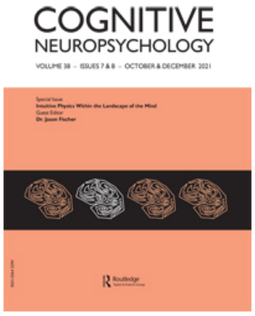

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Bottom-up and top-down modulation of route selection in imitation

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ABSTRACT
The cognitive system selects the most appropriate action imitative process: a semantic process – relying on long-term memory representations for known actions, and low-level visuomotor transformations for unknown actions. These two processes work in parallel; however, how context regularities and cognitive control modulate them is unclear. In this study, process selection was triggered contextually by presenting mixed known and new actions in predictable or unpredictable lists, while a cue on the forthcoming action triggered top-down control. Known were imitated faster than the new actions in the predictable lists only. Accuracy was higher and reaction times faster in the uncued conditions, and the predictable faster than the unpredictable list in the uncued condition only. In the latter condition, contextual factors modulate process selection, as participants use statistical regularities to perform the task at best. With the cue, the cognitive system tries to control response selection, resulting in more errors and longer reaction times.

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Imitation; cognitive control; meaningful and meaningless actions; route selection; statistical learning

Introduction

Imitation is an extraordinary human ability that allows reproducing others' movements and actions. It underlies the development of important communicative and instrumental behaviours and presides over social learning for the entire life (Frith & Frith, 2012; Legare & Nielsen, 2015). Many studies in the context of both social psychology (e.g., Dijksterhuis & Bargh, 2001; Lakin et al., 2003) and cognitive neuroscience (e.g., Brass et al., 2000, 2005; De Renzi et al., 1996; Lhermitte et al., 1986; Tessari et al., 2002) suggested that imitation is an automatic process at least in adults. Some behavioural studies demonstrated that we tend to imitate automatically (Brass et al., 2000, 2001) and without awareness, suggesting that the network involved in imitation partly bypasses conscious awareness (Tessari et al., 2002). Moreover, imitation can be disproportionately augmented or reduced following brain damage. On the one hand, patients with frontal lesions may suffer from imitative behaviour (De Renzi et al., 1996; Lhermitte et al., 1986) due to the lack of inhibition usually exerted by the mediobasal frontal cortex on the parietal lobe. On the other hand, patients with ideomotor apraxia exhibit a dramatic reduction of their ability to imitate actions and often to pantomime on verbal command and visually presented objects (De Renzi et al., 1980): this imitative deficit is particularly evident after lesions of the left inferior posterior parietal cortex (e.g., Buxbaum et al., 2005; Dressing et al., 2018; Goldenberg & Hagmann, 1997; Goldenberg & Randerath, 2015; Tessari et al., 2007; Weiss et al., 2008).

Studies on apraxic patients documented differences between the imitation of known, meaningful and new, meaningless actions, that is clinically observable dissociations between impaired imitation of one but not the other gesture type (Bartolo et al., 2001; Cubelli et al., 2000; Goldenberg & Hagmann, 1997b; Gonzalez Rothi et al., 1991; Mengotti et al., 2013; Tessari et al., 2007). This led to propose the existence of two anatomo-functional mechanisms for the imitation of meaningful and meaningless. A direct route reproduces novel, meaningless actions (but also those already known) and can parse seen actions in subcomponents that the person is already able to perform; a semantic, indirect route reproduces only over-learned, meaningful actions, already stored in long-term memory, recalling each action as a unit/chunk. Some versions of the two-routes model also

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include a specific temporary memory structure, common to both routes, for holding the gestures in memory until they are reproduced (Cubelli et al., 2000, called it "buffer"; Rumiati & Tessari, 2002 referred to it as "motor short-term/working memory"). This short-term/working memory subsystem is also connected to the long-term memory system and allows us to learn new actions (Tessari et al., 2006). Selective deficits in imitating new, meaningless actions are explained with an impairment affecting the direct route (e.g., Bartolo et al., 2001; Goldenberg & Hagmann, 1997a; Tessari et al., 2007). On the other hand, deficits in imitating known, meaningful actions are explained by a selective damage to the indirect semantic route, but with an intact semantic memory which allows recognition of visually presented actions: once the meaningful action is recognized, the indirect route is triggered, but imitation cannot be accomplished due to damage occurring after the access to semantics, and a difficulty in switching to the direct imitation route (which would allow imitation of any action, including the known, meaningful ones), due to a reduced cognitive resources (i.e., a double dissociation; Bartolo et al., 2001; Tessari et al., 2007; Tessari & Cubelli, 2014). Note that when semantics is damaged, either type of action (meaningful or meaningless) is imitated using the direct route. See Figure 1.

Consistent evidence in support to the existence of two separate processes is also provided by imaging and brain stimulation studies investigating the cerebral correlates of the mechanisms involved in actual imitation (e.g., Achilles et al., 2016, 2019; Hoeren et al., 2014; Mengotti et al., 2013; Pastore-Wapp et al., 2021; Peigneux et al., 2004; Reader & Holmes, 2019; Rumiati et al., 2005; Takeuchi et al., 2021; Vanbellingen et al., 2010). Imitation of known, familiar actions and new actions partially overlap in some inferior parietal regions but are also associated with activations in other districts (Achilles et al., 2016, 2019; Bartolo et al., 2001; Goldenberg & Hagmann, 1997b; Hoeren et al., 2014; Mengotti et al., 2013; Peigneux et al., 2004; Rumiati et al., 2005; Tessari et al., 2007). In particular, imitation of new, meaningless actions mainly engages areas of the dorso-dorsal stream, while ventro-dorsal and ventral regions are involved in the imitation of known, meaningful actions (Binkofski & Buxbaum, 2013; Hoeren et al., 2014; Martin et al., 2016a; Martin et al., 2016b; Rumiati et al., 2005).

The two-route model has been recently implemented in a Bayesian model (Proietti et al., 2021) that formalizes how information processing is modulated between different computational processes and provides a basis for generalizations at a cognitive and neural levels. It is proposed that the visuomotor system entails a probabilistic generative hierarchical model for action understanding in which statistical regularities and different kinds of uncertainty originates two forms of information-seeking behaviour, mapped into two distinct computational strategies (Schwartenbeck et al., 2019). More specifically, the direct route has been associated with a visual processing that prioritizes salience and translates the observed action into a short-term, sensorimotor code (low level processing), as implemented in the dorso-dorsal neural pathway. On the other hand, the visual information in the semantic route prioritizes novelty which is then translated into a more holistic processing associated with familiar and skilled actions, implemented in the ventro-dorsal visuomotor pathway (medium level processing; such as the motor engram proposed by Dressing et al., 2018). Lastly, these low and medium levels of action representation are abstracted into more semantic and abstract codes, such as symbolic gestures, associated mainly with the ventral pathway (see Dressing et al., 2018; Tessari et al., 2021).

Bottom-up modulation of the two routes

The modulation of the two cognitive processes is determined by different parameters representing uncertainty, knowledge, novelty and statistical regularities play a crucial role in these parameters trade-offs (Proietti et al., 2021). One of these trade-offs is modulated by the statistical regularities within the context, corresponding to how the actions are presented (Proietti et al., 2021). Indeed, results with both healthy individuals (using pantomimes of object use as meaningful actions, Tessari & Rumiati, 2004); using symbolic, meaningful actions (Carmo & Rumiati, 2009), and brain-damaged patients (Cubelli et al., 2006; Tessari et al., 2007) demonstrated that the composition of the list of the to-be-imitated actions modulates the two routes when limited cognitive resources are available. This is the case of healthy individuals imitating to a deadline: a fast presentation of the stimuli and minimal time given to participants

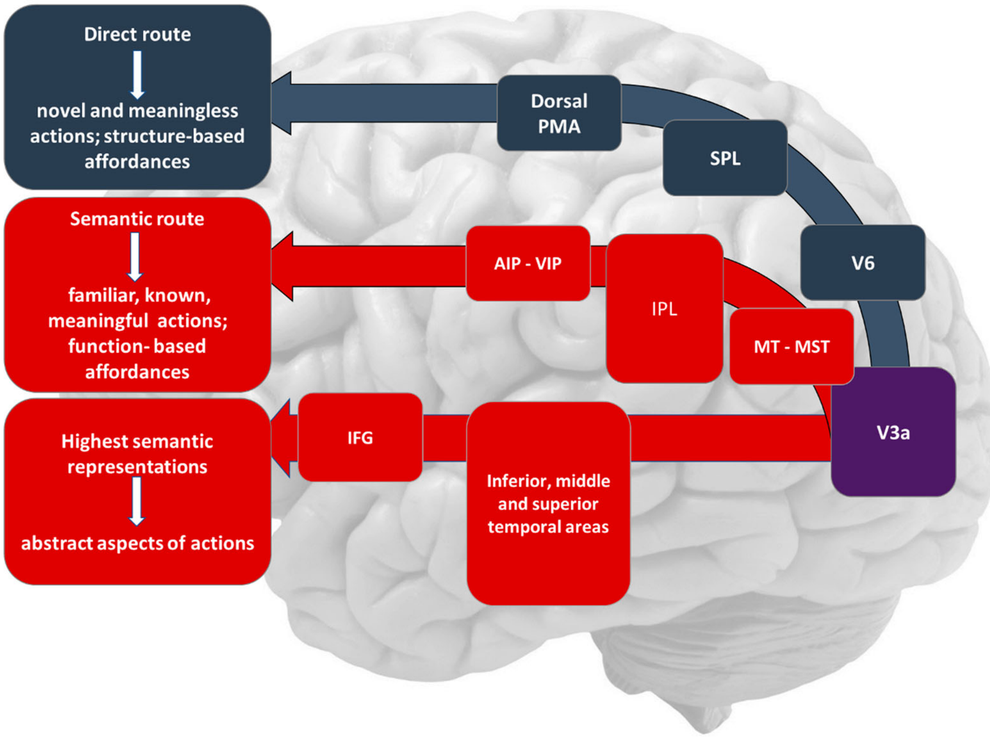

Figure 1. A version of how the cognitive model (Rumiati & Tessari, 2002; Tessari et al., 2007) is implemented in the brain. Two routes are involved in the imitation of known, meaningful, and new, meaningless actions. Visuo-spatial analysis is the first common stage for both routes. Then, if the action to be imitated is meaningless, the direct route, implemented in the dorso-dorsal stream, is selected, whereas if the action is meaningful, then the semantic route (implemented in both the ventro-dorsal stream, for the motor engrams, and in the ventral streams, for the conceptual, abstract aspects) is preferably selected. A motor short-term/working memory subsystem (not neurally represented in this figure), common to both the semantic and direct route, allows holding in memory until they are reproduced and to learn new actions.

to provide a response, temporally reduce the cognitive resources available to perform the imitation task and induces healthy individuals to behave as they were patients both in terms of accuracy and types of errors (Tessari & Rumiati, 2004). In these conditions, the cognitive system modulates the role of the two routes when known, meaningful and new, meaningless actions are presented in a mixed vs. pure list or based on the percentage of one type of action over the other within the list of actions to imitate (i.e., manipulating the probability to be presented with a known or a new action within a mixed list). When the percentage of known actions is higher (i.e., in a pure block of known actions or when 70% of the mixed list is composed of known actions), the computational strategy encoded in the semantic route is used for imitating known actions, bringing to better imitative performance on this kind of action: the more known actions there were in the list, the better the participants imitated them (e.g., Tessari & Rumiati, 2004): Experiments (1A, 2A and 3A). The error analysis, showing a higher percentage of semantic errors (e.g., prototypicalization, body-part-as-a-tool errors, and visuo-semantic errors) in these conditions, supported results from accuracy.

When the probability to be presented with a new, meaningless action is higher (100% or 70% of new action within the list) or is equal to that of being presented with a known one (50%), then the computational strategy encoded in the direct route is used for reproducing both types of action, and the performance is equal for both types of actions (see Tessari & Rumiati, 2004): Experiments (1B, 2B and 3B). This pattern of results has been replicated behaviourally in a PET (Rumiati et al., 2005) study where known and new actions were presented in a pure block or mixed blocks with different percentages of known and new actions. Moreover, a parametric correlation between the regional cerebral blood flow and the probability to be presented with a known and new action within the list showed different results: a significant positive correlation of neural activity with the amount of known actions was observed in the left inferior temporal gyrus only (an area involved in memory processes and belonging to the ventral stream); in contrast, a significant positive correlation with the amount of new actions was observed in the right parieto-occipital junction only (an area devoted to visuo-motor transformation in the dorsal stream). Similar results were observed in studies with brain-damaged patients, whose cognitive resources are reduced by the brain lesion (Cubelli et al., 2006; Tessari et al., 2007): at group level, patients performed better in the blocked than in the mixed condition, irrespective of the side of the lesion; at the single-case level, a classical double dissociation in imitation of known, meaningful and new, meaningless actions emerged thus supporting a relative functional independency of the two routes. We interpreted this result as the dominance of the most appropriate mechanism for action reproduction (Tessari & Rumiati, 2004) based on the ability to extract environmental regularities as already demonstrated to be at work in other cognitive domains (Aslin et al., 1998; Fiser & Aslin, 2001; Garrido et al., 2013; Nissen & Bullemer, 1987; Trueswell, 1996). In particular, such an ability to learn, based on statistical and symbolic manipulation, seems to pervade the whole cognitive system and is not specific to a particular cognitive domain (e.g., Brady & Oliva, 2008; Wang et al., 2017).

Why are such modulatory processes necessary? Some studies suggest that the direct route might play a central role in early development (Meltzoff & Moore, 1977, 1983, 1989), while others suggest that it results from the combination of several cognitive abilities and develops later in life (e.g., Jones, 2007; Oostenbroek et al., 2016). Sebastianutto and colleagues (Sebastianutto et al., 2017), for example, showed that, by the age of three, children have a semantic representation of both transitive and intransitive gestures and that, when new, meaningless gestures and known, meaningful gestures are presented in separate blocks, the latter are imitated via the semantic route. However, at 14 months of age, infants were shown to perform deferred imitation of familiar and novel object-related gestures (Meltzoff, 1988), storing representations of observed gestures into memory for subsequent reproduction, implying that the semantic route might come into play even in an earlier stage of development. It is plausible that the direct route might lose its importance as the child becomes an adult equipped with a broader repertoire of actions. Therefore, once such a repertoire is acquired, the direct route is usually inhibited, with imitation performance relying mainly on the semantic route. However, under some circumstances, environmental factors act on the weight of the two routes inducing a functional balance for performing the imitative task at best (see Tessari & Cubelli, 2014, for a discussion) based on expectations. Indeed, survival in humans often depends on creating expectations about the environment and monitoring them, and on preparing to respond appropriately to eventual violations of these expectations.

Experimental manipulations showed that the composition of the list can drive the bottom-up extraction of statistical regularities and the adaptive modulation of the two routes. Thus, it can be used to study how human observers learn about the stability of the imitative context by taking advantage of the regularities gathered from the environment and guiding the prioritization of the cognitive strategy.

Top-down modulation of the two routes

Top-down influence has been studied to explain how we perform in imitation and visuomotor priming tasks. Many studies have investigated the role of attention during the action observation phase in imitation tasks showing improvement in voluntary imitation performance and learning (e.g., Janelle et al., 2003) but also during automatic imitation (Bach et al., 2007; Chong et al., 2008; Gowen et al., 2010; Hayes et al., 2014; Leighton et al., 2010). Automatic imitation and biological motion seem to be also influenced by prior knowledge and social cognitive processes (Gowen & Poliakoff, 2012; Heyes, 2011; Longo & Bertenthal, 2009; Shen et al., 2011). Influences on imitation have been observed for a wide range of social cues and prior knowledge (Roberts et al., 2016; Y. Wang & Hamilton, 2012), such as animacy (Gowen et al., 2016; Liepelt & Brass, 2010), group membership (Rauchbauer et al., 2015), intentions (Liepelt et al., 2008), obstacle priming (D. Griffiths & Tipper, 2012) and action rationality (Forbes & Hamilton, 2017; Gergely & Csibra, 2003). In general, research highlights the importance of attention, context, knowledge, and social primes and how they may modulate the imitator's mapping of the observed action into her own motor representation. However, top-down modulation in the specific context of the two-route model has not been deeply investigated to date. A study manipulated the composition of the list and detailed instructions on such a composition were given (Experiment 2B in Tessari & Rumiati, 2004). Participants tried to exert voluntary control over selecting the direct or the semantic route. This led to a better performance in imitation of both known and new actions, compared to a condition without detailed instructions on the composition, when presented in separated blocks. However, when known and new actions were presented in a mixed unpredictable list, the general imitative performance decreased, compared to a condition without detailed instructions, as the number of errors increased in the first trial and an advantage in imitation of known action emerged, suggesting a deliberate attempt to recognize the actions as known or new and to exert a top-down modulation over the two routes.

This study

In the present study, we used mixed lists of known and new actions to account for the bottom-up modulation. We manipulated the stability of the context by making it easier or harder for participants to extract the statistical regularities of the environment and optimize the imitative strategy selection. We presented a group of participants with lists composed of 50% of known and 50% of new actions intermingled: a) a list had fixed sequences of known and new actions, with predictable switches; b) the other list had switches that randomly occurred after three, five or seven trials of known or new actions that were not predictable. Moreover, to account for the top-down modulation of strategy selection, we investigated the role of a cue being informative of the type of action that will follow within the experimental list that might induce the cognitive system to control strategy selection at a top-down level. In this perspective, the composition of the list can be considered a contextual bottom-up factor, and the informative cue as a short-term factor that induces top-down cognitive control for gesture selection and initiation. Thus, both lists (predictable and unpredictable) were presented either in an uncued or cued condition. In the uncued conditions, we aimed at reproducing a condition in which the modulation of the most suitable process for imitation is driven by the extrapolation of the probabilities of being presented with a known or new action. We predicted that in these conditions, stimulus-driven modulation should bring to faster performance in the fixed (as the semantic route is faster than the direct one) than in the mixed condition (where the direct route is the preferred one).

In the cued conditions, we investigated whether the role of the two routes is differentially modulated (independently of the composition of the list) when individuals can exert top-down control on their performance, based on the knowledge given by the cue on the type of action that is going to be presented. The cue and interval, intervening between the cue onset and the stimulus appearance, might allow an endogenously driven resolution of the conflict between the process selection and solving any cognitive conflict in allocating cognitive recourses to select the imitative strategy and the initiation of the movement. However, given the competition for cognitive resources, this endogenously driven resolution might increase reaction times and reduce performance. Indeed, deploying top-down attentional control on route selection has a high cognitive cost that leads to a cascade of consequences. First, RTs are elongated and the competition for cognitive resources impedes controlling for interference, thus reducing accuracy, similarly to the disruptive effect of instructions in an unpredictable mixed presentation of known and new actions observed in a previous study (see Experiment 2B in Tessari & Rumiati, 2004).

The study comprised an experiment in which we manipulated either the composition of the action list and the presence of an informative cue in four conditions: In conditions A and B, predictable and unpredictable (respectively) sequences of known and new actions were shown without any cue. In these conditions, the composition of the list had to be extrapolated online during the experiment through statistical learning. On the contrary, in conditions C and D, a predictable and unpredictable sequence of known and new actions with a cue (informative on the nature of the forthcoming stimulus) was used, respectively. In these conditions, the interval intervening between the cue onset and the stimulus might allow the cognitive system to solve the conflict between the two routes.

Method

Participants

Seventy-eight right-handed individuals, all students of the University of Bologna (39 males, average age = 22.92, SD = 2.12), participated in the Experiment (19 in condition A, 20 in condition B, 19 in condition and 20 in condition D). They all had either normal or corrected-to-normal vision. Their handedness was tested using the Edinburgh Inventory (Oldfield, 1971).

A power analysis was conducted on the interaction Type of Action x List based on Tessari & Rumiati, 2004 (Experiments 1 and 2), and Press & Heyes, 2008. We calculated Cohen's D and used G*Power (Faul et al., 2007) to calculate the sample size: with an effect size Cohen's D = 1.64 (calculated for the Type of Action x List interaction), Alpha = 0.05, and Power of 0.80, we would need only 7 participants per conditions. However, we collected a number of participants corresponding to the average number of the aforementioned studies.

Ethics statement

The study was carried out in accordance with the Helsinki Declaration of 1975 and was approved by the ethics committee of the University of Bologna (approval n. 4240).

Stimuli. We used 15 known, meaningful actions (pantomimes of object use: to iron, to pour with a bottle, to screw a light bulb, to write with a pen, to use a toothbrush, to drink with a glass, to shave with a razor, to hammer, to saw, to use a key, to clean with a cloth, to smoke, to mix with a ladle, to eat with a fork, to comb oneself) and 15 matched novel, meaningless actions (obtained by modifying the relationship between hand/arm and trunk of the meaningful actions). They were chosen from an original set of 20 known and 20 new actions used in previous studies (i.e., Press & Heyes, 2008; Tessari et al., 2006; Tessari & Rumiati, 2004). Five independent individuals rated the meaningfulness, on a scale from 1 (minimum) up to 5 (maximum), of the actions from this original set (Cronbach's α = 0.842). The actions that received the best average scores of meaningfulness and meaninglessness from the five raters were selected as experimental stimuli.

Design and procedure

Both known and new actions were presented in a random order five times each. The sequence of events was structured as follows in the *uncued* conditions (conditions A and B): Each trial started with an action that lasted for 1264 ms, followed by a 1000 ms blank interval, at the end of which a beep was played for 250 ms (see Figure 2a). Participants were required to immediately imitate each action after its presentation (i.e., during the blank interval); the next trial appeared immediately after. In the "predictable" condition (A), alternated sequences of 5 known and 5 new actions were presented. All the 30 actions (15 known and 15 new) were presented randomly within sub-blocks of 5 actions each. When the first presentation of the 30 actions was over, the programme randomized the actions again and repeated the sub-block procedure four times. The sub-block structure aimed to avoid presenting the same action many times in a row. In the "unpredictable" condition (B), the same procedure was applied for creating the sub-bocks, but they consisted of alternated random sequences of randomly presented 3, 5 or 7 known and new actions (Figure 2B) in order to have a sufficient number of items before a switch to induce activation of one of the two routes and not to cumulate too many errors in a row. In the *cued* conditions, the trial began with the presentation of a blue or red square (the cue) for 500 ms and an inter-stimulus interval of 150 ms before presenting the action video for 1264 ms, the black screen for 1 sec, and the sound (see Figure 2B). The colour of the square was informative on the nature of the action to be imitated immediately after (i.e., a known or new action). The association between colour of the square and the meaning of the action was counterbalanced across participants. In conditions C, a predictable sequence was used, and in condition D, an unpredictable one. There were 150 trials in all four conditions: 50% of known actions and 50% of new actions mixed presented.

The participants were informed about the composition of the list (i.e., predictable sequences vs. unpredictable sequences), and they were asked to imitate the actions with their right limb immediately after

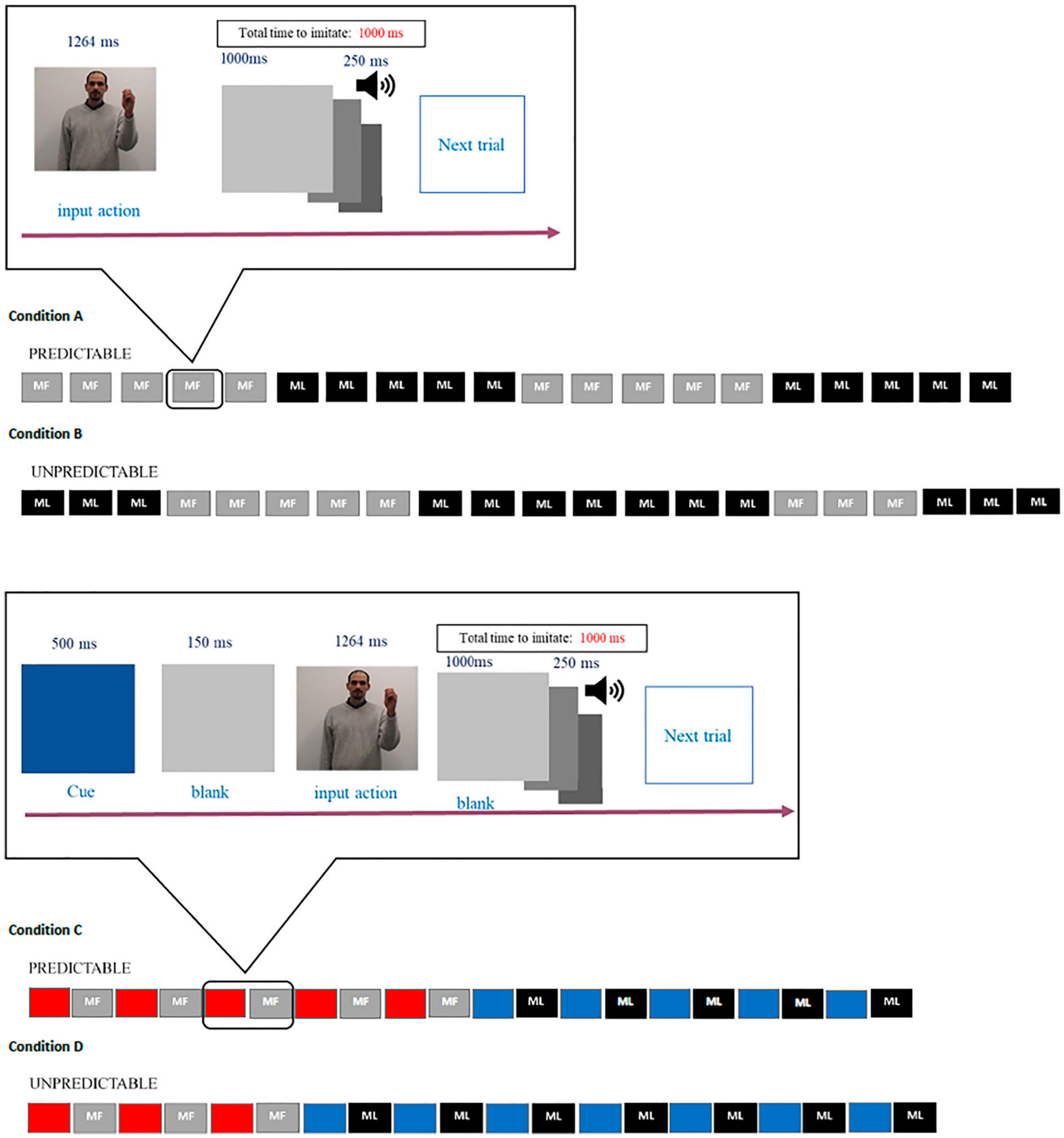

Figure 2. Illustration of the sequence of events in the predictable and unpredictable presentations for either the Uncued (above) and Cued (below) conditions. Details about the structure of the trials are reported in the vignettes. MF stands for known, meaningful action and ML for new, meaningless action.

the video presentation (i.e., delayed imitation) in a mirror configuration. The actor performed the actions with his left limb. Participants' performance was videotaped and later scored independently by two raters (as there was no significant difference between the scores of the two raters in all conditions when disagreement was present about a single trial, they watched it again together and decided whether it has to be considered correct or incorrect). An imitated action was scored incorrect when one of the following error occurred (based on Tessari & Rumiati, 2004): Spatial error (the movement is overall correct, but the hand or the arm are moved in moved in the wrong direction or plane, or on the wrong endpoint); Visual error (a movement visually similar to the shown one, but not included in the list, is reproduce or two gestures in the list are merged); Omission (no gesture is reproduce); Unrecognizable gesture (the reproduced movement is not recognized); early or late start (see below) in imitation. The stimuli were projected onto a white wall through a DELL 2300 projector and had a dimension of 100 cm x 100 cm. The participants were at a distance of 1.5 metres from the projected videos. Close to them, a little table with a response bottom was positioned to collect the exact time they began imitation. This way, we collected reaction times (release time) and controlled that participants did not begin to imitate the stimuli while still on the screen. The experiment was run using the software Presentation (Neurobehavioral Systems) to control the trial sequences and discharge those types of trials from the analyses.

Results

A repeated-measures analysis of variance (ANOVA) was performed with Type of Action (known vs. new) as within-subject factor, List (predictable vs. unpredictable) and Cue (uncued vs. cued) as between-subjects factors. Reaction Times (RTs; only RTs of the correctly imitated actions, in between 150 and 1000 ms, were analyzed) and imitation accuracy (percentage of correctly imitated actions, calculated on the total amount of trials per condition) were the dependent variables.

RTs

RTs analysis was performed on 78.61% of the trials (5.28% early starts and 2.11% omissions).

Type of Action factor was significant ($F(1,74) = 12.32$, $p = .001$, $\eta^2 p = .143$): known actions (mean = 590 ms, SE = 10.15) were imitated faster than new actions (mean = 606 ms, SE = 10.51). Also the Type of Action x List interaction reached significance ($F(1,74) = 6.22$, $p = .015$, $\eta^2 p = .08$): in the predictable lists (two-tailed t-test with Bonferroni correction, $t(37) = -6.06$, $p < .001$), known actions (mean = 569 ms, SE = 14.54) were imitated faster than the new ones (mean = 595 ms, SE = 15.05) but no statistically significant difference emerged in the unpredictable lists (two-tailed t-test with Bonferroni correction, $t(38) = -.588$, $p = .56$; know = 611 ms, SE = 14.17; new = 616 ms, SE = 14.67). See Figure 3. Moreover, Cue factor ($F(1,74) = 15.32$, $p < .001$, $\eta^2 p = .172$) revealed that RTs were faster in the uncued conditions (mean = 558 ms, SE = 14.26) than cued ones (mean = 637 ms, SE = 14.26). At last, List x Cue was significant ($F(1,74) = 10.72$, $p < .005$, $\eta^2 p = .126$): the uncued predictable list (mean = 510 ms, SE = 20.43) was imitated faster than the cued predictable list (mean = 655 ms, SE = 20.43; two-tailed t-test with Bonferroni correction, $t(36) = 5.40$, $p < .001$) but no statistically significant difference emerged for the unpredictable ones (uncued = 607 ms, SE = 19.91; cued = 620 ms, SE = 19.91); one tailed t-test with Bonferroni correction, $t(38) = 0.43$, $p = .69$. Moreover, when the cue was not present, RTs were faster in the predictable list (mean = 510 ms, SE

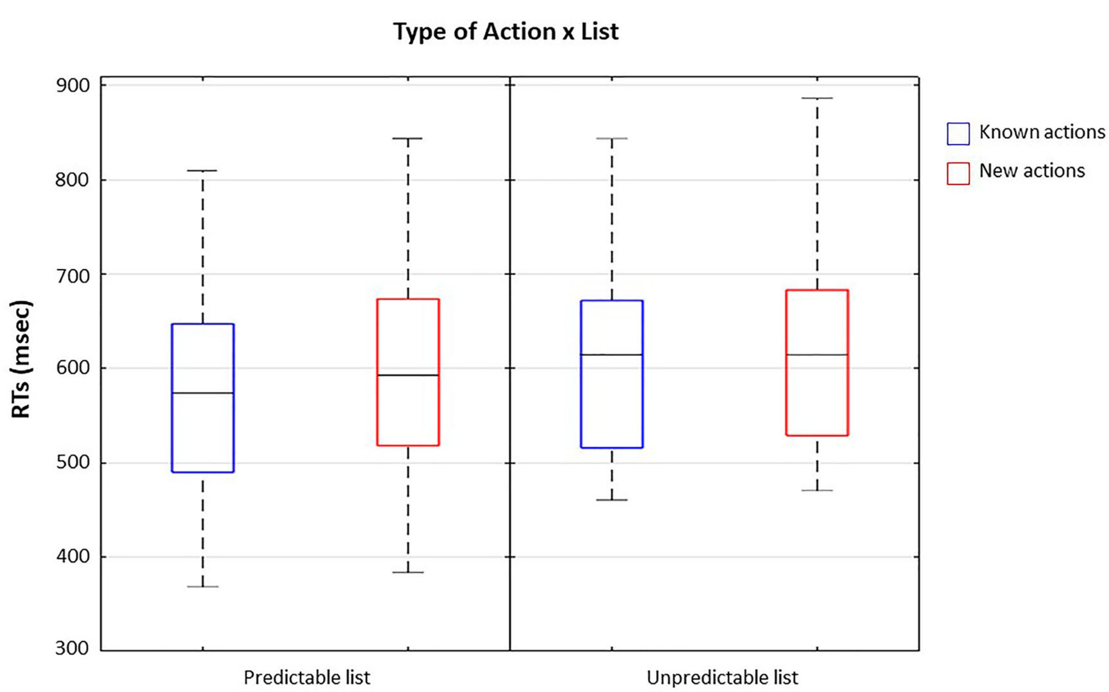

Figure 3. Interaction between Type of Action and List. Reaction times (RTs) for meaningful and meaningless actions are reported in relation to both predictable and unpredictable conditions. In the boxplots the middle portion of the data (the box) is the interquartile range. The black dashed line shows the maximum and minimum values while the horizontal line represents the median.

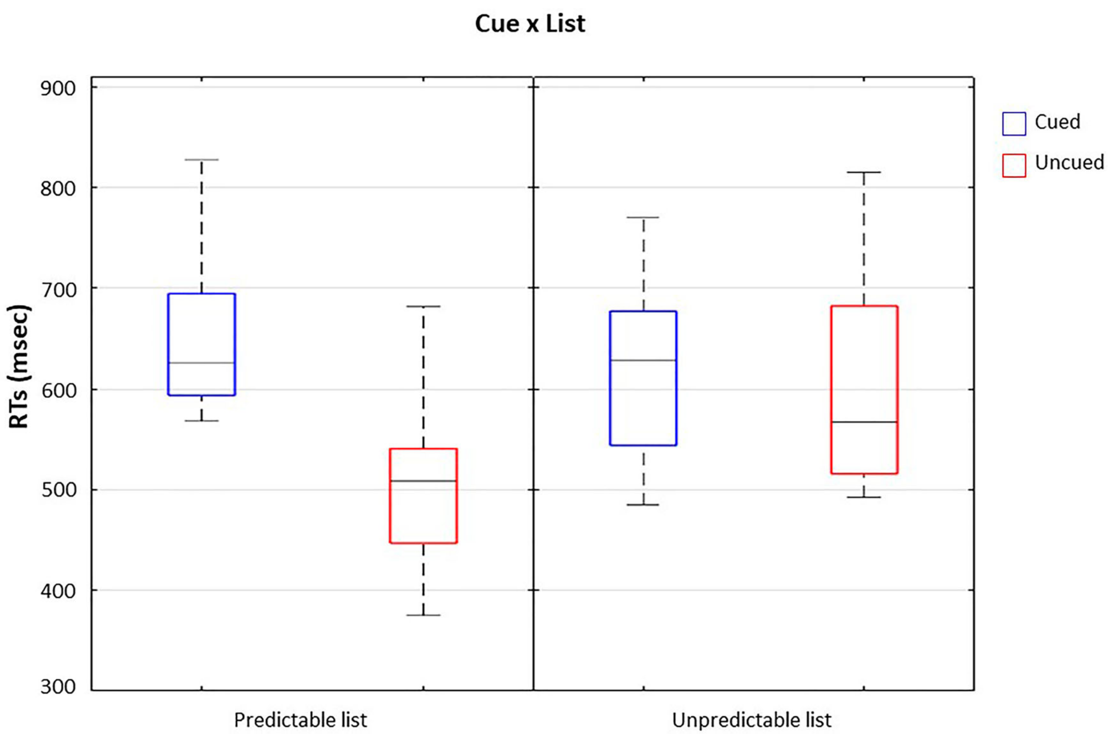

Figure 4. Interaction between Cue and List. Reaction times (RTs) for predictable and unpredictable conditions are reported for cued and uncued conditions. The middle portion of the data is the interquartile range whereas the black dashed line shows the maximum and minimum values and the horizontal line represents the median.

= 20.43) than in the unpredictable one (mean = 563 ms; SE = 14.85); one tailed t-test with Bonferroni correction, t(37) = −3.08, $p = .004$. In the cued conditions, no statistically significant difference emerged between the predictable (mean = 655 ms, SE = 20.43) and the unpredictable lists (mean = 620 ms; SE = 19.91); one tailed t-test with Bonferroni correction, t (37) = 1.38, $p = .174$. See Figure 4. The List factor was not statistically significant (F(1,74) = 2.42, $p = .124$; mean predictable = 582 ms, SE = 14.45 and mean unpredictable = 613 ms, SE = 12.08). For non-significant statistics see the supplementary material.

Accuracy

Type of Action factor (F(1,74) = 13,80, $p < .001$, $\eta^2 p$ = .157) showed that known actions (mean = 80.20%, SE = 1.15) were imitated overall better than new ones (mean = 76.90%, SE = 1.36) in all experiments. An effect of Cue emerged (F(1,74) = 35.21, $p < .001$, $\eta^2 p = .332$) as accuracy was lower in the cued lists (Experiments 2A and 2B; mean = 71.56%, SE = 1.66) as compared to uncued (mean = 85.54%; SE = 1.66). List x Cue interaction factor was significant (F(1,74) = 4,69, $p = .034$, $\eta^2 p = .060$) as predictable lists (mean = 89%, SE = 2.32) brought to a better performance than the unpredictable ones (mean = 82%, SE = 2.38) in the uncued condition (two-tailed t-test t(37) = 2.803, $p = .008$) but no statistically significant difference emerged in the cued condition (t(37) = .871, $p = .389$; mean predictable = 70%, SE = 2.385 and mean unpredictable = 73%, SE = 2.325). For non-significant statistics see the supplementary material.

Discussion

Overall, an advantage of known on new actions emerged in both Accuracy and RTs. Such result is in line with previous literature: known actions are familiar and easily recognized and imitated because there is a corresponding representation in long-term memory (Press & Heyes, 2008; Reader et al., 2018; Rumiati & Tessari, 2002; Tessari & Rumiati, 2004). Moreover, RTs in imitation of known actions were faster than those of new actions in the predictable list, but no difference emerged in the unpredictable list. This result is in line with previous findings on the effect of list composition (Cubelli et al., 2006; Tessari et al., 2007; Tessari & Rumiati, 2004). The two routes work differently in the two types of lists, and the faster semantic route (that works effortless) plays a role in producing such an advantage in the predictable one. Our result suggests that the cognitive system extracts the regularities in the presentation sequence, entails expectations about the forthcoming type of stimulus, and selects the most suitable imitation strategy consequently. As regards the cue, uncued conditions reached a higher accuracy and faster RTs compared to cued ones. It seems that when the cue is presented, the cognitive system tries to exert higher attentional control over the route selection and the action response, but this brings to a higher percentage of errors and slower RTs. Moreover, imitation in the predictable list was faster than the unpredictable one in the uncued condition but not in the cued one, where control was modulated by both the composition of the list and the knowledge about the forthcoming gestures. Moreover, the uncued predictable list showed faster RTs than the cued one, suggesting that consciously trying to exert control on the semantic route slows down its processing speed.

Results suggest that the modulation and control of the two imitative processes may be driven bottom-up by the predictability of the composition of the list, but when the modulation is induced top-down by the cue, performance decreases. Specifically, 650 ms did not allow participants to resolve cognitive conflicts during the preparation of task responses, resulting in a general interference in route selection.

General discussion

We examined how the adaptive modulation of the cognitive processes for action imitation encoded in the two routes model can be driven by the extraction of statistical regularities and by top-down attentional control. A study was carried out to better understand the role of context predictability and whether attending and preparing to deal with such conditions can modulate the selection of imitative processes. We manipulated the composition of the list to investigate stimulus-driven modulation and used an *uncued* and *cued* version of the experiment to investigate top-down attentional modulation.

First, we found that known actions were imitated faster and more accurately than new ones. Regarding the RTs, this was due to the advantage of the known over the new actions in the predictable lists where the semantic route, which is somewhat more spontaneous than the processing of the direct route, is adequately selected when necessary. This is consistent with the assumption that the semantic route is associated with more skilled performance as it permits recognizing and reproducing the known action as a whole (see Tessari et al., 2021 for a detailed discussion of the role of chunking in recalling known, meaningful actions). In contrast, the direct route needs to parse the seen action in simpler motor components to be later reassembled and requires more cognitive and attentional resources than the semantic one. The former is faster and more accurate process in adults, and this is not surprising if we consider that they rarely need to learn or reproduce new actions in daily life. Support comes from developmental studies showing that young children already have a semantic representation of gestures (e.g., Sebastianutto et al., 2017). The meaning factor also interacted with the composition of the list as the known actions were imitated faster than the new ones in the predictable lists but not in the unpredictable ones. Such a result suggests that the predictability of the list exogenously acts on the weight given to the elaboration of the semantic over the direct route. Second, an effect of cue emerged in both RTs and accuracy (longer RTs and lower accuracy in the cued conditions). This result supports the hypothesis that participants tried to exert top-down control over the selection of the two processes and the imitative response. In this case, since the cue informs about the nature of the upcoming stimulus, the route selection is endogenously controlled but imposes a high cognitive resources cost as higher amounts of control are intrinsically costly and require more effort (Norman & Shallice, 1986), which lead to longer RTs while interference induces lower accuracy. Similar results were already reported in a previous study (Experiment 2B in Tessari & Rumiati, 2004) where detailed instructions on the composition of the experimental list were given, and participants exerted voluntary control over route selection: lower accuracy was found in the mixed unpredictable list, with a general decrement in imitation compared to a condition without detailed instructions. Results were interpreted with the deliberate attempt to recognize the actions as known or new and to exert a top-down modulation over the two routes being detrimental. Another possible interpretation of the

RTs pattern is the application of a "criterion-setting" on the time to start imitation, in order to control the process selection endogenously (as found in the language domain; Lupker et al., 1997): the time to begin imitation of known, meaningful actions would be delayed to allow equal time to all the stimuli to be analysed, but become homogeneous with the time necessary to imitate new actions. However, such an interpretation cannot adequately explain the detrimental effects on accuracy.

Results also showed that the cue factor interacted with the composition of the list. In the uncued conditions, when time constraints were imposed in a predictable condition (condition A), the overall performance was faster than that of an unpredictable condition (condition B). However, such an advantage disappeared when the cue was introduced, and the overall performance on the cued predictable and unpredictable conditions (conditions C and D) was similar and slower compared to the uncued predictable condition. Results again suggest that a conscious modulatory strategy on route selection (i.e., higher cognitive control) requires to use cognitive resources, but the cost of this cognitive operation is higher since there is a slowing down of RTs and accuracy reduction compared to the uncued conditions. We suggest that participants try to exert top-down control on route selection by selecting the most appropriate route based on the information we provided them with the cue. However, this control imposes on participants to continuously switch between two processing modes: a global analysis for the known actions (recognized as a chunk by the semantic, indirect route) and a local analysis, based on decomposition/re-composition into elementary motor units, performed by the direct route. Switching between these two modalities burnscognitive resources and puts the two routes in competition thus explaining the reduction in accuracy. Moreover, interpreting the meaning of the cue (as the participants compute its meaning by associating the colour with the category of the action) becomes a metacognitive task that requires further processing as it is apparent in the longer RTs. Crucially, this additional metacognitive task (cue coding) could also make the cue and uncued conditions not comparable (i.e., elaboration of accurate responses in the uncued condition vs elaboration of accurate responses + elaboration of the rules associated with the cue). Increasing the interstimulus interval (e.g., doubling the 650 ms interval used in this study) would allow understanding whether top-down processes require more time to become effective in solving the competition for cognitive resources problem with not detrimental effects on accuracy and RTs.

Results also suggest that the list composition effect is not due to a top-down process but rather to an externally triggered statistical computation that modulates the two routes. Thus, even in the context of the mixed presentation of known and new actions, statistics extraction plays an important role and influences performance according to the predictability of the presentation pattern. This is also in line with Brady and Oliva (2008)'s results suggesting that the brain can rapidly extract statistics, regularities, and repetitive patterns in the environment to find structure and meaning in the incoming sensory signals to help to prepare for future actions. Importantly, they demonstrated that such statistical learning mechanisms operate without conscious intent or awareness and that they also operate at different levels of abstraction, semantic categories included. Our results improve their results as suggest that statistics extraction works better at an unconscious level (like in the uncued conditions in this study) than an aware one (the cued conditions) when the cognitive systems apply top-down control. According to Fischer and colleagues (Fischer et al., 2016), understanding and acting on the world requires intuitive physics, and the ability to plan actions presumes a statistical model of the physical states of the world. For example, this assumption has been demonstrated to hold for other domain of social learning such as tool use: for example, the probabilistic priors acquired from past experiences are essential when the biomechanical information conveyed by tool affordances is ambiguous or noisy or when many competing intentions are equally congruent with a not-yet-completed behaviour (Chambon et al., 2011). A similar result was also obtained in the context of affordances extrapolation (Jacquet et al., 2012). The probability to observe biomechanically optimal or suboptimal behaviours toward an object was manipulated to bias biomechanical expectations elicited by affordances (percentages were manipulated as in Tessari & Rumiati, 2004: 0%, 30%, 50%, 70% and 100%). When the statistical regularities favoured the observation of biomechanically suboptimal behaviours, biomechanical expectations delayed the acquisition of probabilistic priors and hindered the use of priors in solving the uncertainty associated with incomplete actions. In general, it is long known that sensitivity to statistical regularities plays an important role in various cognitive domains such as motor preparation (Nissen & Bullemer, 1987), language parsing (Trueswell, 1996), and judgment (Griffiths & Tenenbaum, 2006). Interestingly, Wang and colleagues (Wang et al., 2017) demonstrated that specific cortico-striatal mechanisms mediate learning of predictive statistics and mediate domain-general learning of complex structures supporting higher cognitive functions (e.g., learning music or language). These experimental results support the computational model based on active inference (Proietti et al., 2021), formalizing how the brain represents the statistical contingencies of the world for action understanding and execution. Physical (e.g., sensorimotor) interactions are necessary to learn and build a semantic map of such statistics. On the other hand, the statistical models in the brain are used to plan and understand further aspects of the physical world in a continuous action-perception (and learning) loop. In other words, actions provide the link between the physical environment and the ability to learn such statistical contingencies (e.g., O'Regan, 2011).

One of the primary tasks of the brain is to extract regularities from the environment in order to make inferences and guide behaviour in novel situations. Sensitivity to statistical regularities also plays an essential role in helping a brain-damaged patient to perform a task at lower costs. Indeed, the predictability of the composition of the list plays a critical role in modulating the route selection also in brain-damaged patients (see Tessari et al., 2007; but also Achilles et al., 2016, 2019; Bartolo et al., 2001; Cubelli et al., 2006; Toraldo et al., 2001). As we recently discussed (Tessari et al., 2021), while assessing apraxia, it is essential to consider not only the gesture meaning but also the list composition, which must become a methodological requirement for future studies when clinically evaluating the status of the semantic and the direct routes in a brain-damaged patient. Moreover, present results suggest that it might be better not to give too much information about the nature of the upcoming actions but leave the cognitive system to extract the list regularities covertly to avoid a re-investment of attention that slows down processing.

In summary, the context drives the modulation of the two routes for action understanding and response based on the extrapolation of statistical probabilities. Furthermore, when sufficient short-term information is provided (the cue), the cognitive system can also try to exert a certain amount of attentional control, which is resource demanding and induces a general interference with response selection. Specifically, stimulus-driven process selection is automatic and unconscious, while top-down induced attentional control is more cognitively demanding (Norman & Shallice, 1986). Following results and interpretation obtained in other domains (e.g., Baluch & Besner, 1991; Tabossi & Laghi, 1992), we might assume that, although the two routes are partially independent, the cognitive system can strategically deploy more resources to either one. Furthermore, our results are relevant for clinical settings as they demonstrated that the presentation order of the types of actions within the testing list triggers the use of different cognitive strategies for performing a task (See Tessari & Rumiati, 2004; Tessari et al., 2007, 2015; Tessari & Cubelli, 2014; for detailed discussion in the domain of ideomotor apraxia). At last, in the clinical assessment, it is crucial to keep in mind that too many indications to the patients may induce an attentional re-investment that may negatively influence the selection of the behavioural strategy and on response control.

Conflict of interest

The authors declare that they have no conflicts of interest.

Data availability

The data that support the findings of this study are available from the first author (AT) upon request.

Disclosure statement

No potential conflict of interest was reported by the author(s).

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