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RESEARCH ARTICLE

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Imitation of novel and well-known actions

The role of short-term memory

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Abstract Four experiments were carried out using the action span paradigm. In experiment 1 we found that well-learnt, meaningful (MF) actions were imitated better than novel, meaningless (ML) actions. In experiments 2 and 3, during the encoding of MF and ML actions, participants were required to carry out different suppression tasks. In experiment 2 we replicated the advantage of MF actions over ML actions and also found that the motor suppression shortened the action span more than the other forms of suppressions (spatial and articulatory). Action encoding and motor suppression tapping the same subsystem, temporarily holding the motor information, could explain the reduced motor span obtained in experiment 2. Two alternative explanations that could have accounted for this effect were ruled out in experiments 3 and 4. In experiment 3 we verified whether the reduction of the action span was produced by the different combination of the articulatory suppression with motor suppression or with the spatial suppression. In experiment 4, we demonstrated that the reduction was not due to the motor suppression being more difficult than the other types of suppression. The critical finding that the spans of well-learnt, MF actions are longer than those of novel, ML actions observed in experiments 1 and 2 was interpreted in terms of different processing routes engaged in the imitation of these two types of actions. MF actions can be imitated along both a semantic, indirect route and a direct route leading from the visual analysis of the action to the motor system. In contrast, the imitation of ML actions is accomplished along the direct route only.

Keywords Imitation · Mirror neurons · Apraxia · Short-term memory · Human

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Introduction

The key question to which some of the most influential theories of imitation have been trying to find an answer is how perception and action are mediated in imitation. The dominant view is that an action performed by another individual is observed and matched directly onto a motor program. The active intermodal mapping theory (AIM) of Meltzoff and Moore (1977), for instance, postulates that humans have an inborn ability to match seen movements of others with felt movements of their own. This theory is based on the series of experiments in which infants match seen facial or manual gestures onto a motor output, supported by the proprioceptive feedback loop.

Neurophysiological and brain imaging studies brought strong evidence to support the direct mapping account of imitative behavior. The basic finding of this line of research is that a common neural network exists in humans (Fadiga et al. 1995; Grafton et al. 1996; Rizzolatti et al. 1996; Binkofski et al. 1999; Iacoboni et al. ss 1999) and in monkeys (Di Pellegrino et al. 1992; Gallese et al. 1996) that sustains both production and recognition of actions. All these studies mentioned a brain region comprising sectors of the Broca's area (Brodmann areas, BA, 44–45, or F5 in the monkey).

The view of imitation as a direct matching, however, does not discuss the role played by the memory components – and in particular the short-term memory – in mediating imitation of actions. For instance, the work done by Smyth and colleagues (Smyth and Pendleton 1988; Smyth et al. 1989) seems strongly to favor the existence of a subsystem which temporarily holds the observed movements until they are actually executed. In 1989 Smyth et al. replicated and developed the results obtained in a previous study (Smyth and Pendleton 1988), finding a double dissociation between the ability to perform a task involving movements directed to targets in space and the ability to perform a task involving hand configurations. In their first experiment, participants were asked to reproduce a hand configuration span (movement memory task) while performing one of two different suppression tasks (the movement suppression task and the spatial suppression task) with either the right or the left hand. Participants had to reproduce the correct sequence with their right hand. Results showed that the movement suppression task on either the right or the left hand interfered with participants' movement span. In a second experiment, the Corsi block task [1] was used as spatial memory task presented together with the spatial suppression task or the movement suppression task involving either the right or the left hand. The performance on the Corsi block test was affected only by the spatial suppression task on either hand, suggesting that a movement pattern is not a critical component in performing movements directed to targets in space and, moreover, that the interference does not act at a peripheral motor control system. The authors concluded that the double dissociation between the ability to perform the task involving movements directed to positions in space (Corsi block test) and the ability to perform a task involving patterns of bodily movements supports the hypothesis that working memory has a dedicated subsystem independent of that of a spatial short-term memory. The finding that interference affects either hand equally suggests that there may be a single control system for both hands.

Is imitation affected by familiarity?

Smyth and Pendleton (Smyth et al. 1989) used movement patterns that carried no particular meaning as stimuli in their 1989 study. However, differences in the imitation of meaningless (ML) and meaningful (MF) actions can be predicted on the basis of a cognitive model of imitation. In such a model (see Fig. 1), ML actions can be imitated *only* using the processing route leading to the motor system (route "a" in the model) from the visual analysis, bypassing the long-term memory (LTM) station. MF actions, on the other hand, can be imitated using both direct, nonsemantic route a and semantic route "b". In fact MF actions are stored in the LTM because they have been previously acquired. Since the imitation of MF actions can be accomplished using both the nonsemantic and semantic routes, whereas the imitation of ML actions relies only on the nonsemantic route, it is reasonable to expect better encoding and imitation of MF than of ML actions.

Evidence supporting the existence of at least two partially independent processing routes is drawn from neuropsychology. On the one hand, four patients have been reported who are not able to imitate ML gestures but show a normal performance on MF gestures (Mehler 1987; Goldenberg and Hagmann 1997). On the other hand, Bartolo et al. (2001) have described a patient whose performance on MF actions falls outside the normal range, in contrast with a normal imitation of ML actions. According to the model sketched in Fig. 1, the deficit in copying of ML actions corresponds to a deficient direct route (route *a* in the model) that leads from vision to-motor control, bypassing the efficient, LTM station where MF gestures are stored (route *b* in the model). In contrast, the selective deficit in imitating MF actions can be accounted for by a fault occurring during the processing along the semantic route.

[1] The Corsi block test comprises nine blocks asymmetrically placed on a table. Participants are required to reproduce sequences of blocks as previously touched by the experimenter in exactly the same order (Milner 1971).

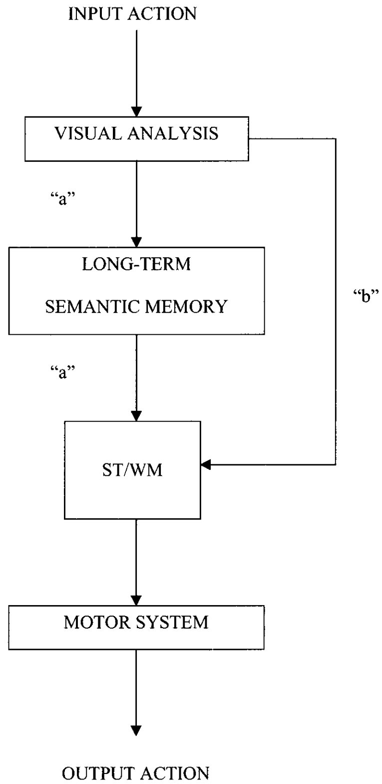

Fig. 1 The model represents the two processes involved in the imitation of meaningful (MF) and meaningless (ML) actions. After the visual analysis, if the action to be imitated is ML, the process *a* is selected, whereas if imitation involves a MF action, both the semantic and nonsemantic processes may be selected (route *b* and route *a*, respectively). (*ST/WM* short-term/working memory)

The present study

A span paradigm was used to verify whether imitation of MF and ML actions relies on different processing routes. It was expected that the span would be shorter when participants were required to imitate ML, since these actions are not stored in the LTM and therefore require more loading of the short-term memory system than the imitation of MF actions does. In order to demonstrate that the short-term system is dealing selectively with motor information, a motor interference was exerted by the participants during the encoding of actions for later imitation (see Smyth and Pendleton 1988). If a motor suppression is performed during the encoding, a shorter action span can be predicted, as well as differences in spans for MF and ML actions.

Experiment 1: Does the meaning of an action influence its imitation?

This experiment was designed to ascertain whether imitation performance is influenced by the familiarity of the action: a better performance was expected on imitation of MF actions.

Method

Participants

Eighteen right-handed participants, all students at SISSA, took part as volunteers in the study. All persons gave their informed consent prior to their inclusion in the study.

Stimuli

Two sets of stimuli were used. The first set included nine MF pantomimes of object use involving a whisk, a comb, a spoon, a razor, a hammer, a fan, a toothbrush, an iron, and a jug (see Appendix 1). Prior to the experiment, ten participants had been asked to name a larger set of MF actions shown on a TV screen at the rate of one every 1.5 s, of which nine, recognized by all participants, were selected for use as stimuli in the real experiment. The second set of stimuli included nine ML actions, involving the same body parts and movements as the MF actions, obtained by modifying the relationship between the hand/arm and the trunk. For instance, the pantomime of combing became a ML action in which similar hand and arm-movements were carried out (see Appendix 2). In this case, however, the movements were performed in a downward movement on the face, instead of around the head, proceeding from the front toward the back. Five participants were asked whether the ML actions resembled a real action or not. None of the ML actions were judged to be consistent with the use of common objects. All actions used in the experiment were performed by an actor using his left hand [2] and video-recorded.

Design and procedure

Both MF and ML actions were presented for recall in serial order. As soon as the presentation of the sequence of actions was concluded, the participants were instructed to reproduce the sequence of actions in the exact order with the dominant hand. Participants began with a span-length of two actions. If they succeeded, they were presented with a sequence of three; if they failed they repeated another sequence of two. The trial ended when a participant failed to perform one span length twice. The final score (span) for each participant was the number of times on which they failed twice, minus one. The participants' performance was video-recorded from the moment they engaged in the suppression task until they imitated the actions, and later scored by two independent judges. An action was scored as incorrect if it involved one of the following errors:

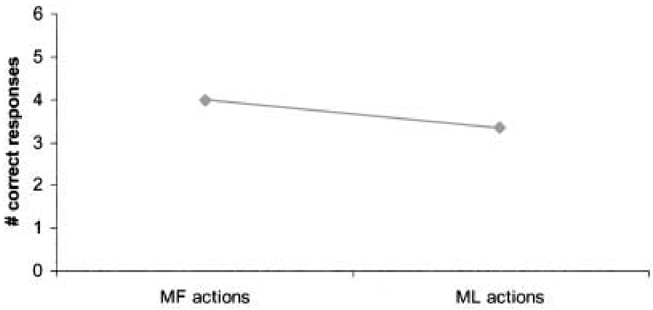

Fig. 2 Means of correct responses for meaningful (MF) and meaningless (ML) actions without any suppression task (baseline condition)

1. *Insertion:* a movement inserted in a sequence to which it does not belong
2. *Blend:* a movement composed of a combination of two items from the original sequence
3. *Deletion:* the omission of an item of the sequence
4. *Transposition:* the participant inverts the order of two items in the sequence
5. *Move:* the participant changes the original order of the items in the sequence
6. *Repetition:* an item is repeated within the sequence
7. *Omission:* failure to give any response
8. *Substitution:* the original movement is substituted with a different movement
9. *Spatial error:* a movement performed in the wrong direction or plan
10. *Body part as a tool (BPAT):* a movement performed by the participant's body part as if it were a tool
11. *Unrecognizable gesture:* a response involving a movement that judges did not recognize

In order to create the stimuli (i.e., sequences of actions of different length), the following procedure was adopted: (1) each of the nine actions was associated with a number from 1 to 9; (2) an action sequence based on the number sequences of the reverse digit span subtest of the Wechsler Adult Intelligence Scale (WAIS; Wechsler 1981) was formed. A complete list of the stimuli used is shown in Table 1. MF and ML actions were presented in two separate blocks and the type of stimuli was counterbalanced across subjects. The actions were shown on a TV monitor. Each action remained on the screen for 1.5 s and there was a blank of 1 s between actions. The study has been approved by the local ethics committee.

Results

Data were treated in a two-way ANOVA for repeated measures. A significant difference was found between the two types of action ($F_{1, 17}$=5.67, mean square, MS=4.00, P<0.05). The mean across participants was 4.00 for MF actions and 3.33 for ML actions (see Fig. 2).

Discussion

The objective was to ascertain what causes the advantage of MF actions over ML actions obtained on experiment 1 and seen also in the studies mentioned in the Introduction. As predicted, the performance (greater span) on MF gestures may be facilitated by the fact that previously ac-

[2] A mirror configuration (i.e., right-hand imitation of left-hand action) was selected because it has been demonstrated that there is a natural tendency to use this configuration when imitating (Kephart 1971; Schofield 1976; but see also Brass et al. 2000, 2001).

Table 1 Stimuli used in experiment 1

	Item					
Span 2	To whisk To eat	To comb To shave				
Span 3	To fan To comb	To whisk To brush	To hammer To eat			
Span 4	To iron To comb	To whisk To hammer	To pour To fan	To hammer To shave		
Span 5	To brush To fan	To eat To brush	To whisk To shave	To shave To comb	To fan To iron	
Span 6	To eat To pour	To iron To whisk	To hammer To comb	To comb To shave	To brush To eat	To shave To fan

quired actions are stored in memory and thus the imitation is primed. With ML gestures, or gestures which are novel to the participants, imitation does not benefit from the same facilitation effect. In addition, whilst the imitation of ML actions is supported only by the nonsemantic route, that of MF actions can be accomplished using both the semantic and nonsemantic routes. The availability of two processes may also explain why the imitation of MF actions is more efficient than the imitation of ML actions.

Experiment 2: Short-term/working memory subsystem and imitation of MF and ML actions

This experiment tested whether a motor suppression task performed during the encoding of actions not only affected the action span more than the other suppression tasks (e.g., articulatory and spatial), but whether it penalized the imitation of ML and MF actions differently.

ML and MF actions were imitated under three different suppression conditions and the results compared. In the first condition, while encoding the actions, the participants were engaged in an articulatory suppression task, in order to prevent them from verbally labeling the actions. The action span observed served as a baseline. In the second condition, the articulatory suppression task was combined with a motor suppression task and, in the third condition, with a spatial suppression task.

Method

Participants

Twenty right-handed participants, all students at SISSA, took part as volunteers in the study.

Stimuli

The stimuli were the same as those used in experiment 1.

Design and procedure

Except where stated otherwise, design and procedure were the same as in experiment 1. Participants were instructed to imitate with the dominant hand the sequence of actions in the exact order they saw it as soon as the presentation of the sequence of actions was concluded. Each subject took part in three experimental conditions: (1) articulatory suppression, (2) articulatory suppression and motor task, and (3) articulatory suppression and spatial task. In condition 1, participants were instructed to count “1, 2, 3, 4, 5” aloud repeatedly while encoding the stimuli to be remembered. All the participants practiced counting aloud at a rate of 5 digits/s for a total of 1 min prior to carrying out the task. In condition 2, in addition to the articulatory suppression, participants were also engaged in a spatial task that involved the repetitive tapping, in correct sequence, of four spatial targets. The hand remained in the same configuration (outstretched index finger with the hand shaped as a fist), though it was moved to different locations in space. In condition 3, the articulatory suppression was performed simultaneously with a motor task consisting of squeezing and releasing a soft tube held in the hand when bending the arm toward the body. In this experiment, the three conditions (articulatory suppression, articulatory suppression and spatial task, articulatory suppression and motor task) were always initiated prior to the presentation of each sequence of stimuli. The order of conditions and that of type of stimuli (ML and ML) were counterbalanced across subjects on a Latin square design.

Apparatus

We used an apparatus similar to that employed by Smyth et al. (1989). The motor suppression equipment consisted of a tube measuring 10 cm long and 5 cm in diameter. For the spatial suppression task, four wooden plates (70×70 mm) were placed in a square, with 25 mm between each plate. Each plate was tapped using the index finger.

Results

Data were treated in a two-way ANOVA for repeated measures. Results are shown in Fig. 3. A main effect for Type of stimulus was obtained ($F_{1, 19}$=14.26, MS=9.07, P=0.001). Action spans were significantly shorter for ML than for MF actions (mean action span for MF actions, 3.33, and mean action span for ML actions, 2.78). A main effect of Type of suppression was also found ($F_{2, 38}$=3.52, MS=2.03, P<0.05). [3]

[3] A Greenhouse-Geisser’s (Greenhouse and Geisser 1959) correction was applied to F, MS, and P-values, since the within-factor Type of suppression had more than two levels. This correction was applied also to the other experiments when necessary.

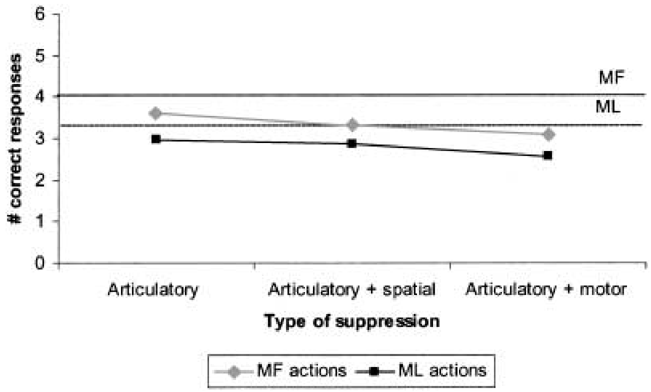

Fig. 3 Means of correct responses for MF vs ML actions according to the different suppression conditions (experiment 2). The baseline for MF and ML action spans is also reported

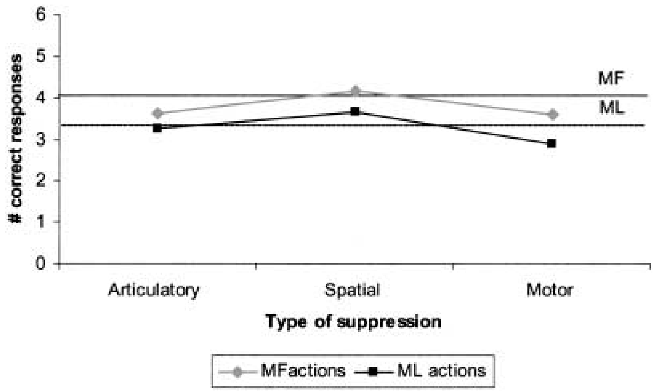

Fig. 4 Means of correct responses for MF and ML actions with and without suppressions (experiment 3)

Action spans were shorter when articulatory and motor suppressions were carried out simultaneously than when either articulatory suppression alone or a combination of spatial and articulatory suppression was carried out [$t(19)=2.40$, one-tailed, $P<0.05$]. However, no significant differences were found in action span between concurrent articulatory suppression alone and concurrent spatial and articulatory suppression combined [$t(19)=1.16$, two-tailed, n.s.]. There was no interaction between the type of stimulus and the type of suppression: the different suppression tasks affected the recall of the two types of actions equally ($F_{2, 38}=0.29$, MS=0.10, n.s.).

Discussion

The finding that the shorter action span was observed when the additional concurrent suppression task was a repetitive movement is in agreement with the idea advocated by Smyth and colleagues that these two activities (the encoding of actions and motor suppression) may bear on the same subsystem.

Besides the short-term/working memory (ST/WM) subsystem hypothesis, there are two alternative explanations that could account for the reduced span when subjects perform a motor suppression task during action encoding. The first holds that the reduction of the action span is the result of the combination of the articulatory suppression with motor suppression as compared to its combination with the spatial suppression; the second alternative that motor suppression may require more resources than spatial suppression. Thus the reduction of the action span in association with the motor suppression would simply reflect the increased effort required during the motor suppression task. These two alternative explanations are addressed in experiment 3 and experiment 4, respectively.

Experiment 3: Single suppression tasks

In experiment 3 the participants were asked to perform one suppression task at time in order to verify whether the reduced action span associated with motor suppression obtained in experiment 2 was due to different combinations of suppression tasks (e.g., articulatory plus motor versus articulatory plus spatial).

Method

Participants

Twenty-four right-handed participants, all students of SISSA, took part as volunteers in the study. None had participated in the previous experiments.

Stimuli

The same stimuli were used as in experiment 1.

Design and procedure

Three suppression tasks (articulatory, spatial, and motor) were performed one at a time by participants during the encoding of actions. The suppression conditions and the stimuli presentation were counterbalanced across subjects in a Latin square design.

Results

The results are shown in Fig. 4. Action span scores were subjected to a two-way ANOVA for repeated measures. A main effect of Type of stimulus was found ($F_{1, 23}=5.54$, MS=10.03, $P<0.05$): action spans were significantly longer for MF actions (mean action span, 3.79) than for ML actions (mean action span, 3.26). A main effect of Type of suppression also emerged ($F_{1, 46}=4.47$, MS=1.43, $P<0.05$). Action spans were significantly shorter when motor suppression was carried out compared with when spatial suppression was performed

Table 2 Types and percentages of errors commited by the participants in experiments 1, 2, and 3 (*ML* meaningless, *MF* meaningful)

Stimulus type		Experiment 1		Experiment 2						Experiment 3					
		MF	ML	MF			ML			MF			ML		
	Suppression type			Articulatory	Articulatory + motor	Articulatory + spatial	Articulatory	Articulatory + motor	Articulatory + spatial	Articulatory	Motor	Spatial	Articulatory	Motor	Spatial
Error type	Insertions	1.47	0.00	10.71	2.15	7.23	2.67	7.46	8.44	8.16	1.27	4.12	6.93	4.76	7.22
	Blending	0.00	1.64	3.57	2.15	3.62	8.00	7.46	6.02	13.27	3.80	4.12	1.98	3.57	5.15
	Deletions	64.71	49.18	50.00	55.91	48.20	45.33	47.76	62.66	34.69	26.58	40.21	50.50	32.14	44.34
	Transpositions	5.89	1.64	8.04	6.45	10.84	9.33	7.46	3.60	17.35	13.92	15.46	5.94	4.76	4.12
	Moves	1.47	1.64	7.14	0.00	3.61	0.00	5.97	2.41	7.14	3.80	5.15	0.99	0.00	2.06
	Repetitions	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.02	0.00	0.00	0.00	1.20	0.00
	Omissions	4.41	3.28	0.00	0.00	0.00	2.67	2.99	0.00	1.02	0.00	0.00	0.00	1.19	1.03
	Substitutions	7.35	14.75	14.28	20.43	13.25	10.67	5.97	10.85	13.27	26.58	19.60	13.86	16.67	16.50
	Spatial errors	5.88	18.03	5.36	7.53	12.05	14.67	11.94	6.02	2.04	13.92	8.25	9.90	29.76	14.43

[$t(23)=2.62$, one-tailed, $P<0.001$]; there was no difference between articulatory and motor suppression [$t(23)=1.01$, n.s.], but articulatory suppression one significantly differed from the spatial [$t(23)=2.03$, one-tailed, $P<0.05$]. The interaction between Type of stimulus and Type of suppression was not significant ($F_{1, 46}=1.3$, MS=0.82, n.s.).

Error analysis of experiments 1, 2, and 3

The error analysis is reported in Table 2. In all the experiments, the types of error that occurred more often were deletions, followed by substitutions and spatial errors. In experiments 2 and 3, insertions and blends were also observed. There were less unrecognizable gesture errors in the experiments 2 and 3 than in experiment 1. Overall there seem to be more transpositions and substitutions for MF than for ML actions. BPAT and transposition errors seem to arise particularly when participants were engaged in the imitation of MF actions, with the former occurring only in the motor suppression condition. It is important to notice that – except for BPAT and spatial errors, which are domain specific – the most frequent types of errors such as deletions and substitutions found in the present study are also the most recurrent types of error in studies investigating the immediate memory for linguistic material in normal subjects (e.g., Conrad 1959).

Discussion

Motor suppression affects the length of action spans more than spatial suppression even when they are not coupled with articulatory suppression. The alternative explanation for the reduction of the action span, i.e., that the results on the motor suppression task are due to the difference between the combination of articulatory and motor suppressions and that of articulatory and spatial suppressions can be dismissed. However, before accepting that the effect of motor suppression on action span is due to the fact that they bear on the same system, it was necessary to demonstrate empirically that the motor suppression task was not more difficult than the spatial suppression task (see experiment 4).

Experiment 4: Word span

This experiment was performed to assessed whether the degree of the effect of motor suppression on the participants' action span could be explained in terms of the motor suppression requiring more general, cognitive resources than spatial suppression. The method of the "specific effect" was used to rule out this explanation (see Sartori and Umiltà 2000). The participants were presented with words representing the objects for which actions had been mimed in experiment 1 and requested to repeat them immediately after presentation. As in experiment 2, the encoding of the stimuli was carried out under the three different suppression conditions (each condition included articulatory suppression and differed only in the addition (or not) of a further motor or spatial suppression task). If no differential suppression condition effect emerges, it could be concluded that the action span reduction observed in experiment 2 is a result of the encoding of the action and the motor suppression task tapping on the same subsystem.

Method

Participants

Eighteen right-handed participants, all students of the University of Trieste, took part as volunteers in the study.

Stimuli

The common names associated with nine objects, the use of which was pantomimed in the actions to be encoded in experiment 1, were used as stimuli: whisk, comb, spoon, razor, hammer, fan, toothbrush, iron, and jug. The words were printed in white on a black ground and were shown on the TV monitor at a rate of one every 1.5 s, spaced with a 1-s blank.

Design and procedure

Unless stated otherwise, the procedure was the same as that used in experiment 2. Participants were requested to repeat the words out loud in the same order in which they were presented. The three suppression conditions were counterbalanced across subjects.

Apparatus

As in experiment 2.

Results

A repeated-measure analysis of variance (ANOVA) was carried out. There were no differences among the three suppression conditions ($F_{2, 34}$=0.22, MS=0.06, n.s.). Results are shown in Fig. 5.

Discussion

The three types of suppression affected the recall of object names equally. It emerged that motor and spatial suppression tasks do not differ in the amount of general resources they require, as no effect of type of suppression was found on the word span. The hypothesis that the effect of the motor suppression on the action span in experiment 2 was due to a resource artifact has therefore been ruled out. Thus the reduction in the action spans when the motor suppression is performed during the encoding could be explained by the existence of a motor subsystem. This is consistent with the finding of Smyth and Pendleton (1988).

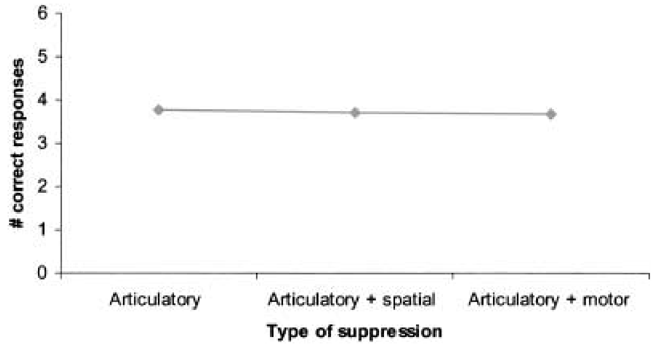

Fig. 5 Means of correct responses for words according to different motor suppression conditions (experiment 4)

General discussion

The objective of this study was to verify the role played by the short-term memory when MF and ML actions are imitated. There are two main findings. First, differences in the imitation of MF and ML actions, with the former being better copied than the latter, were observed in experiments 1, 2, and 3. Second, the action spans of participants engaged in motor suppression while encoding ML and MF actions were shorter than when they carried out either a spatial or an articulatory suppression task (experiments 2 and 3). This reduction cannot be attributed to an effect of particular combinations of motor or spatial suppression with the articulatory suppression (experiment 3), nor to motor suppression being more demanding on resources than the other two forms (experiment 4). These two findings are discussed in depth here.

Imitation of meaningful and meaningless actions

The better imitation performance (i.e., greater span) on MF gestures may be the result of prior acquired actions being stored in memory, thus priming the imitation. However, when the gestures are novel, and unknown to the participants, the facilitation effect is not present. In our model (see Fig. 1), ML actions can *only* be imitated using the processing route leading from the visual analysis to the motor systems (route *a* in the model) and bypassing the LTM station, while MF actions can be imitated by use of the direct route a as well as the semantic route b. The MF advantage over ML actions was not observed by Toraldo, Reverberi and Rumiati (Toraldo et al. 2001) in 86 left-hemisphere brain-damaged patients performing an imitation test devised by De Renzi, Motti, and Nichelli (De Renzi et al. 1980). The authors argued that when patients are required to imitate intermixed MF and ML actions they select the direct, semantic route (route *a* in the model) for imitating both types of actions. This is a more parsimonious choice, since this mechanism can be used for imitating both MF and ML actions. R.I. Rumiati and A. Tessari (unpublished work), using a deadline-technique paradigm, failed to find an advantage of imitation of MF actions when participants were presented with intermixed MF and ML actions. On the other hand, when MF and ML actions were presented in separate blocks, participants performed better on the imitation of MF actions. The reason for the same level of accuracy in the imitation of intermixed MF and ML actions is due to the fact that both stimuli are imitated through the nonsemantic process, which can in fact be used for imitation of both types of stimuli. The facilitation effect observed when MF and ML actions are presented in separate blocks is predicted by our model: unlike ML actions, MF actions are stored in memory and therefore their imitation is primed. Moreover, as opposed to ML actions, MF actions can be imitated using both the semantic and the nonsemantic processes.

Neural correlates of imitation of MF and ML actions

It is not clear whether imitation of MF and ML actions is associated with distinct neural networks. In the first PET study, Decety et al. (1997) found that, irrespective of whether the subjects observed actions for later recognition or later imitation, MF actions, as opposed to ML actions, mainly engaged structures in the *left* hemisphere (i.e., BA 45, 21, and orbitofrontal cortex). It was argued that this neural network is implicated in object processing and in action recognition. In contrast, observing ML actions mainly activate the *right* occipitoparietal pathway, while the activation extends to the premotor cortex when imitation is involved.

In a subsequent study, however, these left/right hemispheric asymmetries associated with the type of stimuli disappear when the perception of stationary hands is used as a baseline (Grèzes et al. 1998). The passive observation of MF actions involves mainly the ventral visual pathway bilaterally, whereas observing ML actions leads to the activation of the dorsal visual pathway also bilaterally. When the aim of perception is to imitate, MF and ML actions share almost the same network, i.e., the dorsal pathway extending to the dorsolateral, premotor cortex, and only in the case of activation ML actions are higher. If the strong association between these areas and the imitation of both types of actions is considered, and the fact that the direct route can process either is kept in mind, it can be speculated that the direct route is associated with these very regions. In this case a visuomotor transformation of the visuospatial characteristics of the action is carried out without accessing the meaning of the actions. Moreover, MF actions also activate the supplementary motor area (SMA), the orbitofrontal cortex, and the left inferior parietal lobule.

Hermsdorfer et al. (2001) have recently conducted a PET study investigating the imitation of hand and finger movements as ML gestures. Subjects presented with paired images of ML hand or finger gestures were required to discriminate whether they were similar or different. There is activation in the left inferior parietal cortex (BA 40) for hand gestures, whereas the right intraparietal sulcus and the medial visual association areas (BA 18/19) are activated for the finger gestures. The lateral occipitotemporal junction (BA 19/37) is activated by both the tasks, but the pre-SMA is mainly active during the hand gesture discrimination task. The hand discrimination task involves areas for the action planning, whereas the finger discrimination task, even if it shares some stages with the hand gesture processing, seems to use bilateral brain structures involved in spatial and form analysis. The authors suggest that the activation of some areas of the dorsal stream implies the existence of a direct route for the imitation of ML gestures, bypassing the semantic memory.

ST/WM subsystem for movements

The finding of a shorter action span associated with the motor suppression task supports the existence of a subsystem temporarily holding the movement information, as suggested also by Smyth and Pendleton (1988). As they did, we argue that the reduced action span is the consequence of the observation of actions and the motor suppression bearing on the same subsystem, which is different to those which process spatial or verbal information.

Such a subsystem is necessary when learning skills from others, including how to use objects or tools. When a person tries to acquire new motor skills from a model through imitation, they retain movements in very much the same way in which a telephone number, heard for the first time, is held in the auditory short-term memory until it is committed in memory. We propose to integrate the observation/execution matching system proposed by Meltzoff and colleagues (Meltzoff and Moore 1977; Meltzoff 1995) and Rizzolatti, Gallese and coworkers (Di Pellegrino et al. 1992; Gallese et al. 1996; Rizzolatti et al. 1996) with a buffer that enables the individuals to temporarily hold the movements from perception to action.

More recently, Bekkering et al. (2000) have pointed out that the direct mapping view cannot account for the errors preschool children make when imitating a model touching a left or right ear (or both) with the left or right hand (or both). Children reach correctly for the object (i.e., ears) but prefer ipsilateral movements (experiment 1). However this ipsilateral preference is not observed when the hand movements are directed to only one ear (experiment 2), or when movements are made in space rather than to physical objects (experiment 3). Bekkering and collaborators argue that a motor pattern is not simply replicated but first decomposed into its constituent components and then reconstructed. Such decomposition-reconstruction process is guided by an interpretation of motor patterns as goal-directed behavior (for a similar view see also Meltzoff 1995). As goals are hierarchically organized, some are dominant over others. As to Bekkering et al.'s (2000) findings, both ears represent the dominant goal in experiment 1 but not in experiment 2, where all movements are directed to the same ear. When the hand became the prevailing goal, it was selected correctly. Future work is needed to understand how the model we have presented here accounts for imitation where a hierarchy of goals is involved.

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Appendix 1

These are the meaningful actions used in experiments 1, 2, and 3:

1. To brush one's own teeth
2. To whisk
3. To iron
4. To comb
5. To eat
6. To fan
7. To pour
8. To shave
9. To hammer

Appendix 2

Descriptions of the meaningless actions used in experments 1, 2, and 3:

1. To brush: a brushing action performed with the right arm extended outwards and the hand held upright
2. To whisk: a whisking action performed in front of the stomach with a larger amplitude
3. To iron: a ironing motion in a diagonal plane
4. To comb: a combing motion in a downwards direction front of the face
5. To eat: a spooning action with the hand moving away and above the right shoulder instead of toward the mouth
6. To fan: a fanning motion using the entire hand, with the arm held horizontal to the floor
7. To pour: a poring action reversed
8. To shave: a shaving action at chest level
9. To hammer: a hammering action on the forehead

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