing the semantic system. All these operations correspond to the semantic route that is used for producing learned gestures. To imitate gestures that are novel, after a perceptual analysis, the model predicts a nonsemantic route that converts the visual input into a motor output. This mechanism is similar to grapheme-to-phoneme conversion, proposed to be employed for reading nonwords or regular novel words.[10]

The semantic route and the nonsemantic route converge in a temporary memory system—called short-term memory (STM) or working memory by Rumiati and Tessari and gestural buffer by Cubelli and colleagues—that holds the motor information until its output is executed.[10,11] Rothi and colleagues also included the "innervatory patterns" which, in the original model, corresponded to motor schemes that are used to perform skilled movements which are thought to be anatomically segregated in the supplementary motor area (SMA).[4] Although the concept of schemas has been used very successfully in modeling higher-level motor processes,[12–14] and linked to brain other than the SMA (*e.g.*, parietal and premotor cortices), innervatory patterns seem to be too course a concept to be included in this cognitive framework (see also Ref. 10 for a similar argument). The main features of the modified model are depicted in Figure 1. Further alterations of the model, like the one dealing with the role of body representations in imitation, will be discussed later in the review.

Despite the availability of this very productive model, neuropsychologists have often continued to use clinical labels such as IA and IMA for describing action-related deficits. Moreover, different neuropsychologists attribute different meanings to these labels. For instance, in Europe the conceptualization of IA and IMA coincides with Liepmann's, whereas in North America IMA is diagnosed on the basis of spatio-temporal errors made when patients demonstrate the use of objects and/or imitate similar or intransitive gestures.

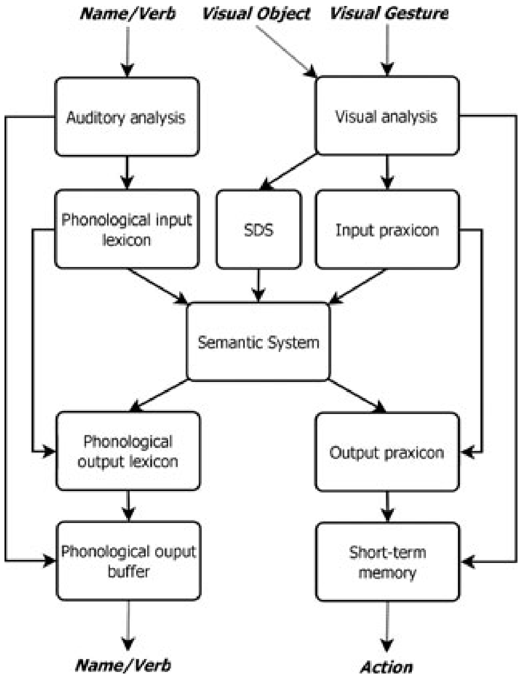

Figure 1. **A modified version of the model of praxis originally proposed by Rothi *et al.* (Ref. 4). According to this model, imitation of familiar gestures relies on the semantic, indirect route that encompasses the input praxicon, the semantic system, the output praxicon, and the short-term memory; imitation of new gestures relies on the nonsemantic route that, from visual analysis, leads directly to the short-term memory.**

Sensorimotor theories of cognition

The common tenet to these theories is that sensorimotor information is implied in many cognitive operations, ranging from object[15] or action recognition,[16] to language understanding.[17,18] However, these theories vary in the extent to which they hold sensorimotor information as being necessary to represent some[19] or all[20] that we know about concrete object and action concepts. This conceptual processing is accomplished by reactivation (or simulation) of the sensorimotor information previously encoded.[15] Sensorimotor simulation is here defined as the activation, in the absence of overt performance, of the same representations and neural structures that are acquired through previous physical interaction with the environment and mediate motor production.

We will refer to this theoretical approach as the *embodied hypothesis* because it is claimed that the conceptual representations are derived from our bodily experience and are situated in the sensorimotor system.[20] Consistent with the *embodied hypothesis*, a number of predictions can be generated. For instance, if the recognition of actions is mediated by processes required in action production (*e.g.*, object use and imitation), then, recognition and production of actions should not be expected to correspond to functionally separable processes. Therefore, it should not be possible to observe patients with a selective deficit in either recognizing or producing actions. In the same vein, if the sensorimotor system characterizes the semantic content of concepts in terms of the way we function with our bodies in the world,[20] then whenever we engage in tasks that require understanding the concept "hammer," for instance, it should be necessary to retrieve the motor programs associated with its use.

There already exist neuropsychological observations that are incompatible with the view that complete re-enactment of motor representations is necessary to successfully recognize and understand objects and actions (for an extended discussion, see Ref. 21). In the following sections, we will discuss how neuropsychological evidence relates to embodied and disembodied theories.

Testing theories

The fundamental task of cognitive neuropsychology is to assess models by evaluating the behavior of brain-damaged patients. This can be accomplished by establishing whether a patient's cognitive abilities dissociate as a consequence of a lesion. Dissociations of abilities provide a strong basis for making inferences about the organization of cognitive abilities in patients, and processes in models.[22] More rarely, useful neuropsychological evidence for constraining cognitive theories is drawn from behaviors that are observed to be consistently impaired or spared together. Two such examples concern the phonological output buffer[23] and the access/storage distinction.[24]

Just as damage to the phonological input lexicon can impair the ability to decide whether a phonological string belongs to the lexicon, so it is predicted that damage to the input praxicon can impair the ability to discriminate actions that already belong to an individual's repertoire from those that are unknown. Damage to the semantic system should result in a selectively impaired ability to understand the content of meaningful actions, objects, or their names. If it is the output praxicon, which is damaged, we should observe defective imitation of meaningful actions and object use, whereas damage to the nonsemantic route would affect only imitation of meaningless actions. A faulty STM/gestural buffer is expected to reduce motor performance in all motor tasks.

Another important prediction concerns the relation between motor and linguistic processes: an impaired ability to produce the gesture of hammering either in imitation (via the semantic route) or in using the actual object should not interfere with an individual's ability to process object or action names ("hammer" or "hammering"), and *vice versa*, unless the breakdown occurs within the semantic system. The relation between motor and language processes can also depend on the extent to which the linguistic task requires access the motor representations associated with words. For instance, if one is asked to explicitly say whether a verb is action-related, one will need to access its semantic representation and, therefore, the associated motor information, whereas this is unlikely to be the case if the task requires counting the syllables contained in a verb.

The neuropsychological analyses of apraxic patients provide a direct means to evaluate the performance of patients on tasks tapping the different components of the models, such as the one summarized in Figure 1. They can also help to establish the extent to which motor processes, in addition to their primary mission of sustaining action production, also contribute to perceptual, conceptual and linguistic processing of action-related information. In the following sections, we will discuss evidence related to mechanisms that characterize the involvement of motor processes in action imitation, action/object recognition, object use, and action-related language processing.

Imitation

Neuropsychologists established over a century ago that, after brain damage, right-handed individuals with right-sided hemiplegia experienced a dramatic reduction in their ability to imitate gestures, suggesting that our tendency to imitate is predominantly sustained by the left hemisphere. We normally manage to keep our tendency to imitate under control[25,26]; however, after frontal lobe damage, patients may experience severe difficulties in inhibiting this tendency.[27–29] Over the years, neuropsychologists have investigated whether differences in imitation depend on the body part used, the action goal, the putative mechanisms involved in imitating different types of gesture (*e.g.*, meaningful and meaningless, or transitive and intransitive), or the strategic control over these mechanisms.

Dual-route hypothesis

Clinically, a reduction of the ability to imitate gestures, considered to be a key symptom of ideomotor apraxia especially by European neuropsychologists,[2,3,7] often affects both meaningful and meaningless actions without distinction.[30] According to the model depicted in Figure 1, imitation can be accomplished using two different routes, depending on whether an action is known or novel. A known gesture can be imitated using the semantic route which, after the visual analysis, encompasses the input praxicon, the semantic or conceptual system, and the output praxicon, whereas a novel gesture can be reproduced by using the nonsemantic route. Each route can be selectively affected: damage to the semantic route reduces the patient's ability to imitate known, meaningful gestures; in contrast, damage to the nonsemantic route impairs the ability to imitate novel, meaningless gestures. We refer to this set of predictions as the *dual-route hypothesis* (see also Ref. 31). This hypothesis was supported as patients with a selective deficit in imitating either meaningful[32,33] or meaningless[7,32–34] gestures were indeed documented. In a study carried out in our laboratory, the imitative ability of 32 consecutive patients with unilateral right- or left-brain damage was tested using separate lists of meaningful and meaningless gestures: six of them were found to imitate meaningful better than meaningless gestures whereas the other two showed the opposite pattern (see Fig. 2).[33] Moreover, there was a classical double dissociation between case 19 and case 31, in that their performance tapping the spared route was as good as that of healthy controls, and the one relying on the impaired route was than that of controls.

It has been suggested that the functional locus of these two patients' deficit in imitating meaningful actions is likely to occur after the semantic system because they were able to understand those gestures that they had trouble in imitating. Why did these patients not use the nonsemantic route to reproduce meaningful actions? Meaningful gestures are

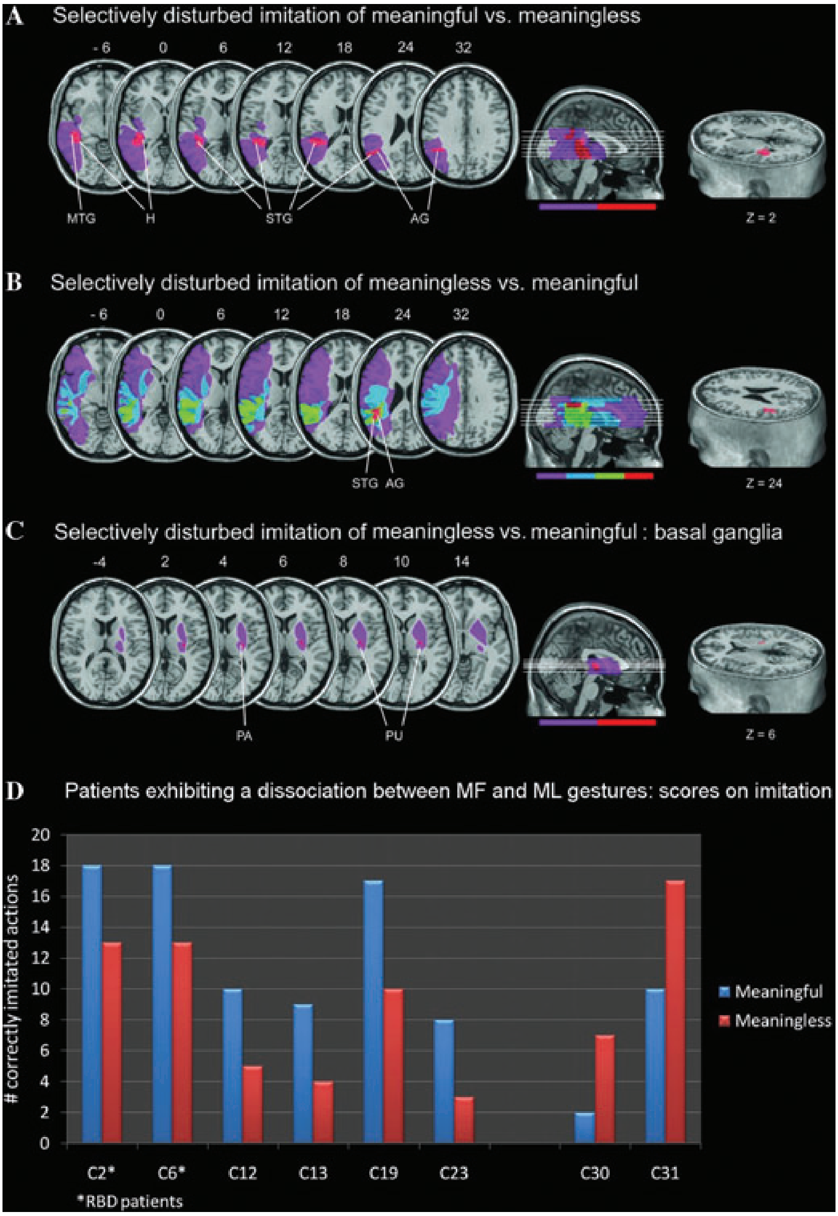

Figure 2. (**A**) Two LBD patients who imitated meaningless (ML) better than meaningful (MF) gestures (cases 30 and 31). (**B**) Four LBD patients who imitated meaningful better than meaningless gestures (cases 13, 14, 19, and 23). (**C**) Two RBD patients who imitated meaningful better than meaningless gestures (cases 2 and 6). In each figure, the number of overlapping lesions is illustrated by different colors coding increasing frequencies from a *violet* ($n = 1$) to *red* (indicating the maximum number of subjects in each group) color. Coordinates of the transverse sections are given. The height of the individual slices is also shown, on the medial view of the MNI template. In the rightmost part of each image the regions lesioned in all subjects of each group are superimposed onto a 3D rendering of the MNI template, which has been sectioned to show deep lesions. H = hippocampus, MTG = middle temporal gyrus, AG = angular gyrus, PA = Pallidum, and PU = putamen. (**D**) The graph plots the performance of individual patients who showed dissociations in imitating meaningful (transitive) and meaningless gestures. These images and data are derived from Tessari *et al.* (Ref. 33).

familiar and their sense of familiarity probably triggered the inefficient semantic route in patients 30 and 31 who proceeded to not revert to the nonsemantic route even though it was intact, because, due to the lesion, they had not sufficient resources for switching operations (see Ref. 10 for a similar case and argument). Case 30 imitated meaningless better than meaningful gestures, but imitated both gesture types below the normal range, thus suggesting that she probably suffered from damage to both the semantic and nonsemantic route.[33]

Direct mapping

In contrast with the *dual-route hypothesis*, the ideomotor theory (IM) posits that observing somebody else executing an action activates an internal motor representation in the observer for perceived and internal actions, in that they share a similar content or code.[35–37] According to this account, imitation is accomplished by a *direct mapping*, or what we might call *single-route hypothesis.* In an elegant series of experiments with healthy volunteers, Brass and colleagues[25,26] demonstrated that simply observing a finger movement evokes a strong tendency to execute that action, which, because it is not always required by the context, is usually inhibited. Proponents of direct mapping agree that, in humans, the neural correlate of direct mapping is the bilateral fronto-parietal Mirror Neuron System (hMNS), engaged both in observation and execution of purposeful actions.[38] Human direct matching—MNS seems to be tuned specifically to purposeful and biological actions.[39–41]

Consistent with the *single-route hypothesis*, some group studies found no difference in patients' imitation of meaningful and meaningless gestures when they were presented intermingled.[10,30,33,42] On the other hand, the *single-route hypothesis* cannot explain the observed double dissociation between the imitation of meaningful and meaningless actions observed in some patients.[7,32–34]

Any deficit in this mechanism should impair imitation of either action type to the same extent. As direct mapping is held to be automatic and unconscious, it resembles more the nonsemantic than the semantic route. In order for the perceived action to activate the corresponding motor representation in the imitator's brain, the mapping process needs to establish correspondences at the level of features that are already in the human motor repertoire, rather than at the level of the whole action representation. What still needs to be established is the nature of these features or, for that matter, the nature of the building blocks which gestures and movements are made up of.

Action recognition and motor production processes

In the model depicted in Figure 1, input and output praxicons are hypothesized to be independent. This means that successful recognition of actions does not necessarily rely on the motor production processes associated with objects and, *vice versa*, action production can occur independently of whether the action recognition has successfully taken place. Evidence in support of this hypothesis comes from individual patients who showed dissociations between the ability to recognize actions and that of using objects or imitating actions. On the other hand, group-level analyses led to quite opposite results, namely to associations of deficits, thus supporting the *embodied hypothesis*, whereby motor production processes associated with objects are at the core of action recognition. Patient M.F., described Bartolo and colleagues could recognize meaningful actions even though she performed poorly on all tests of production of meaningful gestures, including imitation.[32] The abovementioned cases 30 and 31 correctly imitated only 10% and 50% of the object-related pantomimes, even though they correctly identify 90% and 100% of them respectively[33]; differently from M.F., cases 30 and 31 showed normal object use.[33]

Cases of patients with difficulties in recognizing visual gestures, even if able to use objects,[8,10] as well as cases of patients who were apraxic but could accurately recognize gestures,[14,43] have been described in the past. Recently, Negri and colleagues' study reported classical and strong dissociations between object use and pantomime, or between object recognition (evaluated either by means of the pantomime or the object naming task, or by means of a multiple-choice version of the naming task so as to test patients with severe language production impairments) and object use when performance of individual unilateral brain-damaged patients from an unselected sample was analyzed.[9]

However, in sharp contrast with the single-case analysis, in the same study group-level analysis revealed a reliable positive correlation between pantomime recognition and pantomime imitation and a positive correlation between pantomime recognition and object use.[9] This correlational pattern replicated Buxbaum and colleagues' findings.[16] They studied 44 left-brain damaged patients, 21 of whom exhibited IMA apraxia, who performed a number of pantomime imitation and recognition tasks and found that there were strong relationships between object-related pantomime imitation and object-related pantomime recognition, and between imitation and recognition of the hand posture component of object-related actions. These authors found correlations between pantomime recognition and pantomime imitation ($r = 0.80$ and $r = 0.52$ for hand postures and for arm postures respectively). However, a similar correlation between imitation and recognition in Tessari and colleagues resulted only in a trend ($r = 0.32$).[33]

The neuropsychological evidence reviewed above, even though compatible with both the embodied and the disembodied theories, allows us to reject the strongest version of the embodied hypothesis, whereby recognition and production systems coincide. We will discuss later why it is the case that, in some patients, we were able to observe recognition or production abilities either selectively damaged or selectively spared.

Body representations and imitation

Rothi and colleagues did not foresee any particular role for putative body representations within their model. However, it is the case that there might be different levels at which these putative representations of the body might interact with higher-level motor processes.

In addition to the sensorimotor maps,[44] neuropsychologists hypothesized at least three other body representations, based on pattern dissociations: *body structural description, body schema*, and *body semantics* (or *body image*).[45–47] Within this conceptual framework, the *body structural description* is a representation derived primarily from visual input that codes the spatial arrangement of effectors and the relationships between them. Patients with damage to this representation suffer from *autotopagnosia*, which manifests itself with an inability to localize, within the whole body structure, body parts on verbal command, independently of whether the body is theirs or someone else's.[48–52] The *body schema* is an egocentric map that codes the position of one's body parts in space and time by integrating the information derived from sensory and motor modalities.[45–61] Often the integrity of the body schema is assessed using the handedness task[55] in which participants typically have to decide whether a rotated hand was left or right. It has repeatedly been showed that response times linearly increased with the discrepancy between the hand stimulus and participants' own hand, suggesting that they accomplished the task by imagining the movement of their own hand until its orientation matched the one of the hand stimulus. Furthermore, neuropsychological evidence suggests that the body structural description and the body schema can be independent from the *body semantics* (or body image) that is a conscious representation that stores lexical-semantic information about the body and its parts.[45]

In the following sections, we will examine how these putative representations have been considered in relation to higher-level motor processes, imitation in particular. There is no agreement to date on which of the putative body representations is supposed to be damaged so as to cause imitation impairments.

Body structural description

Goldenberg proposed that the imitation deficit is caused by damage to a nonsemantic route as well as to the structural description of the body.[7,56] His proposal was based on the observation that apraxic patients with left-brain damage (LBD) scored worse than LBD patients without apraxia or right-brain damaged (RBD) patients, on an imitation task and on a task in which they were required to reproduce the same postures on a life-sized manikin.[56] What is more, RBD patients' performance on tasks tapping visuo-spatial abilities (*i.e.*, block design and manipulation of beads) was inferior to that of both LBD groups. Goldenberg concluded that patients' reduced ability to reproduce gestures on their own body as well as on a manikin was caused by a unique functional damage to a supramodal body structural description. In addition, the double dissociation between imitation of meaningless gestures and performance on block design, he argued, indicated that the former did not rely on general visuo-spatial abilities. The association of deficits in reproducing postures on the human and on the manikin body was replicated in two patients whose lesions overlapped in the inferior portion of the angular gyrus in the left hemisphere.[7] This was roughly the same area that, according to some authors, was found active in a functional magnetic resonance imaging (fMRI) study in which participants watched a human model performing bodily gestures and then executed either an identical or a different action, using the same or different limbs.[57] The left inferior parietal lobule was associated with a visuo-spatial description of one's own body, whereas visual perception areas in the right occipito-temporal and superior parietal cortices were associated with imitation of simple body gestures, both requiring a visuospatial description of the observed model.[57]

Does imitation need to be dependent upon body mapping procedures, such as Goldenberg proposed? According to an alternative view is the one according to which imitation relies on decomposing-recomposing a visually presented gesture, according to a hierarchy of goals.[58] In a recent neuropsychological study, this issue was directly addressed.[59] Thus, patients with IMA, compared with RBD patients and control subjects, were found to be more impaired in imitating hand gestures and combined finger-hand gestures than finger gestures alone, even though their finger selection was not preserved. For the proponents of the so-called goal-directed theory, imitation of the distal aspects of a gesture, such as reaching for the correct object, is more important than selecting the exact means used to achieve the goal of a modelled action.[58,59]

Body schema

At variance with Goldenberg's view, other neuropsychologists proposed that the defective imitation is caused by damage to the body schema.[45,60,61] Buxbaum and colleagues described a patient, B.G., with progressive IMA, whose performance was severely impaired in imitating meaningless gestures and in tasks requiring spatial and mental sensorimotor transformations of body parts (*e.g.*, the handedness task).[60] These authors proposed that the patient's pattern of deficits was attributable to damage to a unitary set of procedures or representations coding the dynamic positions of the body parts of self and others (*i.e.*, the body schema) and modified the two-route model *à la* Rothi and colleagues in such a way that it could now account for their data.[60] Similarly, Schwoebel and colleagues found that, in left-brain damaged patients, the correlation between action imitation and tasks tapping specific body representations differed depending on whether the action was meaningful or meaningless.[61] More precisely the ability to imitate meaningful gestures correlated with the performance on both the handedness task (held to tap the *body schema*) and a semantic task concerning the meaning of body parts (and therefore held to tap the *body image*), whereas the imitation of meaningless gestures exclusively correlated with the performance on the handedness task.

The studies reviewed above interpret the deficit of the handedness task to be the result of damage to the body schema.[45,60,61] This is consistent with recent imaging work demonstrating that the representation of one's own body parts and the mental transformation thereof can be disentangled.[62] It is therefore possible that imitation deficits described by Buxbaum and colleagues[60,61] might reflect a defective ability to mentally imagine or simulate movements of body parts even though their body structural description is intact. Although there is no doubt that the motor system and the body interact, the nature of the body representation that is engaged in imitation of gestures still remains to be clarified as it is yet to be established whether it is necessary to postulate damage to a body representation in order to account for impaired imitation.

Object recognition and use

The object-use deficit has been considered to be the key-symptom of ideational apraxia because it was first noted in 1905 by Pick, who reported the case of a patient who committed gross errors not only in carrying out complex activities (*e.g.*, lighting his pipe) but also in using single objects like, for instance, using a razor as a comb or scissors to write.[63] Descriptions of patients showing impaired imitation, but normal object and tool use, and patients with the opposite pattern, have been reported, suggesting that these two abilities rely only partially on the same processes.[5,64,65] Double dissociation invalidates the skeptics' belief that IA is simply a more severe case of IMA.[66,67]

The ideational deficit has been interpreted in many ways. For Pick and Dejerine, failure to use objects was a consequence of general mental disorders,[63,68] opinion supported by the frequent association of IA with dementia or confusion.[69] For Liepmann,[70] patients have difficulties in forming the idea or plan an action. According to Morlaas, IA was a special case of "agnosia of use" in that it affected only transitive actions (*e.g.*, waving good-bye).[71] De Renzi and Lucchelli argued that errors such as omission, misuse or mislocation, made by the patients with IA, "reflect a defective idea of how the object must be used" (p. 1181).[5] These authors, therefore, proposed to call this deficit "amnesia of usage", caused by a failure to activate memories of actions. Subsequently, other neuropsychologists associated the deficit in using objects with damage to the conceptual or semantic system.[10,43,60,65,72,73]

In the above mentioned studies, however, the extent to which these apraxic patients could recognize those objects they failed to use, or did not retain conceptual knowledge of, or whether they had lost the sequential organization of complex gestures, was not fully established. In our laboratory, we carried out an extensive assessment of semantic knowledge concerning the objects that two apraxic patients failed to use (F.G. and D.R.).[14,74] We demonstrated that their deficit in using objects could not be caused by a damaged semantic system, in that the patients performed well object-to-action matching and on an action-to-object matching tasks; neither could it be caused by visual agnosia, in as much as they could correctly recognize all objects, nor by a deficit in sequencing the pictures of everyday activities.[14] Moreover, we demonstrated that these two patients retained finer semantic knowledge about the objects they failed to use.[74]

Thus, in order to use objects one does not seem to rely on full semantics. This claim was supported by the observation of seven patients with Semantic Dementia (SD),[74–78] one with Alzheimer's disease,[77] and one with *herpes simplex* virus encephalitis[78] all of whom were diagnosed as being able to use objects in the presence of severe semantic loss and naming difficulties. While in Negri and colleagues'[77] patients' semantic deficit worsened in subsequent testing sessions, leaving their ability of using objects substantially intact, the SD patients studied by Silveri and Ciccarelli[78] could cope with everyday activities, as long as their semantic deficit was not severe (as in the case of SD patients reported in Refs. 79–82).

Taking together, these double dissociations suggest that motor representations are necessarily contacted when we produce an action but not when we understand an action or an object's function. This lack of overlap between processes underlying action production and the ability to understand action and objects is in contrast with the correlation of deficits found in some early studies of apraxia (where patients' semantics was not clearly assessed) and in more recent studies involving SD patients with a severe semantic deficit.

A computational account of tool use and its deficits

The errors that patients F.G. and D.R. of Rumiati and colleagues committed when they used objects included step omissions, subtask omissions, action additions, object substitutions, perseverations, and capture error/usage behavior.[14] In that study we proposed that the errors arose from a disturbance of contention scheduling (CS), a system responsible for the control of routine action, in which action schemas and object features are represented in two distinct networks that are normally mutually interconnected.[12] Another system—supervisory attention—is able to bias the CS when willed control over behavior is needed.[83] In 2007, Cooper has also applied this model to five multiple object tasks typically used in clinical assessment.[13] In preparing an espresso coffee pot using coffee from a tin and a spoon, the parts of the coffee pot, the coffee tin, and the spoon would be represented in the object representation network. Normally, these representations trigger the appropriate action schemas; this triggering is the cognitive equivalent of the Gibsonian notion of affordance,[84] and is supported by empirical studies.[85,86] The reverse links, from schemas to object representations, are activated to ensure that appropriate objects are selected during schema-directed action. Within either domain, lateral inhibition operates between units to ensure that no more than one object representation, or schema respectively, becomes strongly active for a given function at a given time. Cooper lesioned the links between action schemas to object representations, and the reversed links, and reproduced the error profiles of F.G. and D.R. of Rumiati and colleagues, respectively.[13] Consistently with Cooper and Shallice's model, D.R.'s deficit is best accounted for by assuming a complete ablation of a pathway from object representation to schema, whereas F.G.'s deficit is best accounted for by assuming a near complete ablation of the reverse pathway.[12]

"What" and "how" revisited

According to a current dominant view of the visual system (see Ref. 87), the visual processing used in the programming and control of grasping is held to be quite distinct from the visual processing that supports our object perception. Goodale and Milner argued that the visual control of grasping and other visually guided movements is sustained by a dedicated visuo-motor system in the dorsal steam, that from the primary visual cortex reaches the posterior parietal cortex (the "how" system). The perception of objects, they claimed, depends on the ventral stream projecting from the primary visual cortex to the temporal lobe (the "what" system). Evidence for a distinction between "vision-for-action" and "vision-for-perception" comes from the observations of neurological patients. On the one hand, patients with damage to the dorsal stream often show optic ataxia (OA)—a deficit of visuo-manual guidance—despite having a relatively speared ability to recognize objects. The opposite side of the dissociation is represented by patients suffering from visual form agnosia (VFA), a deficit that impairs object recognition without interfering with their ability to reach and grasp objects. More recently, Pisella and colleagues[88] argued that the current available observations do not convincingly support Goodale and Milner's dichotomic view and concluded that it should be revised in favor of a more complex organization characterized by multiple parallel visual-to-motor connections: a dorsal-dorsal pathway, a ventral stream-prefrontal pathway, and a ventro-dorsal stream pathway. The first one, which involves the most dorsal part of the parietal and premotor cortices and supports immediate visuo-motor control, when damaged, gives rise to OA. The second one connects the ventral visual stream to prefrontal areas, by-passing the parietal cortex, and supports "mediate" control; damaged to this pathway gives rise to VFA. The third connection is the ventro-dorsal pathway that comprises the more ventral part of the parietal lobe, the premotor and prefrontal areas, and supports complex planning and programming that rely on high representational levels; damage to this connection gives rise to limb apraxia, spatial neglect or mirror apraxia depending on whether it is located in the left hemisphere, the right-hemisphere or both.

The double dissociation between patients with a selective deficit in using objects and patients with degraded object knowledge is compatible with Pisella and colleagues' framework. We suggest that the "how" system should include higher-level action representations, acquired by past experience, on which the dexterous use of familiar objects relies. They correspond to the nonsemantic, left posterior parietal cortex-based system,[128] the same that might be damaged in ideational apraxic patients.[14,74] Even though they fail to use them appropriately, limb apraxic patients do not necessarily show deficits in grasping and manipulating objects (*i.e.*, they do not have OA), suggesting that the higher-level action representations are functionally dissociable from first-order sensorimotor transformations required in object prehension.

On the other hand, the ventral stream-prefrontal pathway, in addition to computing the intrinsic properties involved in object identification (or "what" stream), would also deal with task-independent conceptual knowledge that comes into play not only in object naming and recognition tasks but also in tasks tapping functional-semantic information about objects. This system seems to be degraded in demented patients, *e.g.*[74,78]. Although this double dissociation reliably shows some degree of specialization between these different levels of object and action representations, under normal circumstances these levels may well interact.

Action-related language processing

It is common to find associations of deficits in verbal and nonverbal domains in neuropsychology, so much so that in the past the nonverbal deficits of aphasic patients were interpreted as being part of a central communication disorder.

There are several studies in which disturbances of gesture comprehension (*i.e.*, understanding what is its meaning) were frequently detected in aphasic patients, as for instance in Gainotti and Ibbia's study.[89] However, it is not clear whether the responses given by the aphasics in the gesture comprehension task were inaccurate because they failed to process gestures correctly or because they used the impaired verbal modality to elaborate their responses. The association of aphasic deficit with an impairment of symbolic gesture interpretation was replicated in a later study by Gainotti and Lemmo.[90] Moreover, the deficit of aphasic patients on a gesture comprehension task correlated closely with a verbal semantic impairment. Duffy and Duffy,[91] expanding the results of their own earlier study,[92] found a strong correlation between impaired pantomime recognition and verbal deficits in 47 aphasic patients. Moreover these aphasics were impaired in both pantomimic expression and recognition and these deficits correlated closely with aphasic deficits. More recently, a subgroup of patients with severe aphasia were reported who were impaired in understanding actions in both verbal and nonverbal modalities (*i.e.*, through reading and pantomime interpretation), although the performance of the larger group of aphasics, to which the severe aphasics belonged, dissociated between the two modalities.[93]

Clinically, in right-handed individuals IMA (defined as a failure to imitate gestures or/and to execute them to verbal command) and IA (defined as a failure to use objects) are mainly associated with lesions in the language-dominant left hemisphere. Association between the two deficits is therefore likely to be due to the encroachment of the lesion upon the contiguous structures, which are differentially dedicated to language and praxis. In line with this view, Ajuriaguerra and colleagues reported that 90% of patients with ideomotor apraxia also suffered from aphasia and that 56% of the aphasics were apraxic.[69] This was supported by the findings of De Renzi, Pieczuro and Vignolo, in which the highest correlation reported was that between aphasia (*i.e.*, comprehension) and ideational apraxia ($r = 0.579$, $P < 0.001$); in their study IA occurred in patients with severe aphasia, and particularly in patients with global and severe Wernicke aphasia.[64] As the aphasics had difficulty in pairing objects with the movements required to use them appropriately, De Renzi and colleagues concluded that an inability to associate different aspects of the same concept was one of the common underlying causes for their failure to perform certain tasks correctly.[64]

However, conclusions based on these and similar observations have been challenged by other findings showing uncorrelated performances[94–96] and dissociations between verbal and action domains.[30,64,93,97,98]

Uncorrelated performance and dissociations

In Bell's study, the ability of aphasic patients to recognize pantomimes did not correlate significantly with their scores on language or praxis, which substantiated the view that their errors in pantomime recognition may be caused by a perceptual-motor deficit in addition to semantic impairment.[94] Goodglass and Kaplan[95] and Wang and Goodglass[96] who tested aphasics both on the production of transitive and intransitive pantomimes with verbal prompts, as well as their comprehension of pantomimes, also found that the performance of these two tasks were not correlated.

Liepmann (quoted by Ajuriaguerra *et al.*[69]) described seven nonaphasic patients with apraxia, six of whom had right-sided hemiplegia.[99] In contrast, Kertesz, Ferro and Shewan found that of 177 left-stroke patients, 6 had severe aphasia but normal praxis abilities.[97] De Renzi and colleagues studied 100 left-brain damaged patients of whom 60 suffered from aphasia; of the 40 nonaphasic patients, 2 showed a deficit in performing the imitation task, whereas 12 of the 60 aphasics did not.[30] However a positive, significant correlation was found between imitation scores and a measure of verbal competence (measured with the Token test). In another large group of 699 Italian patients examined by Papagno, Della Sala, and Basso, 10 were found to have IMA but not aphasia, and 149 aphasia but not apraxia.[98]

In the study by Saygin and colleagues cited earlier, a dissociation was also found in a group-level analysis between pantomime interpretation (using line-drawings) and action comprehension (with sentences), though the stimuli used for both tasks were identical.[93] This clearly suggests that aphasics can interpret observed actions that they cannot understand via language (through verbal material).

To explain the discrepancy between associations and dissociations of language and praxis abilities, some authors suggested that linguistic and nonlinguistic functions might share representations to a variable degree, depending on the extent to which verbal and nonverbal tasks share perceptual and conceptual properties and developmental stages of acquisition.[93] We have directly addressed this hypothesis and provided evidence that, even when task- and stimulus-level factors are as closely matched as possible, double dissociations between language and nonlinguistic representations and processes are still possible.[100] The performance profiles, observed in our and others' patients challenge the extreme embodied view according to which sensorimotor and conceptual systems are thought to be virtually identical.

The anatomy of action perception and imitation

Neuropsychological[7,32–34] and neuroimaging[101,102] studies demonstrated that the two routes, or processes, for imitation have a psychological reality and dedicated neural correlates. Specifically, patients with lesions of the parietal cortex (in particular the angular gyrus) were described as being impaired in imitating meaningless gestures, but were still able to imitate meaningful gestures.[7,33,34,103] Using positron emission tomography (PET), Peigneux and colleagues observed activations in the left angular and middle frontal gyri, in the right supramarginal gyrus and inferior parietal lobule, when subjects imitated familiar gestures, and in the inferior and superior parietal lobes bilaterally when subjects imitated novel gestures.[101] Furthermore, in one of our studies, an increased activation in the inferior temporal, the angular and the parahippocampal gyri of the left hemisphere was found when volunteers imitated pantomimes of object use, relative to imitation of meaningless gestures.[102] Imitation of meaningless gestures, relative to pantomimes, led to an increased neural activity in the parieto-occipital and the occipito-temporal junctions in the right hemisphere, in the superior temporal gyrus in the left hemisphere, and in the superior parietal cortex bilaterally. Thus, in addition to regions that are generally engaged in imitation, there are other regions that are associated only with imitation of either meaningful or meaningless gestures.

In contrast, the neuroimaging studies that aim to test the *single-route hypothesis*, according to which the recognition of an action is mediated by the same neural substrates engaged in the production of the same action, led to the activation of the alleged hMNS: the ventral premotor cortex, the inferior frontal gyrus, the inferior parietal cortex and the superior temporal sulcus[104,105] (see Ref. 106 for a review). These regions are held to be homologous to premotor and parietal regions in the monkey brain, in which about 15% of neurons were found to respond both to observation and execution of a given transitive (but not intransitive) action.[107–110] However, in the imaging studies with human volunteers, portions of the hMNS were found active not only when transitive (goal-directed) gestures were used as stimuli, as in the case of the monkey brain, but also when they were intransitive.[38,111,112]

Whether the brain regions defined as hMNS represent the correlate of the direct mapping mechanism underlying visual processing of gestures and imitation has recently been questioned.[113–115] Many of the neuroimaging paradigms investigating the hMNS searched for regions whose activity was, among other things, *cross-modal*, *i.e.*, modulated by both the perception of a given movement and its execution. However, at variance with the studies on the monkey brain, in which the activity of single neurons was recorded, the studies conducted with humans adopted noninvasive neuroimaging techniques, recording the activity of a large volume of grey matter in which many subpopulations of neurons with different functional properties may coexist. The heterogeneity of the signals recorded with neuroimaging techniques casts doubt on many of the findings that reported brain regions exhibiting cross-modal effects. Rather, any increase in neural activity, both when observing and executing a given action, could reflect the activation of distinct subpopulations of neurons, none of which has cross-modal functional properties.[113,116]

Three studies have recently attempted to overcome this problem by investigating the alleged hMNS using adaptation paradigms.[117–119] Studies employing this paradigm assume that neural cells with selective functional properties rapidly adapt when their preferred stimulus occurs repeatedly[120]; thus, any decreased activation when one stimulus is presented in rapid sequence reflects the adaptation of a subpopulation of neurons within a particular brain region. Dinstein and colleagues described regions in the anterior intraparietal sulcus and in the ventral premotor cortex which adapted when the same gesture (but not different gestures) were either repeatedly observed or executed.[118] However, they failed to find cross-modality effects as no region adapted when the same gesture was first executed and, afterwards, observed. On the other hand, Chong and colleagues found a portion of the right anterior intraparietal sulcus, in which the activity was attenuated when participants observed a recently executed action relative to one that had not previously been performed, thus providing the first evidence in the human brain of neurons exhibiting cross-modal functional responses.[117] As Chong and colleagues used meaningful gestures which were, in many cases, associated with an object (as well as Dinstein *et al.*[118]), their results could reflect adaptation of object-related properties, rather than adaptation of the movement *per se*.[117] This issue was addressed by Lingnau and colleagues who tested cross-modal adaptation paradigms using meaningless gestures and failed to replicate Chong's result, thus leaving the debate about the existence of a neural substrate underlying direct matching open.[119]

The anatomy of object perception and use

Objects and tools are processed by different regions, which can vary depending on the modality in which they are experienced, on their function, on the manner in which they can be manipulated, on their value, weight as well as many other properties. A wealth of functional imaging studies suggested that high-level object processing of object pictures relies on regions in both the middle occipital cortex and the fusiform gyrus bilaterally,[121,122] with the medial fusiform gyrus specifically active whilst processing manipulable objects, such as tools and utensils, compared with living things.[123,124]

On the other hand, neuropsychological studies of patients suffering from ideational apraxia suggest that the human capacity for highly skillful object use relies on the activity of left inferior parietal cortex.[5,14,74,125] Consistent with neuropsychological observations, studies with healthy participants found an involvement of the posterior part of the left inferior parietal lobe when they pantomimed the use of a tool prompted by a picture[126,127] or its name.[128] The activation of this brain area, associated with both the preparation of the gesture and its overt execution, was neither found when participants performed the same gesture through imitation, when they named the object rather than pantomiming its use,[127] nor when they programmed and executed a meaningless gesture.[126,128] Moreover, the neural activity of the left inferior parietal cortex enhances when object-related action schemas are accessed both explicitly (*i.e.*, for overt execution) and implicitly, like for instance in nonmotor tasks involving tools, such as making judgements about actions associated with manipulable objects,[129,130] naming tools[131] and the associated actions,[132] or simply passive viewing tools.[19,131,133]

A recent study reported increased functional connectivity between medial fusiform regions,[133] that in previous studies had been associated with presemantic representations of visually presented objects,[123,124] and a portion of the left supramarginal gyrus close to the one previously reported by Rumiati and colleagues[127] and Johnson-Frey and colleagues.[128] Similar results were observed in a recent PET study when participants pantomimed the use of (or carried out a nonmotor judgement on) an object presented as a name (or as a picture).[134] We found an increased connectivity between the left superior temporal sulcus (implicated in word processing) and portions of the fusiform gyri (implicated in object picture processing) specifically when participants pantomimed the use of an object name. Furthermore, we also found increased connectivity between fusiform regions and the left inferior parietal cortex (previously implicated in the pantomiming task) when participants pantomimed the use of object pictures or object names, thus favouring the explanation according to which object-related action knowledge is better accessed by visual (and not verbal) object representations.

Between associations and dissociations

The neuropsychological and neuroimaging evidence reviewed in the above sections is consistent both with embodied and disembodied views on higher-level motor processes. As Mahon clearly put it, in cognitive neuroscience we are lacking a theory that can explain both the dissociation between action production and recognition, and the association of impairments in action production and recognition.[135] On the one hand, the sensorimotor or embodied theories can account for the associations between motor processes and action recognition but fail to account for the dissociations of their deficits. On the other hand, disembodied theories (see Fig. 1) can easily explain dissociation patterns like the one between action production and action recognition, but find it difficult to explain associations of deficits as being caused by damage to a single process. We suggest that Mahon's argument should be generalized to include the putative role of motor representations in action-related language processing. The evidence gathered thus far strongly indicates that, even though language and action are independent domains, as suggested by the clinical dissociations (*e.g.*, Ref. 98), action-related language processing might also heavily interact with motor processes (see also Ref. 136 for a review). Recent findings, for instance, suggest that healthy participants, engaged in linguistic tasks that contain motor or visuo-spatial operations, can make either an implicit or an explicit use of motor or perceptual representations.[137–140] However, the exact conditions under which the information flows, or does not flow, between the perceptual or linguistic domain and the motor domain have not yet been clearly understood. In the following sections, we will discuss some mental operations that make the cross-talking between action perception (or action-related language) and motor processes possible.

Sensorimotor simulation

The sensorimotor hypothesis holds that understanding language that denotes actions recruits the motor system because this is an integral part of the cortical network in which words are represented.[20,141] Accordingly, in order to understand linguistic descriptions of actions, we mentally simulate the motor content within the same motor substrates that are used to physically perform those actions. Imaging studies have shown that passive reading or listening to action language activated motor and premotor areas,[142,143] whereas electrophysiological[144,145] and magneto-encephalography (MEG)[146] studies clarified that activations involving frontocentral regions occurred about 200 ms from word onset, a time window in which it has been suggested that the lexical-semantic access occurs.[147] However, it is not possible to establish the level of the processing in which participants were engaged when the motor system was activated, because in the above-mentioned studies subjects' emodynamic responses, but not the behavioral ones, were recorded.[142–146]

In our laboratory, we carried out a study in which we aimed to ascertain the contribution of the motor system to the processing of action-related language in a semantic task (*i.e.*, deciding whether a verb was related to an action) and in a morpho-phonological or syllabic task (*i.e.*, counting the number of syllables of those verbs).[148] We delivered TMS to the primary motor cortex (M1) so as to elicit motor evoked potentials (MEPs) in hand muscles and thus obtain a measure of motor excitability. We showed that M1 activation during linguistic tasks, far from being automatic, increased when participants performed semantic judgments on verbs, but not when they performed the syllabic task (Fig. 3). This effect occurred only after a 350 ms postword onset when, according also to independent evidence,[147] the lexical-semantic word processing had already taken place.

The effects found in Papeo and colleagues go in the same direction as those provided by the fMRI study of Tomasino and colleagues, in which M1 was found to be activated only when participants had to explicitly imagine the motor content of action-related phrases, but not when they performed a letter detection task on the same verbal stimuli.[149,150] Taken together, these findings suggest that motor simulation is more likely to be triggered when the motor content of the word is critical for performing a task, and that it can be selected even when not explicitly requested by task instructions.[148–150] Thus the motor activations observed in a study in which participants were not explicitly required to imagine the semantic content of motor verbs (*i.e.*, silent word reading), can be interpreted as being due to simulation of the motor content of those words.[142]

In a TMS study carried out by Roy and colleagues, an increase of M1 activity was observed for rare words compare with frequent words, possibly because as the former words are more difficult they might be better processed by simulation.[151] This effect was observed somewhat beyond the time window in which lexical access normally occurs, thus suggesting that M1 interacts with the lexical-semantic system to assist word understanding under certain, but not all, task conditions. Relevant for our claim that motor simulation might be one of the mechanisms that permits the transfer of information between domains is the observation that the time in which word processing is influenced by the TMS effect, both in ours and related studies on M1, is the same in which mental imagery on similar stimuli takes place. The fact, then, that activations of this region are inconsistently found in imaging studies is probably due to M1 varying according to context and task (see Ref. 152, for a review).

To conclude, the role of sensorimotor simulation in higher-level cognitive processes such action-language comprehension is twofold: it conveys concrete information that enriches our conceptual representations and it provides us with a strategy to perform tasks on verbal stimuli with sensorimotor features that cannot easily be inferred or whose recall is the most effective via simulation.

Strategic control in imitation

Another example that illustrates the reversibility of high-level motor processes is represented by the strategic selection of routes in speeded imitation. A reduction of cognitive resources, caused either by experimental manipulations in healthy participants[31,153–154] or by brain damage[33] in patients seems to influence which route to select for imitating gestures.

In particular, studies with healthy participants revealed that speeded imitation was significantly more accurate for meaningful than meaningless gestures when they were presented in separate lists, whereas when the two types of gestures were presented intermingled, the advantage of meaningful over meaningless imitation disappeared. It was proposed that when gestures were presented in blocks, participants selected the faster semantic route for imitating meaningful gestures, and the nonsemantic route for imitating meaningless gestures, whereas when both gesture types were presented intermingled, only the nonsemantic route was selected[154] (Fig. 4A; see also Ref. 155).

The lack of difference in imitation of meaningful and meaningless gestures in the mixed presentation was not due to meaningless gestures impoverishing overall performance because they require more cognitive effort. In fact, the same pattern as in Tessari and Rumiati[154] was observed when meaningless or both meaningless and meaningful actions were presented for a longer time.[153] In all these studies, the meaningful gestures employed were pantomimes of object use (*e.g.*, hammering) whereas the meaningless ones were gestures obtained by modifying the relationship between the hand-arm and the trunk of the meaningful version. Recently, we have successfully replicated the original patterns observed with object-related gestures using intransitive gestures, thus demonstrating that the strategic control effects are not specific to object-related pantomimes, but they represent a more general way in which the human mind-brain operates in coping with a shortage of resources. We employed the same paradigm adopted in previous studies,[153,154] except that intransitive gestures were presented for a shorter time (−150 ms) in order to make them comparable with transitive gestures, in terms of resources requested.[156] We found that in the blocked condition, participants were more accurate at imitating intransitive gestures with meaning than

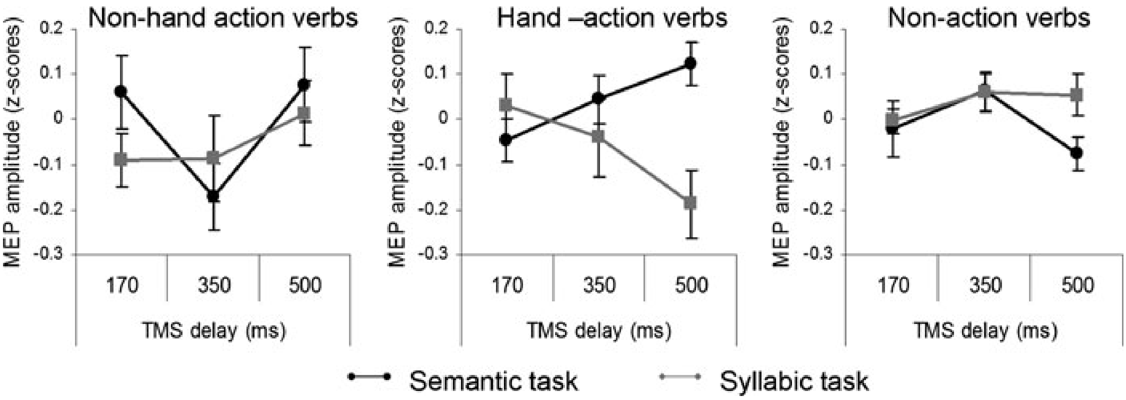

Figure 3. **Analysis of normalized motor-evoked potential (MEP) amplitude for the verb categories (hand-action, nonhand action and nonaction verbs) as a function of the tasks (semantic and syllabic) and the timing of TMS delivery (170, 350, 500 ms) as the only between-subjects factor. MEP amplitude provides a measure of excitability in the left primary motor cortex (M1). At 500 ms poststimulus, MEP amplitude increased when the participants performed the semantic task with hand-action verbs compared with nonaction verbs. It decreased, relative to nonaction verbs, when the participants performed the syllabic task with the same hand-action verbs. A similar dissociation between M1 activity associated with the two task conditions was never observed for the nonhand action verbs. Vertical bars indicate the Standard Error of the mean. Data from Papeo *et al.* (Ref. 148).**

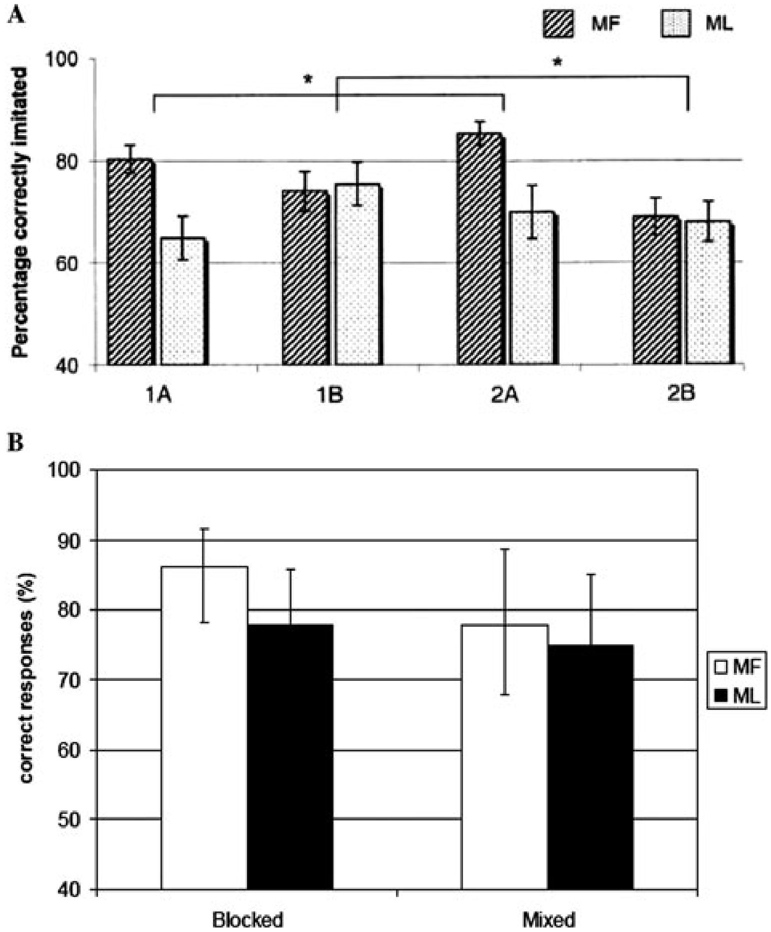

Figure 4. (A) Percentages of correctly imitated meaningful (MF) and meaningless (ML) transitive gestures in Experiments 1 (A and B) and 2 (A and B) are plotted. Experiments 1A and 2A correspond to presentation in blocks; Experiments 1B and 2B correspond to mixed presentation. In Experiments 1, participants were not aware of the composition of the lists whereas in Experiments 2 they were informed about it before performing the imitation task. Bars represent confidence intervals. Brackets refer to comparisons between Experiments 1A and 2A and Experiments 1B and 2B (*$P < 0.05$). Data from Tessari and Rumiati (Ref. 154). (B) Percentages of correctly imitated meaningful (MF) and meaningless (ML) intransitive gestures plotted according to whether they were performed in a blocked or mixed condition. The bars represent the standard deviation from the mean. Data from Rumiati *et al.* (Ref. 31).

without meaning, whereas in the mixed condition, no difference was observed.[31] In general, intransitive gestures are performed more accurately than transitive gestures which pose greater processing demands on the mind-brain, presumably because one inevitably processes the information relative to the corresponding objects, even though these are not physically presented.[155] This finding is consistent with the results of a recent imaging study showing that planning either tool use pantomimes or intransitive gestures was associated with asymmetrical increases in the *same* regions of left parietal and dorsal premotor cortices, irrespectively of the hand used.[156]

The interpretation of these effects in terms of strategic route selection is supported by neuropsychological evidence too: when meaningful and meaningless gestures were presented intermingled, patients' ability to imitate either action type did not differ[33] (see also Refs. 10, 30, 42); however, when we evaluated the patients' imitative ability using separate lists, we found that eight patients selectively failed to imitate either meaningful or meaningless gestures.

Speeded imitation in the mixed condition induced healthy participants to select only one mechanism for reproducing both types of gestures; in doing this, they saved resources that would otherwise be eroded by switching between nonsemantic and semantic mechanisms. This same strategy is also applied by patients who performed the imitation task in the mixed condition; in their case, even if they perform the task without time limits, it is the lesion that reduces their resources.

These strategic effects are not specific to the domain of action perception and imitation. In fact, similar effects on route selection have been found in reading studies: when legal nonwords were inserted in a list of words, readers used the sublexical route to read regular words as well as nonwords, instead of selecting the lexical route.[157,158] In languages with a shallow orthography (*e.g.*, Italian), the lexical route can be selected for reading words already known to the reader but *must* be selected for reading nonfrequent irregularly spelt words, whereas the sublexical route is necessary for reading new words, nonwords or regular known words; this is achieved by applying a set of orthographic-to phonological conversion rules. In contrast, reading in languages with opaque orthography (*e.g.*, English), the lexical route needs to be selected as there are many irregular words that could not be read otherwise (see Ref. 159 for a review).

Thus, route selection does not seem to merely depend on the type of action to be imitated (or word to be read) but seems to be critically sensitive to the amount of cognitive resources available for accomplishing a given task.

Concluding remarks and future directions

In this review we illustrated how, during the last 20 years, the way in which the motor system was viewed by cognitive neuroscientists has changed considerably as a result of diverting the emphasis from its role in producing motor outputs to its central role in many other higher-level cognitive processes including action recognition, object recognition and language understanding. We described two main strands of neuroscientific evidence endorsing either a separation between functions or processes, or a complete overlap between them. Each of these two opposite empirical sets is compatible with a class of theories: while behavioral dissociations, and discrete neural substrates underpinning different higher-level motor functions, are better explained by disembodied theories of higher-level motor processes,[8,10,154] behavioral associations, and common neural substrates underpinning different higher-level motor functions, are better explained by sensorimotor or embodied theories.[20,106] Although we are far from being in the position of offering a unitary theory that can comfortably accommodate all empirical observations summarized in this review, we have tried to point to some operations that seem to play a role in passing information between domains.

We proposed that the apparent conflict in understanding action-related language between behavioral associations and dissociations in brain-damaged patients, or between differential or overlapping brain activations in normal population, can be explained with its resilience to task demands or context, whereas action imitation, the mechanism that is proposed to warrant flexibility in route selection depends on the available resources.

Earlier in this paper we discussed to what extent motor processes are required in order for us to skillfully recognize objects or object-related gestures. It turned out that the overlap between the motor and the conceptual systems need not be massive, as expected on basis of the sensorimotor hypothesis. The computational modeling forwarded by Cooper[12,13] focused on the interplay between the motor system and the object system when we are engaged in using objects during everyday activities. In this theoretical framework a reduction of top-down control can account for unsettled links between the abovementioned systems giving rise to consistent patterns both in patients, and in the model of Cooper.

There are still many questions that need to be answered in order to better define the space between the extreme embodied and disembodied hypotheses. How general are these strategic processes? To which extent they are automatic or conscious? How much effort or resources do they require to be successfully implemented? Future work should try to address these questions while keeping in mind the strong constraints imposed by neuropsychological findings.

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Conflicts of interest

The authors declare no conflicts of interest.

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