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Research article

Implicit action prediction constrains observed biological action reconstruction

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ABSTRACT

Voluntary movements include a predictive control of the sensory-motor consequences of executed or observed actions. The motor system predicts further steps of actions relying on its pure observation. This study seeks to disclose the interference of an implicit motor prediction effect during actions reconstruction. Videos of human actions directed to objects were presented to volunteers. Subsequently, they combined four static frames of those videos randomly arranged on the screen. Such combination could be chronological (from the beginning to the end of the action) or reverse (from the end to the beginning of the action). The observed actions were also biological (human movement) or non-biological (movement of objects). The grasping began with the actor's hand in a resting position over a table (Experiment I), or with his hand in contact with the object (Experiment II). In the first experiment, participants presented lower accuracy in the biological condition rearranging in chronological order. In the second experiment, however, the accuracy was lower in reverse order. The interpretation of such results is that the implicit predictive mechanisms interfered in the rearrangement of the frames. As an example: the expected movement after a grasping action whose outcome is capping a bottle would be the withdrawal of the hand. Therefore, combining frames of a recent seen action, volunteers present less accuracy if the first frame to be placed is counterintuitive.

1. Introduction

In the realm of motor cognition every single voluntary movement is encoded considering the prediction of its sensory consequences. Since the discovery of mirror neurons in the early 90s [1,2], myriad studies have shown the role of motor system in cognitive aspects far beyond than the mere execution of actions [3]. For instance, the action observation is enough to recruit motor circuits. Observers turn on a frontoparietal cortical network (or action-perception network) passively observing movements [4]. Accordingly, the action observation might reflect an online encoding of the action that involves its understanding [5, 6, 7, 8]. The inferior frontal gyrus (IFG) within this action-perception network might be a key cortical area as demonstrated by its active involvement during a process of explicit action reconstruction [9]. In a study by Fazio et al. (2009), short biological and non-biological videos were presented to aphasic patients carrying a lesion in the IFG. Their task consisted in ordering in temporal sequence four pictures taken from those videos. It was demonstrated an impairment in their capability to re-order pictures of human actions.

Actions are usually planned to accomplish a goal [8, 10]. Thus, the general meaning of actions should be computed in a predictive way in the action-perception network. Accordingly, it is well established that action observation generates a prediction related to the outcomes of the ongoing action [11]. Any impairment in the capability to correctly encode observed human actions results in the misprediction of the upcoming events of behavior.

In congruence with the idea that the brain acts predictively [12] by coding action prospectively [13] and based on evidence that the observer's motor system resonates what they are seeing [14], it is reasonable to assume a predictive effect during action reconstruction as well. The main aim of the present study is to examine whether implicit motor predictive mechanisms interfere with an explicit mental

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reconstruction of an action. Two experiments were designed for this purpose: (I) Video clips showed an actor moving his hand towards an object placed on a table. The movement started with the actor's hand in a resting position over the table; and (II), the same video was displayed, backwards, with the actor's hand grasping the object at the beginning of the video.

Based on the above proposal we argue that the observation of videos implicitly evoked the hand returning to the resting position, when the action started from the table (Experiment I) or from the object (Experiment II). Thus, in accordance with the idea that action observation triggers an implicit motor prediction, action reconstruction would be more accurate when the hand is expected to return to the resting position after observing a reaching to grasp action. Thus, in both experiments, the accuracy to reconstruct a reaching-to-grasp action would be determined by how predictable the observed action is. This is in accordance with the idea that action observation triggers an implicit motor anticipation. Moreover, we introduced a control condition that consisted in the reconstruction of physical actions (i.e., objects displacements without biological movement) that allows verifying if such implicit interference in action reconstruction is biologically tuned or not. The present protocol is interesting due to the fact that to explicitly reconstruct a biological action, participants could predict the upcoming expected event of this action based on the previous observation, instead of only static frames or linguistic instructions. The reconstructions of temporal sequence of actions offer to participants possibility to covert imitate the observed scene onto their own motor repertoire. Thus, the next step of the observed biological action is predicted as its immediate implicit consequence when an explicit mental reconstruction is required. Accordingly, an unseen action could interfere in the explicit action reconstruction of a recent visual scene. The same process was not expected to reconstruct non-biological actions.

2. Methods

All experiments of this study were approved by the local institutional Bioethics Committee of the Federal University of Juiz de Fora (CAAE: 36257514.4.0000.5147) and are in accordance with the ethical guidelines of the Declaration of Helsinki as 2008. All participants gave their informed consent and were not previously informed about the main purpose of the study.

2.1. Experiment I

2.1.1. Participants

Twenty participants took part in this experiment (8 men). They were 18–36 years old (21.70 ± 3.88). Ten of them were right handed (5 men) and ten left handed (3 men). All participants had more than twelve years of education. Laterality was assessed using the Edinburgh Handedness Inventory [15] with scores of 85.43 ± 14.84 for right-handed and -83.04 ± 22.45 for left-handed participants. None of them had pathologies of central or peripheral nervous system. They all had normal or corrected vision.

2.1.2. Stimulus

Stimuli consisted of ten video clips of biological and non-biological actions. The screen size was 760 × 540mm. Videos were 2 s long (30 frames/second) in average. The resolution of the biological videos was 800 × 600 and 720 × 480 for the non-biological videos. Five videos were biological, and five were non-biological.

The *biological* videos showed the actor executing transitive hand movements as following: putting a pencil in a cup; bringing a cup to the mouth; lifting a bottle; placing a cork in a bottle; putting a cap on. In this experiment, the videos started with the actor laying his hand over the table in all videos and the video ended when the actor was in contact with the object. All movements in the biological videos were performed with the left hand. These videos were mirrored, resulting in identical actions with the same kinetically parameters of the movement, however performed with the other hand. Thus, each biological video got two versions, one performed with the right hand and the other with the left hand.

The *non-biological* videos presented objects moving without human intervention; i.e., a bottle falling; a chair dragging over the floor; a ball rolling over a table; a door closing and a stick falling down.

Both biological and non-biological videos were recorded by means of the same apparatus (camera and setup) and all biological videos with the same male actor. Four static frames from each video were chosen. The frames represent different and successive sequencing moments of the whole action in each video.

2.1.3. Procedure

Participants were invited to sit in a comfortable chair positioned 60 cm in front of a 15" screen (Toshiba Satellite A205) and oriented to remain with their hands resting over their legs. An experimenter handling the computer mouse was positioned at a table behind the participants out of their field of view.

Each trial was initiated by a black screen containing a centered white cross (5s), followed by the video clips. At the end of each video (2.1.2 Stimuli), a message was displayed on a black screen, indicating the order in which the frames should be organized. These frames consisted of images from the same video just shown (2.1.2 Stimuli). It could be in chronologically order ("Organize the frames from the beginning to the end of the video") or in reverse order ("Organize de frames from the end to beginning of the video"). The possibility to organize frames chronologically or in reverse allowed modifying initial and final features of the action to be reconstructed. The instruction on the screen was read aloud by the experimenter.

Participants should declare verbally the order of frames and the experimenter was responsible to record the frames' order with the mouse. The presentation of the videos was randomized in terms of category (biological and non-biological), and temporal sequence of frames' organization (chronological and reverse) (Figure 1). The data were automatically transferred to an Excel file and analyzed off-line. To familiarize the participants, four trials with different videos were run prior to the experiment. All doubts were clarified before the experiment began. The whole experimental section lasted approximately fifteen minutes.

Each participant watched a total of thirty videos: 10 biological to be organized in the chronological way (5 with the right hand and 5 with the left hand), 10 biological videos to be organized in the reverse way (5 with the right hand and 5 with the left hand), 5 non-biological videos to be organized in the chronological and 5 non-biological videos to be organized in the reverse way. All videos were watched two times and the frames were randomly organized in chronologically and reverse way. Chronological videos mean that participants should organize the frames from the beginning to the end of the action. Reverse videos mean that participants should organize the frames from the end to the beginning.

2.1.4. Statistical analysis

The accuracy, which corresponds to the rate of trials ordered correctly during each experiment, was computed. Wrong trials were those in which the participant indicated the order incorrectly in at least one of the frames.

Two-way ANOVA for repeated measures was used to access differences in accuracy by comparing "conditions" (Biological and Non-Biological) and "temporal sequence" (Chronological and Reverse) within factors. Additionally, the "laterality of the participant and video" (actor performing the action with the right or left member) was investigated to exclude possible confounding effects. The laterality of the actor was considered only when comparing biological videos. There was no effect of participants laterality ($F_{(1,18)} = 0.124$; $p = 0.729$; $n^2_p = 0.007$; $\beta = 0.063$), neither influence of the participants laterality in video laterality ($F_{(1,18)} = 0.080$; $p = 0.781$; $n^2_p = 0.004$; $\beta = 0.058$) as result of "Video *x* Laterality" in ANOVA. Data were analyzed using the program Statistical Package for Social Sciences (SPSS, version 22.0), adopting a

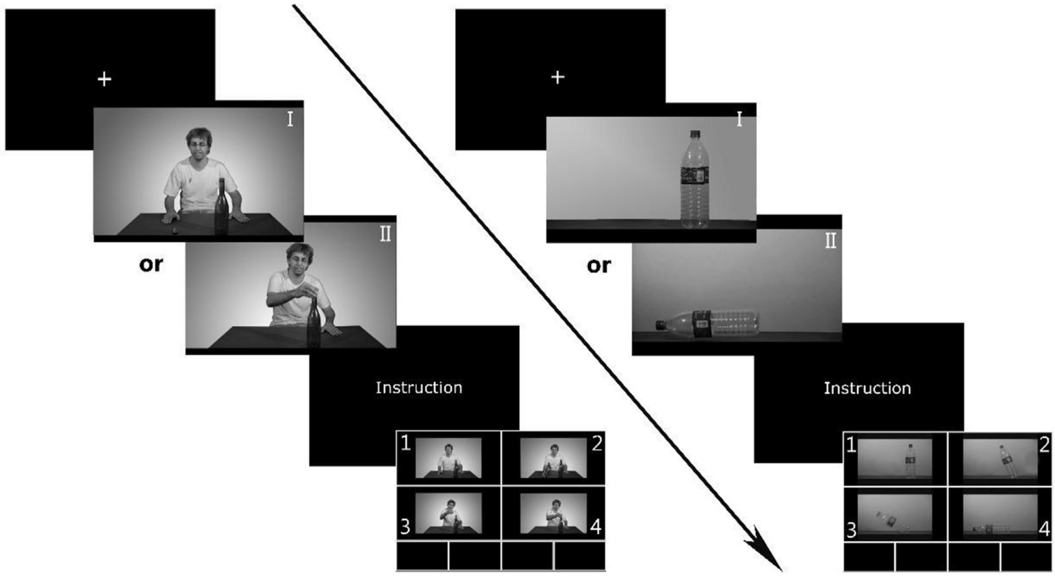

Figure 1. Experimental procedure. Panels on both sides of the diagonal arrow depict successive views of the computer screen during a representative trial of the frame-ordering task. On the left an example of video-clip frames representing the biological condition and on the right the non-biological condition. The experiment started with a white cross in the center of the screen. Once the video-clip was presented, volunteers followed an instruction indicating the temporal sequence (chronological or reverse) in which they should order the frames. They answered verbally by indicating the numbers beside the frames. Upon the experimenter's click the program transferred each frame to the empty dark cells at the bottom of the screen in the indicated order.

significance level of 5% ($p < 0.05$). The post Tukey HSD test was applied when necessary. Results are expressed in mean ± SEM. The effect size was computed based on the partial eta-squared (n^2_p). In addition, the statistical power (β) was indicated whenever applicable.

2.1.5. Results

In the experiment, in which videos started with the actor laying his hand over the table, participants performed worse when instructed to organize the frames in a chronological way. Repeated measures ANOVA revealed an interaction between condition x temporal sequence ($F_{(1,19)} = 8.55$; $p = 0.009$; $n^2_p = 0.31$; $\beta = 0.792$). The post hoc revealed that the accuracy of the biological chronological condition (77.50 ± 3.83) was lower compared to the biological reverse condition (87.50 ± 2.39; $p = 0.007$), chronological non-biological condition (91.00 ± 3.07; $p = 0.0006$) and non-biological reverse condition (90.00 ± 2.71; $p = 0.001$), respectively. There was no statistical significant difference for the non-biological conditions ($p = 0.06$), nor any other effects for condition ($F_{(1,19)} = 3.88$; $p = 0.06$; $n^2_p = 0.17$; $\beta = 0.46$) and temporal sequence ($F_{(1,19)} = 3.96$; $p = 0.06$; $n^2_p = 0.17$; $\beta = 0.47$) (Figure 2).

2.2. Experiment II

2.2.1. Participants

Twenty six different participants took part in this experiment (10 men). They were 18–26 years old (20.346 ± 2.497). Thirteen of them were right handed (4 men) and 13 were left handed (6 men). All participants had more than twelve years of education. Laterality was assessed using the Edinburgh Handedness Inventory [15] with scores of 83.46 ± 16.25 for right-handed and -87.31 ± 19.11 for left-handed participants. None of them had pathologies of central or peripheral nervous system. They all had normal or corrected vision.

2.2.2. Stimulus

In this experiment all videos from Experiment I (2.1.2 Stimuli) were modified to backwards. In this way, biological videos started with the actor's hand in contact with the object, which is the last scene of those biological videos showed in Experiment I (Figure 1). Therefore, the videos were as following: removing a pencil of a cup; removing a cup of the mouth; putting a bottle in the table; removing a cork of a bottle; putting off a cap. The non-biological videos were also put backward.

2.2.3. Procedure

In this Experiment the procedure was the same as in Experiment I, except the way in which videos were presented. In Experiment I, we verified that subjects reconstructed actions with more accuracy in reverse way. In other words, they better reconstructed actions when scenes started with the actor's hand in contact with the object and ended in the

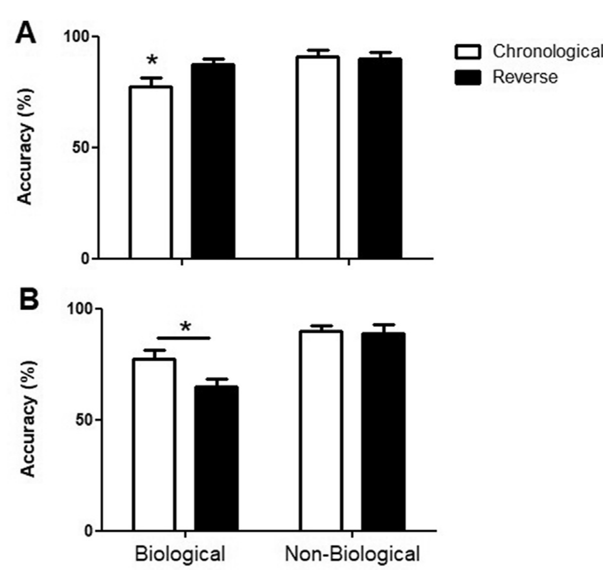

Figure 2. Percentage of accuracy in the frame-ordering task. **A:** The chart represents the mean accuracy of volunteers in the experiment I for the biological condition (bars on the left and non-biological condition, bars on the right). **B:** Same layout in reference to experiment II. Significant differences were only observed for the biological condition. (*) = $p < 0.05$. Biological and non-biological conditions ordered in chronological (white) or reverse (black) way.

rest position. To confirm that results are due to implicit motor prediction, we run a second experiment. Thus, Experiment II consisted in the same procedure, but the original videos were backward.

All conditions were equal as well as the number of trials. The entire duration of the experiment was approximately fifteen minutes.

2.2.4. Statistical analysis

The statistical analysis performed in Experiment II was conducted as in Experiment I.

Two-way ANOVA for repeated measures was used to access differences in accuracy by comparing "conditions" (Biological and Non-Biological) and "temporal sequence" (Chronological and Reverse) within factors. Additionally, the "laterality of the participant and video" (actor performing the action with the right or left member) was investigated to exclude possible confounding effects. The laterality of the actor in the videos was considered as a factor only when comparing biological videos.

There was no effect of participants laterality ($F_{(1,24)} = 0.240$ p = 0.628; $n^2_p = 0.10$; $\beta = 0.076$), neither an influence of participant laterality in the video ($F_{(1,24)} = 3.041$; $p = 0.094$; $n^2_p = 0.112$; $\beta = 0.388$) as result of "Video *x* Laterality" in ANOVA. Data were analyzed using the program Statistical Package for Social Sciences (SPSS, version 22.0), adopting a significance level of 5% ($p < 0.05$). The post Tukey HSD test was applied when necessary. Results are expressed as mean ±SEM. Effect size was computed based on the partial eta-squared (n^2_p). In addition, the statistical power (β) was indicated whenever applicable.

2.2.5. Results

In this experiment videos started with the actor touching an object, the participants performed the test with lower accuracy when they had to organize the frames in the biological condition and reverse order. Repeated measures ANOVA revealed a statistically significant effect for temporal sequence ($F_{(1,25)} = 5.273$; $p = 0.030$; $n^2_p = 0.174$; $\beta = 0.598$) and an interaction between condition x temporal sequence ($F_{(1,25)} = 5.291$; $p = 0.030$; $n^2_p = 0.175$; $\beta = 0.599$). The post-test indicated that participants were more accurate in the biological chronological condition (77.44 ± 3.72) when compared to biological reverse condition (p = 0.009, 64.79 ± 3.72). Accuracy in non-biological conditions was higher when compared to biological chronological condition; non-biological chronological (p = 0.01, 90 ± 2.54) and non-biological reverse (p = 0.01, 89.23 ± 3.72). Moreover, participants were more accurate reconstructing a non-biological action than a biological one ($F_{(1,25)} = 26.600$, $p = 0.000025$; $n^2_p = 0.516$; $\beta = 0.999$) (Figure 2).

3. Discussion

Herein the interference of implicit motor predictive mechanisms on explicit mental reconstruction of an action was tested by applying the observation of forward and backward reaching-to-grasp actions presented in short video clips. The results support the hypothesis that the implicit expectation of participants about the ongoing observed action specifically interferes in biological action reconstruction. It is suggested here that motor circuits are directly involved in this process.

When participants were asked to reconstruct a biological or a non-biological action from random series of snapshots in chronological or reverse order, the accuracy of action reconstruction was higher when the task was congruent with the ongoing action (i.e., reverse condition of experiment 1), only for the biological condition. This finding suggests that returning the hand to the resting position is expected, predicting its natural movement as a consequence of the observed act - the hand reaches the object and must return to the initial position. Indeed, the hand is not even expected to remain holding the object everlasting. Moreover, for the reconstruction of objects motion, no differences between order sequences were found. It is in agreement with previous results demonstrating that the reconstruction of a hidden trajectory of a limb was biologically tuned [16, 17, 18]. For instance, participants were more accurate to estimate the final position of a motion partially hidden when the motion kinematics respects biological rules [16, 18] or the biomechanical constraints of movements [18].

In the second experiment however, the biological condition began with the actor's hand touching the object, suggesting its return to the resting position in chronological action. Accordingly, the reconstruction of this action was more accurate than the biological reverse action, which was in this case the same chronological action displayed in Experiment I. In addition, the reconstruction of action in reverse order in this case (i.e., the hand on the table towards the object) seems to be incongruent with the expectation of what the movement should be. Thus, the next step of the observed biological action is predicted as its immediate implicit consequence when an explicit mental reconstruction is required. Indeed, the sequential order seems to be a crucial factor in action planning [19].

Taken together, these results are in agreement with theoretical proposals as the prospective coding [20] in which the observation of the current state of an action would contain expectations/predictions about its future conditions.

Herein, the prediction of the final goal of the action led to a biological action reconstruction from random static snapshots of the observed action.

Therefore, these findings suggest that implicit prediction of such actions include the movement *continuum* and that such action continuation in absence of visual stimulation would directly interfere, positively, or negatively, in the reconstruction of a previously observed action. Although this phenomenon has not yet been demonstrated during mental reconstruction of actions, a converging beam of evidence has been proposed. In other words, the action perception activates the motor system [21] in a predictive way [22, 23, 24]. Cavallo et al. (2016) [24] have shown that observers could extract kinematic features of pouring or drinking, over the total kinematic pattern of grasping movements observed in point light videos. They suggested that individuals can anticipate others' intentional actions by observation.

Additionally, the absence of differences between temporal sequences for non-biological conditions is particularly interesting for two main aspects. First, it confirms that viewing the last video scene did not facilitate action reconstruction for the reverse (Experiment I) and chronological (Experiment II) conditions. Results of the biological condition also confirm this evidence. If visual reminiscence affected the accuracy of action reconstruction, a greater accuracy for reverse conditions in both experiments would be expected. However, the results of these experiments differ from this prediction, since in the second experiment the accuracy is better for the chronological reconstruction. Accordingly, since the interval was very short (less than one minute) between the last scene viewing and the frames presentation, a working memory influence could not be totally ruled out. However, the effect described herein does not seem to be mainly determined by ultra-fast memory systems [25]. Second, the difference between the biological and the non-biological condition strongly suggests that distinct processes and/or neural networks sustain the action reconstruction of each action.

The observation of a non-biological condition as object movements, for instance, recruit cortical areas involved in the representation of physical laws [26]. In addition, Pickering and Garrod (2013) [28] suggest that the non-biological motor prediction may rely in perceptive processes. On the other hand, it is well established that the observation of biological motion recruits the motor system (mainly the inferior frontal gyrus, the premotor area and the parietal cortex) plus the STS (superior temporal sulcus) according to the motor rules [21, 27]. Using a very similar experimental design, Fazio et al. (2009) [9] emphasized the importance of the inferior frontal gyrus (IFG) for the biological action reconstruction. Indeed, aphasic patients presented a higher error rate to reconstruct biological rather than non-biological actions.

Based on neuropsychological evidence and theoretical models, we propose an involvement of parietal areas during action observation throughout a complex frontoparietal interaction, which directly interferes on action reconstruction, specifically for a biological condition.

For instance, Fontana et al. (2011) [29] demonstrated that the parietal injury affected the readiness potential (i.e. a marker of motor activity preceding the execution and observation of voluntary movements reflecting the motor preparation) when patients had to perform a task to observe and predict action. Interestingly, the authors described the absence of readiness potential prior to the observation of action for patients with posterior parietal cortex lesion, which was not the case for patients with a ventral premotor lesion. Such evidence suggests that the parietal cortex could have a predictive role about the action goal [29] whereas the premotor cortex would encode the observed action [9]. We hypothesize that the interaction between these two cortical areas could explain the difference between experimental conditions (chronological vs. reverse) to reconstruct a biological action by anticipating the implied goal in the observed action. Such assumption remains highly speculative and complementary neuropsychological and neurophysiological studies are necessary.

In conclusion, the results of this study point out that the motor system discloses the upcoming predictions of observed actions by reconstructing their sequence explicitly. Herein, it is argued that the predictive feature of the motor system is a consequence of a space-time representation in a network of action-observation. Particularly, prediction can only make sense as being part of a coherent story in the realm of moving with intentions. Such evidence should help to orient the conception of new protocols and therapies acknowledging the profound predictive nature of action observation.

Declarations

Author contribution statement

Amanda Mara de Assis Chagas, Isabella Alves de Faria: Performed the experiments; Analyzed and interpreted the data; Contributed reagents, materials, analysis tools or data; Wrote the paper.

Ghislain Saunier: Conceived and designed the experiments; Contributed reagents, materials, analysis tools or data; Wrote the paper.

Ruben E Bittencourt-Navarrete: Conceived and designed the experiments; Wrote the paper.

Anaelli A Nogueira-Campos: Conceived and designed the experiments; Analyzed and interpreted the data; Contributed reagents, materials, analysis tools or data; Wrote the paper.

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Data availability statement

Data included in article/supplementary material/referenced in article.

Declaration of interests statement

The authors declare no conflict of interest.

Additional information

No additional information is available for this paper.

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