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The case of communicative intransitive gestures:
Further developments on a dual mechanism for motor control of action in imitation.

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Abstract

Imitation is classically thought of as a mechanism that allows learning from demonstration. Several are the models that offer an explanation of how human imitation is accomplished. Observations of brain damaged patients, healthy subjects and brain imaging data can be found in support of both unique mechanistic models and dual route models (Chapter 1) . Two sets of evidence from neuropsychology and normal experimental psychology support the need of independent mechanisms that can account for either imitation of novel, meaningless actions or familiar, meaningful actions.

In Chapters 2-3, I reported several behavioural experiments that tested whether a putative indirect semantic route for imitation is able to process not only object-related gestures but also communicative gestures. Moreover I investigated whether subjects are able to select a given route for imitation based on some strategic, implicit assessment of the context and resources or whether route selection was stimulus-driven.

In Chapter 4, by means of event-related-potentials recordings I demonstrated that imitation of familiar actions and novel actions dissociate, as novel actions recruit an anterior left lateralized supplementary process.

In chapter 5, by showing that autism spectrum disorder children have preserved imitation of both object-related and communicative familiar actions while performing poorly at imitation of novel actions, I explain autism in the light of a dual route model.

Throughout this thesis my aim was to gain in-depth comprehension of dual mechanisms for imitation of actions, as I believe that, compared with unique mechanistic models, it adds explanatory value.

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Chapter 1

Introduction

1.1. Dual function of imitation

Imitation is classically thought of as a powerful learning mechanism that allows humans to acquire new skills without the burden of trial and error processing that might produce costly or even fatal consequences (Bandura, 1974). However, learning might not be the only cognitive function that imitation subserves. Uzgiris (1981), for instance, has suggested that imitation may serve a dual function; it might help understanding observed acts or puzzling events and it can signal shared mutuality with another, with a clear stress on the aspect of interpersonal interaction.

More recently, Byrne (2005) called for the distinction between two kind of imitation, each of which would attain different end-goals: "Social Mirroring" and "Learning by Copying". While

the latter would be achieved by powerful perceptual cognitive processes, social mirroring would be achieved by a much simpler cognitive process, because it would not require anything new to be learnt. The overt imitation of actions already present in one's own repertoire is suggested to fulfill a social-like function in human interaction as, for instance, empathy and mutual identification (Byrne, 2005) or interpersonal bonding (Chartrand & Bargh, 1999). Certain types of imitation (e.g. automatic imitation) may function as a social glue by which humans coordinate their behaviour or develop affiliative tendencies towards each other (Bertenthal et al., 2006); yet it seems unlikely that it functions as a skill transfer device, given that it only involves the activation of action representations that are already present in one's own repertoire (Byrne, 2003).   Whether imitation learning and mimicry (mirroring) depend on distinct neurocognitive processes or whether the same structures are involved in both cases is still a matter of debate (Heyes, 2009)

1.2. Apraxia studies and models of praxis

Apraxia (loss of skilled movement) is a term that has been used to describe a wide variety of neurobehavioral disorders. Apraxia is generally defined as ''a disorder of skilled movement not caused by weakness, akinesia, deafferentation, abnormal tone or posture, movement disorders such as tremor or chorea, intellectual deterioration, poor comprehension, or uncooperativeness''(Heilman and Rothi, 1993).

Apraxia can selectively affect different body segments, as for instance limb apraxia. The type of limb apraxia that has received most attention and that we are concerned here is the Ideomotor Apraxia (in short IMA). The key feature in IMA is a failure to imitate, and it is mostly caused by left hemisphere damage (De Renzi, Motti & Nichelli, 1980). IMA patients are characterized by comminting spatial and temporal errors when performing movements with their left, non –paretic hand. Errors may concern use of objects or tools as well as movements performed without external objects, like for instance pantomime of object use. Patients may commit errors

even when the correct movements are demonstrated and they only have to imitate them (Goldenberg, Hermsdorfer & Spatt, 1996; Rumiati, Papeo & Corradi Dell'Acqua, 2010).

Another concept, introduced by Liepmann, is the idea of one movement as being equivalent to one visual mental image of the intended movement that he named "movement formula". These representations of movements have been proposed to be stored in the inferior parietal lobule and be contacted when one imitates a gesture, pantomimes the use of objects or actually use them (see Heilman & Rothi, 1993).

The fact that several patients have been reported to make errors when imitating meaningless (ML) gestures but are then able to perform meaningful (MF) gestures as pantomime of object use on command or on imitation, led Rothi et al. (1991) to put forward a model of praxis postulating the existence of two routes for gesture production as well as imitation. One route passes via long term memory representations (engrams), and processes MF actions, but cannot be used for ML gestures as ML gestures are novel and are not associated with a stored representations in memory. The second route is the direct route as it bypasses gesture engrams and provides a direct link from vision to motor control. This route can be used to process both MF and ML actions. If a direct route is damaged or interrupted, gesturing of MF actions could still be achieved by the first route, thus accounting for the dissociation often found of impaired performance of ML gesturing.

Another important distinction that can be found in the literature on apraxia is the one between transitive, or object-related actions (e.g. hammering), and intransitive actions, that is actions which have nothing to do with objects, and typically convey communicative content (e.g. waving goodbye). The disparity of performance of transitive and intransitive actions in apraxic patients is still poorly understood (Buxbaum, et al. 2007). The fact that patients with ideomotor apraxia have often less difficulty with intransitive gestures than transitive object-related gestures prompted Buxbaum (Buxbaum, 2001; Buxbaum, 2007) to propose a model where a dedicated mechanism for object-related skilfull gestures is described along with a mechanism that is sought both for intransitive and meaningless actions. Buxbaum's model differs from the competing dual

route apraxia model of Rothi (Rothi et al. 1991) for the latter makes no predictions relevant to differences in transitive vs. intransitive gesture imitation (Buxbaum et al. 2007). Buxbaum's model is centered on the division of labor of the dorsal stream (action execution) and the inferior parietal lobe (IPL) (action representation) systems. Left IPL stores information about postures and movements of body and hand for skilfull manipulation of familiar gestures and the bilateral fronto-parietal dynamic processing provides online updated information about current position of body or body parts, for familiar and novel, transitive and intransitive movements. For this author there would be two types of IMA: a representational IMA and a dynamic IMA. The representational apraxia is proposed to reflect a damage to the IPL and lead to deficits concerning stored features of skilled object-related actions. On the other hand, Dynamic IMA arises from damage to the dorsal stream structures and entails a failure in online transforming stored gesture representations or visual input into motor output. While in Representational IMA subjects are expected to be more impaired in imitation of transitive (object-related) than intransitive (symbolic) gestures, in Dynamic IMA subjects should be equally impaired in both gesture types (Buxbaum, 2001; Buxbaum, et al., 2007). Buxbaum and colleagues (2007) reported that stroke patients with left inferior parietal lobe were more impaired in transitive than intransitive gesturing or meaningless gesturing, whereas patients with bilateral fronto-parietal damage due to corticobasal degeneration showed the opposite pattern.

In contrast with the previous view, Kroliczak and Frey (2009) proposed that a common network over the left hemisphere represents both familiar tool use pantomimes and communicative gestures. The fact that to date no clear reverse dissociation has been reported (impaired intransitive gestures and intact transitive pantomimes) raises the possibility that the transitive pantomimes may simply place higher demands on a representational system (see Fig 1.1). Using fMRI, these authors showed a remarkable degree of overlap in the left parietal, frontal and temporal areas involved in planning tool use pantomimes and communicative gestures that do not involve objects Kroliczak and Frey (2009) (see Fig 1.1).
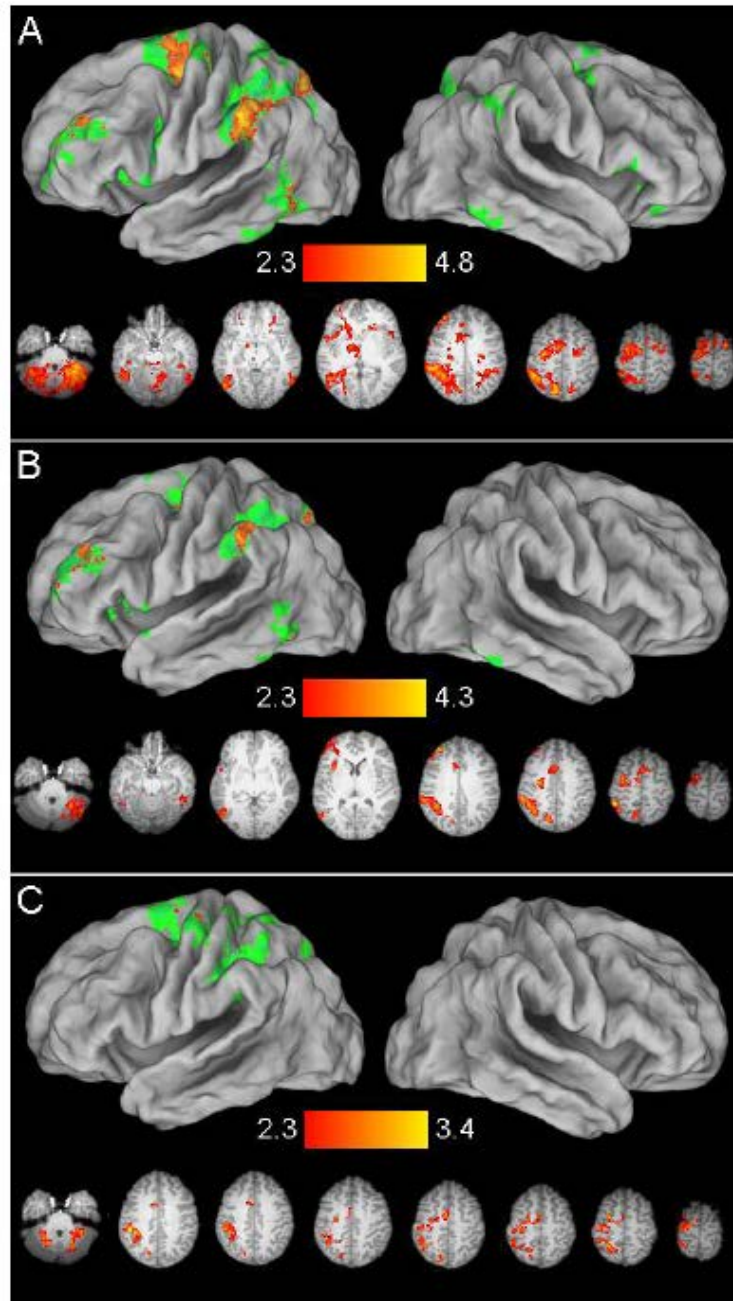
Fig. 1.1 Brain areas showing increased activity during transitive and intransitive gesture planning for execution with the dominant right hand. In A) Planning transitive actions vs. a linguistic control condition. In B) Planning intransitive actions vs. the linguistic control condition. Activation of similar regions as transitive action planning described above. C) A direct comparison between conditions revealed that transitive vs. intransitive planning is associated with greater increases in activity for transitive actions (within and along left IPS and extending into the SMG, in SPG, rMFG and PMd). Taken from Kroliczak and Frey (2009).

1.3. Models of human imitation: Unique mechanisms

The seemingly incommensurability of the visual input and motor output in imitation of action is one of the most challenging and non-trivial question in human imitation studies. In fact,

several models have offered highly diverse solutions to it. The correspondence problem, as it is called, refers to how one's own motor system selects the appropriate muscles that would lead to the observed movement (Brass & Heyes, 2005). The most influential models of human imitation will be briefly described here: emphasising their main features and fundamental findings, and their relation to the correspondence problem envisaged solution.

The core assumption of the *common-coding approach* between perception and action is that both perceived events and planned actions share a common representational code and are, therefore, commensurate (Prinz, 1997). The common coding approach implies that if perception and action share the same representational domain, then traces of perception in action should be established and observed, in the course of imitation. Both induction paradigms, where perceptual stimuli induce or enhance certain actions due to the similarity of shared features, and interference paradigms, where perceptual events and actions interfere with each other, have provided considerable empirical substantiation. The spatial compatibility effect between stimuli and responses is a simple experimental demonstration of the putative interplay between perception and action. In a choice reaction task with two assigned responses for each of the two stimuli, when the task assignment is compatible, as stimulus and response share a common spatial feature (e.g. left response key and stimuli presented to the left of a fixation cross), subject's response are clearly superior (both in accuracy and reaction times) to incompatible assignments (Prinz, 1997; Hommel, Musseler, Aschrsleben & Prinz, 2001).

Within the general framework of a common coding stands the Active Intermodal Mapping (AIM) hypothesis (Meltzoff & Moore, 1997). In order to account for the finding of early facial imitation, where no visual guidance about own body parts is available or learning and experience is plausible at such early age, a mechanism is proposed in which an inter modal representational domain unifies observation and execution of motor acts. According to AIM, imitation is a matching-to-target process whereby a proprioceptive feedback loop allows infants' motor performance to be evaluated against the seen target. The common supramodal representational

domain enables infants to detect equivalences between their own acts and the ones they see. The AIM model encompasses three main features. The organ identification is the first step in generating an imitative response, by which infants relate their own body parts to the corresponding ones of the adult, as it is said to be innate and renders body parts and movements of self and others commensurable. The second step in developing imitative responses is the body babbling or how movement components are mapped. Infants learn by body babbling what muscle movements do achieve a particular body configuration, i.e, by moving their own limbs and facial organs in a repetitive body play, infants acquire knowledge and build a map between organs and organ-related end states and movements. At last, organ relations, as tongue-to-lips, refer to a common metric between the self and others that infants can use in imitation, by parsing the observed act into its organ relations. This description level cuts across the modality of perception and thus renders commensurate the observed but not experienced action of others, and the experienced but not seen facial action (Meltzoff & Moore, 1997).

Additionally, advocates of the common coding approache to imitation find in the discovery of mirror neurons in the monkey brain a potential neural substrate for human imitation (see Box 1).

Nonetheless, some behavioural findings of children's imitative performance are less consistent with models based on a common coding approach. Bekkering, Wohlschlager and Gattis (2000) showed that when asked to imitate simple actions, children's performance often deviates from the model. When asked to copy movements to a right or left ear (the object), using their ipsilateral or contralateral hand (the agent), performing a movement parallel to the body or crossing the body line (movement) or crossing their arms (salient feature), children tend to select the appropriate object or the agent thus neglecting the movement path or the salient feature. The fact that children do not always show a veridical match between observed and executed action led Bekkering et al. (2000) to develop a model in which human imitation is driven by action goals. The theory of goal-directed imitation (GOADI) assumes that a perceived act is cognitively decomposed into separate components, called goals, that can either be the object, agent or movement. The

selected goals are hierarchically organized by virtue of the functionality of actions, i.e., if end-states are present they are hierarchically more important than the means to achieve them (effectors used or movement paths).

Box 1. Mirror Neuron System

Mirror neurons were first identified in the monkey brain by Rizzolatti and colleagues (Di Pellegrino et al, 1992; Gallese et al., 1996; Rizzolatti et al., 1996): a class of visuo-motor neurons in the area F5 of the monkey ventral pre motor cortex was shown to be activated both during execution and observation of hand actions. Later, similar type of neurons have been described as well in the inferior parietal lobe of the monkey brain, and the whole neuronal network involved in both execution and observation of action has been called as mirror-neuron system (MNS) or action execution/observation matching system.

The observed actions capable of inducing a discharge of the mirror neurons include placing or taking objects from a table, grasping food and manipulating objects (Gallese et al., 1996; Rizzolatti et al., 1996). There is a clear congruence between the effective observed and executed actions (Di Pellegrino et al., 1992). Some of the mirror neurons are activated during observation and execution of only one type of action, whereas others show broader congruence and their activation is merely defined by the goal of the action. The monkey mirror neurons do not discharge when only an object or agent is present, and MN activation is not limited to hand actions. The discovery of mirror neurons has led to many different speculations about their functional role. The most prominent proposals suggest that mirror neurons generate an internal representation of the action that can be used for different functions, including recognition and understanding motor events and imitation (Gallese et al, 1996; Rizzolatti et al., 1996).

Several functional brain imaging in humans have provided some evidence about existence, circuitry and function of mirror neuron system in humans (but see Dinstein et al., 2008 for a critical view). In humans the mirror neuron system is a potential candidate for a direct perceptual-motor mapping as it would provide a common coding that could be used either in action understanding or imitation (Rizzolatti, Fogassi & Gallese, 2001). The support for similar system in humans comes essentially from the findings of a motor facilitation during action observation (Fadiga et al., 1995) and from overlapping brain activity, during both observation and execution of actions, in the 2 putative mirror neuron areas: left inferior promoter cortex and right superior parietal lobe. (Iacoboni, 1999).

The process of decomposing-recomposing the observed act depends critically on the availability of resources which would explain why some aspects (e.g. what effectors are used) are neglected by infants when imitating. Imitation is thus an elaborate and interpretative process rather than a simple re-enactment of the means used by the demonstrator. (Bekkering, et al., 2000; Wohlschlager, Gattis & Bekkering, 2003).

Contrary to the models just described, the Associative sequence learning (ASL) model suggests that correspondence problem needs not be solved by a specialist theory of imitation but that a generalistic theory of learning can provide a good explanatory account of it (Brass & Heyes, 2005). According to the ASL model the capacity to imitate is a product of general processes of associative learning. ASL explains imitation not only of transparent actions, such as finger movements, but also opaque actions such as facial expressions, and all kind of actions where the observers' image of the model is not similar to the sensory feedback received during performance of the same action. The ASL model does this by postulating that each action guiding representation is a compound of two action representations: one encoding visual information and the other containing somatosensory information and motor commands. Imitation is enabled as the visual and motoric representations become linked through the Hebbian associative learning of contingent co-occuring events. The ASL also predicts that whether a person is able to imitate will depend on their past experience (i.e. one will be able to imitate a certain action if one had the opportunity to form the link between the visual and motor representation of that action). ASL highlights the importance of learning as opposed, for instance, to the AIM model that claims imitation skills are innate. Using a paradigm of automatic imitation (interference of compatible-incompatible actions), evidence in support of ASL model has been found, showing that sensorimotor learning can enhance, abolish or even reverse the automatic imitation (Bird, Brindley, Leighton & Heyes, 2007; Brass & Heyes, 2005). For instance, an enhancement effect was found in a study comparing imitation of human hand against imitation of robotic hand movements (Press, Gillmeister & Heyes, 2007). If at pretest, the robotic hand was weak in inducing interference in imitation as compared to the human hand, 24

hours after compatible sensorimotor training with the unfamiliar robotic hand movements the robotic movement elicited as much automatic imitation as the human movement. Moreover, for these authors, much of the sensorimotor imitogenic experience of human infants comes from sociocultural sources that are not available to other animals or species; hence they are the ultimate factor in developing imitation skills. Imitation skills could generally be enhanced from intensive face to face interaction and from the mirror play or the kind of play, dance and exercise programs that favour and reward synchronous actions (Catmur, Walsh & Heyes, 2009).

1.4. Models of Human Imitation: Dual mechanisms

A set of findings from both healthy subjects and brain damaged patients cannot be easily explained by the previous models. First, brain damaged patients have been reported with selective deficits in imitation of either meaningful (MF) familiar actions or meaningless (ML) novel actions (Goldenberg & Hagmann, 1997; Peigneux et al., 2000; Bartolo et al., 2001). Selective deficits can hardly be accounted for by unique mechanistic models, as they predict no obvious differences in imitation of different type of movements. There are two main strands of evidence in support of my argument. First, behavioural findings from our lab showed that healthy individuals have larger memory span for MF actions than ML actions (Rumiati & Tessari, 2002). Second, healthy subjects when under time pressure (by a deadline experimental procedure) imitate more accurately familiar MF actions than ML novel actions when presented in separate list, but imitated with the same accuracy when both type of actions were presented intermingled. This behavioural pattern was observed whether or not participants were aware of the composition of the list of the to-be-imitated actions. This differential performance on imitation of ML and MF actions has been explained with a dual route model (Cubelli et al., 2000; Rothi, 1991; Rumiati & Tessari, 2002; Tessari & Rumiati, 2004), according to which selective deficits in imitating actions are due to the malfunctioning of a single mechanism, as a reduction in cognitive resources, caused either by experimental manipulations with healthy participants or by brain damage seems to influence the selection of the

action imitation mechanism. Within this theoretical framework, a sub-lexical direct mechanism is mainly (but not solely) dedicated to reproduce ML actions, while a lexical-semantic indirect route can only be used for producing actions that have already been acquired. While the direct route puts greater demands on a short-term working memory system, the lexical-semantic route relies on accessing stored representations of motor plans (Tessari & Rumiati, 2004). The studies with healthy participants revealed that speeded imitation was significantly more accurate for MF than for ML gestures when they were presented in separate lists, suggesting that two different routes were used. In contrast, when the two types of gestures were presented intermingled, the advantage of meaningful over meaningless imitation disappeared, suggesting that participants selected the direct route for imitating both stimulus types (Tessari & Rumiati 2004). The decrease in accuracy with MF actions in the mixed condition has been interpreted as being due to a strategic selection of a single mechanism (the direct route), capable of processing both action types, in order to avoid the high costs of switching between the two mechanisms. In all these studies, the MF gestures employed were pantomimes of object use (e.g. hammering), while the ML ones were gestures obtained by modifying the relationship between the hand–arm and the trunk of the meaningful version.

The analysis of the errors made by subjects also provided information about the mechanism selected during imitation (Tessari & Rumiati 2004). Subjects made more semantic errors (e.g. prototypicalizations and visuo-semantic errors, see Appendix D) when imitating MF gestures in the blocked condition than in the mixed condition indicating that the semantic mechanism was selected more often in the former than in the latter condition. Lexicalization errors (i.e. a MF gesture that is visually similar to the ML target one but that is not included in the list, but see Appendix D) were made when subjects imitated ML gestures, and were more numerous in the blocked than in the mixed condition when the non-semantic strategy subserved imitation of both ML and MF gestures.

Similar behavioural pattern was observed in 32 unilateral brain-damaged patients (either left-brain damage or right-brain damage) (Tessari et al. 2007). When MF and ML gestures were

presented intermingled, patients' ability to imitate either action types did not differ. However, when patients' ability to imitate was evaluated using separate lists, six patients showed a selective imitation deficit for ML actions.   This study suggests that patients performing the imitation task in the mixed condition selected the non-semantic route because it allowed the reproduction of all gestures and avoided high costs of switching between routes. The selective deficits observed in the blocked condition suggest that the individual imitative mechanisms were selectively damaged. Thus, route selection does not seem to depend exclusively on the type of action to be imitated (meaningful and meaningless), but also on other factors such as external (list) and internal (resources) conditions.

Press and Heyes (2008) have replicated both the effects of superiority of MF actions and the effect of list composition (blocked vs. mixed) with both accuracy and reaction times (RT) as dependent variables. The fact that this pattern of results was obtained with RT of imitative performance, as well as with accuracy, as in previous studies, suggests that the effect is rather robust, and therefore can provide important insights into the processes mediating imitation (Press & Heyes, 2008). Yet at variance with the idea of a strategic selection of routes to imitation, Press and Heyes (2008) argued that, in the mixed condition, participants' performance was contingent upon stimulus properties and not upon the type of list, thus no strategic selection of the dual mechanism or top-down control is possible for subjects. In particular, they found that reaction times were longer for both MF and ML actions when they were preceded by a ML action trial (i.e. *carry-over* cost of the preceding trial).

1.5. Further developments on the dual route model

A dual route account for human imitation has proven to provide a comprehensive account of both neuropsychological findings, as well as behavioural ones obtained with healthy participants. A good model of human imitation should consider not only imitation of actions already present in

one's own repertoire but, more importantly, imitation of novel actions, regardless of whether they are processed by the same unique mechanism or not.

Whether the dual route model can account for imitation of intransitive communicative gestures is still an empirical question. As it is formulated, a critical distinction made by the dual route model regards familiarity or novelty of the to-be-imitated action, given a representation of the movement is present or absent from long term-memory. To date, all studies that have interpreted imitation within the dual route model have used transitive gestures (e.g. Rumiati & Tessari, 2002; Rumiati et al., 2005; Tessari & Rumiati, 2004; Tessari et al, 2007). As proposals for independent mechanisms regarding imitation of transitive and intransitive actions can be found in the neuropsychological literature (e.g. Buxbaum, 2001) it is crucial to show that indeed the dual route model and its central distinction of familiarity vs. novelty are valid when using different type of stimuli, and that the model is not only restricted to transitive actions, as pantomimes of object use.

Chapter 2 of the thesis deals with the issue of imitation of transitive and intransitive actions, by showing that healthy subjects imitate transitive actions less accurately than intransitive actions (Experiment 1). These findings suggest that there is no need to assume the existence of independent mechanisms (as in Buxbaum, 2001) to account for differential performance of apraxic patients on transitive and intransitive actions. Rather, the reason why patients may fail to imitate transitive actions is because they are generally more difficult to process than intransitive actions (see for instance Kroliczak & Frey, 2009). In Experiment 2, I used the same paradigm as in Tessari & Rumiati (2004) with healthy subjects imitating intransitive MF and ML gestures, in a blocked and in a mixed list condition. I have decreased the time allowed to imitate (from 500 ms to 350 ms) since we have learned from experiment 1 that intransitive actions are easily imitated. MF actions in the blocked conditions were better imitated than ML actions, but no difference between imitation of MF and ML was observed when the two action types were presented intermingled (mixed condition). These results fully replicate the findings of Tessari and Rumiati (2004) but also add that

action meaning and the strategic control effects are not specific of object-related pantomimes and that they represent a more general mechanism of human imitation. The fact that imitative performance of ML actions in both conditions and of MF action in the mixed condition improved across the experiment provides some support that the non-semantic can be effectively used for learning through imitation.

In **chapter 3**, the criticisms regarding the strategic selection of the dual mechanism of imitation (Press & Heyes, 2008) are considered. I carried out two experiments with the aim of verifying which of the two accounts - the strategic selection by Tessari & Rumiati (2004) or stimulus driven by Press & Heyes (2008) - better explains the effects found in imitation of MF and ML actions. In Experiment 1, healthy participants imitated intransitive MF gestures faster than ML gestures in the blocked condition and than intransitive MF actions in the mixed condition. Moreover, in the latter condition we replicate the main effect of preceding trial. In Experiment 2, we directly tested the *carry-over costs* of ML imitation on subsequent trials (Press & Heyes, 2008), by comparing 3, one blocked and two mixed, conditions with different amount of switches between action types. I failed to find an effect of switching cost in either of the 2 mixed conditions, but in the mixed condition with fewer switches, I found the presence of both mixing cost and of a preparatory effect for the forthcoming switch. This pattern is consistent with participants adopting a top-down strategic selection of the routes when they imitate mixed MF and ML gestures. Both in experiment 1 and 2 we make use of RT measures as they have proven to be a sensitive measure for highlighting the selection mechanism in imitation (see Press & Heyes, 2008), and importantly these findings with RTs suggest that the two routes for imitation are quantitatively and qualitatively different: the direct mechanism, that has been characterized as more prone-to-errors, is slower; in contrast, the indirect, semantic mechanism not only is more accurate but is also faster.

The mirror neuron (MN) system has been generally accepted to be involved in understanding the actions of others (Rizzolatti & Sinigaglia, 2008), but also to be the neural substrate of human imitation (Iacoboni, et al., 1999). Mirror properties are not sufficient to allow

imitation of actions that do not belong to one's own repertoire and further mechanisms are required (Buccino, et al. 2004b; Vogt, et al., 2007). In action understanding, it is unclear whether the MN network is recruited when subjects have to extract the meaning of the actions and do not only passively observe actions. In **Chapter 4** of this thesis, I present a study where event-related potentials (ERPs) were recorded when subjects perform both an imitative task and an action discrimination task. In this study, subjects observed both MF familiar actions and ML novel actions either for later imitation or for later recognition. Two dissociations between imitation and discrimination are reported. Importantly, an early frontal left lateralized component was observed for ML actions in the imitation condition hence consistent with the idea that for imitation of novel actions there is the need of supplementary processes and in agreement with the observation of the involvement of the left middle frontal areas in imitation learning (Vogt et al., 2007).

In **Chapter 5**, I tested the dual model of imitation in autism. Several authors have suggested that imitation can be deficient in autism (e.g. Hamilton, 2008; Williams et al., 2004). However whether this deficit is restricted to a specific class of gestures or affects all action classes (e.g meaningful, meaningless, transitive or intransitive) is still under debate. In this study, high-functioning autistic children and age-matched typically developing children were asked to imitate several types of gestures which could be either already known or novel to them. The known gestures could either convey a communicative meaning (i.e. intransitive gestures) or involve the use of objects (i.e. transitive gestures). A significant interaction was observed between type of gesture and group of participants, with autistic children performing better known gestures than novel ones . However, imitation of intransitive and transitive gestures did not differ across the two groups. Autistic children were also found to perform more poorly than controls on two mental rotation tasks. All these findings are discussed in the light of a dual-route model for action imitation (i.e., Tessari & Rumiati, 2004), that can fully account for selective imitative deficits depending on the nature of the actions.

Chapter 2

Imitation of Communicative Intransitive Actions

2.1. Imitation of transitive and intransitive actions in healthy individuals

Neuropsychological studies of limb apraxia have informed us as to how actions are represented in the brain. The imitative deficit observed in IMA patients (De Renzi, Motti, & Nichelli, 1980) can affect some types of actions selectively while sparing others. There are now a number of reports of patients who show selective deficits for imitation of either meaningless (ML) or meaningful (MF) actions (Bartolo, Cubelli, Della Salla, Drei, & Marchetti, 2001; Goldenberg & Hagmann, 1997; Peigneux et al., 2000; Tessari, Canessa, Ukmar, & Rumiati, 2007). These differences in imitation of ML and MF have been explained within a dual route model (Rumiati &

Tessari, 2002; Tessari & Rumiati, 2004). According to this account, a deficit in imitating ML actions is interpreted as due to a defective sublexical, direct route, necessary to translate a gesture unknown to the subject into a movement output. A deficit in imitating MF gestures has been interpreted as due to a malfunctioning lexical-semantic, or indirect route (Tessari et al., 2007). Unlike the sublexical route, the lexical-semantic route deals with actions which are stored in the long-term memory of the imitator. Among the actions that are represented in memory, an important distinction has been made between transitive or object-related actions (e.g. hammering), and intransitive actions, that is actions which have nothing to do with objects, and typically convey communicative content (e.g. waving goodbye). However, the empirical evidence in favour of dedicated mechanisms for the imitation of other types of actions is still inconclusive. At the group level, patients have been reported who find it more difficult to perform transitive actions (e.g. Buxbaum, Kyle, Grossman, & Coslett, 2007; Foundas et al., 1999; Haaland, Harrington, & Knight, 2000; Roy, Square-Storer, Hogg, & Adams, 1991). The way in which patients' action responses were elicited differed substantially from study to study. In Haaland et al.'s study (2000), patients were requested to imitate transitive actions; in Foundas et al.'s (1999), patients were requested to perform transitive actions that were prompted verbally; and in Roy's et al. (1991), both types of elicitation were used. Two single-case studies also documented a selective deficit in producing transitive actions. Dumont, Ska, and Schiavetto (1999) described a patient, PF, with a left temporo-parietal lesion, who was impaired at producing transitive gestures irrespective of the modality used to prompt them (verbal command, photographs of objects, real use of objects, and imitation). However, PF was normal in producing intransitive and meaningless actions. Rapcsak, Ochipa, Beeson, and Rubens (1993) presented the case of a right-handed man, with an almost complete disruption of the left-hemisphere, who was impaired at pantomiming transitive gestures and at imitating novel actions performed with the hand ipsilateral to the lesion. In contrast, he performed actual object use, intransitive gestures, and axial movements in response to verbal requests relatively well.

Based on the existing neuropsychological literature, and given the absence of any report on the complementary selective impairment of intransitive actions, we cannot conclude that transitive and intransitive actions are processed by different mechanisms (see Buxbaum, 2001, for a similar position). It seems more likely that transitive actions pose greater processing demands on the cognitive system, because they are intrinsically more complex due to their association with the object representations. In addition, the fact that they are performed without the object in hand makes them also less familiar. Consistently, Mozaz, Rothi, Anderson, Crucian, and Heilman (2002) found that, like apraxic patients, elderly healthy subjects performed intransitive better than transitive gestures on verbal request. How actions may be represented can be studied by requiring healthy individuals to perform a speeded imitation task (Rumiati & Tessari, 2002; Tessari & Rumiati, 2004).

In this chapter, we asked healthy adults to imitate, under time pressure, transitive and intransitive actions in separate blocks. If we are correct in hypothesising that transitive actions are more difficult and less familiar than intransitive actions, participants' accuracy will be likely to be worse with the former than with the latter actions. All MF actions were simple, one-step gestures, performed by using only the left arm and hand. The video display of each action, irrespective of whether it was transitive or intransitive, lasted for exactly the same length. In addition to length, we also made a great effort in matching as much as possible MF transitive and MF intransitive actions. We have also included ML transitive and ML intransitive actions, derived from the original MF transitive and MF intransitive actions respectively. Should there be a difference in the imitation of ML intransitive and transitive of actions, one could argue that the differences between these two action types are due to the intrinsic kinematic complexity of the gestures. In addition, as predicted by two-route models, we expected participants to imitate MF actions better than ML actions. In general, ML actions pose greater demands on a short-term memory system for movements because, as they have no stored representation, they must rely on online processing. Moreover, as MF and ML actions

resembled each other kinematically, eventual differences in imitation between MF and ML actions, can hardly be interpreted as them being different in terms of motor complexity.

Since ML actions have no stored representation, any difference between ML transitive and ML intransitive gestures should be attributable to differences in the functioning of the online visuomotor conversion (or direct, sublexical route). The analysis of the errors made by the participants we will contribute to clarify these issues.

2.1.1 Methods

Subjects

Fifteen right-handed individuals took part in the experiment (9 females). Their mean age was 27.4 (SD = 5.15). Their handedness was evaluated using the Edinburgh Inventory (M = 77.35, SD = 25.89).

Stimuli

Four sets of actions were used: MF transitive, MF intransitive actions, ML transitive and ML intransitive actions. The MF transitive actions (N = 18) were pantomimes of object use and were the same as those employed by Tessari and Rumiati (2004) (see appendix A); the MF intransitive were communicative actions (N = 18) (see appendix B). The two sets of meaningless actions were derived from the meaningful actions by modifying the original relationship between hand-arm and trunk. Thus, the transitive ML actions (N = 18) were those based on transitive MF actions, and the intransitive ML actions (N = 18) were those based on intransitive MF actions. In total each subject was presented with a total of 72 different actions, repeated four times each. Action stimuli were performed by a male actor who used his left hand and presented as short movies to the subjects who performed the actions using their right dominant hand.

Procedure

Each trial started with the video display of an action, followed by a 0.5 s black screen, at the end of which a sound rang for 0.25 s, indicating the beginning of the next trial. Subjects were tested individually and were asked to imitate each action immediately after its presentation and before the following trial began. They were asked to press a button with their right hand at the onset of the video. Once the video had ended, they were asked to release the button and to immediately imitate the presented gesture as accurately as possible. By doing this we wanted to make sure that subjects kept the same hand position at the beginning of each trial.

MF and ML actions were presented separately in two blocks. In one block, all actions were meaningful (both transitive and intransitive) for a total of 144 trials. In the other block, all actions were meaningless (both transitive and intransitive) for a total of 144 trials. Transitive and Intransitive actions were presented as mini-blocks. In either mini-block, the actions were divided into four lists of eighteen actions; actions were randomized within each list. Subjects could start the experiment with either a block of MF actions or a block of ML actions; within which subjects could began either with an intransitive mini-block or with a transitive mini-block. The order both blocks and the mini-blocks was counterbalanced across subjects, with the order of mini-blocks being kept the same for both main blocks (e.g. transitive actions first). Thus, approximately one quarter of the subjects started with ML transitive actions. The remaining subjects began the experiment with either ML intransitive mini-block, a MF transitive mini-block or a MF intransitive mini-block.

All subjects gave their informed consent for taking part in the study which was approved by SISSA Ethics committee. They were not aware of the aim of the study and their performance was recorded and later scored by two independent raters. Based on previous studies (e.g. Tessari & Rumiati, 2004), for each incorrect action raters were asked to code the error with one of 16 apriori defined error-types (see appendix C). To assess the agreement of the two raters' observations, a Cohen's kappa coefficient was calculated. The Kappa value obtained was 0.46, corresponding to a fair-to-good agreement. In the next section, we will report first the analysis performed on the

average scores of both raters and, subsequently, the analysis carried out on the scores provided by the blind rater only. The same effects found in the former are replicated in the latter analysis.

2.1.2 Results

Participants' imitative performance is depicted in Fig. 2.1 A repeated- measures Analysis of Variance (ANOVA) was carried out on correct responses, with Meaning (meaningful vs. meaningless) and Context (transitive and intransitive) as within-subjects factors.
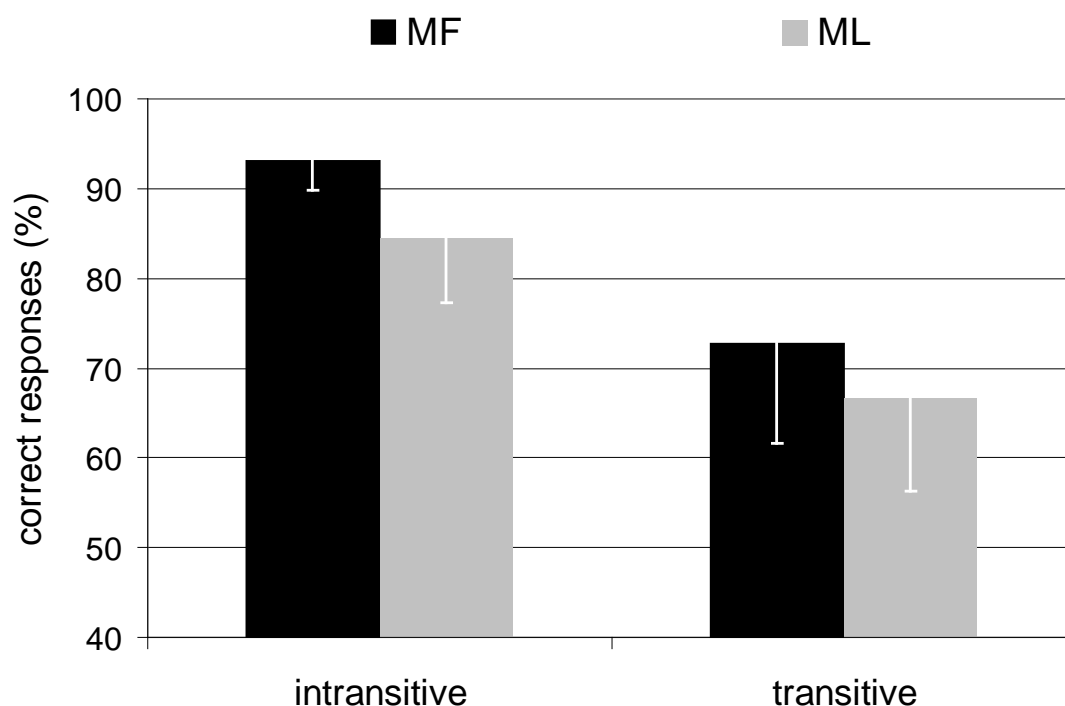
Fig 2.1 Percentage of correctly imitated actions according to whether they had or not a meaning (meaningful vs. meaningless), or whether they implied or not the use of an object (transitive, intransitive. The bars represent the standard deviation from the mean.

Accuracy: Analysis on both raters

The two main effects of meaning ($F(1,14) = 59.97$, $p < 0.001$) and context ($F(1,14) = 8.15$, $p < 0.01$) were found to be significant, but not the context x meaning interaction ($F(1,14) = .163$, $p =$

.692). Overall, MF actions were imitated better than ML actions (M = 77.06, SD = 2.11; M = 70. 74, SD = 2.08, respectively), and intransitive actions (M = 83.61, SD = 1.21) were performed better than transitive actions (M = 64.19, SD = 2.83). MF actions were performed far better when they were intransitive (M = 86.99, SD = 1.09) than when they were transitive (M = 67.13, SD = 3.51) (paired-wised t (14) = 6.52, p < 0.001). The same holds for the ML actions: intransitive actions were imitated more accurately than transitive actions (M = 80.23, SD = 1.81; M = 61.25, SD = 2.85), for t(14) = 7.98, p < 0.001.

Accuracy: Blind rater analysis

The two main effects of meaning ($F(1,14) = 14.938$, p = 0.002) and context ($F(1,14) = 90.839$, p < 0.001) were found to be significant, but not the context x meaning interaction ($F(1,14) = .727$, p = .408). Overall, MF actions were imitated better than ML actions (M = 82.92, SD = 1.63; M = 75.56, SD = 2.01, respectively), and intransitive actions (M = 88.75, SD = 1.03) were performed better than transitive actions (M = 69.72, SD = 2.41). MF actions were performed far better when they were intransitive (M = 93.06, SD = .824) than when they were transitive (M = 72.78, SD = 2.88) (paired-wised t (14) = 7.48, p < 0.001). The same holds for the ML actions: intransitive actions were imitated more accurately than transitive actions (M = 84.44, SD = 1.83; M = 66.67, SD = 2.67), (paired-wised t (14) = 8.01, p < 0.001).

Error analysis

Since subjects did not commit all types of errors (see Appendix D.), we collapsed different error types together into broader categories in the following way: Spatial errors included hand, arm and finger errors, plus orientation errors and errors of movement endpoint; Perseveration errors, included perseveration and global perseveration errors, whereas other errors were collapsed together with omissions and unrecognized errors. The other categories of errors remained the same.
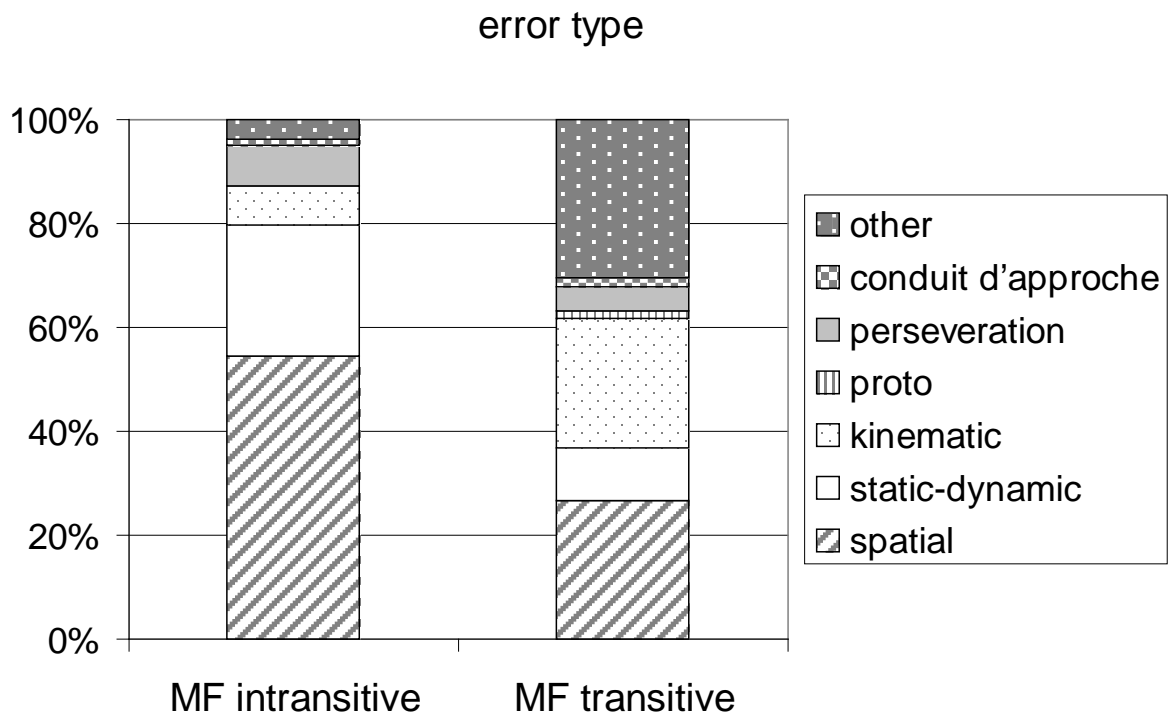
error type

Fig 2.2 Percentage of different error types plotted for MF transitive and intransitive actions.

In order to test whether MF transitive and intransitive actions gave rise to specific errors, we analyzed error types when subjects performed MF actions only (see Fig. 2.2). When they performed transitive gestures, subjects made more kinematic (24.91%), spatial (26.6%) and other errors (30.37%); when they performed intransitive gestures, they made more static-dynamic (25.31%) and spatial errors (54.43%). Using the Independent Wilcoxon signed-rank tests (with Bonferroni correction), we found that kinematic errors ($Z = - 3.417$, $p < 0.006$) and other errors ($Z = - 3.203$, $p < 0.006$) significantly differed for intransitive and transitive actions. In particular, subjects made more kinematic ($M = 6.46$, $SD = 4.07$) and other errors ($M = 7.4$, $SD = 8.03$) when imitating transitive than intransitive actions (respectively, $M = 0.2$, $SD = 0.56$; $M = 0.46$, $SD = 0.74$).

2.1.3 Discussion

In this experiment, we aimed to clarify whether the difficulty in imitating transitive actions as compared with intransitive ones, observed in patients with apraxia, are also observed in normal healthy adults performing the task under time constraints. The time-constrained procedure for imitation does not allow subjects to perform at ceiling. Poorer performance on transitive actions than on intransitive ones would be consistent with the claim that behavioral differences found in performance of apraxic patients are due to transitive actions being more difficult, and probably less familiar (in the sense that individuals might be less experienced with), than intransitive actions.

Consistent with this prediction, we found that normal healthy subjects under time pressure imitated MF intransitive gestures significantly better than MF transitive gestures. Our findings are also consistent with the fact that elderly subjects have greater difficulty in producing transitive actions over intransitive actions on verbal command (Mozaz et al., 2002). This typical shortage of cognitive resources for elderly individuals, or the deficits exhibited by brain-damaged patients, is consistent with the observation that performance of both of these groups is not at ceiling. Likewise, with the manipulation of speeded imitation we were able to reproduce a shortage of cognitive resources that led to the production of imitative errors by healthy subjects. Surprisingly, participants performed ML intransitive actions better than ML transitive actions also when they imitated ML actions. As ML actions were obtained by modifying the spatial arrangement between body parts of the corresponding MF actions, this difference can be interpreted as ML transitive actions taxing more than the ML intransitive actions the operations necessary to convert the visual input into a motor output, i.e. the direct route for imitation. We analyzed the types of errors participants committed when they imitated transitive and intransitive actions, in the attempt to better understand why the observed differences came about, and which action dimensions were more likely to be affected during imitation. We found that imitative performance of pantomimes of object use and symbolic communicative gestures, under time pressure, differed in the amount kinematic errors subjects made. In fact, communicative symbolic gestures are better characterized by a static hand-finger configuration and just a few, for instance ''go away'' in our list of actions, are strictly

dependent on the particular movement associated to it. In this experiment we also found that the performance on ML actions was worse than that on MF actions (i.e. both transitive and intransitive). This superiority effect of known, or familiar, actions over novel actions (Rumiati & Tessari, 2002; Tessari & Rumiati, 2004) can be explained within a dual-route model of imitation (Rumiati & Tessari, 2002; Tessari et al., 2007; Tessari & Rumiati, 2004), where a dedicated mechanism can be used for imitation of meaningful, familiar gestures, through the access of its motor representation stored in memory. MF actions are stored in memory and retrieved as a whole and for these reasons they tend to be more easily imitated. In order to imitate novel actions, one cannot use this mechanism as new actions are not stored in memory, but subjects must rely on a visuo-motor conversion mechanism that bypasses the long-term memory system. In conclusion, in the current study we have observed that subjects found transitive gestures as generally more difficult to imitate than intransitive gestures. Given that the complementary dissociation has not been reported so far, the complexity of the movements seems to be the best explanation for the neuropsychological observations (Dumont et al., 1999; Foundas et al., 1999; Haaland et al., 2000; Rapcsak et al., 1993; Roy et al., 1991). This task difficulty effect seems to be driven by the actions' own motor complexity, and maybe by factors like familiarity. The finding that intransitive actions are easier to imitate is consistent with the task difficulty argument applied to explain the selective impairment of transitive actions found either in single or group of patients with apraxia. Taken together these findings suggest that there may not be different mechanisms, and hence different brain structures, dedicated to the imitation of transitive and intransitive gestures.

2.2. Extreme speeded imitation of intransitive gesture experiment

So far, studies on the dual route were concerned with how we imitate transitive, object related gestures (e.g. hammering); however, whether the dual route account holds true also for intransitive gestures (e.g. waving goodbye) still needs to be demonstrated. Experimental psychology studies with healthy adults showed that both transitive and intransitive gestures are subject to

automatic imitation as demonstrated by Brass et al. (2000, 2001) and by Press et al. (2008), respectively. Neuropsychological group studies typically showed that apraxic patients have more difficulties in producing transitive than intransitive gestures on verbal command (Foundas et al. 1999), by imitation (Haaland et al. 2000; Buxbaum et al. 2001, 2007; Rumiati , Carmo, Corradi Dell'Acqua, 2009) or in both modalities (Roy et al. 1991). Two left-brain-damaged patients have also been described with a complete preservation of the ability to perform intransitive gestures paired with a severe deficit at pantomiming transitive gestures (Rapcsak et al. 1993; Dumont et al. 1999). These reports seem to imply that there are independent mechanisms for processing transitive and intransitive gestures (e.g. Buxbaum, 2001). As a clear complementary dissociation has not yet been reported (Cubelli et al., 2000), it is premature to conclude that transitive and intransitive actions are imitated by different mechanisms. Recently, we have reported that healthy adults, engaged in a speeded imitation task, performed meaningful intransitive gestures significantly better than meaningful transitive gestures, suggesting that, compared with the intransitive ones, transitive gestures pose greater processing demands on the mind–brain, presumably because of the involvement of objects (Carmo & Rumiati, 2009). While, in general, the production of transitive gestures seems to be affected more by left hemisphere lesions (Bartolo et al., 2001; Tessari et al., 2007), the ability to generate intransitive gestures can be equally disrupted by damage to either cerebral hemisphere (Buxbaum et al. 2007). But, there are also studies suggesting that defective performance with both transitive and intransitive gestures is more likely to follow left than right hemisphere damage (Hanna-Pladdy et al., 2001). A recent imaging study showed that planning either tool use pantomimes or intransitive gestures was associated with asymmetrical increases in the same regions of left parietal (the intraparietal sulcus, the supramarginal gyrus and the caudal superior parietal lobule) and dorsal premotor cortices (Kroliczak & Frey, 2009). Interestingly, these effects were greater for tool use pantomimes, but only when performed with the right hand. Kroliczak and Frey (2009) concluded that transitive and intransitive actions are represented in a common, left lateralized praxis network, irrespective of the hand used.

With this experiment, we aimed at verifying whether the dual route hypothesis, already tested for transitive gestures (Rumiati & Tessari, 2002; Tessari & Rumiati, 2004; Tessari et al., 2007), holds true for intransitive gestures. From the imaging results just mentioned (Kroliczak & Frey, 2009), it seems plausible that one would obtain a common pattern across the two action types. In the present experiment, we allowed subjects only 350 ms for imitation - 150 ms less than the time subjects were allowed in Tessari & Rumiati (2004) - because intransitive gestures are easier than transitive gestures (Carmo & Rumiati 2009).

A successful replication of the original findings would demonstrate that the action meaning and the strategic control effects are not specific to object related pantomimes, rather they represent a more general way in which the human mind–brain operates when it has to cope with a shortage of resources.

2.2.1 Methods

Subjects

Thirty-nine right-handed (on the Edinburgh Inventory, mean = 81.75, s.d. = 23.93) subjects (mean age of 23.1, s.d. = 3.3) participated in this experiment. Subjects were randomly assigned to one of the two conditions (condition is a between-subject factor): 19 subjects (eight males) performed the task in the blocked condition and 20 (six males) performed the task in the mixed condition.

Stimuli

The set of intransitive actions used was the same as in the previous experiment and comprise 18 meaningful (see appendix B) and 18 meaningless actions.

Procedure

In the blocked condition, meaningful and meaningless gestures were presented separately, whereas in the mixed condition, they were presented intermingled. Each condition comprised four sub blocks; in the mixed condition, each sub-block contained 36 gestures (18 meaningful and 18

meaningless) presented in a random order that varied from sub-block to sub-block. In the blocked condition, two sub-blocks contained 36 meaningful gestures each and two contained 36 meaningless gestures each. Each subject performed a total of 144 trials. In the blocked condition, the order of type of stimulus (meaningful or meaningless) was counterbalanced across subjects. Each trial started with the video display of a gesture that lasted for 1500 ms, followed by a 350 ms blank screen, at the end of which a sound of 250 ms went off, warning the subject that the following trial was about to start. Subjects were asked to reproduce each gesture (performed by the actor using his left hand) with their right limb, immediately after its presentation and before the next trial started, and they were asked to press a button with their right hand at the onset of the video. They were asked to release the button as soon as the video had ended and to imitate immediately the seen gesture as accurately as possible.

Their performance was recorded and subsequently scored by two independent raters. Subjects were not informed about the composition of the lists or the purpose of the study, and they all gave their informed consent for taking part in the study, which was approved by SISSA Ethics Committee.

2.2.2 Results

The analyses reported herewith are based on scores averaged across the two raters (level of agreement between them on a Cohen's kappa = 0.50, s.e. = 0.01). A repeated-measures ANOVA was performed on correct responses as a dependent variable, with Meaning (meaningful, meaningless) as a within-subject factor and Condition (blocked, mixed) as a between-subject factor. The main effects of Meaning ($F_{1,38} = 19.45$, $p > 0.001$) and Condition ($F_{1,38} = 4.69$, $p < 0.05$), as well as the Meaning x Condition interaction ($F_{1,38} = 4.65$, $p < 0.05$), were significant.

Two paired-wise t-tests revealed that in the blocked condition, MF (mean = 86.15, $p < 1.99$) were performed significantly better than ML gestures (mean = 77.85, s.e. = 2.08), ($t (17) = 3.93$, $p = 0.001$); in the mixed condition, there was no difference in accuracy between MF (mean = 77.88, s.e.

= 1.95) and ML (mean = 75.03, s.e. = 2.03) gestures. Two independent one-way ANOVAs showed that MF gestures were performed significantly better in the blocked (mean = 86.15, s.e. = 1.99) than in the mixed condition (mean = 77.88, s.e. = 1.95) ($F_{1,37}$ = 8.78, $p < 0.01$). Conversely, no difference in performance was found for ML gestures ($F_{1,37}$ = 0.934, $p > 0.01$) (with Bonferroni correction). Results are plotted in figure 2.3.
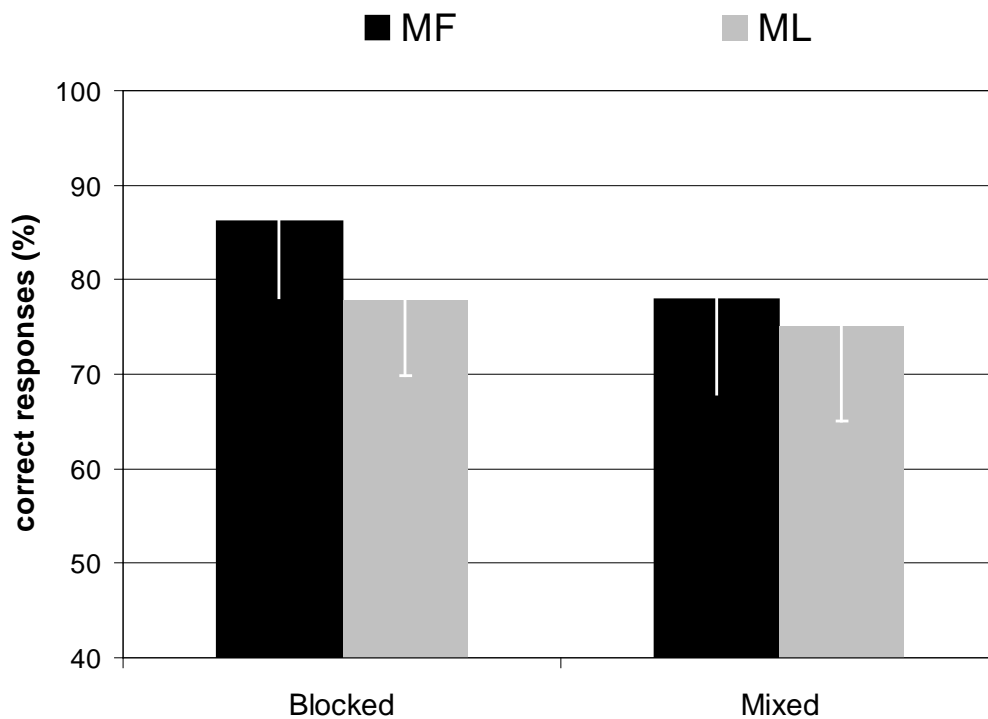
Fig 2.3 Percentages of correctly imitated meaningful (MF) and meaningless (ML) gestures plotted depending on whether they were in a blocked or mixed condition. The bars represent the standard deviation from the mean.

Further analyses: learning effects

In order to verify whether subjects' performance changed during the experiment, average slopes across the four sub-blocks were calculated for MF and ML gestures in each condition (mixed and blocked), and each compared with a non-increasing function. Results are plotted in Figure 2.4.
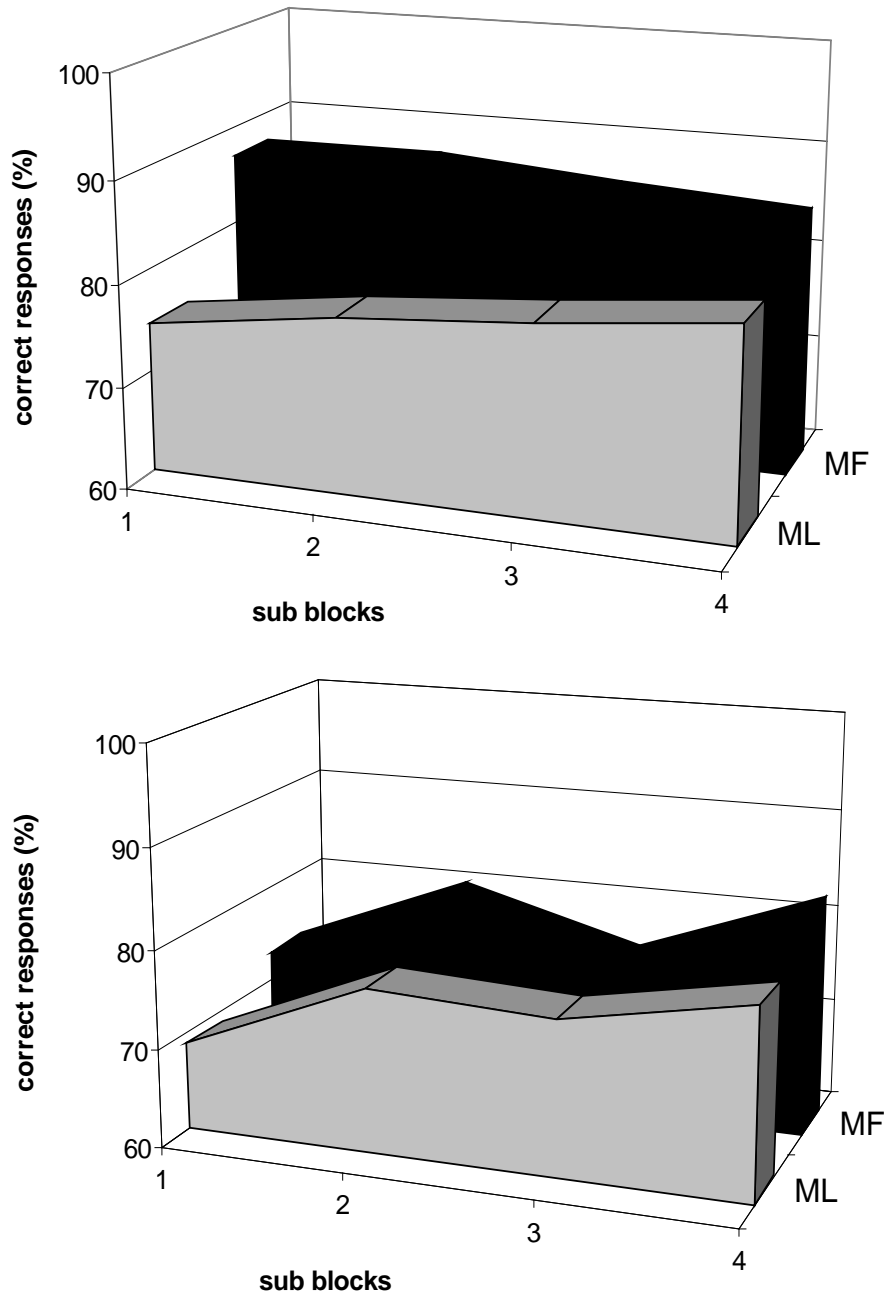
Fig 2.4 Percentages of correctly imitated gestures, performed in the blocked condition (upper plot) and mixed condition (lower plot), plotted as a function of meaning [meaningful (MF, black) and meaningless (ML, light grey)] and of sub-blocks.

In the mixed condition, a significant increase in accuracy was observed for both MF and ML gestures (t(19) = 4.05, p < 0.001, and t(19) = 3.55, p < 0.01, respectively), whereas in the blocked condition, a significant increase in accuracy was observed only for ML gestures (t(18) = 2.3, p ,< 0.05; MF actions: t(18) = 1.24, p > 0.1). In the mixed condition, at the beginning of the experiment

(i.e. the first sub-block), there was no difference in the imitation of MF and ML gestures (t(19) = 1.732, p > 0.05). At the beginning of the experiment, the ability to imitate ML actions did not change as a function of the experimental condition (F1,37 = 2.106, p > 0.05), whereas the ability to imitate MF gestures in the blocked condition was significantly higher than in the mixed list (F1,37 = 15.629 p < 0.001).

2.2.3 Discussion

In this experiment, we replicated the effects previously found using transitive gestures (e.g. Tessari & Rumiati 2004). Consistent with the dual route hypothesis, in the blocked condition, subjects were more accurate at imitating intransitive gestures with meaning than those without meaning, while in the mixed condition, no differences were observed. Likewise, in the mixed condition, to save resources that would otherwise be eroded by switching between non-semantic and semantic mechanisms, normal subjects selected only one mechanism for reproducing both types of gestures. When the non-semantic route was presumably selected, such as, for instance, when subjects imitated ML gestures in the ML blocked condition and both MF and ML gestures in the mixed condition, a significant increase in accuracy was systematically observed.

In contrast, when the semantic mechanism was presumably selected, such as, for instance, in the MF blocked condition, we failed to observe an increase across sub-blocks. We suggest that the non-semantic route can be effectively used for learning through imitation, whereas the semantic route has very poor learning properties.

2.3 Conclusions of chapter 2

In this chapter we have shown that healthy subjects imitate intransitive actions better than transitive actions (experiment 1). This finding is consistent with the idea that differences in complexity might be the reason why apraxic patients are often found to be more impaired in

transitive actions than on intransitive actions; without the need to presume the existence of independent mechanisms (as in Buxbaum, 2001).

Regarding the dual mechanism, we have found that intransitive actions are imitated better than meaningless actions when presented in separate lists. When actions are presented intermingled, this superiority of MF actions is erased and MF and ML actions are imitated similarly. This pattern of results replicates both the superiority and type of list effect found by Tessari and Rumiati (2004) using intransitive communicative actions, and suggests that the semantic route can process not only object-related actions (as in previous studies) but also communicative intransitive actions, as for both cases, representations can be retrieved from long term memory.

Chapter 3
Selection of routes to imitation: differential mixing cost and preparatory effect

3.1 Introduction

Brain damage patients have been reported to be selectively impaired in imitating either meaningless (ML) actions or meaningful (MF) actions (Bartolo, Cubelli, Della Salla, Drei, & Marchetti, 2001; Goldenberg & Hagmann, 1997; Peigneux, et al., 2000; Tessari, Canessa, Ukmar, & Rumiati, 2007). The differential performance on imitation of ML and MF actions has been explained with a dual route model (Cubelli et al., 2000; Rothi, 1991; Rumiati & Tessari, 2002), according to which deficits in imitating actions are due to the malfunctioning of a single route. The dual route model of action imitation has also been used to account for the finding that healthy

subjects under time pressure imitate ML actions less accurately than MF actions (i.e. superiority effect) (Tessari & Rumiati, 2004). It has repeatedly been demonstrated both with transitive (Rumiati et al., 2005; Tessari & Rumiati, 2004; Tessari et al., 2007) and intransitive (Rumiati, Carmo & Corradi-Dell'Acqua, 2009) gestures that when MF and ML actions are presented intermingled, accuracy is the same for both action categories (i.e. list composition effect). The decrease in accuracy with MF actions in the mixed condition has been interpreted as being due to a strategic selection of a single mechanism (the direct route), capable of processing both action types, in order to avoid the costs of switching between the two routes.

Press and Heyes (2008) have replicated this effect of list composition with both accuracy and reaction times (RT) as dependent variables. In particular, they found that while imitation of MF actions led to shorter RT than ML actions when they were imitated in separate blocks, in mixed lists this advantage disappeared as participants spent more time for imitating MF gestures. In addition, they showed that, in the mixed condition, the time required to imitate either action type was always slower when the preceding trial involved the imitation of a ML action. According to Press and Heyes, this effect is due to working memory related *carry-over cost* of ML actions that could account for the list composition effect, and proposed that stimulus type, and not the composition of the list, is responsible for the selection between the direct and lexical-semantic route for imitation (Press & Heyes, 2008). Accordingly, these authors proposed a stimulus-driven selection hypothesis whereby ML actions can only be imitated by the direct route, while MF actions activate always the semantic route. ML actions processed by the direct route deplete working memory resources, causing a detrimental effect on performance of any subsequent trial (Press & Heyes, 2008).

From Press and Heyes's account, however, imitation of ML actions is expected to be different in the mixed condition compared with the blocked condition (Press & Heyes, 2008): while in the blocked condition, ML actions are always preceded by ML actions, in the mixed condition this only occurs in approximately half of the trials. One would therefore predict that ML actions are imitated better in mixed condition compared with blocked condition, due to a release of carry-over

costs. Inconsistently with the carry-over cost hypothesis, no evidence of improved imitation of ML actions in the blocked condition compared with the mixed condition was found neither in their study (Press & Heyes, 2008) nor in the original studies on the dual routes from our laboratory (e.g. Rumiati et al., 2009; Tessari & Rumiati, 2004).

If participants were actually switching between two different mechanisms, the pattern of results observed by Press and Heyes (2008) - namely a differential effect on RT depending on whether the previous trial involved either a ML or a MF action and interpreted as being due to carry-over costs - could also be explained as being due to *asymmetric switch-costs* produced by different task-sets, whereby longer RT are observed when subjects switch to a dominant task than to a less dominant task.

Task switching paradigms have been commonly used to investigate processes of cognitive flexibility and control processes and, in particular, task-set reconfiguration processes (e.g. Monsell, 2003; Rogers & Monsell, 1995). Task-set is an organization of mental resources that will accomplish a particular cognitive task, given an appropriate input; in task switching paradigms, when a task changes from one trial to another, a reconfiguration of the task set is expected to occur. Task-set reconfiguration can be to a certain extent endogenously (internally) driven, that is one can adopt a task-set at will, in advance of the stimulus as one has the foreknowledge that the stimulus will be a member of a specified class (Rogers & Monsell, 1995). In addition, to the endogenous component of task-set, the stimuli itself can activate or evoke a given task-set normally associated with it. This exogenous control (i.e. stimulus-driven) occurs irrespective of prior intentions and, sometimes, in conflict with prior intentions (Rogers & Monsell, 1995). Hence, in order to directly investigate whether the route selection to imitation is consistent with a stimulus-driven hypothesis (as in Press & Heyes, 2008) or whether the cognitive system exerts a top down control over it and can, in specific circumstances (i.e. mixed condition), strategically switch between the two different task-sets (i.e. routes to imitation, as in Rumiati & Tessari, 2002; Tessari & Rumiati, 2004) we employed a task-switching paradigm.

The basic observation in task switching paradigms is that when participants change between two different task sets a switch cost occurs: performance drops (longer RT or higher error rate) when they change task (switch trial) than when they repeat the task (repetition trial) (e.g. Monsell, 2003; Kiesel, et al., 2010; Roger & Monsell, 1995, for a review). A switch cost asymmetry is a well-known phenomenon in task switching and refers to the observation of higher switch costs when participants switch to the stronger, more dominant task from a pair of tasks (e.g. Meuter & Allport, 1999; Monsell, Yeung & Azuma, 2000).

In the present chapter we carried out two experiments with the aim of evaluating whether route selection for imitation is stimulus-driven, as proposed by Press and Heyes (2008), or whether it is strategically driven (Tessari & Rumiati, 2004). In Experiment 1, we tested whether both the superiority effect and list composition effect found with RT with transitive gestures by Press and Heyes (2008) could also be obtained using communicative intransitive gestures. In Experiment 2 in addition to the blocked condition, in which MF and ML actions were presented separately, participants were also presented with two mixed conditions in which MF and ML actions were intermingled. More precisely, in one mixed list the action type (MF, ML) changed every 4 or 5 repetitions (rare switches condition), while in the other the number of alternations was every 2 or 3 repetitions (frequent switches condition). Consistently with the carry-over cost account, for MF actions we expected to observe a steady increase of overall RT proportional to the amount of switches in each condition. For ML actions we predicted shorter RT with a decrease that too should be proportional to the amount of switches in the given condition.

In contrast, consistently with the strategic selection account, we predicted that in the rare switches condition it could still be advantageous for the subject to switch between the direct and indirect route, so differences between MF and ML actions are anticipated, as participants could be using different routes for each type of action; while for the frequent switches condition as the strategic selection of the direct route would be more advantageous, no differences between MF and ML actions were expected (Rumiati, Carmo & Corradi-Dell'Acqua, 2009; Tessari & Rumiati,

2004). Overall, RT should be longer when participants perform imitation in the condition in which there are more switches (frequent switches condition) and shorter in the blocked condition with no switches.

In addition, a local inter-trial comparison between switch trials and subsequent trial (first repetition trial) will allow us to establish whether there is an asymmetric switch cost between the time spent to imitate MF actions and that spent to imitate ML actions, and whether both frequent switches condition and rare switches condition lead to differential switching costs. Asymmetric switch costs can be observed when a task-set is more dominant than another. In studies on imitation with adults participants, it has been suggested that the semantic task-set might be more dominant than the direct route (Brass et al., 2001; Tessari, Cretella, & Rumiati, 2009). If this is the case, then differential effects could be expected, with higher switch costs when one changes to the dominant semantic route and little costs when one changes to the direct route.

Another phenomenon that relates to task switching performance are mixing costs, observed when comparing repetition trials in mixed task conditions to single-task conditions (Los, 1996; Poljac, Koch & Bekkering, 2009; Rubin & Meiran, 2005). In reaction time experiments, where the design involves pure blocks or mixed blocks of trials, it is often found that subjects respond slower in the mixed blocks than in pure blocks (Los, 1996). Some models emphasize more strategic principles and attribute mixing costs to suboptimal preparedness for the forthcoming events in mixed blocks relative to pure blocks by, for instance, assuming that a stage or a process can be prepared, as a task-reconfiguration happens in anticipation of a forthcoming event (Los, 1996). In contrast, stimulus-driven models stand from a local inter-trial variability perspective, and emphasize aspects of processing where the dynamics in a given trial leave behind activation-related traces which either aid or impede subsequent processing (Los, 1996). Here we aimed at evaluating whether different mixing costs would be observed when comparing repetition trials both from the frequent switches condition and rare switches condition versus the pure blocked condition. If participants strategically select one route only in order to avoid switching between the two

mechanisms, as proposed by Tessari and Rumiati (2004), smaller mixing costs should be observed in the frequent switches condition compared with the rare switches condition.

3.2 Experiment 1

The aim of this experiment was twofold. First, we tested whether the pattern reported by Press and Heyes (2008) could be obtained also using new stimuli both with RT as well as accuracy. As mentioned earlier, these authors found that while in the blocked condition participants were faster at imitating MF actions than ML actions, in the mixed condition that there were no differences in RT between imitation of MF and ML actions. These RT findings replicate those originally reported by Tessari and Rumiati (2004, see also Rumiati, Carmo & Corradi-Dell'Acqua, 2009), suggesting that these effects are robust. Here, instead of pantomimes of object use as in Press and Heyes (2008) and as in previous studies from our laboratory (Rumiati et al. 2005; Tessari et al. 2007) we employed a set of intransitive, object non related MF gestures, all with a communicative content as for instance "waving goodbye" and a set of ML gestures (as in Carmo & Rumiati, 2009; Rumiati, Carmo, & Corradi-Dell'Acqua, 2009) presented in blocks in one condition and intermingled in another one. Second, as in Press and Heyes (2008), we examine imitation of both MF and ML actions in the mixed condition as a function of the action type performed on the preceding trial.

3.2.1 Method

Subjects.

Twenty-nine undergraduates (mean age was 23.72±3.61) participated in the experiment. Participants who were all right handed on the Handedness Edinburgh Inventory (M = 85.43±16.6) and had normal to correct-to-normal vision acuity were randomly assigned to one of the two list conditions (n = 14 for the mixed conditions and n = 15 for the blocked conditions).

Stimuli.

The set of MF actions used was taken from an ideomotor apraxia test and comprised 18 intransitive symbolic gestures like, for instance, waving goodbye, "come here" or the stop sign (already used in Rumiati, Carmo, Corradi Dell-Acqua, 2009). The set of meaningless actions comprised 18 actions that were obtained by modifying the relationship between hand, arm and trunk of the MF actions used. All actions were performed by an actor using his left hand and video-recorded; each video-clip lasted for 1500 ms.

Design and procedure

The procedure was kept similar to the one found in Tessari and Rumiati (2004) except for the time allowed to the participants for imitation that was now increased up to 1000 ms. Subjects were randomly assigned to one of two conditions. In the blocked condition, the same list of 18 meaningful actions and the same list of 18 meaningless actions were presented four times in two separate blocks (one for MF and one for ML actions). The order of actions was randomized within each list while the order of MF and ML blocks was counterbalanced across subjects. In the mixed condition, the same list of 18 meaningful actions intermingled with 18 meaningless actions was presented four times. Each subject performed a total of 144 trials.

Each trial started with the video display of an action that lasted for 1500 ms, followed by a 1000 ms blank screen, at the end of which a sound of 250 ms went off, indicating the beginning of the next trial. Subjects were tested individually and they were asked to imitate each action immediately after its presentation and before the next trial started. Subjects had to press a button with their right hand as soon as the video started and keep it pressed while observing the modelled action, once the video ended, they were asked to release the button and to immediately imitate the presented gesture as accurately as possible. We used this procedure in order to make sure that subjects kept the same hand position at the beginning of each trial. RT was measured upon release of target button, as we aimed at examining differences in time latencies of the imitative

performance. Subjects' imitative performance was recorded and scored offline independently by two raters.

Subjects were not informed about neither the composition of the lists nor the purpose of the study. All subjects gave their informed consent for taking part in the study which was approved by SISSA Ethics committee.

3.2.2 Results

Reaction Times. Subjects' RT are plotted in Figure 3.1. A 2x2 repeated measures analysis of variance (ANOVA) on RT with meaning (MF and ML) as a within subjects variable, and list (blocked and mixed) as between subjects variable was performed. RT of trials that were considered incorrect by any of the two raters were excluded from analysis, as well as trials that fell out of two standard deviation scope for each condition. A significant main effect of meaning was found (F(1, 27) = 18.35, $p < .001$) with longer RT for imitation of ML actions (M = 429.75 SD = 86.01) than MF actions (M = 406.38, SD = 92.56). A Meaning x List interaction was found (F (1, 27) = 7.68, $p < .001$), showing that the benefit of MF actions occurred mainly in the blocked condition. This interaction was subsequently analysed with two one-way ANOVAs which revealed that while there was no difference between imitation of ML actions in either blocked or mixed condition ($F < 1$), there was a significant difference between imitation of MF actions in both conditions (F(1, 27) = 8.38, $p < .01$). On average, the time spent for imitating MF actions in the blocked condition (M = 384, SD = 48) was shorter than the time spent for imitating ML actions (M = 429, SD = 33). Paired *t*-test revealed that there was no difference in imitation latency in the mixed condition (t (13) = 1.29, $p > 0.05$), but importantly, in the blocked condition MF actions lead to a shorter latency (M = 384, SD = 48) than ML actions (M = 423, SD = 39) (t (14) = -4.42, $p = .001$).

Accuracy. The average percentage of correct responses was of 88.34% (SD = 7.76) in the mixed condition and 90.23 % (SD = 5.5) in the blocked condition, with MF actions being performed correctly on average at 92.56 % (SD = 4.49) and ML actions at 86.01 % (SD = 7.00)

A 2 x 2 ANOVA on correct responses led to a significant main effect of meaning (F (1, 27) = 23.95, $p > 0.001$) while the main effect of presentation type (F(1,27) = 1.18, $p > .2$) and the list x meaning interaction (F(1, 27) = .14, $p > .7$), were not significant. A paired t-test showed that the main effect of meaning was driven by MF actions being imitated better than ML actions only in the blocked condition (t (14) = 5.64, $p < 0.001$), while in the mixed condition, no significant difference was found (with Bonferroni correction).
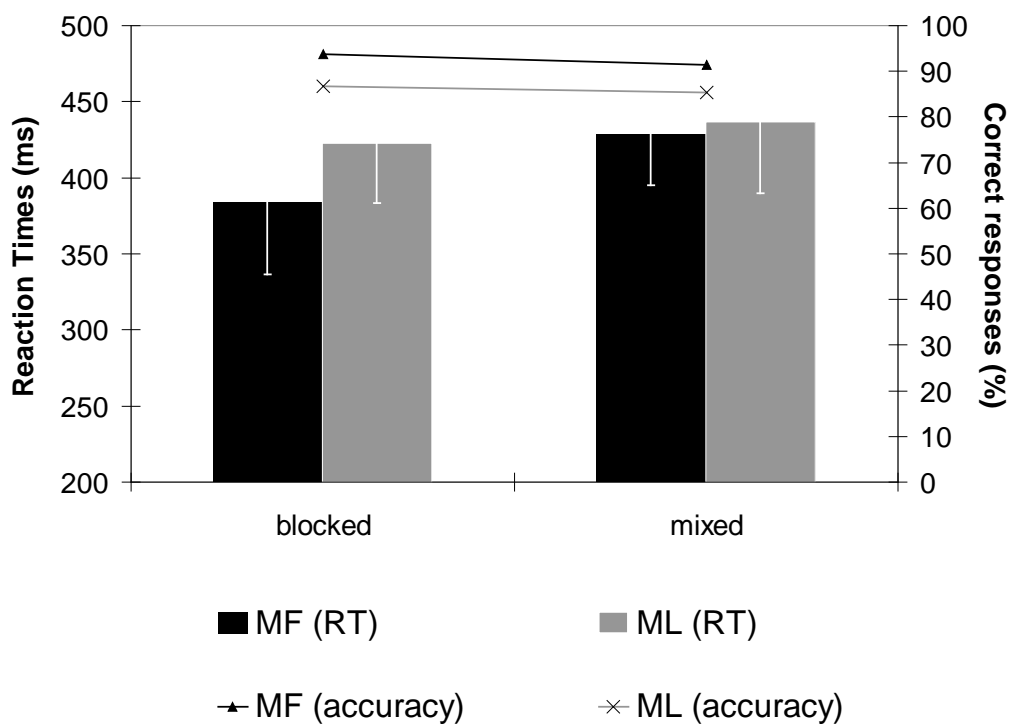
Fig 3.1 Average RT and percentage of correct responses for MF and ML actions whether in a blocked list or in a mixed list condition.

Carry-over costs

In the following section we tested whether Press and Heyes's (2008) explanation of both the advantage in imitation of MF over ML actions in the blocked condition and the route strategic selection in the mixed condition as being due to the preceding trial holds true also for our set of data. To this end, for the mixed condition a repeated measures ANOVA was performed on correct responses with both meaning and preceding trial type as a within subjects variable, as in Press and

Heyes (2008) (see Fig. 3.2). All trials were categorized as preceded by MF action and preceded by ML action. In agreement with Press and Heyes (2008) the main effect of preceding trial was found to be significant ($F(1, 13) = 11.26$, $p < 0.01$), showing that imitation was generally slower when the to-be-imitated action was preceded by a ML action. No other effects were significant.
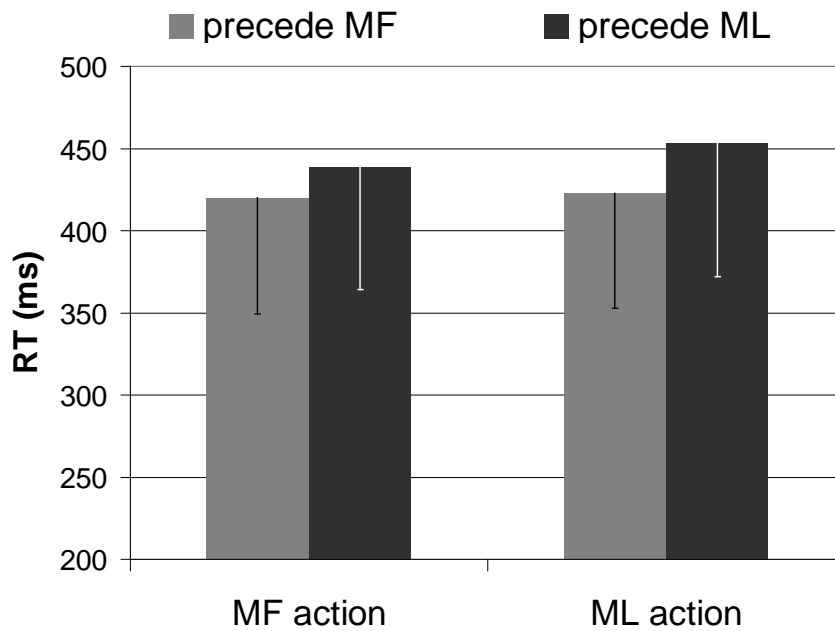
Fig. 3.2 Average RT for MF and ML actions as function of whether the preceding trial comprised a MF or ML action.

3.3 Experiment 2

In Experiment 2 we examined switching and mixing costs in order to address the issue of whether, in mixed conditions, subjects strategically select one mechanism for imitation of both MF and ML actions, or whether the selection of the mechanism depends on the nature of the stimuli itself. If subjects indeed switch between routes, we should observe both switching and mixing costs.

In switching studies, a trial is categorized as switch cost trial when the previous trial belongs to a different category, or as a repeat trial when only the first repetition after a switch considered. This procedure ensures that both switch and repeat trials are equally represented as the same amount of trials are considered for the analysis.

Three groups of subjects performed the imitation task under three different conditions. One group performed a blocked condition in which MF and ML actions were presented separately (blocked condition, also referred as baseline); the other two groups performed one of two different mixed conditions. In both mixed conditions, MF and ML actions are presented intermingled but presented in two different sequential sets. In one set, trials of the same type (MF, ML) are repeated for 4 or 5 times (rare switches condition), whereas in the other mixed set the number of overall number of switches are higher, given that action type changes every 2 or 3 trials (frequent switches condition).

In this experiment we introduced these two mixed conditions with the aim of evaluating if the increased amount of switches leads to an overall increase in RT when imitating MF actions, and a decrease in imitating ML actions compared with the corresponding blocked condition. As a direct test of the carry-over hypothesis, we expected higher carry-over costs in a condition with higher amount of switches, fewer carry-over costs in a condition with fewer switches, and no cost in the blocked (baseline) condition (Press & Heyes, 2008). We further investigated whether asymmetric switching costs between MF and ML actions were found in either mixed condition, or whether RT in the mixed lists reflected mixing costs due to an advanced preparation of a forthcoming change in stimulus type.

3.3.1 Methods

Participants. Thirty-nine participants, 11 males, took part in the experiment. They had a mean age of 24.23 years (SD = 4.13) and they all were right-handed as assessed by the Edinburgh Inventory (M= 81.90 %, SD = 18.74), and had normal or corrected-to-normal vision acuity.

Stimuli. The stimuli were the same as in Experiment 1.

Procedure. Each trial procedure was identical to Experiment 1. Subjects were randomly assigned to one of the three conditions.

In the blocked condition, the set of MF actions and ML actions were presented separately into two blocks. As in Experiment 1, one block comprised a list, repeated four, of 18 meaningful actions repeated four times and one block comprised 18 meaningless actions, repeated four times. The order of actions was randomized within each list and the order of each block (MF or ML) was counterbalanced across all subjects.

The second and the third condition were mixed conditions, in which MF and ML actions were presented intermingled. In both mixed conditions, subjects were presented with a list of 36 intermingled MF and M actions repeated four times. In the first mixed conditions, subjects were presented with pseudo-random sequences of 4 or 5 actions of the same type. That is, after a sequence of 4 MF actions there would be a sequence of 4 or 5 ML actions. In second mixed condition, the switches between MF and ML actions were set every 2 or 3 repetitions of an action of the same kind. The first action type of the entire experiment was counterbalanced across subjects.

Subjects who fell in any of the three conditions, either blocked or mixed, underwent a total of 144 trials. As in Experiment 1, in addition to accuracy, RT were recorded upon button-release. All subjects gave their informed consent for taking part in the study which was approved by SISSA Ethics committee.

3.3.2 Results

Subjects' RT for imitating MF and ML actions in the three experimental conditions are depicted in Figure 3.3. A repeated measures ANOVA was performed on RT as the dependent variable with meaning (MF and ML) as a within subjects factor and list type (blocked, frequent switches, and rare switches) as a between subjects factor. Incorrect trials as well as trials that fell out of two standard deviation scope were excluded from analysis.

The main effects of meaning ($F(1,36) = 11.31$, $p = .002$) and list type ($F(2,36) = 3.92$, $p = .029$) were significant. Overall MF actions were imitated faster (334,72, SE = 9.01) than ML actions (355,78 SE = 8.64). Subjects were faster when imitating actions in the blocked condition

(315,54, SE = 14,30) than in the mixed condition with frequent switches (248,23, SE = 14,30) they were slower in the mixed condition with rare switches (371,98, SE = 14, 30). The meaning x list type interaction was not significant ($F(2,36) = .01$, $p = .98$).
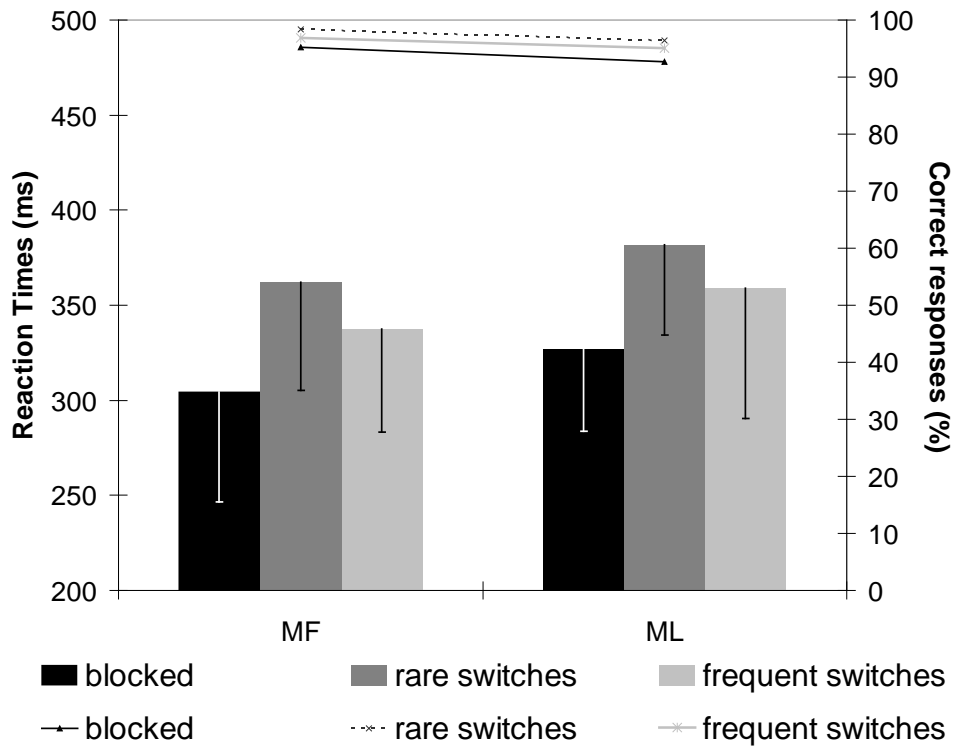
Fig. 3.3 Average RTs and percentage of corrected imitated MF and ML actions plotted depending on whether they were performed in blocked list, rare switches and frequent switches conditions.

Post hoc analysis showed that main effect of list type is driven mainly by the difference between Blocked list and rare switches list (Fisher $p = .008$). No other effects were significant. No speed-accuracy trade-off was detected since participants were more correct on average when imitating MF actions of 96.83 % (SE = .54) than ML actions 94.68 % (SE = .61) (Meaning: $F(1,36) = 9.68$, $p = .004$).

Switching and mixing costs.

Switching costs were analysed by comparing first trials of sequences of either MF or ML actions (a switch trial) to the subsequent trial of the same action type (repeat trial). Although within-

subject design is more commonly found in switching studies (for a between-subject design in task switching see, for instance, Koch, Prinz & Allport, 2005), we kept the same number of repetitions of each action as in previous studies by having a between-subjects design (e.g. Rumiati, Carmo & Corradi Dell'Acqua, 2009; Tessari & Rumiati, 2004), given that novel actions are critical in our design, and strong learning effects have previously been reported (Rumiati, Carmo & Corradi Dell'Acqua, 2009). A repeated measures ANOVA was performed on RT with both meaning and trial type (switch, repeat) as a within subjects variable for the condition with 2/3 repetitions and the condition with 4/5 repetitions (Figures 3.4 and 3.5 respectively). Only the main effect of meaning was found to be significant ($F(1,24) = 6.686$, $p = .016$). Switching costs were not found for neither Trial type condition (main effect of Trial type and Trial x List type interaction both with all $ps > .4$) neither meaning (interaction Trial type x Meaning, interaction Trial type x Meaning x List type with $ps > .1$).
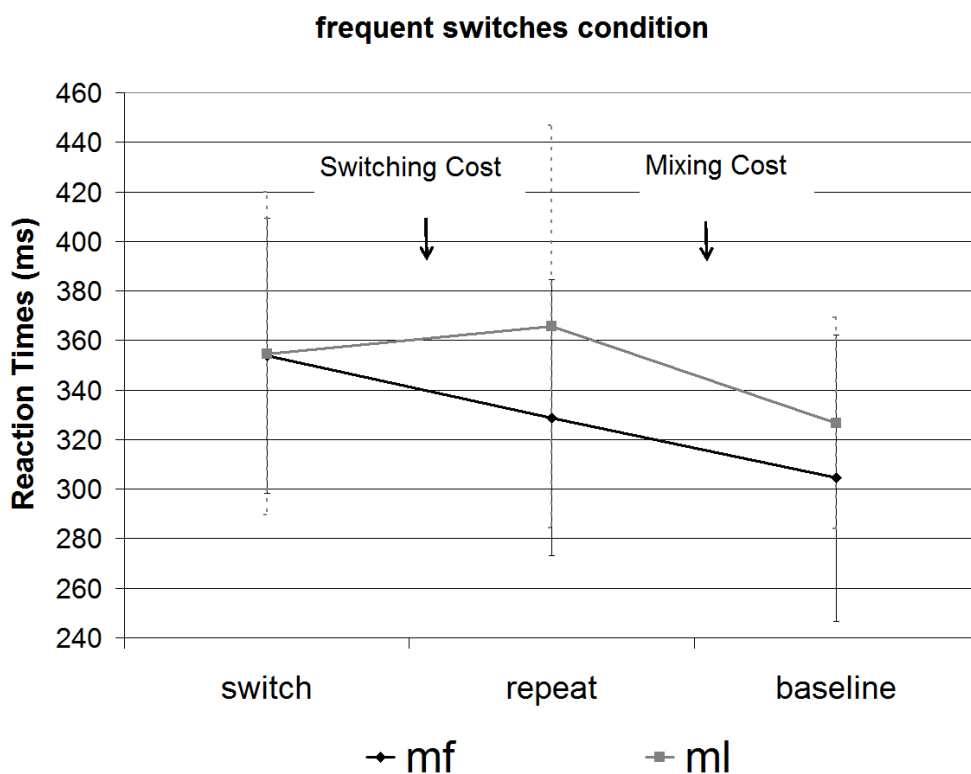
Fig. 3.4 Average RT for MF and ML actions in the baseline condition (blocked list) and in the switch trial, repeated trial in the frequent switches condition.

rare switches condition
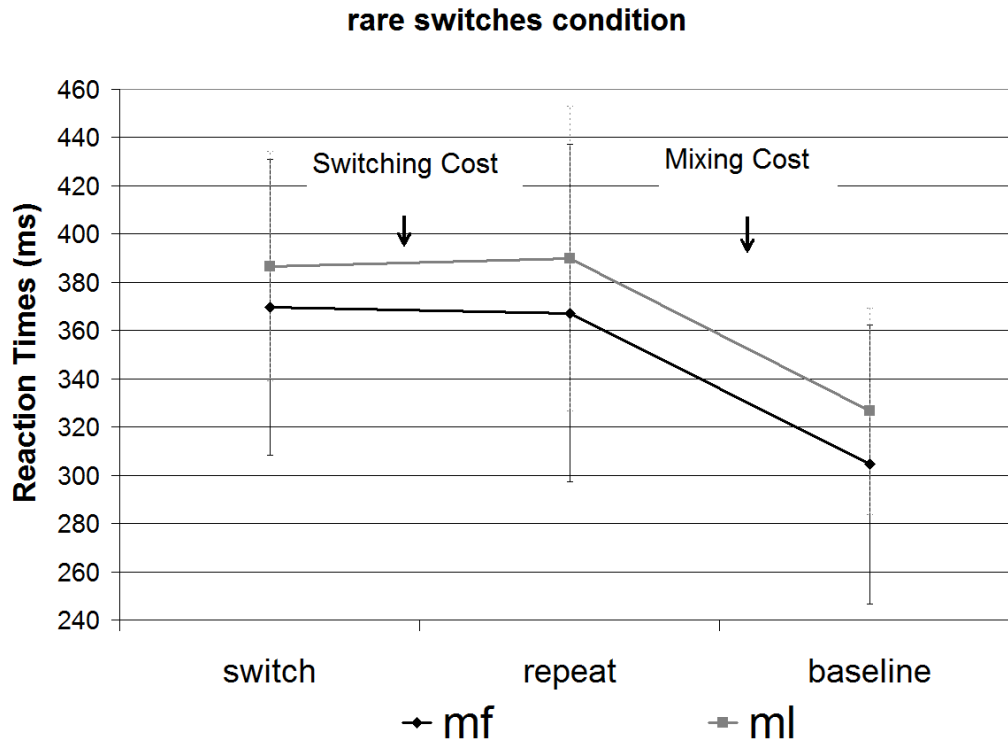
Fig. 3.5 Average RT for MF and ML actions in the baseline condition (blocked list) and in the switch trial, repeated trial in the rare switches condition.

In order to evaluate mixing costs of the two mixed conditions (with frequent switches and rare switches respectively), we compared subjects' RTs for repetition trials and the pure repetition trials. In the blocked list condition, pure or baseline repetitions trials comprise either MF or ML actions. Repeated measures ANOVAs were performed on RTs with trial type (repeat, baseline) as a between subjects condition. Regarding the frequent switches group, an effect of meaning was found ($F(1, 24) = 10.17$, $p = .004$), with MF actions giving rise to faster responses (316,66, SE = 11.11) than ML actions (346,10, SE = 12.73). No significant mixing costs were found (Trial type: $F(1,24) = 2.06$, $p = .16$, nor a significant interaction of Trial type x Meaning ($F < 1$). For the rare switches group both Meaning and Trial type were found significant (respectively, $F(1, 24) = 5.835$ $p = .024$, $F(1, 24) = 8.714$, $p = .007$). Baseline trials led to slower RT (315, SE = 15.08) than repeat trials in the condition with rare switches. No interaction effects were found ($F < 1$).

Preparation effect.

In task-switching, the relation between endogenous and exogenous control of task set is such that the endogenous component can modulate and bias the competition between task-set driven by exogenous input (Norman & Shallice, 1986). When individuals have foreknowledge of an upcoming task, they often prepare ahead of time so that their performance on the task proceeds more smoothly (Altmann, 2004). As far as the influence of endogenous and exogenous components in task set reconfiguration in our experiment is concerned, observing signs of advanced preparation for the forthcoming event would indicate that, to some extent, subjects can exert control over route selection.
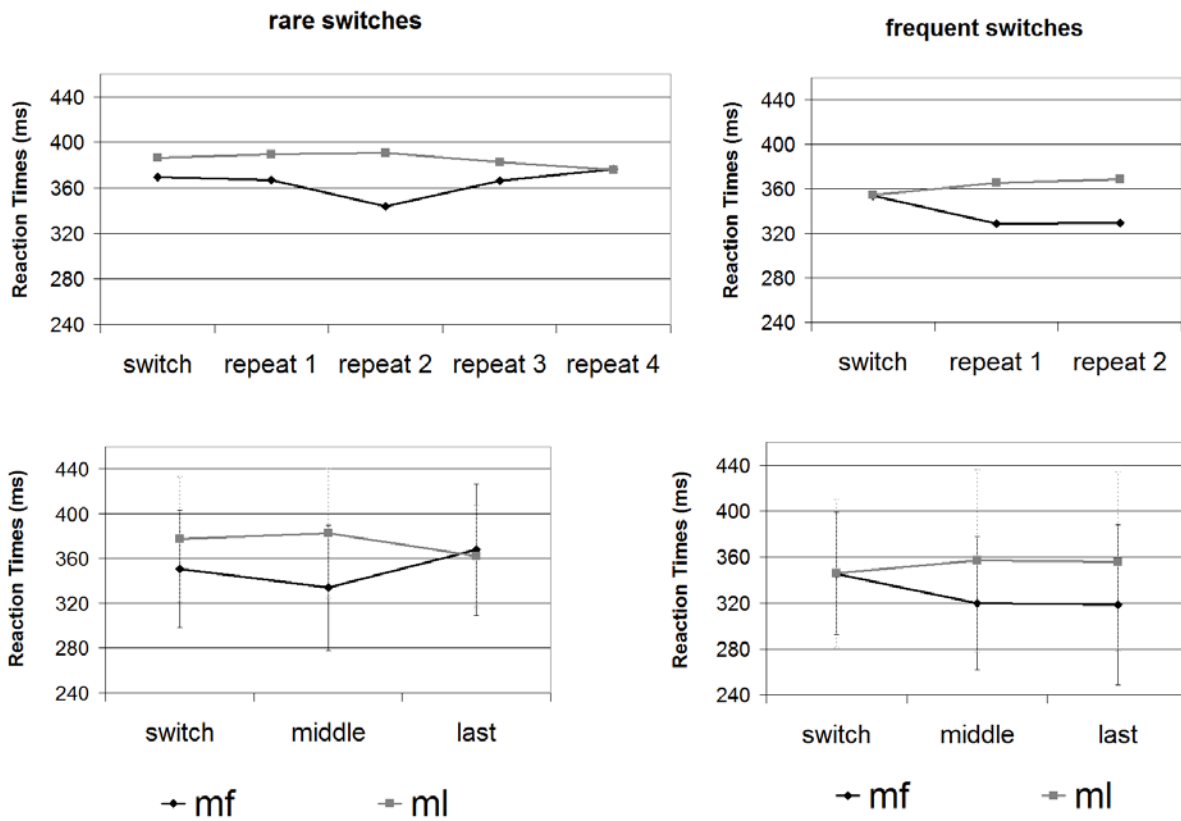
Fig. 3.6 In the upper plots: Average RT for both MF and ML condition for each trial in a sequence for the rare switches condition (left upper plot) and for the frequent switches condition (right upper plot). Lower plots: Average RT for switch, middle and last trial of a sequence, both for MF and ML actions, depending of whether they were imitated in the rare switches condition (lower left plot) or in the frequent switches condition (lower right plot).

In order to investigate preparatory effects we inspect the whole data by taking into account all repetitions trials, and a clear pattern was observed that contrasted visibly from the rare switches condition to the frequent switches condition (see Fig. 3.6, upper plots), particularly the increase in RT in last trials of a sequence of MF actions in the rare switches condition; in addition there was virtually no differences in RT between MF and ML actions when subjects imitated the first action of a sequences in the frequent switches condition. To explore this pattern of results, we compare 3 trial types that were common to the 2 mixed lists: the first, switch trial; the middle trial and the last trial of a sequence.

Given in particular the pattern observed for the rare switches condition that suggests that subjects are familiarized with the structure of the imitation sequence, we decided, for the subsequent analysis to exclude the first block of actions (first set of 18 actions), where subjects could not yet have an idea neither of the constitution of the list nor its alternation pattern.

A repeated measures ANOVA on RT was performed with Meaning (MF, ML) and Trial type (Switch, Middle, Last) as within-subjects variables and List type (the rare switches condition, frequent switches condition) as a between-subjects variable (see Fig. 3.6, lower plots). A main effect of Meaning was found to be significant with the recurrent superiority of MF actions (339,29, SE = 10.56) over ML actions (363.45, SE = 11.71) ($F(1,23) = 14.98$, $p = .001$). The interaction of Trial type and Meaning showed a tendency but did not reach significance ($F(1,23) = 2.76$, $p = .07$) but most importantly the 3 way interaction Trial type x Meaning x List type was found to be significant ($F(1,23) = 3.46$, $p = .040$) To better understand this interaction subsequent post hoc analysis were run.

In the frequent switches condition no differences were found between MF and ML actions at the switch trial (Fisher p =.98), where for both middle trial and last trial MF actions lead to shorter RT (respectively, Fisher p = .009, Fisher p = .008). ML actions did not differ nor from the switch to the Middle trial (Fisher p =.42) nor from the middle to the last trial (Fisher p =.95). Hence the

difference from Switch to Middle trial seems to be driven mainly by the marginally significant decrease in RT on MF actions (fisher p =.06).

For the rare switches condition, in contrast, significant differences were found between MF and ML actions in the Switch and Middle trial (respectively, Fisher p = .06, Fisher p =.001) but not in the Last trial (Fisher p = .68). RT of ML actions did not differ neither from switch to middle trial (Fisher p = .73), nor from middle trial to Last trial (Fisher p = .16). For MF actions there was no significant difference between Switch and middle trial (Fisher p = .24), whereas the difference between the middle and last trial was significant (Fisher p = .02). As supplementary information, the same analysis without excluding the first bin led only to a main effect of meaning ($F(1,23) = 13.34, p = .001$)

3.4 General Discussion

In this study, we aimed at further exploring the dual-route model of action imitation by having participants to imitate intransitive communicative gestures instead of pantomimes of object. In addition to accuracy, we also measured RT as they have proven to be a sensitive measure for highlighting the selection mechanism in imitation (see Press & Heyes, 2008).

In Experiment 1, we observed a superiority effect of MF actions and the list composition effect. An effect of the preceding trial was found as well, as imitation of ML action led to an increase in RT in the subsequent trial, partially supporting the carry over costs hypothesis by Press and Heyes (2008). In Experiment 2, we directly tested the carry over hypothesis and, in addition, we exploited the concepts of switching cost and mixing cost used in paradigms of task-set switching. In Experiment 1, we observed shorter RT when subjects imitated MF actions compared with ML actions, in the blocked condition. In the mixed condition, no differences in RT were found between MF and ML actions with MF. In addition, a main effect of preceding trial was found, with subjects being slower when imitating either a MF action or a ML action when the preceding trial was ML one. We were able to demonstrate using RT as a dependent variable the superiority effect of MF

actions that we have previously observed when accuracy in imitation was analyzed (e.g. Tessari & Rumiati, 2004; Rumiati, Carmo, Corradi-Dell'Acqua, 2009). In particular, these findings suggest that the two mechanisms are quantitatively and qualitatively different. The direct mechanism, that has been characterized as more prone-to-errors, is slower; in contrast, the indirect, semantic mechanism not only is more accurate but is also faster.

In Experiment 2, when we compared performance in the blocked condition, the mixed condition with rare switches and the mixed condition with more frequent switches, we failed to reveal a decrease in RT for ML actions, as it would be expected by the release of carry-over costs. In fact, on the contrary, RT were longer in the mixed condition with rare switches. Regarding performance on MF actions, an increase in RT was observed when comparing the blocked and the mixed condition with rare switches.

No overall differences were found when comparing the frequent switches condition against the blocked condition, nor against the rare switches condition. Nevertheless, RT for both MF and ML actions are shorter than those in the mixed condition with rare switches and are longer than those in the blocked condition. Carry-over cost, as proposed by Press and Heyes (2008) seem therefore unlikely to provide an accurate description of these data.

The analysis at the level of single trials showed an absence of switching costs for both mixed conditions. Hence we can exclude altogether the hypothesis of putative asymmetry in switching costs. Conversely when we examine mixing costs, by comparing repeat trials to pure repeat trials, we found that the 2 mixed lists led to a differential pattern. With rare switches group showing shorter RT in pure repetition trials. This effect was equivalent for both MF and ML actions. The lack of mixing cost in the frequent switches condition and its occurrence in the rare switches condition suggests that participants might be exploiting different strategies to approach the imitation task in the 2 mixed conditions, by choosing to use the direct route for both type of actions in the frequent switches condition while still affording to change between the two mechanisms in the condition where alternations are more sparse.

One problem with this interpretation is that the pattern of results observed in the frequent switches condition (Experiment 2) does not replicate the one observed in the mixed condition of Experiment 1, where no differences between MF and ML actions have been found. Although in both conditions, it would be advantageous for the subjects to strategically select the indirect route, given that in either cases switches between the two action types often more frequent, in the mixed condition of Experiment 1, as the switches between MF and ML actions occurred at random, subjects could not predict the forthcoming event; in the Experiment 2, however, as switches between the two types of action were highly predictable, subjects could indeed use that knowledge when performing the task. In addition to factors such as composition of the list and the proportion of the stimuli, that have already been proposed as potentially affecting the selection of route process (Tessari & Rumiati, 2004), the predictability of the stimuli could as well have an influence on the strategic selection. When stimuli alternate considerably and the pattern of alternation is unknown, subjects seem to find advantageous selecting one route only for imitation of action in a mixed condition (Tessari & Rumiati, 2004). In our experiment, as sequence of stimuli are predictable, subjects might still have found advantageous changing between the two routes to imitation, at least in some trials within each sequence. In order to evaluate whether the differential mixing costs found were consistent with a top-down advanced preparation for the forthcoming shift (Lost, 1996) in route to imitation we compared first, middle and last trials of every sequence of MF and ML actions. Supporting the previous finding and interpretation we found that in one hand, in the rare switches condition there was a main difference in RT from the first and middle to the last trial of a sequence, with an increase in RT for the semantic route (MF actions). In the other hand at beginning of each sequence subjects seem already prepared for each action type with the most appropriate route, so the superiority effect of MF action is observed. These findings seem to indicate that rather than a stimulus-driven selection of routes to imitation, participants take into account the structure of the lists and are capable of a more controlled behaviour by choosing in advance how to approach the imitation task at hand. Regarding the frequent switches condition, we

did not observe the expected effect of advanced preparation. In this condition, the direct route seems to have been used for all ML actions but also for the first trial of a sequence of MF actions. Since the decrease in RT is only observed in the middle trial, it could be that the main difference between the results of Experiment 1 and those of the frequent switches conditions are indeed related to the predictability of the type of condition (i.e. MF and ML actions being presented in mixed or blocked lists).

Taken together, the results on mixing cost and the subsequent analysis on the preparatory effect are in agreement with an endogenous, strategic task reconfiguration, in which mixing costs are attributed to preparation for the forthcoming event (Los, 1996). Moreover, they are supportive of our interpretation that the differential pattern found for the rare switches condition and frequent switches condition reflect two different approaches to the imitation task at hand. In the rare switches condition subject might be indeed switching between the two routes and even preparing for the subsequent task-reconfiguration, where in the frequent switch no mixing costs are observed nor any sign of preparation which is suggestive of a strategic selection of one route only for imitation.

Inconsistent with the stimulus-drive hypothesis put forward by Press and Heyes (2008), the differential pattern between the two mixed condition is demonstrative that the cognitive system is endowed, to some extent, with more flexibility when has to deal with an imitation task, and that at least a combination of both endogenous and exogenous components has to be granted for control processes over imitation.

Chapter 4
Understanding and imitating actions: dissociable neural mechanisms

1. Introduction

In imitation learning, a novel observed action is incorporated into the observer's own motor repertoire (Vogt et al. 2007). From functional neuroimaging studies, an extended overlapping of the brain activity engendered by imitation of familiar and novel actions has been reported (Grezes, Costes & Decety, 1998). A fronto-parietal network has been proposed as a reasonable candidate for the neuronal underpinnings of human imitation (Iacoboni et al., 1999). In the monkey's ventral premotor cortex and inferior parietal cortex, neurons have been described that discharge both when the monkey performs a specific action and when it observes another individual performing the same

action (mirror neurons system) (Di Pellegrino et al. 1992; Rizzolatti et al. 1996; Gallese et al. 1996; Rizzolatti & Sinigaglia, 2008). The existence of a similar execution-observation matching system in humans has been proposed and includes two main areas: the inferior section of precentral gyrus plus the inferior frontal gyrus, and the inferior parietal lobule (Rizzolatti & Sinigaglia, 2008). This is consistent with the proposal of a direct-matching hypothesis, whereby an observed action activates the stored motor-related representations, if the mechanisms underlying imitation of actions are already present in one's motor repertoire (familiar actions) (Iacoboni et al., 1999; Rizzolatti & Craighero, 2004). In contrast, in imitation of novel motor patterns a supplementary mechanism, related to activity within the middle frontal gyrus, has been proposed (Buccino, et al. 2004b; Vogt et al. 2007).

Previous studies on the brain mechanisms subserving imitation differed greatly in the experimental procedures. This makes the comparison between them troublesome. Some used novel gestures (Tanaka et al., 2002; Buccino et al., 2004b), familiar actions (Montgomery, Isenberg & Haxby, 2007) or simple pre-determined movements (Iacoboni et al., 1999). Other studies employed two types of actions that differed in familiarity favouring the observation of both commonalities and differences in brain activations in imitation of novel and familiar actions. In some of these studies, direct activations from novel and familiar actions can be observed. Some results have been obtained by contrasting the task against a baseline condition (Tanaka et al., 2001; Grèzes, Costes & Decety, 1998), while others contrast novel and familiar actions against each other (Decety & Grèzes, 1997; Grèzes, Costes & Decety, 1999; Rumiati et al., 2005; Vogh et al., 2007).

Areas in the premotor cortex (SMA, BA6) have been consistently found to be active during imitation of both familiar and novel actions (Buccino et al. 2004b; Grèzes et al., 1998; Grèzes et al., 1999; Rumiati et al., 2005). Activation of the inferior frontal cortex (ventral premotor, BA44), bilaterally or in the left hemisphere has been reported during imitation of novel gesturing (e.g. Tanaka et al., 2002; Nishitami & Hari 2000; Vogt et al. 2007), whereas it has been reported once with familiar actions (Montgomery, et al. 2007), or with prefixed movements (Iacoboni et al. 1999).

Less consistent across studies is the activation of the superior parietal cortex, found for familiar actions in two studies (Grèzes et al., 1998; Grèzes et al., 1999) and for novel actions in other studies (e.g. Tanaka et al., 2001; Rumiati et al., 2005; Buccino et al. 2004b). The participation of the orbito-frontal areas (BA11) in imitation was only found for familiar actions (e.g. Grèzes et al. 1998; Vogt et al. 2007). In addition, two studies with imitation of more complex novel actions (playing the guitar) reported activations in the middle frontal gyrus (BA9, BA46) (Buccino et al., 2004b; Vogt et al., 2007), areas that for the authors suggest are specifically related to imitation learning mechanisms.

One magnetoencephalographic (MEG) study provided valuable information about the time-course of active areas involved in the mirror neurons system during action imitation and observation (Nishitani & Hari, 2000). The activation begins in the left occipital areas, then it is observed in the left inferior frontal cortex (BA44), which is followed 100-150ms later by activation at the left sensorimotor cortex (BA4) and only 100-200ms later by activity at the right BA4. The timing patterns obtained were similar for both imitation and observation tasks used, but activation was stronger during the imitation task.

The involvement of the MN system has generally been accepted for understanding others' actions (Buccino, Binkofski, & Riggio, 2004a; Rizzolati & Craighero 2004, Rizzolatti & Sinigaglia, 2008), as it has been demonstrated that during observation of actions there is a recruitment of the same neural structures that would be normally involved in the actual execution of the observed actions (Buccino et al. 2001; Grafton et al. 1996). In these studies, likewise in many others (e.g. Hari et al. 1998, Grezes et al, 1998, Jonas et al., 2007), it is difficult to assess which processes subjects were engaged in, since they passively observed actions and received no specific instruction. The studies in which the intention behind action observation has been controlled for vary considerably. Participants, for instance were asked to either perform a memory-related task (Decety et al. 1997; Hermsdorfer et al. 2001), tasks involving visuo-perceptual analysis of the scene

(e.g. Calvo-Merino et al. 2006; Shie et al. 2008), or a task in which participants were required to extract the meaning of the observed actions (Lui et al. 2008).

Differences in brain activation due to subjects' intention in action observation have been already discussed (Grezès, Costes & Decety, 1998). Moreover observing actions for later execution (vision for action) or simply watching them (vision for perception) did not lead to marked differences in brain activity and MN areas were recruited in both cases. However when the intention to observe actions had the specific goal of recognizing the viewed action, (vision for recognition) the observed activity was along the ventral visual pathway (Decety & Grèzes 1999; Grèzes & Decety, 2001; but also Gallagher & Frith, 2004). Additional activation of the superior temporal sulcus (STS) when subjects observed hand actions has been reported (Iacoboni et al. 2001; Chong et al., 2008), supporting its key role in action understanding (Rizzolatti & Sinigaglia, 2008).

In the current study we aimed at evaluating the similarities/discrepancies in the brain activity of participants when they observed meaningful and meaningless actions with the intention to imitate or to perform a meaning judgment task. We used Event-related potentials (ERPs) to investigate differences in the temporal sequence of events in the brain of individuals when performing either an action imitation task or a discrimination task that could have been concealed when using other techniques with less temporal resolution. Moreover ERPs enable the evaluation of the scalp topography of electrical brain activity without subtractions between tasks.

The imitation task allowed us to ascertain whether imitation of novel actions is accomplished by the same functional mechanisms engaged when imitating familiar actions or by different ones. In fact, the substantial contribution of areas with mirror properties seems insufficient to account for imitation of actions not yet part of one's own repertoire (Buccino et al. 2004b; Vogt et al., 2007).

In the discrimination task subjects were instructed to evaluate whether the simple hand gestures presented in a video were known or novel, prompting them to access the semantic knowledge associated with the actions, and enabling us to examine brain mechanisms that might be

contributing to action understanding. With the discrimination task, we aimed at evaluating whether novel actions and familiar actions lead to marked differences and whether the activity is more consistent with typical mirror neuron mechanisms, ventral pathway activity, or both. Finally, if both understanding and imitation of actions are accomplished by the same neural structures, no differences should be found in either ERP time-course or scalp topography.

2. Method

Participants

Eighteen Italian right-handed adults participated in the study (5 males; mean age: 22 years, range: 20-27 years). Handedness was assessed with the Edinburgh Handedness Inventory (mean=84, SD=20). All participants had normal or corrected-to normal vision acuity. Participants gave informed consent as approved by SISSA bio-ethical committee and received 20 Euros for their time.

Stimuli and design

The stimuli used in both tasks comprised 12 simple meaningful (MF) and 12 meaningless (ML) hand gestures (24 different gestures in total). The video-clips last 2000 ms each and were performed by a male model. The set of MF actions comprised 12 object-unrelated, symbolic gestures (e.g. wave goodbye), while the set of ML actions was obtained by modifying the relationship between hand–arm and trunk of each of the 12 MF actions.

The experiment was conducted in a sound-attenuated room. Each trial started with a fixation cross that lasted for 2000 ms. After this period, the video-clip was presented for 2000 ms followed by a 500 ms blank slide, at the end of which the response slide was presented until the subjects' response. During the video presentation, for either the discrimination or the imitation task, subjects were asked to keep one button pressed with their right index finger. Discrimination and imitation tasks differed only at the response slide, and were presented in a block manner. In the

discrimination task, subjects were prompted to answer the question "Does it have a meaning?" (in Italian: "Ha un significato?"), and required to press one of two additional buttons labelled 'Yes' and 'No'. In the imitation task, subjects were prompted with "Now imitate the gesture" ("Ora imita l'azione!") and were instructed to release the target button and imitate with the same hand as in the observed action. At the beginning of each task session subjects had a practice session of 12 trials. Both sets of MF and ML actions were repeated 4 times in each task, for a total of 192 trials. The order of administration of the two different tasks (imitation vs. discrimination) was counterbalanced across participants. In the middle of each task, a short pause was given to allow some rest and checking electrode offsets. In order to exclude incorrect trials, participants' performance was video-recorded and scored off-line by one experimenter.

Electrophysiological recordings and data pre-processing

EEG signal was continuously sampled at 256 Hz using a BioSemi active-two system (http://www.biosemi.com/) from a pre-cabled 128 Ag/AgCl active electrode cap (of a modified 10-20 system montage). Skin preparation was not necessary with active electrodes. Eight additional drop-down electrodes were attached around the subject's face: horizontal electro-oculographic (EOG) signals were recorded at the left and right external canthi, vertical EOGs were recorded right below the eyes, and 4 additional electrodes were placed bilaterally on the mastoids and peri-auricular sites. Individual electrodes were adjusted until the electrode offset was below 40 mV.

Pre-processing of the EEG data was done in EEGLab v7.2.9.19b (Delorme & Makeig, 2004). All electrodes were referenced offline to the average-reference. Continuous EEG signal was high-pass filtered at 0.1 Hz and low-pass filtered at 30 Hz to remove high-frequency noise produced by muscle-related activity and external electrical sources. Continuous EEG was segmented into epochs from 400 ms before video onset to 2000 ms after, for correctly performed trials only. On average, correct trials were 93.68% (SD = 3.89) for imitation, and 90.61% (SD = 4.93) for discrimination. Channels with amplitude exceeding the threshold of +/- 150 µV in more than 30% of trials were interpolated. An automatic epoch rejection algorithm was used, with threshold set to -/+ 1000 µV

and allowing a maximum of 5% of rejections per iteration. In order to detect and remove eye-artifacts, the EEG signal was decomposed using Independent Component Analysis (as implemented in EEGLab), and independent components attributed to blinks and eye-movements after visual inspection were eliminated from the data. For each condition, before event-related potential (ERP) averaging, we further excluded from single epochs the electrodes in which more than 10 time-points (out of 614) overcame the threshold of +/-100 µV. All ERPs were baseline-corrected using the 400 ms pre-video period. For the ERP analyses, on average, there were 36.2 good trials (SD = 5) in the discrimination task and 37.2 good trials (SD= 3.7) in the imitation task.

ERP data analysis

We assessed the difference in mean amplitudes across all subjects of the ERPs from MF and ML trials for both imitation and discrimination tasks. Based on visual inspection and topographic activity distribution for both task conditions, we chose 3 scalp regions of interest (ROIs) and their homologous counterpart in the opposite hemisphere, that describe the most prominent effects observed in our study. Each ROI encompasses the electrode that shows the maximum MF vs. ML difference in a given task and the 3 closest neighbouring electrodes (see figure 4.1). For each ROI, a time-window of 150 ms was chosen and centered at the time point of MF and ML maximum difference in amplitude.

A clear dipolar voltage pattern can be identified with negativity at the left frontal sites and positivity at right posterior sites in the ML-MF contrast for the imitation task at the first time-window (565-715ms). This effect shows the maximum difference between MF and ML conditions at electrode F5' around 640 ms after video stimuli onset. The left frontal ROI thus comprises the electrodes closest to F5': AF5', F7', AF7' (a standard 10/10 system nomenclature is used here instead of the Biosemi one, to favour the comparison with the literature). The right counterpart is the region that includes electrodes F6', AF6', F8', AF8'.
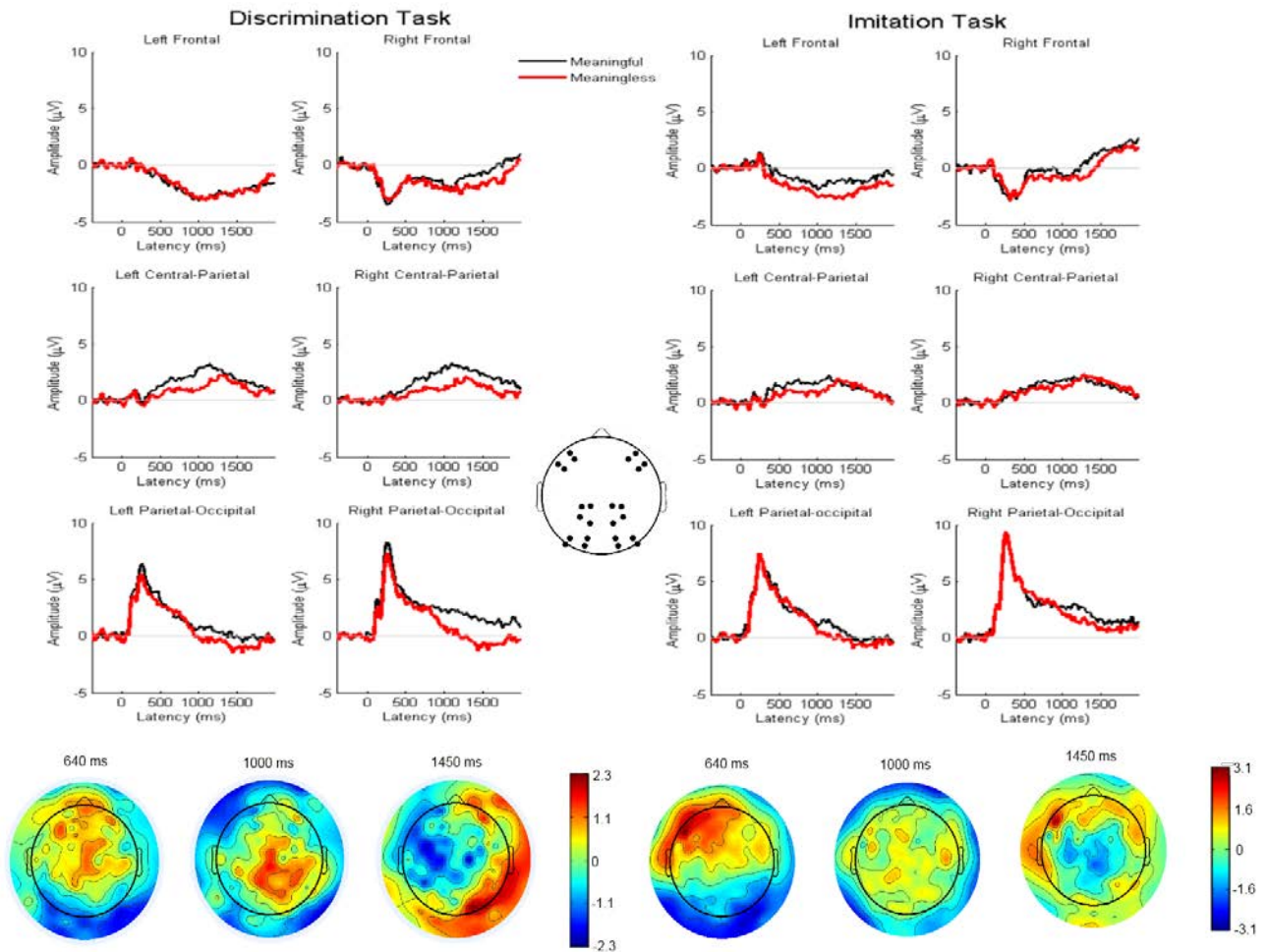
Fig. 4.1 Grand average from imitation task (right pannel) and discrimination task (left pannel) for meaningful and meaningless actions, for the frontal, centro-parietal and parietal-occipital ROIs. Central panel: schematic illustration of location of electrodes that each ROI comprises. At the botton: topografic distribution of amplitude difference between meaningful and meaningless conditions including all scalp sites for discrimination (left) and imitation tasks (right), at 640 ms, 1000 ms, and 1450ms.

At a middle time-window (925-1075 ms) a central-parietal right-lateralized positivity was identifiable for the discrimination task (see fig 4.1). The electrode CP2' corresponds to the place where this effect reaches its maximum in amplitude differences, and this occurs at 1000 ms after stimulus onset. This central parietal region comprises the electrodes CP2', E35, CP2' and P2' in the right hemisphere, while its left counterpart included electrodes CP1', E6, CP1' P1'.

For the discrimination task, a final dipole voltage parieto-occipital right-lateralized effect was observed much later (1475-1525ms). To explore this effect we selected the PO4´electrode that

shows the maximum difference between MF and ML actions from topographic map inspection. The time-window for this effect was centered at 1450 ms after stimulus onset, point where the difference reaches its maximum at the region's central electrode. The right parieto-occipital region comprises the closest neighbouring electrodes to PO4': PO2', PO6', PO8'. While the left counterpart is the region that includes electrodes PO1', PO3', PO5', PO7'.

For each time-window, a repeated measures ANOVA was performed on the mean amplitude values of correct trials for each subject, with Task (Discrimination, Imitation), Meaning (Meaningful, Meaningless), ROI (Frontal, central-parietal, parieto-occipital) and Lateralization (Left hemisphere, Right hemisphere) as independent variables.

3. Results

Left Frontal Component Activity (565-715 ms)

At this time-window, a broadly distributed negativity was observed over the most anterior region with its inverted counterpart towards the most posterior regions (main effect of ROI: $(F(2,34) = 22.5, p < .0001)$. Although we observed an overall lower mean amplitude potential for the right hemisphere than for the left hemisphere (main effect of hemisphere, $F (1, 17) = 16.1, p < .001$), there was an interaction between hemisphere and ROI $(F(2,34) = 5.1, p = .011)$ due to this effect not being present at the central parietal (Tukey: $p = .99$), or at the parieto-occipital scalp sites (Tukey $p = .31$) but only at the frontal sites (Tukey: $p < .001$). If overall ML actions have a lower mean amplitude than MF actions (Main effect of meaning, $F(1, 17) = 6.6, p = .01$), this is not the case for the most posterior scalp region (Tukey $p = .88$) where this effect was slightly reverted (Meaning x ROI interaction, $F (2, 34) = 4.1, p = .025$).

Most importantly at this time-window, a Task x Meaning x ROI x Hemisphere interaction $(F(2, 34) = 3.97, p = .028)$ was found. Based on subsequent separate ANOVAs for each of the 3 ROI, we were able to detect that this difference between imitation and discrimination task was present

mainly at the left frontal region (Task x Meaning $F(1, 17) = 8.87$, $p = .008$), Task x Meaning x Hemisphere $F(1, 17) = 15.80$, $p = .001$), while it did not occur in the Central-Parietal ROI (Task x Meaning $F(1, 17) = 1.78$, $p > .1$; Task x Meaning x Hemisphere: $F(1,17) = 1.79$, $p > .2$), and it was reversed in the Parieto-occipital ROI (Task x Meaning $F(1, 17) = 2.56$, $p > .1$; Task x Meaning x Hemisphere; $F(1,17) = 6.22$, $p = .02$).

Post-hoc comparisons further confirmed that this 3-way interaction found at the frontal ROI (Fig. 4.2) is driven by greater negativity for ML actions as compared to MF actions at the left hemisphere in the imitation task (Tukey: $p < .001$); while the difference between MF and ML actions is not present in the discrimination task (Tukey: $p = .99$). The 3-way interaction found at the parieto-occipital ROI is driven mostly by the absence of differences between the 2 hemispheres for ML action in the imitation task (Tukey $p = .09$), as overall the right hemisphere leads to a higher mean amplitude than the left hemisphere.
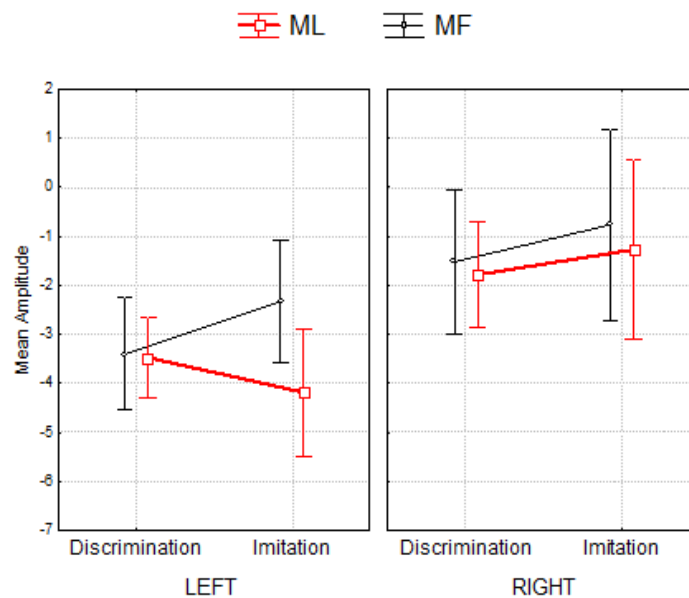
Fig. 4.2 Mean Amplitude from imitation and discrimination tasks, MF and ML actions for the frontal ROI at the first time window (565-715ms).

Right Central-Parietal Component (925-1075ms)

At this time-window overall MF actions show a higher mean amplitude than ML actions (main effect of Meaning, $F(1,17) = 25$, $p < .001$). The meaning x ROI interaction ($F(2,34) = 4.4$, $p = .02$, see Fig 4.3), suggests that not all regions are contributing equally. Indeed, a higher amplitude of MF actions as compared to ML actions is only visible in the central-parietal region (Tukey: $p < .001$), while MF and ML actions did not differ significantly in the frontal region (Tukey: $p = .97$) and parieto-occipital ones (Tukey: $p = .09$).
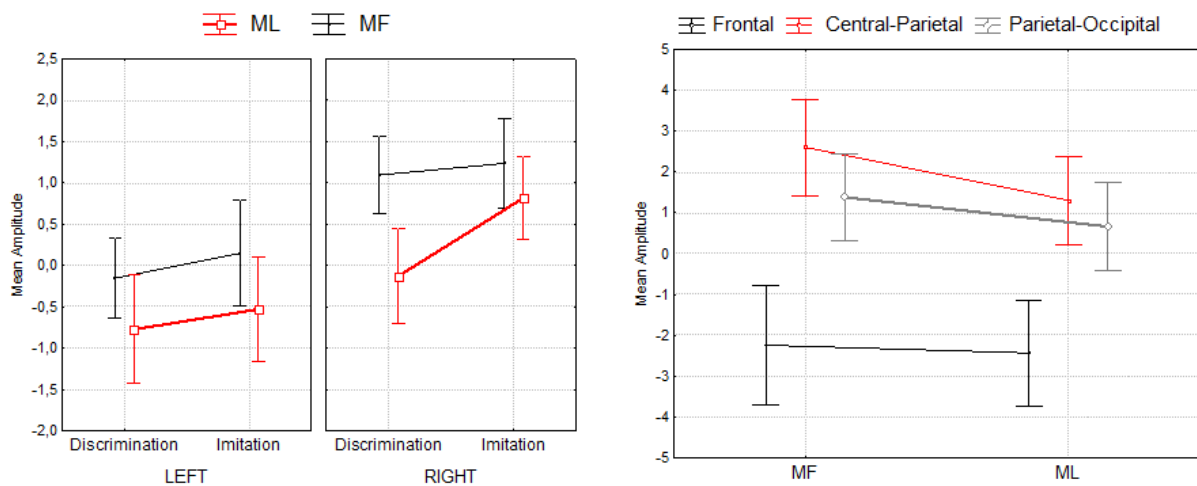
Fig. 4.3 Mean amplitude of MF and ML actions at the middle time window *(925-1075ms)*. Right plot depicts overall mean amplitude of MF and ML actions for each of the 3 ROIs. Left plot depicts mean amplitude of MF and ML actions for each task (imitation, discrimination) in the left and right hemisphere.

Moreover, a Task x Meaning x Hemisphere interaction was found ($F(1,17) = 11$, $p = .004$, see Fig 4.3), suggesting that the difference between MF and ML actions found previously in the central-parietal region was not equally driven by both tasks, and not equally present in both hemispheres. Although at the left hemisphere MF and ML actions differ both for the Discrimination task (Tukey $p = .003$) and the Imitation task (Tukey: $p = .001$), at the right hemisphere this difference was even enhanced for the discrimination task (Tukey: $p = .0001$) but disappears for the imitation task (Tukey: $p = .071$).

Right parieto-occipital component (1475-1525ms)

At the latest time-window a Task x Meaning x Hemisphere interaction was found (F (1,17) = 11.76 , p = .003, see Fig. 4.4), with the difference between MF and ML actions being present for the discrimination task in the right hemisphere (Tukey p < .001) but not at the left hemisphere (Tukey p = .7) (Fig. 4). In the case of the Imitation task, no differences between MF and ML actions were found in either hemisphere (Tukey ps >.15).
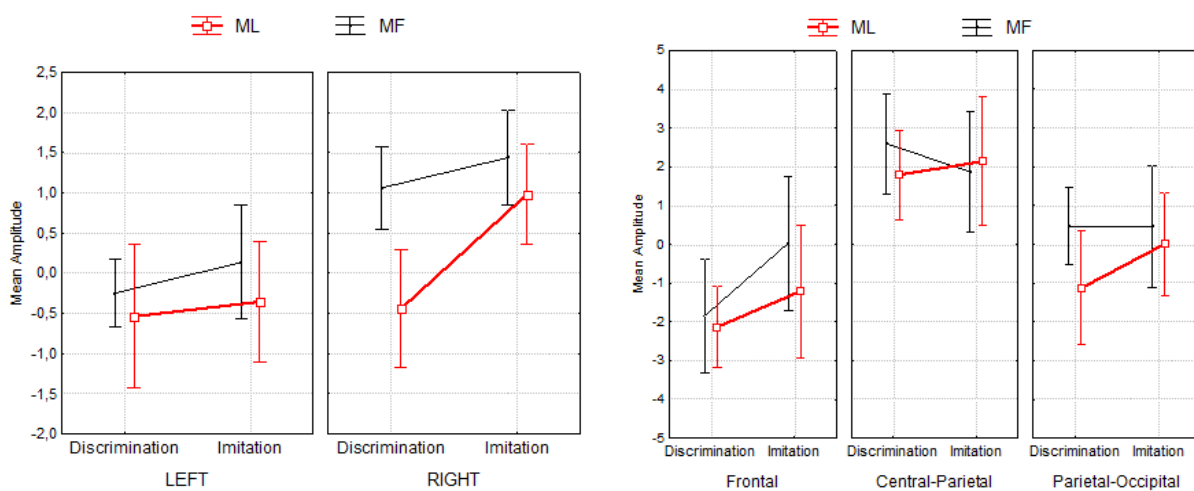
Fig. 4.4 Mean amplitude of MF and ML actions for both tasks (imitation, discrimination) at the latest *(1475-1525ms)* time window, for each hemisphere (left panels) and for each ROI (right panels).

The difference between MF and ML actions found in the discrimination task in the right hemisphere is supported by a Task x Meaning x ROI interaction (F (2,34) = 4.49, p = .01) in which, for the discrimination task, Meaning did not differ for the most anterior region or for the central region (Tukey ps >.5) but only in the parieto-occipital region (Tukey ps = .01). For the imitation task, no significant differences between MF and ML actions were found (Tukey ps > .1).

4. Discussion

In this study, event-related potentials were recorded upon observation of novel or familiar communicative gestures. The exact same video stimuli were used both when subjects observed

actions with the intention to imitate and when they had to perform a meaning judgement task. The key result is a sustained negative component with a first peak at around 640 ms at anterior left scalp sites. This frontal component is more pronounced for novel meaningless actions when the intention behind action observation was that of subsequent imitation. The fact that this was not observed with familiar actions or when subjects were not required to learn them for later reproduction (i.e. in the discrimination task), suggests that this component is involved in imitation learning mechanisms. In imitating novel actions, a translation between the visual input and motor output is needed (Tessari & Rumiati, 2004), as no representation can be retrieved from memory. Hence, this learning mechanism is plausibly more dependent on working memory and under supervisory control of the left dorsolateral prefrontal cortex, as proposed already by Vogt et al. (2007). Strong evidence has been provided for frontal involvement in memory encoding (Buckner, Kelley & Peterson, 1999).

Moreover, a hemispheric asymmetry has been proposed for frontal lobes involvement in different aspects of encoding and retrieval of episodic memory, leading to the Hemispheric Encoding/Retrieval Asymmetry (HERA) model (Tulving et al., 1994). On this model, the left frontal lobe is supposed to be more involved in the encoding of novel aspects of incoming information, while right frontal lobe is more involved in episodic memory retrieval (Tulving et al., 1994; Tulving et al., 1996). Novelty of the incoming information plays a central role, as elaborate encoding processes are applied as a function of it, and determine long-term storage likelihood (Tulving et al., 1996; Kim, Vallesi, Picton & Tulving, 2009). Critically, slow negative potentials recorded from scalp sites over the left dorsolateral frontal sites have been reported to strongly correlate with associative learning level (Lang et al., 1988).   The idea of a supplementary activation during imitation of novel actions is consistent both with the proposal of an indirect MN mechanism that could account for "true imitation" or mimicry (Ferrari, Bonini, & Fogassi, 2009) as well as with the proposal by Catmur, Walsh, and Heyes (2009) that MN representations need not be innate and that general learning processes, by concurrent experience of observing and executing actions, could account for their development.

A dissociation between imitating and observing actions was also found both at a middle time window (around 1000 ms) and at the latest one (1550 ms). Earlier over right central-parietal and later on over right parieto-occipital scalp sites, an increased negativity was found for novel actions when subjects performed the discrimination task. This finding is probably due to the more complex and demanding process of visual spatial inspection of novel actions. In particular, the right superior-posterior parietal cortex is presumably involved in processing novel translations between visuo-spatial information and of motor or body-related information (Halsband & Lange, 2006). However an equally substantial or even higher participation of the right superior parietal cortex would be expected as well for observation of novel action in imitation, which was not the case here.

Alternatively, this right lateralized component over parieto-occipital areas could be driven by the STS. This structure has been implicated in visual perception of biological motion, as it is selectively active for biological-like motion as opposed to non-biological, random motion (Pelphrey et al., 2003; Puce & Perrett, 2003). Although right, left or bilateral activations of the STS have been observed regarding perception of biological motion (Puce & Perrett, 2003), it is likely that these differences in laterality are related to the type of stimuli used, as left activations have been shown for object-related actions and right activation for intransitive actions or fine-grained gesturing (Iacoboni et al., 2001), such as those used in the current study.

Besides the general role played by the STS in perception biological motion, two studies have shown that, for eye gaze movements (Pelphrey Singerman, Allison, McCarthy, 2003), and grasping movements (Pelphrey, Morris & McCarthy, 2004), when subjects observe an incorrect movement that violates the observer's expectancies (goal directed action vs. non-goal directed action), STS is strongly engaged. These findings led the authors to propose that this structure plays a critical role in social perception, and particularly in the analysis of the intentions of others (Pelphrey et al., 2003; Pelphrey et al., 2004; Pelphrey & Morris, 2006). Likewise, in our study, it could be the case that when subjects observed ML actions compared with familiar gestures, because of their apparent lack of a goal, a greater engagement of the STS occurs.

The notion of common coding and shared action representation in the brain raises the issues of how self versus others distinction comes about, which neural mechanism are engaged in discriminating the representation of one self and those activated by external agents (Decety & Chaminade, 2003; Brass & Heyes, 2005), and how we prevent automatic imitation in everyday life (Brass, Ruby & Spengler, 2009; Spengler, Von Cramon, & Brass, 2010). The temporo-parietal junction (TPJ) within the inferior parietal role has been proposed to play a key role in the sense of agency (Decety & Chaminade, 2003; Brass et al. 2009), with the specific involvement of the right TPJ being systematically associated with 1st person versus 3rd person spatial transformations and perspective taking tasks (Decety & Lamm, 2006). Recently, some authors have suggested that preventing motor mimicry recruits the same underlying computational mechanisms also involved in higher-level social cognitive processing, such as self-other differentiation (Brass, Derrfuss, & Von Cramon, 2005; Spengler et al., 2010). Brass et al. (2005) have shown that inhibition of latent imitative tendencies recruits also the right TPJ. It could be the case that when no representation is yet available, and no imitation processes are operating, as in the case of the observation of novel actions, the self – other distinction becomes unnecessary, and that could lead to a marked difference in the need for suppressing or not automatic imitation ongoing processes.

Overall, the early recruitment of left lateralized frontal processes does not contradict the findings of Nishitani and Hari (2000) where activations of sensorymotor cortex take place only after activation of the left BA44.

In this study with ERPs we have found two dissociable components when subjects imitate an action compared with a condition where subjects observe an action. An early negative component was found over the anterior left lateralized scalp sites when subjects imitate ML novel actions, which is suggestive of the engagement of general associative learning mechanisms when one has to imitate a novel action. At the middle time window (around 1000 ms) over the right central-parietal scalp sites and at the latest time window (1550 ms) over the right parieto-occipital scalp sites, an increased negativity was found when subjects observed novel actions. Two

alternative explanations within a general social cognition framework are discussed: if on one hand, this brain activity could be driven by activity at the STS as novel actions could lead to a violation of the observer's expectancies, on the other hand the activity recorded could be product of right TPJ's activity, engaged in self-other differentiation.

Chapter 5
Preserved imitation of familiar gestures in high-functioning autistic children

5.1. Introduction

The relationship between autism and imitation deficits was envisaged long ago by Ritvo and Provence (1953), short after autism was originally described in the work of Kanner (1943). The imitative ability is acknowledged to play an essential role in normal development (Uzgiris, 1981), as it can be used by infants to acquire and master new behaviors. In recent years, the relationship between autism and imitation has been investigated more systematically. It has been argued, for instance, that children with an Autism Spectrum Disorder (ASD) are consistently impaired in performing imitative tasks (Williams et al., 2004) relative to children with other developmental delays (matched for chronological age, verbal IQ-mental age and expressive language, see Rogers,

Bennetto, McEvoy & Pennington, 1996; Stone, Ousley & Littleford, 1997), or to normal controls matched for mental age (Stone et al. 1997; Smith & Bryson, 1998). ASD children performed more poorly on imitation tasks than matched-to-language-impaired controls or younger children matched for receptive language and mental age (Smith & Bryson, 1998), thus ruling out the interpretation that the imitation impairment is due to a linguistic deficit. Neither can the imitative deficit of ASD children be attributed to defective gesture recognition (Smith & Bryson, 1998; Rogers et al., 1996) or visuo-motor coordination (Smith & Bryson, 1998). Moreover, irrespective of whether they are low or high functioning, autistic children seem to have difficulties in imitating gestures that disable children and typically developing children do not show (Vanvuchelen, Roeyers & De Weerdt, 2007).

Whether the reduced imitation of ASD children is a true deficit or a delay in development is still under debate. This "deficit" is already present in children as young as 20 months and is, in general, more apparent in children than in adults (Williams et al., 2004). Consistently, an improvement in performance was observed when young ASD children (with an average age of 31 months) were retested about one year later (with an average age of 45 months) (Stone et al., 1997).

5.1.1. Imitation is not an unitary mechanism

Williams et al. (2004) propose that observing a meaningful object or gesture triggers the release of a previously rehearsed program, and that observing a desired outcome might lead the observers to reach a goal by applying their own problem solving ability (emulation). Hence, imitation itself would be especially required for copying meaningless gestures that do not have an obvious goal or associated knowledge (Williams et al., 2004). This would explain why ASD children seem to experience more difficulty in imitating meaningless than meaningful actions or actions involving objects (Rogers et al., 1996; Stone et. al., 1997).

Regarding object-related imitation, Hamilton, Brindley and Frith (2007) showed that ASD children imitate goal-directed actions as well as healthy children with the same verbal mental age.

These authors argued that the ability to imitate (and understand) the goal of hand actions is intact in ASD children, and suggested that these children might fail on those imitation tasks in which they cannot rely on a hand-goal strategy as in the case of meaningless actions. They also concluded that it is unlikely that a unique neurocognitive mechanism underlies imitative behavior in either the typical or autistic brain. Consistently with this view, Hamilton (2008) put forward a dual route model for Emulation and Planning vs. Mimicry (EP-M model) and proposed that the latter is impaired in autistic children.

However, as far as the ability of ASD children to imitate communicative gestures (such as waving a hand as goodbye) is concerned, the results are not conclusive. While in some studies, these gestures have been included in the assessment but were analysed together with other types of gestures (e.g. Stone et al., 1997), in a particular study, in which communicative gestures were analysed as a separate class, they were found to be imitated correctly (Rogers et al., 1996). The result from the latter study is difficult to interpret because participants' ability to imitate is confounded with action execution on verbal command. In fact, in addition to the instruction to imitate, participants were provided with verbal encouragement (e.g., "Show someone that you are a champion"). Moreover, different studies used different tasks and included participants of different age.

If, according to the EP-M model, autistic children have a selective damage to the mimicry route (Hamilton et al., 2007; Hamilton, 2008), one would predict that they should be equally impaired in imitating meaningless as well symbolic communicative gestures. In fact, as these two latter action types do not have an obvious outcome, children cannot rely on an emulation and/or problem solving. However, a different set of predictions can be drawn based on a dual-route model of action imitation (Tessari & Rumiati, 2004). The key feature of this model is the presence of two different mechanisms subserving imitation: a sub-lexical route necessary for reproducing novel, ML actions, and a lexical-semantic route that can only be used for imitating over-learned, MF actions. Since both symbolic communicative (i.e. intransitive) and transitive gestures are familiar to the

subjects, imitation of either type of gesture should be comparable in terms of accuracy. After brain damage, each mechanism can be selectively impaired, giving rise to different imitation deficits affecting either MF or ML actions (Bartolo et al., 2001; Goldenberg & Hagmann, 1997; Peigneux et al., 2000; Tessari, Canessa, Ukmar & Rumiati, 2007). In particular, when the direct route is damaged, patients cannot imitate novel actions, while when the lexical-semantic route is damaged, they cannot use it to imitate meaningful actions. These findings were observed when meaningful and meaningless actions were presented in separate lists.

In the present study we aimed at clarifying how high-functioning autistic (HFA) children imitated the following types of actions: meaningful symbolic communicative, pantomime of object use, or meaningless actions.

5.1.2. Mental rotation in ASD

For imitation to be successful, it is critical that the observed movement is mapped onto the observer's body representation (e.g. Alaerts et al., 2008; Gardner 2002; Wapner & Cirillo, 1968). This mapping can be obtained by using one of two mental transformations: the object-based transformation that consists in imagining an object that rotates according to its reference frame, and the egocentric transformation whereby the imitator imagines an object that rotates according to his/her point of view. Both these operations require an updating of the relationships between the objects' and the observer's egocentric reference frame. These relationships are updated by two mental transformations that might be implemented by two dissociable neural systems (Tomasino et al., 2003; Zack et al., 2000). Recently, a group of ASD children were found to outperform typically-developing children (Falter, Plaisted & Davis, 2008). Moreover, these authors show that in their sample ASD children performed better on visual or other non-rotational aspects of the mental rotation task, indicating that they might have been using an alternative strategy to solve the task.

In the current study we tested whether imitation deficits of HFA children could be explained as being due to a pathological mental rotation. Participants were required to perform two different

mental rotation tasks: the "Little Man" task (Radcliff, 1979) and the left-right hand decision task (e.g., Tomasino & Rumiati, 2004). In the Little Man task, subjects are shown pictures of a man in different orientations, holding a black disk in one hand and they are asked for each picture which hand holds the black disk. In the left-right hand decision task, a picture of a hand is shown and participants are required to judge whether it represents a left or a right hand. While in the Little Man task subjects mentally re-orient the stimuli itself (Ratcliff, 1979), in the left-right hand decision, subjects mentally rotate the motor image of their own hand (Parsons, 1994).

5.2. Methods

5.2.1. Participants

Thirteen high-functioning autistic children (M= 7.31, SD = 1.79; all males) and 14 normally developing children (M = 7.00 years old, SD = 1.71; all males) participated in study. Age did not differ between the two groups (F(1,26) = .21, p >.1). All children were right-handed (HFA: M = 90.91%, SD = 15.02, Controls: M = 89.89%, SD = 16.62). All autistic participants had a clinical diagnose of Pervasive Development Disorder- Not Otherwise Specified, according to DSM-IV and the Autism Diagnostic Observation Schedule (ADOS). Intelligence scales and autism specific scales were administered by each child responsible therapist. High-functioning autistic participants were selected if they had a full scale IQ > 70, and they scored above threshold on the Autism on the Children Autistic Rating Scale (CARS) or ADOS (see Table 1). None of the patients had co-morbid Attentional Deficit and Hyperactivity Disorder (ADHD), seizure disturbance or any other associated disorder known to cause autism. Children with autism were recruited through the clinical services of "La Nostra Famiglia" day hospital, (Pasian di Prato, Udine, Italy), a non-profit organization of social utility whose purpose is to promote and safeguard health care, education and services for people with special needs, in particular children and adolescents. Typical children were recruited from local schools and were administered an intelligence scale (WISC, verbal subscale) by the

experimenter. Ethical permission for the study was granted by SISSA ethical committee, and informed consent was given by one parent of each child.

Table 1. Demographics of the participants. All data is given as mean (standard deviation) and min-max.

	N	Age	Verbal IQ (WISC, Griffiths)	Performance IQ (WISC, Griffiths)	Full Scale (WISC, Griffiths or Leiter)	CARS	ADOS
Autistic group	13	7.31 (1.79) 5-11	86.91 (21.61) 54-116 (n=11)	89.92 (19.53) 66-126 (n=12)	88.58 (17.72) 70-118 (n =13)	42.35 (4.18) 35.5-48 (n =10)	12.33 (6.66) 8-20 (n=3)
Control group	14	7 (1.71) 4-10	127.38 (25.10) 92-156	-	-	N/A	N/A

5.2.2. Imitation task

All children attended the experimental session for approximately 1 hour. Stimuli consisted of five sets of 12 simple, non-sequential gestures each. Of these, three sets included MF gestures: 12 transitive gestures *without* objects like, for instance, pretending to pour from an imagined bottle (all taken from Tessari and Rumiati), 12 intransitive symbolic gestures like for instance waving goodbye, "victory", "come here" (all taken from Rumiati, Carmo, Corradi Dell-Acqua, 2009), and 12 transitive gestures performed *with* an object like, for instance, pouring from a real bottle. The remaining two sets included 24 meaningless (ML) gestures, obtained by modifying the relationship between hand, arm and trunk of the MF transitive and intransitive gestures. ML and MF actions were as much as possible matched for complexity. Each action was displayed up to two times for 3 seconds on a computer screen using (Presentation software, Neurobs). All actions were modelled by a female adult using her right hand-arm; subjects were only given the instruction "do what she does" without mentioning the hand they should use. When performing the gestures, the model kept

the gaze fixed straight ahead, thus avoiding confound effects regarding the possibility of reading intentions from gaze (Becchio, Pierno, Mari, *et al.* 2007).

Participants' performance was video-recorded and scored off-line by a rater blind to the predictions of the study who was instructed to code each action in a 3 point-scale system: 0 for totally incorrect, 1 partially correct, and 2 for correct imitation. For the partially incorrect imitative performance, the rater was asked to code the errors with one of 15 *a priori* defined error-types (see Appendix D), and report the hand used in each trial. Participants could begin the experimental session either with MF (3 blocks) or ML gestures (2 blocks) and this order was counterbalanced across participants.

Two types of assessment were carried out in order to ascertain what participants knew about the intransitive and transitive gestures employed in the study. For the symbolic intransitive actions, participants were asked to say whether they knew the meaning of each action (n=12) they watched; for the transitive gestures, participants were presented with the corresponding object and asked to demonstrate how it is normally used. This latter task allowed us also to evaluate participants' hand dominance, given that no instructions were provided to the children as to which hand they should use with the object placed on the table in front of them. The order of the imitative tasks and of the knowledge assessment tasks was counterbalanced across subjects.

5.2.3. Mental rotation tasks

Mental rotation tasks were always administered after participants completed the imitation tasks. Prior the two rotation tasks proper, children' ability to perform a left-right discrimination was assessed. In this task, children were instructed to point to a black circle that could appear either to the left or to the right of a vertical line. Children that succeeded on this test were then administered with the two mental rotation tasks: the Little Man task and left-right hand decision task. A reduced version with 16 trials of the Little Man task (Radcliff, 1979) was employed. The Little Man is shown either upside down or upright; in half of the trials the Little Man faces the participant, while

in the other half he turns his back. The Little Man has always a black disk in one hand and a white disk in the other hand, half of the times the black disk is in one hand in the rest in the other hand. Participants were asked to decide which hand holds the black disk. A version with 20 trials of the left-right hand decision task was used (from Rumiati et al., 2001). Here, children had to decide whether the hand depicted in the picture was left or right. These stimuli were presented in different views, (palm, back, or side views: thumb or little finger) and orientation (45°, 90°, 180°, and 360°). Half of the pictures represented a right hand and the other half the left hand. The experimenter took note of the participants' responses (correct or wrong) on sheet of paper.

5.3. Results

5.3.1. Imitation

For each participant, MF (transitive or intransitive) gestures that were not recognized were not included in the analysis. HFA children were able to recognize on average 74.36 % (SD = 14.22) and Control children 85.61 % (SD = 5.16) of the intransitive gestures. HFA children were able to demonstrate the use of objects (transitive actions) on average 98.71% (SD = 3.13) and Control children 100%.

Regarding Imitation performance, a repeated-measures ANOVA on percentage of correct responses with Meaning (ML, MF) and Context (transitive, intransitive) as within-subjects independent variables and with Group (HFA, controls) as a between-subjects variable (see Fig. 5.1) was performed. Overall, the HFA group imitated more poorly (M = 73.26, SE = 3.96) than the control group (M = 90.10, SE = 3.82); meaningful actions (M = 89.10, SE = 2.22) were performed better than meaningless (M= 74.28, SE=3.54), and the accuracy with intransitive actions (M = 82.33, SE = 2.72) and transitive actions was comparable (M = 81.01, SE = 3.32).

Main effects of Group and Meaning were found to be significant ($F(1, 26) = 9.355$, $p = .005$; $F(1, 26) = 45.84$, $p < .001$, respectively) but not the main effect of Context, $F(1, 26) = .26$, $p > .05$). As predicted, the two-way interactions Group x Meaning ($F(1, 26) = 6.21$, $p < .05$) was significant

but not the two-way interaction Group x Context (F(1, 26) = .26, $p > .05$) nor the 3-way interaction (Group x Context x Meaning: F(1, 26) = .35, $p > .05$). Context x Meaning were also found significant (F (1, 26) = 14.59 , $p = .001$ respectively).
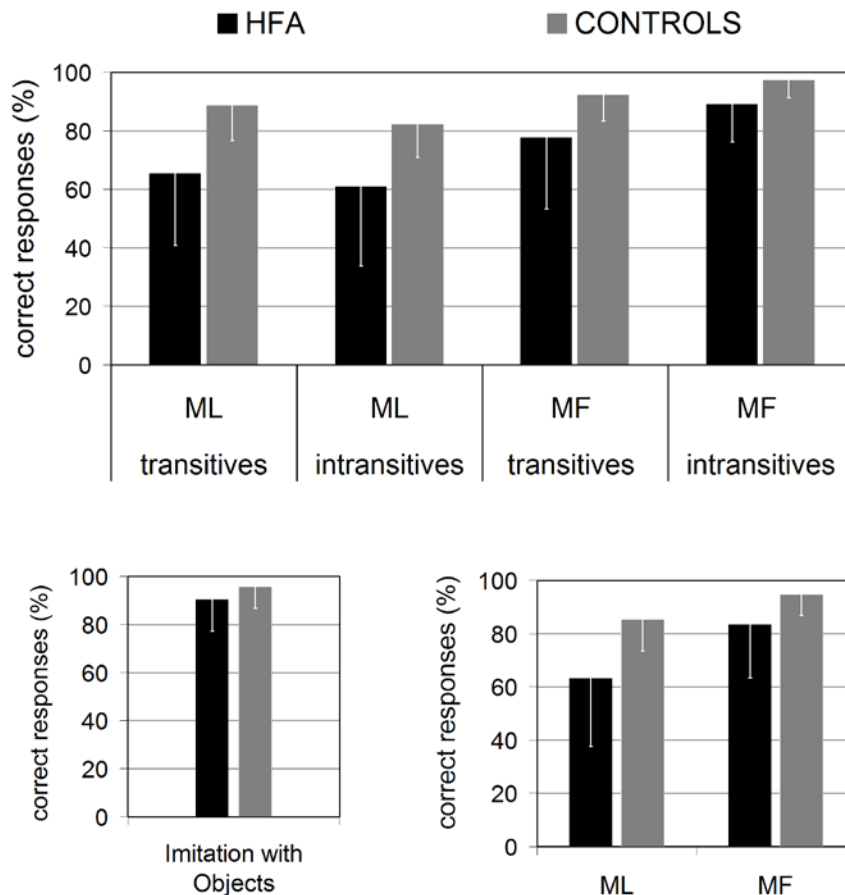
Fig. 5.1 Accuracy on the imitative tasks for the experimental HFA group (in black) and control group (in grey). The bars represent standard deviations from the mean. Upper plot depicts imitative correct responses on meaningless (ML) and meaningful (MF) according to whether they are transitive or intransitive.

In order to better understand the interactions, we performed subsequent post hoc analysis. As to the Meaning x Group interaction, no differences were found between HFA and Control children in imitation of MF actions (Tukey, $p > .1$), whereas differences were found for imitation of ML actions (Tukey $p < .05$). The difference between Imitation of MF and ML actions is driven mostly by HFA children who imitated ML actions more poorly (Tukey $p < .001$). Control children imitated MF actions somewhat better ML actions (Tukey p = .024, see Fig.1). Regarding the

context x meaning interaction, no significant differences were found in imitating transitive and intransitive ML actions (Tukey $p > .1$), while intransitive MF actions were found to be better imitated than transitive MF actions (Tukey p = .019). However the Context x Meaning interaction seems to be mostly driven by differences in imitating intransitive actions: differences between imitation of intransitive MF actions and imitation of transitive ML actions was highly significant (Tukey $p < .001$) (with Bonferroni correction for p values).Regarding imitation of actions using real objects, the two groups did not differ significantly (F (26,1) = 1.59, $p > .05$). Moreover, we found no correlation between each subject's IQ quotient and the imitative performance neither on ML actions (r= .34, $p > .05$) nor on MF actions (r=.32, $p > .05$).

5.3.2. Does age matter?

Does imitative performance on both MF and ML actions improve with participants' age? Having failed to observe either the main effect of context or the context x group interaction, we correlated the performance on imitation of MF and ML actions, regardless of whether they were transitive or intransitive, with the age of the control participants and of the HFA children respectively (see Figure 5.2).
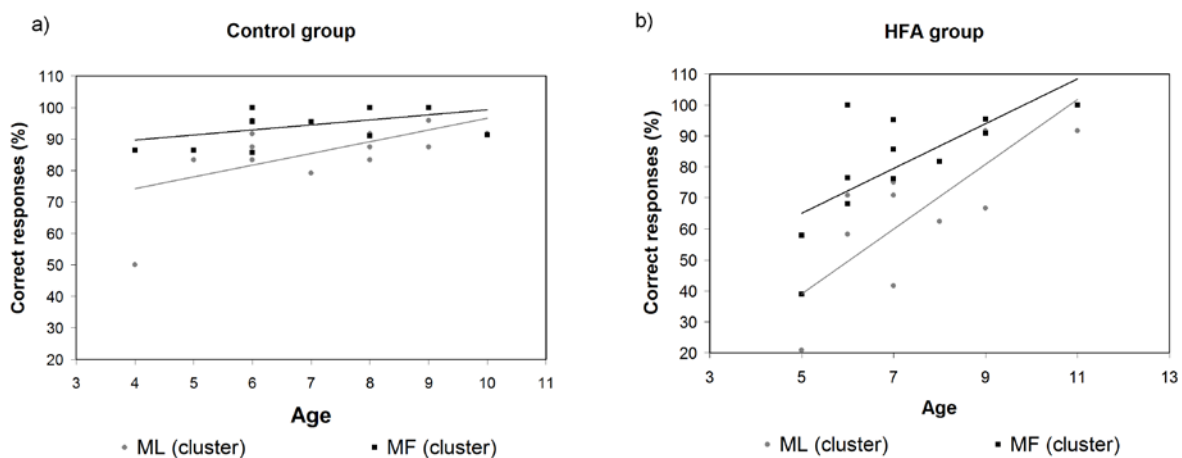

Fig. 5.2 Overall imitation of ML and MF actions correlated with age of subjects for a) control group and b) HFA group.

The imitative performance of the Control group on ML actions (but not that of meaningful actions, r = .51, $p > .05$) correlated significantly with increasing subjects' age (r = .56, $p < .05$), while the imitative performance of the HFA group on either type of gesture significantly correlated with their increasing age (MF: r = .72, $p < .05$) ML: r = .79, $p < .001$).

5.3.3. Specular and Anatomical Imitation

Participants could imitate a gesture by selecting the same limb used by the model (i.e. anatomical imitation) or by using the one on the same side of the model's body as if they were looking in a mirror (i.e. specular imitation). It has often been claimed that typically developing children at a young age tend to prefer specular over anatomical imitation, and that the preference becomes apparent later in life (when they are about 12 year old) (Wapner & Cirrilo, 1968). Which kind of imitation ASD children prefer is still not clear. In one study, unlike controls, adults with autism did not benefit from viewing other person's mirror-image movements (Avikainen et al., 2003), while in another one both control and ASD children showed a preference for mirror imitation of hand actions (Hamilton et al., 2007). In these studies, since the model performs the action using in half of the trials the left hand, and the imitator tends to use the dominant right hand, it is difficult to establish whether participants preferred the specular to the anatomical imitation.

Figure 5.3 plots the percentage of trials in which participants used the left-hand (specular imitation) to imitate the different types of gestures. Although the autistic group made more use than the control group of specular imitation in all imitative tasks, on the Mann-Whitney U test for independent samples, no significant differences were found between the two groups on imitation of transitive (U = -.46 , $p > .1$) and intransitive ML gestures (U = -.20, $p > .1$), transitive with (U = -1.6, $p > .1$) and without (U = -.23, $p > .1$) the actual object at hand, and intransitive MF gestures (U = -.41, $p > .1$).
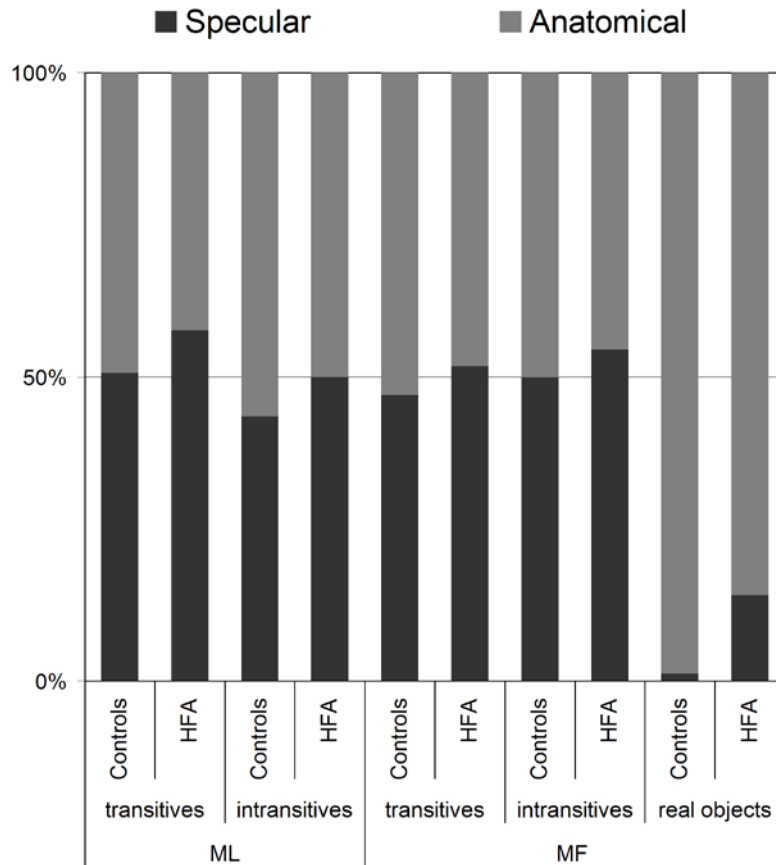
Fig. 5.3 Percentage of specular and anatomical imitation for each type of imitative task.

5.3.4. Mental rotation

Eleven (out of 14) control children and 8 (out of 13) HFA children succeeded in the left-right discrimination test and hence they were administered with the two rotation tasks. For both the Little Man rotation task and left-right hand decision task we run two separate Mann-Whitney U tests, in which we compared the accuracy of the control group and the HFA group (see Fig. 5.4).

Control children (mean accuracy 14.45, SD = 1.81; M = 18.27, SD = 1.919.13) were more accurate than HFA children (mean accuracy 10.87, SD = 3.04; M = 16.12, SD = 2.29) on the Little Man task and on the left-right hand decision task ($Z = -2.44$, $p < .05$. and $Z = -2.07$, $p < .05$ respectively).
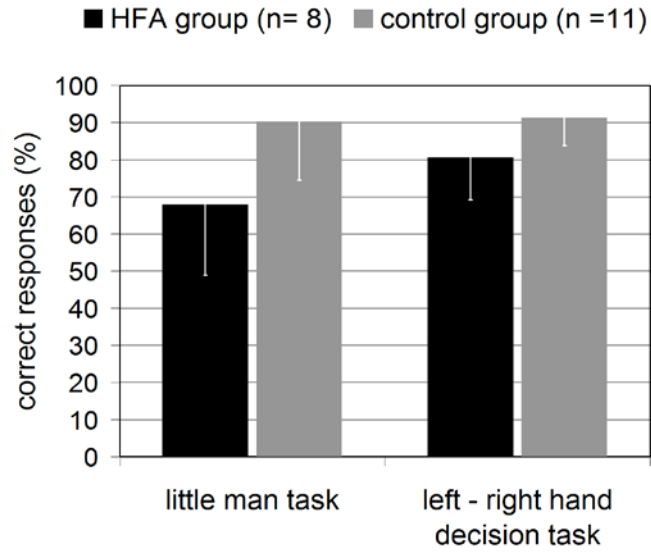
Fig. 5.4 Performance accuracy for both rotation tasks in percentage.

5.2.5. Do imitation and mental rotation correlate?

In order to understand whether the ability to carry out the two different mental rotation tasks influenced participants' imitation performance, we correlated the scores on each mental rotation task with the accuracy on imitation of ML and MF gestures (see Figures 5.5-5.6). Performance on the Little Man task did not correlate with imitation of either ML ($r = .34$, $p > .05$) or MF gestures ($r = .38$, $p > .05$). In contrast, performance on the left-right hand decision task moderately but significantly correlated with both imitation of MF ($r = .46$, $p < .05$) and ML actions ($r = .54$, $p < .05$).
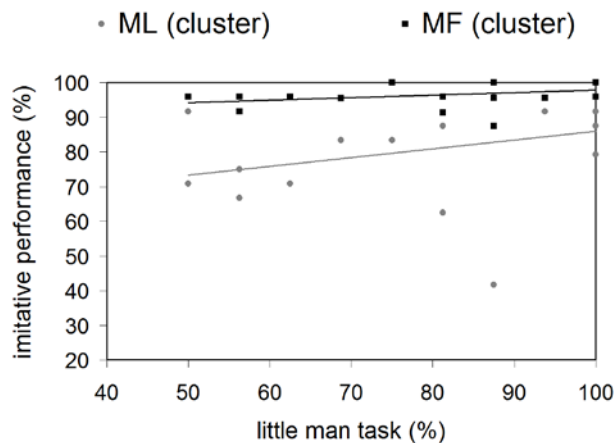
Fig. 5.5 Overall imitative performance for ML and MF actions correlated with the performance on the Little Man rotation task

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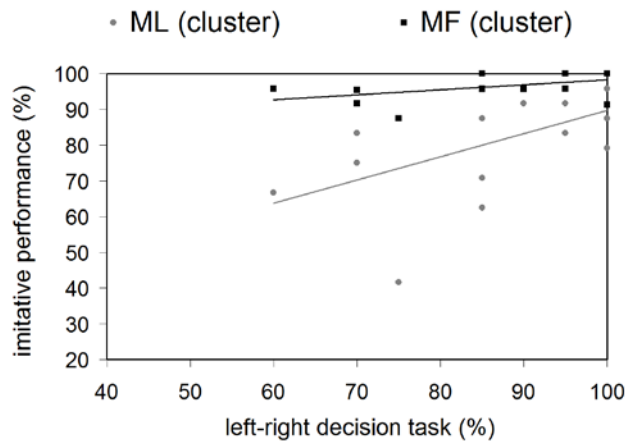
Fig. 5.6 Overall imitation of ML and MF actions correlated with the performance on the left-right hand decision task

5.4. Discussion

In the current study we aimed at verifying the types of gestures that autistic children succeed or fail to imitate. We therefore tested a sample of high-functioning children with a clinical diagnosis of autism and an age-matched sample of typically developing children for their ability to imitate either meaningful or meaningless gestures. Gestures could, or could not, involve the presence of an object (transitive or intransitive). In agreement with Williams et al.'s (2001) view, we found that, relative to control children, high-functioning autistic children were more impaired in imitating ML than MF actions. In addition, we found that the imitative performance of either group of participants was not dependent on whether the gesture implied the use of an object or not (transitive vs. symbolic communicative), as both MF transitive and symbolic communicative gestures were imitated equally well by both groups.

In particular, the finding that imitation of object-related actions as well as symbolic communicative gestures is preserved in ASD children is inconsistent with the hypothesis put forward by Hamilton (2008). According this author's proposal, autistic children are able to imitate only gestures that imply the use of an object (or include a clear goal) as its presence allows the emulation of the action instead of mimicry. An individual emulates an observed action by first

extracting the goal of the action and then, planning and reconstructing it by her own means (Hamilton, 2008). The fact that HFA and control children imitate equally well MF actions that do not have an object associated (i.e. symbolic communicative gestures) challenges the view that autistic children are only able to emulate.

The finding that, in HFA children, imitation of both transitive and intransitive MF actions is intact while imitation of ML actions is impaired, strongly suggests that they suffer from a selective damage to one of the two putative mechanisms for action imitation hypothesised by Tessari and Rumiati (2004): the indirect, non-semantic route. The access to the lexical-semantic system for actions stored in memory appears to be intact in these children.

Our results might have useful implications for an early diagnose of the disorder, in that we suggest that only the use of ML actions is appropriate for assessing imitation skills. Due to several factors, the diagnosis of autism is still often made quite belatedly (around 6 years of age, Hoewlin & Moorf, 1997) mostly because it is based on the assessment of language skills that do not develop before the first year of life. Our study demonstrates that testing imitation could be used for identifying the eventual presence of the disorder without having to wait for the emergence of linguistic abilities.

Regarding imitation of ML gestures, the accuracy of both autistic children and control children tended to improve with participant's increasing age. The recovery of symptoms in ASD has long been debated and mechanisms that might promote it have been systematically scrutinized (see Helt et al., 2008, for a review). Although our results cannot be taken as definitive evidence, they are in agreement with the hypothesis that the imitative ASD children's difficulties might not represent a true deviance but rather a delay in development, as they ameliorate as children get older. Therefore the imitative deficit could be expected to back down as the child gets older.

We failed to find any difference between specular and anatomical imitation. In approximately half of the trials, participants did prefer to imitate with their non-dominant hand,

mirroring the observed movement. Overall, our results suggest that, for both autistic and typically developing children, imitating an observed movement in a specular manner might be beneficial.

5.4.1 Mental rotation in HFA children

With respect to issue of whether ASD children are able to mentally rotate stimuli, we found that they performed poorly on both the Little Man task and for the left-right hand decision task compared with age-matched controls. Overall imitation of MF and ML actions correlated equally with performance on either mental rotation tasks. However, partial correlations revealed that, while the performance on the Little Man task did not correlate with either action type, imagining the rotation of our own hands correlated with imitation of both MF and ML actions. The fact that only egocentric mental rotation, implicated in left-right hand decision task, correlated with imitation performance suggests that rotating external objects, as in the Little Man, plays a less critical role in imitation task we used.

To the best of our knowledge, this is the first report in which deficits on mental rotation tasks in ASD have been reported. Our results are not consistent with the findings reported in a study in which ASD outperformed controls in non-rotational aspects of mental transformations (Falter, Plaisted, & Davis, 2008). They are also in part at variance with a recently reported dissociation between impaired visual perspective taking and normal performance on a mental rotation task (Hamilton, Brindley, & Frith, 2009). In this latter study, performance on the visual perspective taking task was a good predictor of the poor mentalising abilities of their sample of autistic children.

Given that this is the first time that this pattern has been observed, it is not without caution that we draw our remarks here. More research is needed to investigate further the role of mental rotation in imitation tasks. Nonetheless, if the difficulty of autistic children in mental rotation tasks is to be confirmed, then we should take more seriously the possibility that this deficit might impair the ability of these children to imitate the actions made by others.

Chapter 6

General discussion and concluding remarks

An open question in the field of human imitation regards whether imitation of transitive and intransitive actions is accomplished by the same mechanism or rather by independent mechanisms. On the one hand, Buxbaum (Buxbaum et al., 2007; Buxbaum, 2001) holds that imitation of intransitive and transitive actions is engendered by different mechanisms. Importantly, this position accounts for observations of brain damaged patients who were more impaired in imitating transitive actions than intransitive actions (e.g. Buxbaum et al., 2007; Haaland et al., 2000; Roy et al., 1991). On the other hand, in a neuroimaging study (Kroliczak & Frey, 2009) it has been found that

imitation of transitive actions and imitation of intransitive actions involve a common brain network. Kroliczak and Frey (2009) claimed that a simpler and parsimonious explanation for the selective deficit in imitating transitive actions is that this action type may simply place higher demands on a representational system that is shared by both action types. Consistently with the latter argument, in Chapter 2, I reported that subjects found transitive gestures generally more difficult to imitate than intransitive gestures (Experiment 1). Given that the complementary dissociation (impaired intransitive gestures and intact transitive pantomimes) has not yet been reported, the complexity of the movements seems to be the best explanation for the existing neuropsychological observations. Additionally, I have shown a successful replication of the original findings of the dual route model of action imitation (Tessari & Rumiati, 2004) using intransitive communicative actions (Chapter 2, Experiment 2). The pattern of results obtained replicates both the superiority and type of list effects found by Tessari and Rumiati (2004), suggesting that the semantic route can process not only object-related actions, but also communicative intransitive actions, as for both types of stimuli, representations can be retrieved from long term memory. Taken together the findings presented in Chapter 2 suggest that there may not be different mechanisms, dedicated to the imitation of transitive and intransitive gestures.

One main feature of the dual model for action imitation (Tessari & Rumiati, 2004) is the flexibility by which subjects can process both MF and ML actions through the direct route. The observed list effect, i.e no differences in imitation of MF and ML actions in a mixed condition as compared with a blocked condition, (Tessari & Rumiati, 2004; Rumiati, Carmo & Corradi-Dell'Acqua, 2009) led the authors to propose that, while in the blocked condition, participants select a lexical-semantic route for imitating MF actions and the direct route for imitating ML actions, in the mixed condition, they imitate either action type by strategically select the direct route.

At variance with this view, Press and Heyes (2008) argued that, in the mixed condition, participants' performance was contingent upon stimulus properties and not upon the type of list, so

that, for imitation of MF actions the semantic route was always selected while imitation of ML actions relied on the direct route. As evidence, these authors showed that in the mixed condition carry over costs of ML actions inflicted on the subsequent trial could explain the List effect found (Press & Heyes, 2008).   In Chapter 3, I further addressed this issue of route selection in action imitation, as I investigated whether the route selection to imitation is consistent with a stimulus-driven hypothesis (as argued by Press & Heyes, 2008) or whether the cognitive system exerts a top down control over route selection and can, under specific circumstances (i.e. mixed condition), strategically switch between the two different task-sets (i.e. routes to imitation, as in Rumiati & Tessari, 2002; Tessari & Rumiati, 2004). To that end, we employed a task-switching paradigm (Chapter 3, Experiment 2), as task switching paradigms have been commonly used to investigate processes of cognitive flexibility and control processes of task-set reconfiguration (e.g. Monsell, 2003). In this experiment, we directly tested the *carry-over costs* of ML imitation on subsequent trials by comparing the blocked condition with two mixed conditions having different amounts of switches between action types. We found no relief of *carry over costs* for ML actions in conditions with fewer switches between the two action types, as in previous experiments from our lab in which transitive actions (Tessari & Rumiati, 2004) or intransitive actions were used (Chapter 2, Experiment 2, and Chapter 3, Experiment 1). Moreover, in Experiment 2 (Chapter 3), only in the mixed condition with fewer switches, the presence of both *mixing costs* and of a preparatory effect for the forthcoming switch was observed. The results on *mixing costs* and the subsequent analysis on the preparatory effect are in agreement with an endogenous, strategic task reconfiguration, in which mixing costs are attributed to preparation for the forthcoming event (Los, 1996), hence, consistent with participants adopting a top-down strategic selection of the routes when they imitate mixed MF and ML gestures.

While the dual route model for action imitation has been tested studying brain damaged patients (e.g. Tessari et al., 2007), healthy subjects (Tessari & Rumiati, 2004, Rumiati & Tessari, 2002; Chapters 2-3 of the present thesis) or with neuroimaging techniques (Rumiati et al., 2005;

Chapter 4 of this thesis), in Chapter 5 I proposed Austim Spectrum Disorders as a suitable model for investigating the dual mechanism of imitation, as it can fully account for the selective imitative deficits observed in high-functioning autistic (HFA) children. In Chapter 5 we observed a significant meaning (MF, ML) and group interaction, with HFA children performing known MF actions better than novel ML gestures compared with the group of control children. Importantly, and in agreement with the findings of Chapter 2, imitation of intransitive and transitive gestures did not differ across the two groups. In Chapter 5, we also reported that HFA children's performance on two mental rotation tasks was poorer than that of control children (Little Man Task and Left-right hand decision task). Correlations revealed that rotation of external objects (as in Little Man Task) did not correlate with imitation of either action type, whereas imaging the rotation of our own hands (as in Left-right hand decision task) correlated both with imitation of MF and ML actions. The fact that only egocentric mental rotation correlated with imitation performance suggests that rotating external objects, as in the Little Man, plays a less critical role in the imitation task we used, but seriously raises the possibility that deficits related to spatial mental transformations might impair the ability of HFA children in imitating the actions of others. Furthermore these findings suggest that the interplay between mental rotation processes and imitation processes seems to be a prolific research field, and that the role of mental transformations in control of action that has already been addressed by some authors (e.g., Buxbaum, 2001) should be continued not only within ASD but also with normal population.

6.1. Learning effects

The involvement of the human mirror neuron (MN) system has been proposed as being the neural substrate of action understanding (Buccino, Binkofski, & Riggio, 2004a; Rizzolati & Craighero 2004, Rizzolatti & Sinigaglia, 2008) as well as of imitation (Iacoboni, et al., 1999). However, as brain activity with mirror properties seems insufficient to provide a good description of imitation of actions that do not belong to one's own repertoire, supplementary processes have

been proposed (Buccino, et al. 2004b; Vogt, et al., 2007). In Chapter 4, we investigated whether action observation requires different processes, and recruits different brain resources, depending on whether the ultimate goal is to imitate or to understand the presented action. In addition, we evaluated whether imitation of MF and ML actions led to different patterns of brain activity, as it should be expected if MF and ML actions are processed by different mechanisms. Our key result, of an anterior left lateralized component observed for meaningless actions while subjects imitated gestures, is consistent with the idea that imitation of novel actions requires supplementary processes involving left middle frontal areas that suggest the engagement of general associative learning mechanisms. This finding regarding the recruitment of a supplementary process allegedly involved in learning of new actions, gives support to the idea that the direct route can be effectively used in learning trough imitation. In Chapter 2 (Experiment 2) we had already shown that in the conditions in which the non-semantic route was presumably selected such as, for instance, when subjects imitated ML gestures in the ML blocked condition and both MF and ML gestures in the mixed condition, a significant increase in the subjects' accuracy was systematically observed throughout the experiment (learning effects). The fact that performance improved only when the direct route was presumably operating (i.e. MF actions in blocked condition) suggests that the semantic route might have reduced learning capabilities. Notwithstanding the fact that we have shown consistent behavioural and ERP data that seems to indicate the differential participation of the dual route in general learning, empirical evidence that bridges the gap between behavioural and brain related activity is still lacking. Further research that would show that the supplementary neural processes reported are indeed needed for the acquisition of new motoric representations is highly recommended.

6.2. Time-course of the dual mechanism

Following Press and Heyes (2008), we have shown too that both superiority effect and list effects can be observed with RT. In Chapter 3 (Experiment 1), we consistently observed slower

responses for all the conditions where the direct, sub lexical route is thought to be primarily operating (i.e., ML actions in blocked condition and mixed conditions), while the indirect (MF actions in the blocked condition) led to a faster processing of the to-be-imitated action. This finding allows a better understanding of the mechanisms underlying imitation, as it makes possible a characterization of the dual route in terms of their time-processing span. It has been previously reported (Tessari & Rumiati, 2004) that the lexical-semantic mechanism to imitation of actions gives rise to a superior performance when subjects imitate under time pressure (i.e. a deadline procedure). The observation that this same processing mechanism also leads to shorter latencies of the imitation output discards the idea that the superior performance accuracy characteristic of the semantic route is due to a more cautious and slow process. In addition, the poor performance of the direct route does not seem to be due to a fast and hurried processing; surprisingly, the direct route is featured by much slower latencies. The two mechanisms are not only characterized by different time courses but importantly they seem to differ in their efficiency. The reason behind redundant mechanisms, where one is highly inefficient (i.e. direct route), thus seemingly unnecessary or pointless, is unclear. For a more exhaustive view, one should take into account the discrepancy in learning rates already reported (Chapter 2, Experiment 2). The learning properties of the dual operation and the differential time-course featured by each route are critical for understanding the competence of each route and suggest that the two routes fulfill different functions. As others have suggested (Byrne, 2005; Urziris, 1981), imitation plays two conceptually different roles. The first mainly regards the learning of new actions and understanding of the world - learning through imitation - and the second one might serve a social bonding function, as an expression of shared mutuality. As suggested by Byrne (2005), the latter is a much simpler process that would entail anything new to be learned. In fact, we are now able to describe an operation that on expenses of very poor learning properties is a quick alternative to imitation that could be put to use when the relevant task at a given moment is to force social bonding. Otherwise, a mechanism dedicated to

learning can be selected - the direct route – more prone to errors and slow, yet with the great advantage of enabling the acquisition of new actions thought the observation of others.

For a deeper understanding of imitation in humans it is critical to specify what kind of imitation one is referring to. Not every imitation model that is currently available tackles both learning through imitation and social interaction facilitation, hence, a good practice would be to refer explicitly which psychological function a given model addresses.

More, the use of a measure with increased objectivity, as RT, gives strong support to the dual route model. Given it is not dependent on subjective ratings, it carries a considerable improvement in the methodology employed up to now, and should therefore be extensively used in subsequent studies regarding the dual route model.

6. 3 Concluding remarks

The aim of this thesis was to investigate the dual route model regarding some known issues and criticisms, and to explore and provide support for main attributes, as learning effects or time-course. Taken together, the results of various experiments that focused either on behavioral findings from healthy individuals and ASD individuals, or on brain related activity, give support to a model of human imitation that assumes the coexistence of two singular mechanisms, that draw, at least partially, upon differential neural mechanism.

Appendixes

Appendix A

Meaningful transitive actions (from Tessari and Rumiati, 2004)

(1) To clean a surface with a cloth

(2) To comb

(3) To paint (a wall)

(4) To iron

(5) To drink

(6) To eat with a fork

(7) To put on lipstick

(8) To pour with a bottle

(9) To brush one's own teeth

(10) To stir

(11) To hammer

(12) To play tennis

(13) To strike a match

(14) To saw

(15) To cut with a knife

(16) To screw in a light bulb

(17) To use a key

(18) To smoke

Appendix B

Meaningful intransitive actions (for the Italian culture)

(1) Silence: Closed hand with index finger upright, close to the lips.

(2) Hungry: Straight hand, palm down, hitting repeatedly on the same side of the torso.

(3) Go away: Hand folded at 90º, with fingers pointing down, moving towards the left.

(4) Military Salute: Open hand, diagonally close to the forehead.

(5) Ok: The tips of the index finger and of the thumb make a

circle, with the other fingers being open.

(6) Be strong: Arm bent in 90º, with hand up and closed. On the same side of the body.

(7) More or less: hand open in front of the body; moving repeatedly 45º to the left and to the right (relative to themidline of the body).

(8) Sleepy: Open hand; palm on the ipsilateral cheek (right)

(9) Listen: slightly folded hand; close to the ear.

(10) Come here: Closed hand, with index finger opening and closing repeatedly.

(11) Good luck: Index finger and middle finger crossed, with all the other fingers closed.

(12) Victory: Index finger and middle finger drawing a V shape.

(13) No: Index finger upright, with the remaining fingers closed, moving 45º to the left and to the right (relative to the midline of the body), repeatedly.

(14) Stop: Open hand, away from and in front of the body.

(15) Bye Bye: Open hand, moving 45º to one side and the other, repeatedly.

(16) Later: Hand bent in 90º to the left; index finger straight out, moving in a circular way.

(17) Hitchhiking: Arm bent in 90º; hand closed, thumb out. Arm repeatedly moving away from the body to the right side.

(18) Crazy: Index finger sticking out of a closed hand;, hitting repeatedly the forehead.

Appendix C

Error classification

(1) Spatial Error of the hand: The overall movement of the limb is correct but the hand posture is wrong;

(2) Spatial Error of the arm: The arm posture is wrong;

(3) Spatial Error of fingers: The overall movement of the limb and hand is correct but finger posture is wrong;

(4) Spatial orientation error: The arm is moving in the wrong direction or in the wrong plane;

(5) Spatial Error of movement endpoint: The movement endpoint is not reproduced correctly;

(6) Static-Dynamic Spatial error: A Static imitation of a movement is produced when a dynamic action is presented (i.e., the position and configuration of the body parts are correct, but the correct rhythmic or repetitive movement associated with the gesturing is not reproduced); or a dynamic (rhythmic or repetitive) movement is produced when the target action does not require it.

(7) Kinematic error: This is a movement that is generally correct except for one kinematic dimension such as velocity or smoothness;

(8) Prototypicalization: (for MF actions only). A prototypical version of the action is performed;

(9) Visuo-Semantic: The action is visually similar and semantically related to the target action. (for MF actions only);

(10) Perseveration: A movement is composed of a combination of items included in the list;

(11) Global Perseveration: An action included in the list, is reproduced instead of the target action;

(12) Lexicalixation: A MF action, visually similar to the ML target action (but not included in the list), is produced. (for ML actions only);

(13) Substitution: A visually similar meaningful action (not include in the list), is produced instead of the meaningful action that was presented. (for MF actions only);

(14) Omission: Imitation of the target action is not performed;

(15) Unrecognized error: The response involves a movement that the raters failed to recognize;

(16) Conduit d'approche: Faulty attempts to imitate the action, but only eventually is a correct answer provided.

Appendix D

Error Classification

(1) Spatial Error of the hand: The overall movement of the limb is correct but the hand posture is wrong

(2) Spatial Error of the arm: The arm posture is wrong

(3) Spatial Error of fingers: The overall movement of the limb and hand is correct but finger posture is wrong

(4) Spatial orientation error: The arm is moving in the wrong direction or in the wrong plane (e.g. plane)

(5) Spatial Error of movement endpoint: The movement endpoint is not reproduced correctly.

(6) Static-Dynamic Spatial error: Static imitation of movement is produced when a dynamic action is presented or a dynamic movement is produced when the expected target action involves rhythmic or repetitive movement (a static instead of dynamic or dynamic instead of static)

(7) Kinematic error : movement in the wrong direction, different velocity, different trajectory ;

(8) Prototypicalization: Just for Meaningful actions. A prototypical version of the action is performed.

(9) Visuo-Semantic: The action is visually similar and semantically related to the target action. (just for MF actions)

(10) Perserveration: A movement is composed of a combination of items included in the list.

(11) Global Perserveration: An action included in the list, is reproduced instead of the target action.

(12) Lexicalixation: A meaningful action, visual similar to the meaningless target action (but not included in the list), is produced. (just for ML actions)

(13) Substituition: A visual similar meaningful action (not include in the list), is produced instead of the meaningful action that was presented. (just for MF actions)

(14) Conduit d'approche: Faulty attempts to imitate the action, but only eventually is a correct answer provided.

(15) Crossing, not crossing: correct gesture but in the wrong side of the body

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