Title: Motor resonance meets motor performance.

Authors: Guido Barchiesi, Luigi cattaneo

Center for Mind/Brain Sciences (CIMeC), University of Trento, Via delle Regole, 101, 38123 Mattarello (TN), Italy

ABSTRACT

The aim of the present work is to explore which of two different models better explains facilitation/ interference effects when participants have to conditionally react to an observed action with a movement. The Dimensional Overlap model assumes two parallel routes, an automatic route and a rule-based one, that interact only when the stimulus-set and the response-set share some dimensions. In the alternative model, a motor resonance for rule-based reaction, the automatic visuo-motor transformation is always an obligatory step that provides the correct categorization of the observed action as the input for the rule-based route, thus linking the two routes in a serial fashion. We explicitly tested which of the hypotheses fits better the data by asking participants to perform one of two different actions in a twochoice reaction paradigm. In one condition participants were required to perform the opposite action compared to the one they saw (COUNTER task: see A-do B, see B-do A), while in the other they were required to perform two actions that did not share any dimension with the stimulus-set (NEUTRAL task: see A-do C, see B-do D). We predicted an advantage for the NEUTRAL task if the Dimensional Overlap model was correct, while a similar performance was foreseen if the motor resonance-based model was correct. Since the interpretation of these results was not straightforward, we conducted a distributional analysis of participants' response accuracies in order to understand whether a serial or a general parallel model explained better the data. We found clear evidence that participants responded above chance before the motor representation of the action observed was activated. We conclude that two separate systems in the human brain can transform observed actions in own motor representations. One is stimulus-driven, while the second is rule-driven. Likely, their activity is mutually independent along parallel pathways.

1. Introduction

Action observation is a field of research that focuses on the cognitive and neural effects of observing a specific event, an action executed by others (Gallese et al., 1996; Rizzolatti et al., 2001). The interest in this field has been prompted by the discovery of mirror neurons in the monkeys' premotor cortex 23 years ago (di Pellegrino et al., 1992; Gallese et al., 1996). Action observation has been studied with different techniques, both in monkeys and humans, showing that observing actions performed by others not only involves high-level visual representations but, more interestingly, it recruits representations that are active during the execution of motor acts thanks to an automatic visuo-motor transformation, called almost interchangeably "motor simulation", "motor resonance", or "mirror mechanism" (Avenanti et al., 2007; Cattaneo et al., 2009; Fadiga et al., 1995; Ubaldi et al., 2013).

A mirror mechanism is defined as "the mechanism that unifies perception and action, transforming sensory representations of others' behavior into motor representations of the same behavior in the brain (Rizzolatti and Sinigaglia, 2010)"; according to Rizzolatti et al. (2001) indeed "…when we observe a hand grasping an object the same population of neurons that controls the action execution of grasping movements becomes active in the observer's motor areas (Rizzolatti et al., 2001)", or "each time an individual sees an action done by another individual, neurons that represent that action are activated in the observer's premotor cortex. This automatically induced motor representation of the observed action corresponds to that which is spontaneously generated during active action and whose outcome is known to the acting individual (Rizzolatti and Craighero, 2004)". According to a version of the motor theory of action understanding, the motor resonance process allows the observer to understand the action observed (Rizzolatti et al., 2001; Nelissen et al., 2005).

If motor resonances is required for rule-based reaction this implies that a rule-based motor reaction to an observed action first of all should cause the observer's motor system to resonate (allowing the observer to categorize the action), and only subsequently the observer would be able to change the resonant motor representation in order to react in a non-imitative way (according to the observer's goal). Recently we proposed a model based on neurophysiological data that aimed to describe the evolving dynamics of the state of the motor system when participants observed an action in order to react to it following a rule-based visuo-motor matching (Ubaldi et al., 2013). Data showed that requiring the observers to react to an observed action with the opposite one (see action A-do action B, see action B-do action A), caused their motor system to react first by activating the motor representation correspondent to the action observed, and then by activating the task-required motor representation.

Researchers have found data compatible with the motor resonance for rule based reaction hypothesis not only in the neurophysiological domain, but also in the field of behavior (Heyes, 2011). This effect, called "automatic imitation" has been demonstrated exploiting a paradigm that presents participants with two possible stimuli (e.g. S1 and S2) to which participants have to respond with a pre-specified visuo-motor rule (when seeing S1 perform "action A", when seeing S2 perform "action B"). A task irrelevant stimulus is then presented along with the task relevant stimulus; these task irrelevant stimuli could be either the "action A" or the "action B". Responding to the task relevant stimuli with "action A" when the task irrelevant stimulus is the "action A" shortens the RTs compared to a situation in which task irrelevant stimuli represent a different kind of event. Conversely, responding to the task relevant stimulus with the "action A" when the task irrelevant stimulus presented is the "action B" causes the delaying of the RTs (Brass et al., 2000; Heyes et al., 2005; Stürmer et al., 2000). Even in the case in which the task relevant stimulus was the action itself, response compatibility effects have been shown; again, if the participants were presented with the "action A" and they had to respond with the "action B" (counter-imitative task) they were slower and less accurate compared to when the "action A" had to be performed in response to "action A" (imitative task) (Barchiesi and Cattaneo, 2013)

The automatic imitation effect however can also be considered a special case of stimulus-response compatibility effect. Stimulusresponse compatibility refers to the influence of some stimulus feature on the participants' motor response. Effects of this kind are usually elicited when stimulus and response sets share a common dimension. In the case of experiments studying automatic imitation effects, stimuli and responses are strictly linked because they represent the same actions in different modalities.

The most popular model used to explain these category of effects is the Dimensional-Overlap model by Kornblum et al. (1990), Kornblum and Lee (1995). This model involves the activity of two different routes, a rule-based route, and an automatic route for transforming vision in action. However, in order to obtain

stimulus-response compatibility effects, a condicio sine qua non is that the stimulus-set (the possible events that can be perceived) and the response-set (the possible responses that can be performed) have to be overlapping with respect to some features, that is, they have to share some dimensions. For example, in a classic Simon task participants have to conditionally react with the right hand or with the left hand to colored stimuli. If for example the stimulus appears on the right side of the screen, then if the correct response requires a right hand response, participants will be faster compared to the situation in which the correct response has to be provided with the left hand. In this case the dimension that links the stimulus-set to the response-set is the space: stimuli appearing on the left will automatically trigger responses with the left hand, and the same link relates stimuli on the right side and responses with the right hand. The same applies to automatic imitation effects, indeed there is dimensional overlap because the stimulus set (see action A or B) and the response set share some dimensions (perform action A or B).

Overall it seems that, in order to explain data on automatic imitation and automatic imitation-like effects, a model that implies at least two functional routes, an automatic route and a rulebased one, is required.

At least two possible dual-route models can account for facilitation/interference effects when participants are required to react conditionally to observed actions. One model, the motor resonance for rule-based reaction, assumes seriality between the two routes (Serial model, SM): the automatic activation of the motor representation correspondent to the action observed (through motor resonance) takes place. This step is automatic and it is required if participants aim to categorize the action observed. After this step the executive system is informed on the action that has been observed, so the task-related rule can be applied, substituting the resonant motor representation with the correct one (unless the task requires imitation).

Another possibility is that the two routes are parallel from a very early perceptual stage, but one route (the automatic one) is always faster than the other. This sub-model can also account for a biphasic behavior found in previous works, but in this case the automatic route is neither causative, nor necessary for the rulebased one.

According to the Dimensional Overlap model (DOM) if the response set does not show any shared dimension with the stimuli, then no stimulus-response compatibility effects should occur, because the stimulus does not automatically activate the motor representation correspondent to the action observed. However if motor resonance is supposed to be both automatic and required in order to react appropriately to an observed action, then the activation of the motor representation of the action observed is always a mandatory step in order to perform the correct task-related visuo-motor matching.

When dealing with two choice reaction time paradigms, the DOM model predicts that imitation (see A-do A, see B-do B) is the fastest visuo-motor matching (indeed there is concordance between motor representations activated by both routes), the counter-imitation (see A-do B, see B-do A), is the slowest (there is competition between motor representations retrieved by both routes, so the two have to compete); a "neutral" response rule (see A-do C, see B-do D) is intermediate between the previous two, because the response set does not share any dimension with the stimulus-set (the automatic route does not take place).

Instead SM makes the same predictions as the DOM model does both on imitation and counter-imitation, but not when stimulus and response sets do not share dimensions. Indeed in a serial model the motor representation of the action observed is always activated in all three visuo-motor couplings, even in the neutral one. After the executive system has selected the correct motor representation, then the

resonant motor representation should be suppressed, generating a conflict similar to the ones in the counter-imitative task (Fig. 1).

Thus we decided to compare only the counter-imitative task vs. a neutral task since the two models make the same prediction on the imitative task, hypothesizing it as the fastest visuo-motor coupling among the three.

Thus in order to distinguish between SM and DOM, we asked participants to undergo a two-choice reaction time paradigm observing two different actions and responding to them with two different motor sets. In one session participants were asked to do "see action A (B)-perform action B (A)" (COUNTER task), while in another session instead they were required to do "see action A (B)-perform action C (D)" (NEUTRAL task). The predictions of the

SM hypothesis are that the motor simulation to actions A or B is required to inform the rule-based route on which action the observer has seen in both the COUNTER and NEUTRAL task. This serial step should be reflected in a similar performance for the two conditions because the timing of motor resonance is similar in both tasks and the selection of a correct response can occur only after motor resonance has occurred. Given that the two sets of actions to be executed are different between the COUNTER and the NEUTRAL task, it was theoretically possible that any detected difference between those conditions was to be due to different complexity of the performed actions; in order to exclude this potential confound, we also asked participants to perform an arbitrary visuo-motor matching with non-action cues as a control condition (colored dots).

2. Materials and methods

2.1. Participants

Fifteen voluntary participants (5 males, mean age¼21, 2 were left-handed) took part in the experiment after giving written consent. The experiment was approved by the ethics committee of the University of Trento. The experiment was conducted in compliance with the Declaration of Helsinki.

2.2. Stimuli

Participants were presented with two categories of stimuli: HAND or DOT stimuli. Stimuli of both categories consisted in a sequence of 2 still frames, the second of which provided the cue to respond. The first frame of HAND stimuli was constant and showed a right hand from the radial profile with the thumb and fingers half-open (see Fig. 2). The second frame was either the hand with closed fingers or the hand with fingers wide open. Two small objects were present on the scene in such positions that the closed fingers grasped one of the two objects (brown object) and the open fingers touched the other one (green object). In such way the two actions were fully goal-directed (Fig. 2). The hand could be presented randomly from either an egocentric perspective or from an allocentric perspective. Given that the object that the hand acts on laid on the horizontal midline of the screen, the hand was displayed above the horizontal midline when showed in an allocentric perspective, and below when presented in an egocentric perspective. The hands presented belonged to four different people. The DOT stimuli showed a gray dot that could turn either light blue or yellow. As the hands, the dot could appear randomly either above the screen horizontal midline or below it. HAND stimuli were approximately 4 cm high (finger tips to wrist distance) 2.8 cm wide (fingers to thumb distance in the initial state), while the DOT was presented with a diameter of 3.5 cm.

2.3. Procedure

Participants sat on a comfortable chair approximately 60 cm away from the computer screen with their right hand and arm placed on a custom-made response-box (Fig. 3). The right forearm was oriented strictly parallel to the computer screen, with the fingers pointing leftwards; the arm orientation prevented participants to be influenced by any spatial compatibility effect as the participants' hand was orthogonal with respect to the HAND stimuli in both possible orientations. The custom-made response box was constituted by two force sensors; one placed under the participants' index and middle finger (the thumb was put below the support of one force sensor and kept stable to that position) the other on the external portion of the middle part of the forearm. The choice of the force sensors have been used in order to (a) provide participants with their reaction times, (b) track the state of the effectors at every time point of each trial. Both sensors were kept tightly in contact to the hand and the forearm by means of elastic bands. The experiment was divided in two consecutive sessions. In each session participants were presented with 6 alternating blocks which were in turn composed by 48 stimuli each. Odd blocks showed HAND stimuli, even blocks showed DOT stimuli. Within each block in single consecutive trials, the presentation of the two possible events and the orientation of the visual target were randomized.

In one session (COUNTER task) participants were explicitly instructed to open their fingers (without moving the wrist) "whenever they saw the target fingers grasping the brown object", while they were required to grasp the force sensor under their fingers "whenever they saw fingers touching the green object" (see Fig. 2). In the DOT blocks, 7 participants opened their hand in response to the dot becoming yellow and closed their hand in response to it becoming light blue. The remaining 8 participants performed the opposite visuo-motor mappings.

In the other session (NEUTRAL task) 7 participants were required to either abduct or adduct their forearm respectively when they observed the hand grasping the brown object or touching the green object; the remaining subjects were required to perform the alternative visuo-motor matching (abduct if touching, adduct if grasping). In DOT blocks 7 participants responded adducting their forearm on yellow dots, while the remaining subjects abducted the forearm on light blue dots. After the setup of the participant's hand in the response box, two practice blocks were performed by the participants, one for each type of stimulus. In both tasks participants were asked to perform the actions required both as fast and as accurately as they could without favoring one criterion over the other. Seven participants performed the COUNTER task first, while the remaining performed the NEUTRAL one first. In total participants underwent a total of 576 trials (288 COUNTER, 288 NEUTRAL). The number of trial repetitions per condition was of 144 in each of the 4 cells of a 2 task (COUNTER or NEUTRAL) 2 stimulus category (HAND or DOT) design.

2.4. Trial structure

The sequence of events in each trial was organized by the E-Prime 2.0 software (Psychology Software Tools). Each trial started with the initial frame presented for a random time between 500 and 1000 ms followed by the final frame without solution of continuity. This transition provided in the HAND condition the sensation of apparent motion. The screen refresh rate was set to 60 Hz. Participants were required to respond after the presentation of the final frame because it contained the only informative cue. The final frames lasted until participants' responses or for a maximum time of 1017 ms. Subsequently a feedback screenshot was displayed for 400 ms providing participants either with their response time (expressed in ms) if the response was correct, with a text string saying "Wrong!" if the response was not correct, or finally with a text string saying "NO RESPONSE" if the response was not detected by the system at the end of the 1017

ms. After the feedback frame, a fixation cross was displayed until 2730 ms were elapsed from the onset of the trial, i.e. from the onset of the initial frame (Fig. 4). In this way trial duration was constant but the appearance of the final frame (the cue) was randomly jittered with respect to t¼0 over a period of 500 ms and was therefore unpredictable to the participant.

2.5. Response logging and data processing

The response box contained two force sensors (Brand: Sparkfun Electronics model SEN-09376) that were integral with the box, which in turn was fixed to the table. On the other side, the participants' hand was linked to the sensors by means of two rubber bands. In this way both sensors at rest provided a non-null signal, thus allowing the recording of both positive (push) and negative (release) responses. The two force sensors were connected to 5 V a circuit with an additional serially mounted resistor of 330 Ω. The variable resistance of the force sensor determined changes in the output voltage that were read in parallel by an Arduino Uno board (Arduino™) and by an analog-digital converter (1401 CED) using the Signal™ software. Both devices sampled at 4000 Hz. The Arduino board was used to produce the þ5 V potential feeding the circuit and to provide to the presentation PC a digital signal of the subject's response that was used by the e-prime software to compute the online feedback information to be displayed at every trial. The force sensor outputs read through the 1401 unit were stored for offline analysis from 283 ms before to 1017 ms after the onset of the final frame.

Trial sweeps that were logged with the Signal software were then exported as MATLAB™files. They were analyzed offline by means of an algorithm, created in MATLAB™ (Mathworks), performing the following steps: each trial was divided in "baseline" (the period before the onset of the final frame) and "data sweep" (the period after the onset of the final frame). For each trial the median value of the baseline was computed. Each baseline median was subtracted then from the correspondent data sweep in order to normalize them (Norm_data_sweep). For each Norm_data_sweep the algorithm marked as reaction time (RT) the timepoint in which the force sensor output exceeded 0.03 N/cm^2 (0.1 V) or 0.03 N/cm^2 (0.1 V). In order to exclude trials with excessive voluntary activity prior to the cue, the algorithm checked whether the variation range in the baseline period was under 0.021 N/cm^2 (0.07 V), if not the trial was excluded from the analysis. It is worth noting that a sensor providing continuous information on the state of the effectors is capable of revealing trials in which participants change their decision during the actual performance of a movement, a behavior known as "partial error" (Coles et al., 1995). Using an "on–off" (discrete) response-box, these trials would have been resulted in a slower RT compared to the others in which an early correct response was provided, but in the analysis they would not have been treated as errors. Our set up however allows to identify them and to treat them as errors.

2.6. Statistical analysis

RTs lower than 150 ms were excluded from further analysis. The dependent variable for the following analysis consisted in the median value of RTs and the accuracy calculated within each cell of a 2 2 design with TASK (COUNTER or NEUTRAL) and STIMULUS CATEGORY (HAND or DOT) as factors. Two 2 2 repeated measures ANOVAs were performed separately for median RTs and accuracy values. Planned comparisons were foreseen comparing HAND vs. DOT stimuli in the two tasks with 2 pairwise t-tests. The critical p-level was therefore Bonferroni-corrected to 0.025.

3. Results

3.1. ANOVAs on RTs and accuracy

The total percentage of rejected trials was 1.9% (0.2% HAND, 0.2% DOT in the COUNTER task, 0.7% HAND, 0.8% DOT in the

NEUTRAL task). The ANOVA on RTs showed a main effect of the TASK (F(1,14)¼27.06, p¼0.0001) with responses to the COUNTER task slower than those in the NEUTRAL task (344 ms vs. 306 ms). A trend to significance was found for the main effect of STIMULUS CATEGORY, (F(1,14)¼3.37, p¼0.088) with responses to HAND stimuli generally slower than those to DOT stimuli (332 ms vs. 318 ms). A significant TASK STIMULUS CATEGORY interaction was found (F(1,14)¼44.26, p¼0.00001) with responses to HAND stimuli significantly slower (t(14)¼4.05, p¼0.001) than those to DOT stimuli in the COUNTER task (367 ms vs. 320 ms). Conversely in the NEUTRAL task responses to HAND stimuli were significantly faster (t(14)¼–3.29, p¼0.005) than those to DOT stimuli (297 ms vs. 315 ms) (Fig. 5).

The ANOVA on accuracies yielded two main effects. One main

effect of the TASK factor (F(1,14)¼8.51, p¼0.011), with lesser accuracy in the COUNTER task than in the NEUTRAL (0.89 vs. 0.92). The main effect of the STIMULUS CATEGORY (F(1,14)¼9.79, p¼0.007) consisted in lesser accuracy in HAND trials compared to DOT trials (0.88 vs. 0.92). Interestingly a significant TASK STIMULUS CATEGORY interaction was found (F(1,14)¼10.59, p¼0.0058) with significantly more errors (t(1,14)¼3.72, p¼0.002) produced in response to HAND stimuli compared to DOT stimuli in the COUNTER task (0.85 vs. 0.92). Conversely, in the NEUTRAL task no significant difference (p¼0.28) in accuracy was found between the HAND and the DOT stimuli (0.91 vs. 0.93).

4. Interim discussion

In this experiment we aimed to compare two dual route models describing different dynamics between perception and action during a choice reaction time upon the observation of two different actions. In particular, we wanted to understand if motor resonance is a necessary step in order to perform rule-based visuo-motor transformations, or instead, it is more likely that the interaction between action observation and action performance was more easily explained by a parallel model such as the Dimensional Overlap (DOM). The two models make different predictions when considering the performance of a counter-imitative coupling vs. a neutral one. The DOM predicts that if there is no dimensional overlap between the stimulus set and response set, then no processing is carried out by the automatic route, resulting only in the activation of the rule-based route for vision-to-action transformation. If this is the case, by definition then the two routes are parallel given that one is acting without the other. The SM instead assumes that the motor representation of the observed action is always accessed because it is a required step to categorize the observed action and to perform rule-based visuo-motor matching.

Results fit better with the predictions of the Dimensional Overlap model (Fig. 5). Both tasks required a non-imitative response, thus, according to the SM, the sequence of events in both tasks should have been first of all the motor activation correspondent to the observed action (in order to categorize the observed action), followed first by the selection of the correct taskrequired response, subsequently by the substitution of the resonant motor representation with the task-required motor representation, and eventually by the production of the correct response. The present data do not fulfill this prediction. On the

contrary, we found a behavioral advantage both in terms of RTs and accuracy of the NEUTRAL task compared to the COUNTER task.

Noticeably, the observed actions serving as visual cues were identical for the two tasks. This finding rules out the possibility of a purely perceptual explanation. On the other hand, the two response actions were different between the two tasks, potentially confounding the interpretation of the differential performance. The comparison with performance in the control task (DOT stimuli) unequivocally rules out the possibility that this difference is due to distal output processes. Indeed it could have been possible that some actions were more difficult to perform compared to others, in this case opening or closing the hand could have been easier or more difficult compared to adducting/abducting the arm. If no DOT condition was performed, then differences in RT could have been ascribed simply to the fact that one pair of responses was easier/more difficult to provide compared to the other pair. Instead contrasting HAND vs DOT in both COUNTER and NEUTRAL tasks rules out this potentially confounding explanation.

Although the data fulfill the prediction of the DOM, the current interpretation of the can be challenged by making different assumptions about the way different representations interact with each other. As specified in the serial model predictions of the NEUTRAL task (Fig. 1, third column), when participants observe action B, the correct response to provide is the action D; in order to perform the correct response D, first of all participants need to suppress the resonant motor representation B activated automatically by the mere observation of the action (Fig. 1, third column, boxes third to fifth), otherwise, if the subject decided to move before the action B suppression, the action B would have been produced instead of the action D. So for example if arm adduction is required to the observation of a grasping action, then every other motor representation at the same hierarchical level has to be suppressed. If the resonant motor representation of the grasping action is activated then, time is required to suppress it and substitute it with the arm adduction before participant decides to move (Fig. 1, removal of the white cross on the movement square, fourth and fifth boxes). The processing stages do not differ from those described in the COUNTER task (Fig. 1, both models, first and second column). Indeed also in the case of the COUNTER task, the motor representation of the action B has to be suppressed in favor of the action A, otherwise imitation would have been produced. If this assumption is correct, then the DOM model has to be preferred, given that the SM requires to suppress the resonant motor representation activated both in the COUNTER and in the NEUTRAL tasks (see Fig. 1) while the DOM model does not require it in the NEUTRAL task.

However, it is also possible that the pre-selection process that determines the response-set is performed hierarchically after the motor representation considered (i.e., hierarchically lower compared to the level of the motor representation activated by the motor resonance). For example in the NEUTRAL task the motor representation of a grasping action will never be one potential response option for the task, indeed the grasping action is not part of the response-set. According to this view the paths from the resonant motor representation downward to the muscles would be set as not available without inhibiting directly the resonant motor representation (the unavailable path to the muscles is represented in Fig. 6 as black crosses between the motor representation and the movement box). If this is the case, both the SM and the DOM models make the same predictions in terms of performance. According to the serial model, in the NEUTRAL task the information provided by the resonant motor representation is required for the rule-based route to categorize the action observed, but without resulting in an actual action to be inhibited (Fig. 6). Essentially the difference between the initial and the alternative interpretation relies on the fact that in the alternative one the resonant representation does not need to be directly inhibited because it is the path to the muscles that has been excluded by the pre-selection process that determines the responses-set, not the motor representation itself. This way, as described in Fig. 6 (third column), the resonant motor representation is

active when observing its corresponding action, allowing the executive system to be informed on which action participants have observed, but excluding the distal consequences of its activation. As depicted in Fig. 6 if the alternative assumptions were preferred, then the SM and the DOM model make exactly the same predictions. Consequently it is not possible to distinguish between a SM and a DOM model based on our results.

Given the ambiguous interpretation of the previous analysis we decided to conduct a distributional analysis on participants' accuracy based on their reaction times. The goal of this analysis is slightly different from the primary one that was focused on distinguishing between two models, the SM and the DOM model. The present distributional analysis instead redirects the question to differentiate between a serial model and a parallel one (SM vs. PM) without specifying which kind of parallel model. A parallel model does not imply DOM, meaning that it does not imply that the motor representation correspondent to the action observed is inaccessible when there is no dimensional overlap; however it implies that the possible automatic activation of the motor representation correspondent to the observed action has not a causal role in classifying the action observed.

Previous research on neurophysiological data showed that motor resonance is more likely to appear in early time windows with respect to the onset of the observed action (Ubaldi et al., 2013). If data are in accordance with SM, then the accuracy of responses before motor resonance would be at chance both in the COUNTER and in the NEUTRAL task. According to SM, when motor resonance takes place the resonant motor representation of the action observed is activated; this leads to the prediction that in the COUNTER task the accuracy time course should show a decrease in accuracy below 0.5, that is, participants do not respond by chance, but they tend to imitate the action observed. At the same time points no decrease from the chance level should be observed in the NEUTRAL task; indeed no automatic activation of arm adduction/abduction is present (differently from the COUNTER task) and no categorization can be processed since motor resonance is still taking place. After the motor resonance has been performed, the performance should increase in both tasks.

Other results would be more in accordance with a PM model; one of these results would be that in which motor resonance takes place in parallel or after the action categorization process. If this is the case, then response accuracy in the COUNTER task should increase above chance, then it should decrease and eventually it should increase again.

In order to find the time-windows in which motor resonance takes place, the accuracy on the HAND stimuli have been compared to those of the DOT stimuli in the same time-windows. The rationale of this is that DOT stimuli should not produce motor resonance by definition.

It is worth noticing that this distributional analysis does not aim to answer the question of whether the motor representation correspondent to the action observed has been automatically activated in the NEUTRAL task as it was aimed by the previous one, but it clarifies whether or not the executive system necessitates of motor resonance in order react according to a rule.

5. Distributional analysis

The distributional analysis was carried out by grouping trials in accordance to their RT. To do this we considered consecutive bins of 50 ms (from 151–200 ms to 1001–1050 ms). First we calculated the number of valid responses (i.e. showing a stable signal in the baseline period and no-response trials) and the number of correct responses provided by each participant in each bin for each stimulus category. Then we calculated the accuracy within each bin by dividing the number of correct responses by the number of valid

responses. Given that the participant's' behavior was variable both between and within subjects, the external bins turned out to be thinly populated by trials in most subjects. For this reason, we established an arbitrary cutoff and in each subject we considered only bins with at least 10 valid responses for both HAND and DOT stimuli but separately for each of the two tasks. None of the participants fulfilled this criterion in the 151–200 ms bin and only one of them did so in the 450–500 ms bin. Therefore the final analysis has been performed on five bins: 201–250 ms, 251–300 ms, 301– 350 ms, 351–400 ms and 401– 450 ms. For all 4 conditions of the task x stimulus category design. According to this procedure the participants present in each bin for the HAND and the DOT stimuli were exactly the same within tasks, but needed not be so between tasks (Tables 2 and 3).

At this point we had obtained for each participant 4 sets of 5 (one for each time-bin) accuracy values. To test whether the population of subjects was responding randomly, we ran for each of the 4 conditions 5 single sample t-tests against the null-hypothesis of the mean value¼0.5 (corresponding to a random production of responses). The critical p-value was therefore Bonferroni corrected (p-corrected¼0.05/10¼0.005). At this point we finally compared the proportions of correct responses between HAND and DOT stimuli by means of 5 separate pairwise t-tests separately in the two tasks (critical p-values were Bonferroni corrected for 5 comparisons to p¼0.01).

It is worth noticing that according to our previous works in the action observation domain (Barchiesi and Cattaneo, 2013; Ubaldi et al., 2013) the duration of the persistence of an imitative motor pattern in the corticospinal system during a counter-imitative task is in the order of 100–150 ms. Such phenomenon has therefore an intrinsic temporal frequency of around 10 Hz. This evidence leads us to sample the responses accuracies at a sample frequency of 20 Hz (50 ms bins) according to the Nyquist's rule.

We have chosen to test the response accuracy within time windows that represent absolute delays from the action presentation on the screen assuming that the delay of the motor resonance onset is invariant among participants. This assumption has its basis on previous work studying the cortical excitability of the motor system while performing tasks similar to the one used in the present work, both within the action observation domain (Barchiesi and Cattaneo, 2013; Ubaldi et al., 2013) and within more general stimulus-response compatibility experiments (Michelet et al., 2010).

5.1. Distributional analysis results

The distributional analysis shows for all conditions that in none of the 5 bins did the accuracy of the participants' population correspond to a response at chance level (mean value¼0.5). All pvalues were o0.005 and are indicated in Table 1.

The pairwise comparison between accuracy levels in response to HAND vs. DOT stimuli in the COUNTER task showed a significant difference only at the 251–300 ms bin, with responses to HAND less accurate than those to DOT (corrected p-valueo0.01, Table 2, Fig. 7 right panel). On the contrary in the NEUTRAL task the analogous pairwise comparison between accuracy in HAND vs. DOT stimuli did not yield any significant differences at any time-bin (Table 3, Fig. 7, left panel).

5.2. Distributional analysis discussion

The distributional analysis clarifies that the motor resonance phenomenon, is not a required condition to inform the rule-based route. First of all we showed that participants always responded above chance in all time-bins in all conditions. Subsequently, our analytical strategy was based on comparing the performance within the same task between HAND and DOT stimuli, the rationale of this being that DOT stimuli imply no

motor resonance by definition, and HAND stimuli instead should evoke motor resonance that manifests itself as a drop in accuracy in implementing the counter-imitative rule. In other words the prediction of the SM hypothesis would again be that of a sequential activation of the motor resonance response followed by the rulebased response in a strict early-automatic and late-executive sequence as demonstrated in other tasks (Barchiesi and Cattaneo, 2013; Ubaldi et al., 2013). The present data indeed show a drop in accuracy at one time-bin in the COUNTER task/HAND stimuli condition, between 251 and 300 ms (Fig. 7 right panel) and this trend prolonged to the next bin (301–350 ms) but without reaching the significance (p40.01). Crucially, the preceding bin (201–250 ms) does not show any evidence of interference, as demonstrated by the HAND vs. DOT comparison (Fig. 7, right panel).

This result is in line with our previously debated idea (Barchiesi and Cattaneo, 2013; Ubaldi et al., 2013) that at least two neural pathways coexist in the mind/brain transforming vision into action (see Section 1). One produces a stable stimulus-driven motor representation of the observed action, and the other(s) performs rule-driven arbitrary visuo-motor matching and the two pathways appear to be independent and compete for motor output. From the distributional analysis of the present data, however, we partly correct our model based on categorizing responses as early and late. Here we provide even stronger evidence that stimulus-driven responses and rule-driven responses are mediated by two separate pathways, as in our model. However, in previous work we claimed that the two pathways were necessarily following each other in a strict temporal order, up to the point that we labeled as "early" and "late" (Barchiesi and Cattaneo, 2013). Here we confirm the existence of two separate pathways, but we provide evidence that they are not necessarily serial in timing. Indeed, in the COUNTER

task there is evidence of rule-based responses in absence of stimulus-driven responses in the 201–250 time-bin. Evidence for the recruitment of simulative patterns becomes clear only in the later bin, 251–300 ms.

Results on the NEUTRAL task show accuracies always above chance and never different from the DOT stimuli. According to the SM, HAND stimuli should show accuracy at chance level before and during motor resonance; if we consider motor resonance to activate the motor representation correspondent to the observed action between 251 and 300 ms, as in the COUNTER task, then it is possible to conclude that even if the motor resonance takes place, it is not required to inform the rule-based route in order to react appropriately to the observed actions.

One technical aspect that should be made clear for the sake of comparison of our data with the previous literature is that the timing of motor behavior reported here corresponds to reaction times and is therefore largely delayed with respect to the corresponding cortical phenomena that are measured by TMS of the motor cortex and that are described in the previous literature. It is reasonable to expect that given a total conduction time of 20 ms from the motor cortex to the distal upper limb, an electro-mechanical delay of around 20–40 ms in hand muscles and a further delay due to joint stiffness, a delay of around 50–70 ms could be a reasonable correction factor to compare TMS studies with the present one.

6. Conclusions

Taken together these data indicate that some forms of transforming action observation into motor responses do not require motor resonance, or, going back to the theoretical aim of the present work, the

activation of motor representations is not a required condition for applying rule-based visuo-motor transformations, favoring a parallel model instead of a serial one.

The first comparison aimed to differentiate not only between SM and a general PM model but more specifically between SM and DOM models. Data showing a clear and solid performance advantage for the NEUTRAL task left however space to alternative interpretations that do not favor one model over the other. In particular it is possible that the cognitive system sets the stage for the responses in the response set, i.e. it sets the pre-selected responses by inhibiting/not allowing the access to particular muscle districts from higher motor representations (in this case from the resonant motor representation).

Given the ambiguity of the results of our first analysis we exploited the time-course of the responses accuracies to determine whether data fitted better with serial or a general parallel hypothesis.

These data further confirm the plausibility of a dual route model for action observation. One stimulus-driven route produces motor resonance phenomena which are used for categorizing observed actions, in agreement to the bulk of data that demonstrate causal effects of motor performance on perception of actions similar to those performed (Barchiesi et al., 2012; Cattaneo et al., 2011; Schütz–Bosbach and Prinz, 2007). The second route is ruledriven and allows the observer to react to an action in a flexible way accessing directly whatever motor representation is necessary to fulfill a visuo-motor rule, without the need of a two-phase access to the motor system. It could be argued that automatic motor activation during action observation can occur very early in time as demonstrated by Lepage et al. (2010). However the automatic motor activation demonstrated by Lepage et al. (2010) was a nonspecific modulation, that occurred irrespective of the action observed.

The present results are also in line with a double neural route for action understanding and are strikingly similar to the model hypothesized by Rizzolatti et al. (2001), in which aside from the motor resonance pathways, the observer can understand observed actions also by means of non-motor or non-simulative processes, which is described as the "visual hypothesis", in opposition to the Direct Matching Hypothesis (Rizzolatti et al., 2001). Similar models describing two routes for action understanding have also been hypothesized by independent groups (Kilner, 2011).

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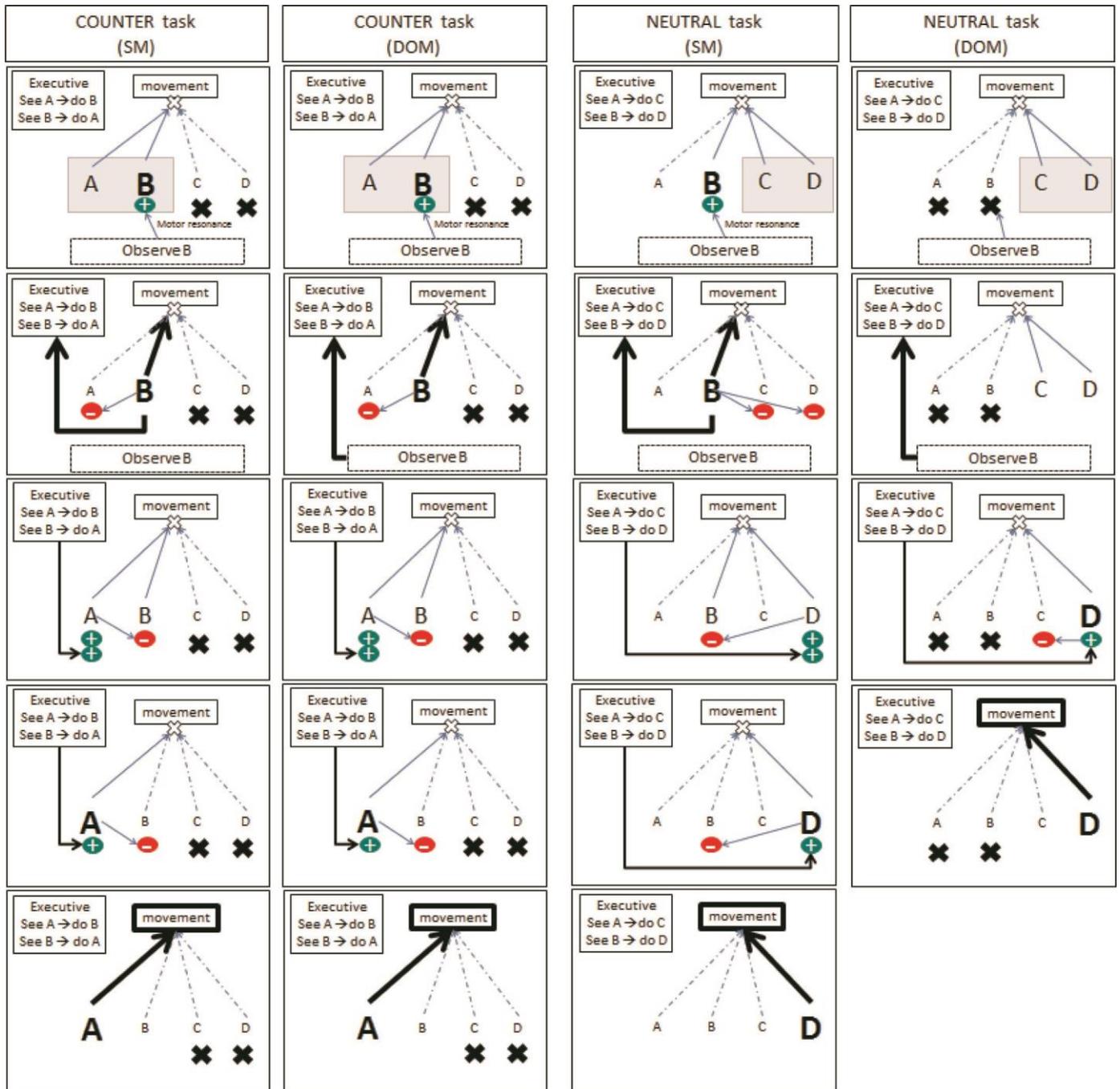
Fig. 1. Timeline developing from top to bottom. Bold letter followed by a thick line¼active motor representation. Medium sized letter followed by thin line¼facilitated motor representations. Small letter followed by a dashed line¼inhibited motor representation. Gray Square¼response-set. Black Cross¼next step never accessible. White Cross¼conditional access to the next step. Plus¼excitation, minus¼inhibition. Dynamics of the information processing model describing (from left to right): COUNTER task according to SM, COUNTER task according to DOM, NEUTRAL task according to SM, NEUTRAL task according to DOM. (For interpretation of the references to color in this figure, the reader is referred to the web version of this article.)
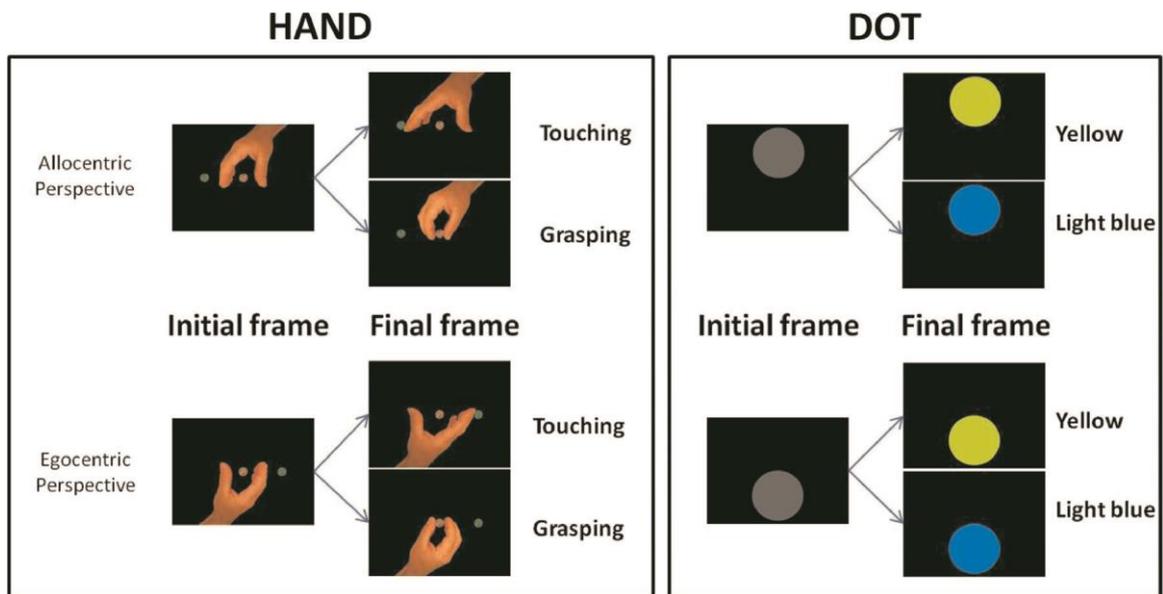
Fig. 2. Stimuli: HAND stimuli on the left, DOT stimuli on the right. On the left side of each panel the initial configuration of the stimuli is depicted, while the right side shows the two possible events for each stimulus category. (For interpretation of the references to color in this figure, the reader is referred to the web version of this article.)
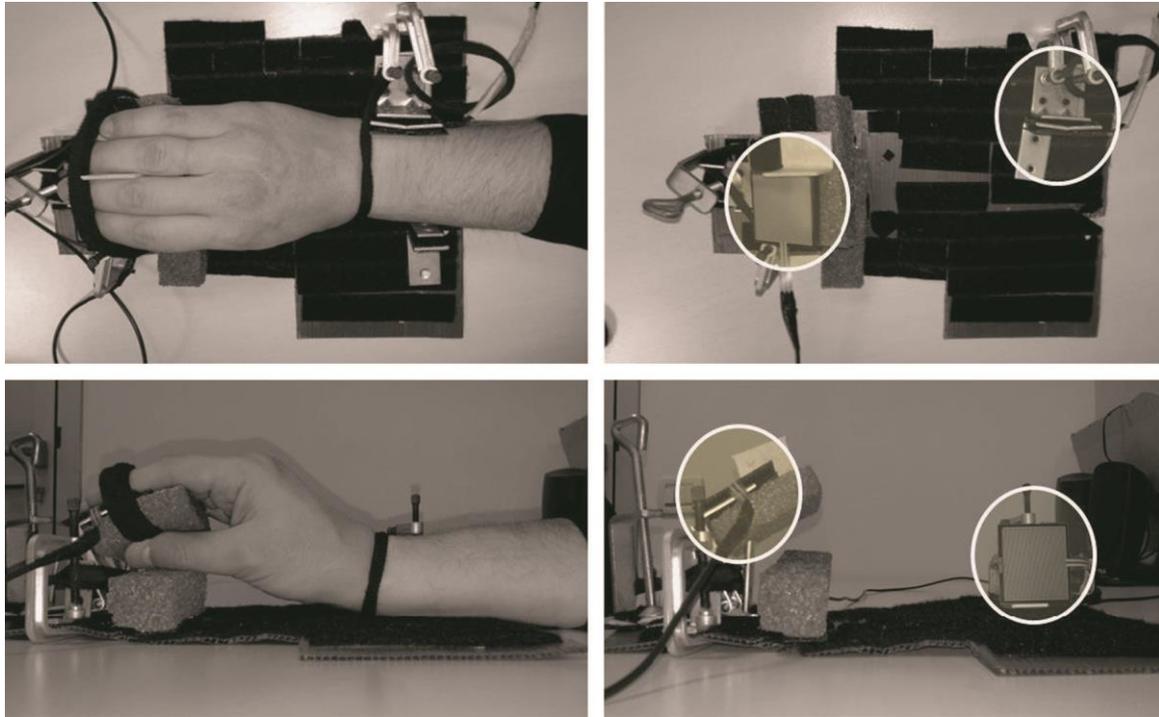
Fig. 3. Response box: custom-made response box built for the experiment. The box is composed by two force sensors one placed under participants' index and middle finger, the other placed caudally with respect to the wrist. The first provided the responses for the COUNTER task, the other for the NEUTRAL task.
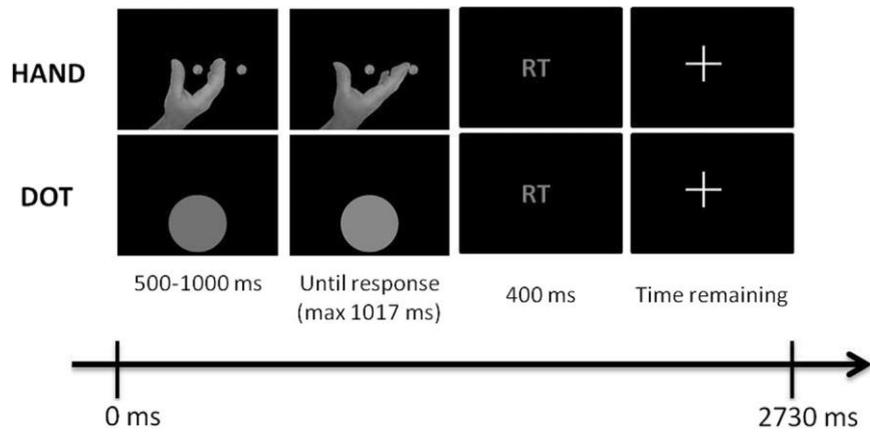
Fig. 4. Trial example: time-course of the trials (HAND trial above, DOT trial below)
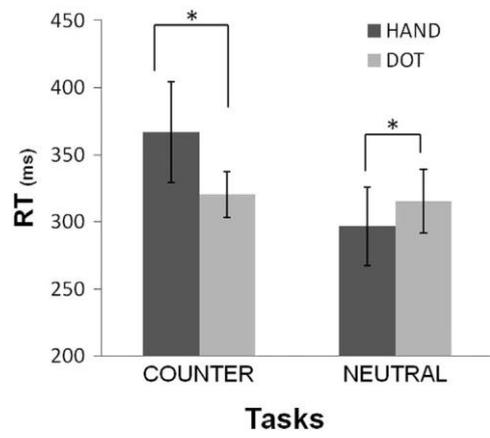
Fig. 5. RTs: Results for RTs analysis. Bars indicate confidence intervals at the alpha level of 0.025 (Bonferroni corrected for 2 comparisons).
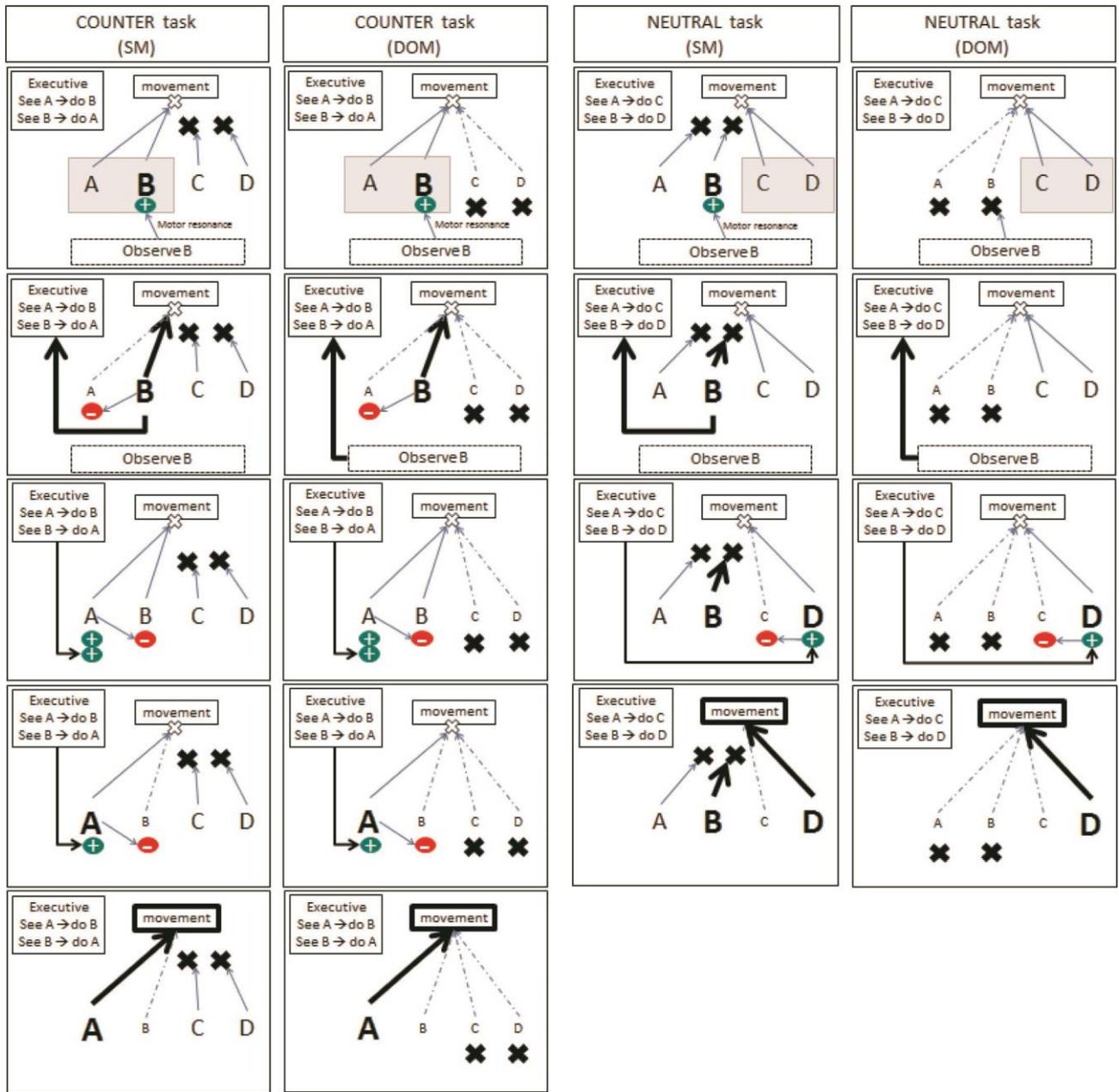
Fig. 6. Timeline developing from top to bottom. Bold letter followed by a thick line¼active motor representation. Medium sized letter followed by thin line¼facilitated motor representations. Small letter followed by a dashed line¼inhibited motor representation. Gray Square¼response-set. Black Cross¼next step never accessible. White Cross¼conditional access to the next step. Plus¼excitation, minus¼inhibition. Dynamics of the information processing model describing (from left to right): COUNTER task according to SM, COUNTER task according to DOM, NEUTRAL task according to SM, NEUTRAL task according to DOM.
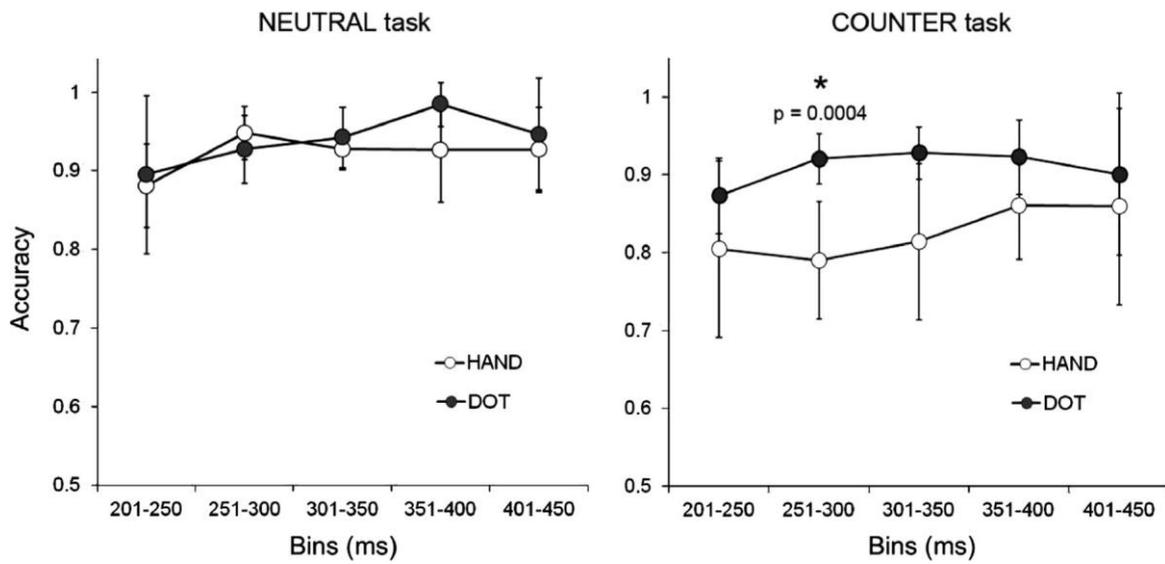
Fig. 7. Distributional analysis: HAND and DOT proportions of correct responses for the NEUTRAL (left) and the COUNTER task (right) at each time bin. Bars indicate confidence interval at the alpha level of 0.01 (Bonferroni corrected for 5 comparisons). The star indicates significant differences at the alpha level of 0.01.

Table 1
Results of the t-tests performed for each task (COUNTER and NEUTRAL) against the null hypothesis of random responses (proportions of correct responses¼0.5).

Task	Stimulus	Range (ms)		t	df	p
COUNTER	HAND	201	250	6.94382	6	0.000442
COUNTER	HAND	251	300	9.89895	9	0.000004
COUNTER	HAND	301	350	8.05612	11	0.000006
COUNTER	HAND	351	400	13.51346	13	0.000000
COUNTER	HAND	401	450	7.36696	4	0.001809
COUNTER	DOT	201	250	19.88156	6	0.000001
COUNTER	DOT	251	300	33.48401	9	0.000000
COUNTER	DOT	301	350	32.97283	11	0.000000
COUNTER	DOT	351	400	22.96263	13	0.000000
COUNTER	DOT	401	450	9.90471	4	0.000583
NEUTRAL	HAND	201	250	18.49684	7	0.000000
NEUTRAL	HAND	251	300	34.37039	13	0.000000
NEUTRAL	HAND	301	350	42.87399	13	0.000000
NEUTRAL	HAND	351	400	16.60900	5	0.000014
NEUTRAL	HAND	401	450	20.26925	2	0.002425
NEUTRAL	DOT	201	250	10.11128	7	0.000020
NEUTRAL	DOT	251	300	25.53911	13	0.000000
NEUTRAL	DOT	301	350	29.51353	13	0.000000
NEUTRAL	DOT	351	400	45.12556	5	0.000000
NEUTRAL	DOT	401	450	16.13986	2	0.003817

Table 2
Proportion of correct responses for each bin for HAND and DOT stimuli in the COUNTER task. Empty cells mean that the participant has not at least 10 valid responses for both HAND and DOT stimuli and the second row shows the number of participants on which the test statistic has been performed. The star marks the time bin at which comparison between accuracy on HAND vs. DOT stimuli resulted significant at an alpha level of 0.01 (Bonferroni corrected).

COUNTER task										
Bins (ms)	201–250		251–300		301–350		351–400		401–450	
No. participants per bin	7		10		12		14		5	
	HAND	DOT	HAND	DOT	HAND	DOT	HAND	DOT	HAND	DOT
s1			0.82	0.92	0.89	0.91	0.98	0.88		
s2	0.69	0.87	0.94	0.98	1.00	0.91	1.00	0.90		
s3	0.76	0.87	0.72	0.88	0.76	0.90	0.81	0.77		
s4							0.91	1.00		
s5			0.72	0.88	0.81	0.97				
s6	0.88	0.84	0.71	0.89	0.84	0.95	0.86	1.00		
s7					0.44	0.91	0.63	0.88	0.67	0.83
s8	0.73	0.90	0.69	0.90	0.76	0.83	0.79	1.00		
s9							0.87	0.94	0.92	1.00
s10	0.94	0.95	0.70	0.96	0.76	0.98	0.85	1.00		
s11	0.96	0.89	0.91	0.93	0.86	0.94	0.94	0.87		
s12					0.88	1.00	0.89	1.00	0.91	1.00
s13	0.69	0.79	0.82	0.89	0.89	0.93	0.95	0.89	0.92	0.85
s14			0.86	0.97	0.87	0.93	0.84	0.90		
s15							0.72	0.89	0.88	0.83
Average	0.81	0.87	0.79	0.92	0.81	0.93	0.86	0.92	0.86	0.90
p (t-test)	0.1179		0.0004		0.0132		0.0644		0.4065	
Bonferroni (corrected p¼0.01)	n.s.		n		n.s.		n.s.		n.s.	

Table 3

Proportion of correct responses for each bin for HAND and DOT stimuli in the NEUTRAL task. Empty cells mean that the participant has not at least 10 valid responses for both HAND and DOT stimuli and the second row shows the number of participants on which the test statistic has been performed. The star marks the time bin at which comparison between accuracy on HAND vs. DOT stimuli resulted significant at an alpha level of 0.01 (Bonferroni corrected).

NEUTRAL task										
Bins (ms)	201–250		251–300		301–350		351–400		401–450	
No. participants per bin	8		14		14		6		3	
	HAND	DOT	HAND	DOT	HAND	DOT	HAND	DOT	HAND	DOT
s1			0.98	0.86	0.92	0.89	0.92	1.00		
s2	0.91	1.00	0.90	0.98	0.87	0.85				
s3			0.93	0.94	0.95	0.91				
s4	0.81	1.00	0.98	0.92	0.96	0.91				
s5	0.77	1.00	0.94	0.84	0.93	0.97				
s6	0.91	0.84	0.93	0.85	0.91	1.00				
s7					0.92	0.84	0.85	0.97	0.89	0.91
s8	0.91	0.90	0.96	0.95	0.89	0.93				
s9			1.00	1.00	1.00	1.00	1.00	1.00	0.92	1.00
s10	0.91	0.90	0.95	0.96						
s11	0.93	0.85	0.82	0.96	0.90	0.98				
s12			1.00	1.00	0.97	1.00	1.00	1.00		
s13	0.91	0.68	0.95	0.82	0.87	0.98				
s14			0.94	1.00	0.96	1.00	0.92	0.94		
s15			1.00	0.91	0.93	0.95	0.87	1.00	0.97	0.93
Average	0.88	0.90	0.95	0.93	0.93	0.94	0.93	0.98	0.93	0.95
p (t-test)	0.8005		0.3603		0.3142		0.0686		0.5982	
Bonferroni (corrected p¼0.01)	n.s.		n.s.		n.s.		n.s.		n.s.	