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Research Report

State-dependent TMS of inferior frontal and parietal cortices highlights integration of grip configuration and functional goals during action recognition

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ABSTRACT

Understanding the object-directed actions of conspecifics not only implies recognition of the object (e.g., a pen) and processing of the motor components (e.g., grip configuration), but also identification of the functional goal of the action (e.g., writing). Motor components and goal representations are both known to be critically involved in action recognition, but how the brain integrates these two pieces of information remains unclear. Action priming was used to tune the cognitive system to the integration of grip and goal representations. We evaluated the effect of briefly presented primes sharing grip and/or goal information with the target on recognition of action photographs. Single-pulse transcranial magnetic stimulation (TMS) was applied at target onset over the inferior frontal cortex (IFC) or the inferior parietal lobule (IPL) to evaluate their involvement in integrating grip and goal information. IFC and IPL stimulation specifically reduced integration of these two pieces of information. These results demonstrate, for the first time, the existence of specialized neuronal populations dedicated to grip/goal integration within a fronto-parietal network, supporting the importance given to this network by sensorimotor and predictive models of action recognition.

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1. Introduction

As social animals, human beings have to take their conspecifics' actions into account to properly plan and carry out their own actions (Jacob & Jeannerod, 2005; Sebanz & Knoblich, 2009). Those actions are complex, organized and goal-directed (Cooper, Ruh, & Mareschal, 2014; van Elk, van Schie, & Bekkering, 2014). For example, a person's action may involve not only reaching for and grasping (the motor components of the action) a glass of water (the object), but also an ultimate goal, such as drinking. Both the action's motor components – dynamic and static parameters – and goal-related information are important for action understanding (Baldwin, Baird, Saylor, & Clark, 2001; Decroix & Kalénine, 2018, 2019; Hrkać, Wurm, & Schubotz, 2014; Novack, Wakefield, & Goldin-Meadow, 2016; Tidoni, Borgomaneri, di Pellegrino, & Avenanti, 2013; van Elk, Van Schie, & Bekkering, 2008; Zacks, Tversky, & Iyer, 2001). Yet how motor components and goal representations contribute to action understanding and how the two representations are integrated in the brain remains poorly understood (Thompson, Bird, & Catmur, 2019).

Understanding how information about goals and motor components is represented in the brain first requires the two components to be experimentally manipulated independently (Decroix & Kalénine, 2018, 2019; Kalénine, Shapiro, & Buxbaum, 2013; van Elk et al., 2008). Decroix and Kalénine (2018) used a priming paradigm involving object-directed action pictures containing grip and/or goal violations to assess the relative timing of grip configuration processing (i.e., the specific operationalization of the motor components) and goal activation processing when observing actions. In that study, target pictures of object-directed actions were briefly primed by an action picture ($\leq$300 msec) sharing i) only the same action goal; ii) only the same grip configuration; iii) both the same goal and the same grip; or iv) neither the same grip nor the same goal. The authors reported facilitatory priming effects for both grip and goal information: participants were faster at accurately judging the target actions (i.e., whether the action was correct with the typical use of the object) when the prime showed the same grip/goal information relative to when it showed different grip/goal information. Remarkably, when the prime lasted 220 msec, action recognition was slower following primes with either a similar grip or a similar goal, but not both, compared to primes with both similar or both dissimilar grip and goal dimensions – a phenomenon known as the partial-repetition cost (Hommel, 2004). This effect may be considered a behavioral hallmark of the integration of grip configuration and goal dimensions during action observation (Decroix & Kalénine, 2018). Yet prior behavioral work has not clarified which brain region is causally involved in the integration of goal and grip configuration during action observation.

Potential candidates for integrating grip configuration and goal information lie within the so-called action observation network (AON) – a widespread cortical network including occipito-temporal visual areas and fronto-parietal sensorimotor brain regions. The inferior frontal cortex (IFC) and the inferior parietal lobule (IPL) are considered key "motor" nodes of the AON that are involved in coupling visual representations of observed actions with motor representations of the same actions (Avenanti, Candidi, & Urgesi, 2013; Caspers, Zilles, Laird, & Eickhoff, 2010; Molenberghs, Cunnington, & Mattingley, 2012; Ocampo & Kritikos, 2011; Spunt & Lieberman, 2012; Thill, Caligiore, Borghi, Ziemke, & Baldassarre, 2013; Urgesi, Candidi, & Avenanti, 2014; van Elk et al., 2014; Van Overwalle & Baetens, 2009). Interestingly, prior imaging (e.g., Schubotz, Wurm, Wittmann, & von Cramon, 2014; Wurm & Lingnau, 2015) and theoretical work (Kilner, 2011; Lingnau & Downing, 2015) suggested that fronto-parietal nodes of the AON integrate information about the goals and the motor components of the action. However, whether the IFC and/or the IPL play a critical role in this process remains unclear. Notably, there is growing evidence that the IFC and the IPL are critical for action processing, as brain lesions or neurostimulations of the two nodes lead to impaired action recognition (Avenanti, Paracampo, Annella, Tidoni, & Aglioti, 2018; Candidi, Urgesi, Ionta, & Aglioti, 2008; Cattaneo, 2010; Cattaneo et al., 2011; Cattaneo, Sandrini, & Schwarzbach, 2010; Fontana et al., 2012; Jacquet & Avenanti, 2015; Kalénine, Buxbaum, & Coslett, 2010; Kalénine et al., 2013; Koch et al., 2010; Michael et al., 2014; Pobric & Hamilton, 2006; Tidoni et al., 2013; Urgesi, Candidi, Ionta, & Aglioti, 2007; Valchev, Tidoni, Hamilton, Gazzola, & Avenanti, 2017). However, these studies did not evaluate which neural regions are critical for integrating grip configuration and goal information during action observation.

The present study aimed to overcome the aforementioned limitations by investigating the neural bases of the integration of goal and motor components of observed action within the two key fronto-parietal nodes of the AON, i.e., the IFC and the IPL. We built upon the previous work of Decroix and Kalénine (2018) and developed a behavioral task that could reveal the roles of the IFC and the IPL in selective processing of grip configuration, selective processing of goals or the integration of grip and goal information. Participants were asked to evaluate target photographs of object-directed actions that were briefly primed by an action photograph sharing only the same action goal, only the same grip configuration, both the same goal and the same grip or neither the same goal nor the same grip. Prime stimuli lasted for 220 msec and were followed by a mask lasting 66 msec, as in Decroix and Kalénine's (2018) study. Their results showed that this duration is sufficient not only to elicit both grip and goal priming effects separately (i.e., priming a specific grip/goal facilitated recognition of the same grip/goal in target pictures), but also to induce a partial-repetition cost (i.e., faster action recognition following primes with both similar or both dissimilar grip and goal dimensions than primes with either a similar grip or a similar goal).

Importantly, to test the causal role of the main fronto-parietal nodes of the AON, we administered single-pulse transcranial magnetic stimulation (TMS) at target onset over the left IFC and the left IPL. As a control, we administered sham TMS over the vertex, which served as a baseline session. TMS over a neural region causally involved in selective processing of the feature shared by the prime and the target stimulus (i.e., the grip or the goal) would result in a *selective* alteration of the grip/goal priming effect (Cattaneo, 2010;

Cattaneo, Rota, Vecchi, & Silvanto, 2008; Cattaneo, Silvanto, Battelli, & Pascual-Leone, 2009), thus demonstrating a state-dependent TMS effect (Lang et al., 2004; Siebner et al., 2004; Siebner, Hartwigsen, Kassuba, & Rothwell, 2009; Silvanto & Cattaneo, 2017; Silvanto, Muggleton, & Walsh, 2008). This would reveal neuronal populations dedicated to processing the grip and/or the goal in the stimulated region (Cattaneo, 2010; Cattaneo et al., 2008; Romei, Thut, & Silvanto, 2016; Silvanto & Cattaneo, 2017; Silvanto & Pascual-Leone, 2008). On the other hand, an alteration of the partial-repetition cost (Hommel, 2004) would reveal neuronal populations dedicated to the *integration* of the two dimensions in the stimulated region. The choice of a TMS-priming paradigm was motivated by i) the need to control the timing of action processing and target a particular time when we know that both grip configuration and goal information have been independently processed and integrated (Decroix & Kalénine, 2018) and ii) the possibility of detecting changes in facilitative priming effects (independently for grip or goal processing) as well as partial repetition costs (grip and goal integration). As mentioned above, the IFC and IPL are two equally good candidates for processing grip configuration and goals independently, as well as for integrating the two components. Thus, our paradigm allowed us to test whether the IFC and the IPL contain functionally relevant neural populations involved in integrating grip and goal information or selectively processing grip or goal information independently.

2. Methods

2.1. Participants

Eighteen participants[3] (6 males, $M_{age} = 24$ years, range: 21–29 years) were recruited for the study. All were right-handed according the Edinburgh Handedness Inventory (EHI; *M* = .83, range: .37–1; Oldfield, 1971) and reported normal or corrected-to-normal vision and no history of neurological or psychiatric disease. They all provided written informed consent. The experiment was approved by the bioethical committee at the University of Bologna and was carried out in accordance with the Declaration of Helsinki (World Medical Association, 2013).

2.2. Stimuli

Twenty objects were selected. For each reference object, four color 1024 × 683 px photographs were taken, all involving hand-on-object actions. Actions were always performed with the right hand by the same female actor, and photographs were framed in such a way that only the forearm, the right hand and the object were visible. Photographs only showed the tool-object without the recipient (e.g., a nail for an action with a hammer) to minimize the influence of contextual information outside of the hand-object interaction on action processing.

For each reference object, actions could be typical or atypical in terms of grip configuration and/or action goal. Typical grips were defined according to the typical manipulation of the object. For instance, a precision grip applied to a pencil is considered typical, whereas a power grasp is not. Typical action goals were defined according to the typical function of the object. For example, an upright pencil allows one to write (typical goal possible), whereas an upside-down pencil does not (typical goal impossible). Importantly, the typical goal could still be achieved even when the grip was atypical, and vice-versa. Thus, grip configuration and action goal dimensions were manipulated independently, resulting in four possible combinations of grip configuration (typical or atypical) and action goal (typical or atypical). Example stimuli are shown in Fig. 1. The full set of stimuli is available as Supplementary Material.

2.3. Design and procedure

The pictures were presented in a priming paradigm. All four types of picture could be presented as prime. Only the fully typical actions showing both typical grip and typical goal ("correct targets") or the fully atypical actions showing both atypical grip and atypical goal ("incorrect targets") could be presented as targets. This resulted in four prime–target relations for each reference object: "Grip similar, Goal similar"; "Grip similar, Goal dissimilar"; "Grip dissimilar, Goal similar"; "Grip dissimilar, Goal dissimilar".

There was a total of 2 grip similarity levels (Grip similar; Grip dissimilar) x 2 goal similarity levels (Goal similar; Goal dissimilar) x 2 response types (Yes = "correct target"; No = "incorrect target") x 20 objects = 160 trials. Each trial was repeated in three TMS blocks corresponding to the stimulated areas (IFC; IPL) and sham. Each TMS block was divided into two blocks of 80 trials, resulting in six blocks of eight minutes each with a break between blocks of ~5 min. Block order and trial order were fully randomized. Overall, there were 80 trials x 6 blocks = 480 trials. The experiment was conducted with E-Prime V2.0.10.353 software (Psychology Software Tools,

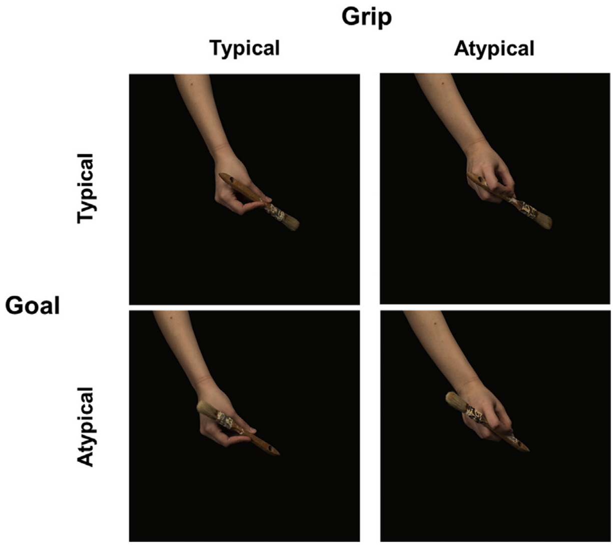

Fig. 1 – Example of stimuli.

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[3] Based on the relevant literature (Cattaneo, 2010; Cattaneo et al., 2010; Jacquet & Avenanti, 2015), we estimated that about 16 participants would be necessary for this experiment.

Pittsburgh, PA). The design of the experiment and the stimulated sites are shown in Fig. 2.

Each trial started with a fixation cross for 5000 msec, then the prime for 220 msec, then a pixelated black and white mask for 66 msec and finally the target that was displayed until the participant's response. Participants were required to judge as quickly and accurately as possible whether the target action was correct or not according to the typical use of the object (forced choice). They were required to press "c" or "b" on a keyboard using their left hand. The correct/incorrect pattern was counterbalanced between participants. As in previous studies, TMS was delivered at target onset (Cattaneo, 2010; Cattaneo et al., 2008). The prime duration of 220 msec was chosen based on our previous priming study with a similar design in which a 220-ms prime followed by a 66-ms mask was sufficient to trigger both grip and goal priming effects (Decroix & Kalénine, 2018). Response times (RT) and response accuracy were recorded. Participants first performed a training session with twelve representative trials on which they received feedback. The training session involved three additional objects that were not included in the experimental session. The experimental session was equivalent to the training session but without feedback. Participants could take breaks between the blocks.

Participants first filled in the consent form and the EHI. The TMS setup was then calibrated (see below). The training session and the 6 experimental blocks were performed. At the end of the experiment, participants were debriefed. Overall, the experiment lasted ~2 h.

2.4. Transcranial magnetic stimulation (TMS)

TMS pulses were delivered with a figure-of-eight coil (70 mm) and a Magstim Rapid2 stimulator (Magstim, Whitland, Dyfed, UK). The individual resting motor threshold (rMT) of each participant was identified as the minimal stimulation intensity producing motor evoked potentials (MEPs) of a minimum amplitude of 50 μV in the right first dorsal interosseous (FDI) muscle with 50% probability (Rossini et al., 2015). MEPs were recorded by means of a Biopac MP 35 electromyograph (Biopac Systems, Inc., USA). EMG signals were band-pass filtered (30–1000 Hz) and digitized (sampling rate: 5 kHz). Pairs of silver/silver chloride surface electrodes were placed over the right FDI muscle using a belly/tendon montage. The intensity of stimulation used during the experiments was set to 110% of the individual rMT.

Prior to the experimental session, the coil position was identified on each participant's scalp using the SofTaxic Navigator system (EMS, Bologna, Italy). In a first step, skull landmarks (nasion, inion and 2 preauricular points) and about 60 points providing a uniform representation of the scalp were digitized by means of a Polaris Vicra Optical Tracking System (Northern Digital, Inc., Waterloo, ON, Canada). Coordinates in Talairach space were automatically estimated by the SofTaxic Navigator from a magnetic resonance imaging (MRI)-constructed stereotaxic template. Then we selected the scalp sites corresponding to the IFC and the IPL in the left hemisphere using the coordinates of the activation peaks reported for observation of hand-object pictures in the meta-analysis of Caspers et al. (2010). The IFC was targeted in the anterior–ventral part of the precentral gyrus (ventral premotor cortex) at the border with the pars opercularis of the inferior frontal cortex (coordinates: $x = -51$, $y = 7$, $z = 30$), corresponding to Brodmann's area 6/44 (Avenanti, Annela, & Serino, 2012; Avenanti, Annella, Candidi, Urgesi, & Aglioti, 2013; Caspers et al., 2010; Urgesi et al., 2007; Van Overwalle & Baetens, 2009). The IPL was targeted in the anterior sector of the intraparietal sulcus ($x = -58$, $y = -24$, $z = 36$), corresponding to Brodmann's area 40 (Avenanti et al., 2012; Caspers et al., 2010; Van Overwalle & Baetens, 2009). The IFC and IPL scalp sites were marked on a bathing cap with a pen. Then the neuronavigation system was used to estimate the projections of the scalp sites onto the brain surface (IFC mean surface Talairach coordinates ± SD: $x = -52 \pm 2$, $y = 6 \pm 1$, $z = 30 \pm 2$; IPL: $x = -58 \pm 3$, $y = -24 \pm 1$, $z = 35 \pm 1$). IFC and IPL stimulation was carried out by placing the coil tangentially over the marked scalp sites. Sham stimulation was performed by

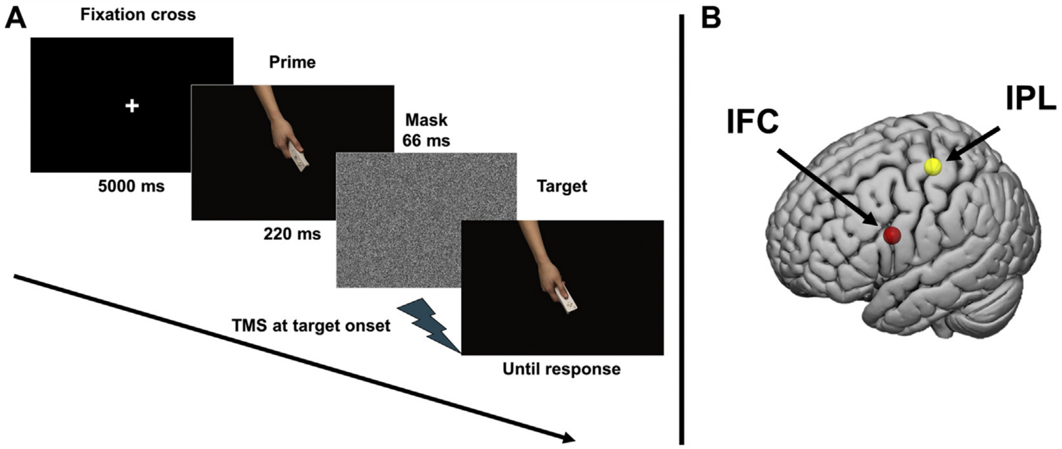

Fig. 2 – **A. Design of the experiment. B. Sites of stimulation for the inferior frontal cortex (IFC) and the inferior parietal lobule (IPL) reconstructed on a standard template using MRIcron software. Mean surface Talairach coordinates ±SD for the IFC site were: $x = -52 \pm 2$, $y = 6 \pm 1$, $z = 30 \pm 2$. Surface coordinates for the IPL site were: $x = -58 \pm 3$, $y = -24 \pm 1$, $z = 35 \pm 1$.**

placing the coil tilted at 90° over the vertex, so that no current was induced in the brain.

2.5. Data preprocessing

The task was relatively easy to perform ($M_{accuracy} = 94.5\%$, range: 79.6–99.6%). First, trials with errors and/or RTs greater than 1500 msec or less than 150 msec were considered conceptual outliers (i.e., data not related to the processes of interest) and removed (5.65% of the data). In the remaining trials, RTs greater or less than 5 median absolute deviations from the median (Leys, Ley, Klein, Bernard, & Licata, 2013), computed separately for each condition and each participant, were considered statistical outliers (i.e., data not representative of the RT distribution) and removed (1.24% of the remaining data). See Table 1 for RT and accuracy data averaged per condition.

2.6. Data analysis using mixed-effects models

A mixed model approach was used to take both individual participants and items into account as sources of variation and to consider their possible interactions with the factors of interest (e.g., a given participant or a given item, may be more sensitive to IFC stimulation than another one). Mixed models were fitted with restricted maximum likelihood (REML) using the *lme4 1.1-17* package in R (Bates, Mächler, Bolker, & Walker, 2015). Overall main effects and interactions were evaluated with *F* statistics obtained using Satterthwaite's approximation of degrees of freedom for the denominator, implemented by the *lmerTest 3.0-1* package (Kuznetsova, Brockhoff, & Christensen, 2017). This method has been proven to produce acceptable type 1 error rates (Luke, 2017). *t*-tests of individual parameter estimates were then used to evaluate the contrasts of interest. Effect sizes for individual parameter estimates were computed using a variant of Cohen's *d* adapted for mixed-effects models, hereafter called "Westfall's *d*" (Brysbaert & Stevens, 2018; Judd, Westfall, & Kenny, 2017; Westfall, Kenny, & Judd, 2014). Westfall's *d* is computed by dividing the difference between estimated means by the square root of the sums of the variance of the random parameters. Bonferroni corrections were applied to account for the two comparisons of the IFC and the IPL to sham.

Accuracy was analyzed first to ensure the absence of any speed-accuracy tradeoff induced by TMS. Mean accuracy was obtained for each participant in each condition by averaging the data over all items. The full model used to analyze mean accuracy included Grip similarity ("Grip similar", "Grip dissimilar"), Goal similarity ("Goal similar", "Goal dissimilar"), Response type ("Yes", "No"), TMS condition ("IFC", "IPL", "Sham") and their respective interactions as fixed effects. It also included random intercepts and random Response type slopes for participants.

The full model used to analyze RTs included Grip similarity ("Grip similar", "Grip dissimilar"), Goal similarity ("Goal similar", "Goal dissimilar"), Response type ("Yes", "No"), TMS condition ("IFC", "IPL", "Sham") and their respective interactions as fixed effects. It had random intercepts for participants and items, random Grip similarity, Goal similarity, TMS condition and Response type slopes for participants and random Goal similarity and TMS condition slopes for items. For each Yes and No model, Grip similarity ("Grip similar", "Grip dissimilar"), Goal similarity ("Goal similar", "Goal dissimilar"), TMS condition ("IFC", "IPL", "Sham") and their respective interactions were included as fixed effects. The random structures included random intercepts for participants and items

Table 1 – Mean reaction time (in ms), standard deviation (SD) and accuracy as a function of Response type, Grip similarity, Goal similarity and TMS condition.

Response type	Grip similarity	Goal similarity	TMS condition	Accuracy (%)	Mean (ms)	Standard deviation
no	Grip dissimilar	Goal dissimilar	IFC	98.06	566.40	82.92
no	Grip dissimilar	Goal dissimilar	IPL	95.83	561.07	88.42
no	Grip dissimilar	Goal dissimilar	Sham	96.94	556.38	74.37
no	Grip dissimilar	Goal similar	IFC	94.72	607.64	87.63
no	Grip dissimilar	Goal similar	IPL	91.11	585.25	75.42
no	Grip dissimilar	Goal similar	Sham	95	593.87	72.23
no	Grip similar	Goal dissimilar	IFC	96.94	593.37	85.24
no	Grip similar	Goal dissimilar	IPL	93.89	578.26	91.99
no	Grip similar	Goal dissimilar	Sham	95	574.30	66.52
no	Grip similar	Goal similar	IFC	95.56	532.23	94.46
no	Grip similar	Goal similar	IPL	94.72	543.15	95.03
no	Grip similar	Goal similar	Sham	95.56	518.55	73.70
yes	Grip dissimilar	Goal dissimilar	IFC	92.78	580.08	78.51
yes	Grip dissimilar	Goal dissimilar	IPL	93.61	565.79	91.68
yes	Grip dissimilar	Goal dissimilar	Sham	93.06	560.06	64.34
yes	Grip dissimilar	Goal similar	IFC	91.67	567.03	91.74
yes	Grip dissimilar	Goal similar	IPL	94.17	571.94	89.26
yes	Grip dissimilar	Goal similar	Sham	93.06	566.12	74.17
yes	Grip similar	Goal dissimilar	IFC	94.72	571.70	92.14
yes	Grip similar	Goal dissimilar	IPL	92.22	555.17	75.46
yes	Grip similar	Goal dissimilar	Sham	91.67	553.56	74.81
yes	Grip similar	Goal similar	IFC	95.83	517.31	112.07
yes	Grip similar	Goal similar	IPL	95.56	492.84	81.25
yes	Grip similar	Goal similar	Sham	96.67	475.06	56.86

and random Grip similarity, Goal similarity and TMS condition slopes for participants. For all models, the maximum random structure supported by the data was fitted (Barr, Levy, Scheepers, & Tily, 2013; Bates, Mächler, Bolker, & Walker, 2015; Matuschek, Kliegl, Vasishth, Baayen, & Bates, 2017). An iterative procedure based on principal component analysis was used to exclude redundant parameters and to select an appropriate random structure (see Bates, Kliegl, et al., 2015).

3. Results

Participants were required to answer, as quickly and accurately as possible, whether the target action was correct or not according to the typical use of the object. Both RTs and accuracy were recorded. Accuracy was analyzed first before performing the main analysis on correct trial RTs where participants gave the correct answer (see *Data preprocessing* section).

Mean accuracy across items and RTs was analyzed as a function of Grip similarity ("Grip similar", "Grip dissimilar"), Goal similarity ("Goal similar", "Goal dissimilar"), Response type ("Yes", "No") and TMS condition ("IFC", "IPL", "Sham") using a mixed model approach (see *Data analysis using mixed-effects models* section for details).

Statistically, the main effects of Grip similarity ("Grip similar" *vs* "Grip dissimilar") and Goal similarity ("Goal similar" *vs* "Goal dissimilar") evaluated grip and goal priming effects, respectively, while the Grip similarity x Goal similarity interaction evaluated the partial-repetition cost effect (i.e., the cost of sharing the same grip but not the same goal or sharing the same goal but not the same grip, compared to sharing both the same grip and the same goal or sharing neither). The Grip similarity x Goal similarity interaction was thus considered a statistical marker of grip and goal integration. Therefore, we evaluated whether stimulating the IPL or the IFC, compared with sham stimulation, would affect the Grip similarity x Goal similarity interaction. We also included the factor Response type in the analysis as prior studies have consistently reported an influence of yes/no response effects on action judgements (Decroix & Kalénine, 2018; Yoon, Humphreys, & Riddoch, 2010), although the direction of the effect of Response type on action priming, in interaction with IPL/IFC stimulation, was difficult to anticipate *a priori*.

There was no main effect of TMS condition on accuracy ($F_{2,374} = 1.45$, $p = .23$) and no interaction between TMS condition and any of the other factors (all $p > .30$).

The first model of the RT data showed the expected main effects of Grip similarity ($F_{1,16.2} = 79.81$, $p < .001$) and Goal similarity ($F_{1,25.5} = 14.09$, $p < .001$), as well as the expected Grip similarity x Goal similarity interaction ($F_{2,7874.8} = 5.56$, $p < .001$). This confirmed the presence of grip and goal similarity priming effects in our experiment, as well as the partial-repetition cost demonstrated by the Grip similarity x Goal similarity interaction. Importantly, the analysis also revealed a significant Grip similarity x Goal similarity x TMS condition x Response type interaction ($F_{2,7874.8} = 5.56$, $p = .004$). To directly test the influence of TMS on the partial-repetition cost effect (i.e., on grip and goal integration), we further investigated this interaction by carrying out separate analyses for yes and no responses. The Grip similarity x Goal similarity x TMS condition interaction was significant for both yes responses ($F_{2,3904.9} = 3.63$, $p = .026$) and no responses ($F_{2,3937.3} = 4.45$, $p = .012$). For yes responses, the cost of repeating one action dimension ("Grip similar, Goal dissimilar" or "Grip dissimilar, Goal similar") compared to repeating both action dimensions ("Grip similar, Goal similar") or neither dimension ("Grip dissimilar, Goal dissimilar")—i.e., the partial repetition cost—was reduced by 43 msec after IFC stimulation compared to sham (estimate = −42.91 msec, $SE = 17.31$, $t_{3971.04} = -2.48$, $p_{\text{corrected}} = .026$, Westfall's $d = .32$). In contrast, there was no significant difference between IPL stimulation and sham (estimate = −14.05 msec, $SE = 17.27$, $t_{3971.04} =$ - .81, $p_{\text{uncorrected}} = .419$, Westfall's $d = .10$), and the difference between IPL and IFC stimulation approached significance before Bonferroni correction (estimate = −28.86 msec, $SE = 17.29$, $t_{3971.03} = -1.67$, $p_{\text{uncorrected}} = .095$, Westfall's $d = .21$). Interestingly, the inverse pattern was observed for no responses: compared to sham, the partial-repetition cost was decreased by 36 msec after IPL stimulation (estimate = −36.05 msec, $SE = 16.03$, $t_{3938.35} = -2.25$, $p_{\text{corrected}} = .048$, Westfall's $d = .26$) but not after IFC stimulation (estimate = 8.27 msec, $SE = 15.97$, $t_{3988.69} = .52$, $p_{\text{uncorrected}} = .604$, Westfall's $d = .06$). The difference between IPL and IFC stimulation was also significant (estimate = −44.32 msec, $SE = 16.01$, $t_{3988.60} = -2.77$, $p_{\text{corrected}} = .010$, Westfall's $d = .32$). Results are displayed in Fig. 3 (also see supplementary Figure S1). No other effects involving the factor TMS condition were significant (all $p > .07$).

4. Discussion

This study investigated the critical roles of the IFC and the IPL in processing grip configuration and goals when observing object-directed actions performed by others. We used state-dependent TMS over the left IFC and IPL to evaluate whether either brain regions contain neuronal populations causally involved in i) processing grip configuration, ii) processing action goals or iii) integrating these two dimensions. TMS was found to disrupt the integration of grip configuration and action goal. Action recognition was affected by both left IFC and left IPL stimulation in comparison to sham. Remarkably, different results were revealed when considering the response type; namely, IFC stimulation influenced the processing of correct action targets (i.e., yes-response items), whereas IPL stimulation impacted the processing of incorrect action targets (i.e., no-response items). This double dissociation rules out the possibility of a non-specific effect of TMS. Overall, our results highlight specialized neuronal populations in both the IFC and the IPL dedicated to the integration of grip configuration and goal dimensions.

The partial-repetition cost was observed, as participants were slower to judge a target action when it was primed by a photograph sharing only one of the two dimensions compared to when the target was primed by a photograph sharing both dimensions or neither of the two dimensions. When TMS was applied at target onset, this cost was reduced, with participants being faster at judging target actions preceded by primes sharing only one of the two dimensions in comparison to the sham stimulation condition. The mechanisms underlying priming effects are complex, and prior exposure to information

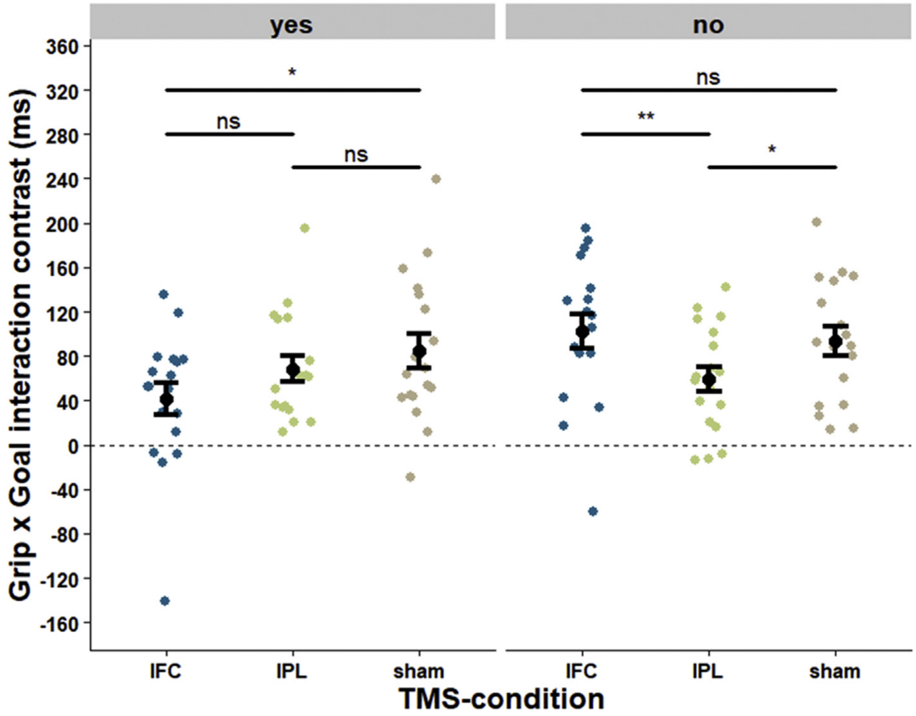

Fig. 3 – Grip similarity x Goal similarity interaction contrast in milliseconds as a function of Response type (Yes, No) and TMS condition (IFC, IPL or sham). Dots above the zero line indicate individuals' partial-repetition costs, i.e., higher response times for prime target pairs sharing partial information (either the grip or the goal dimension, but not both) than for prime target pairs showing either similar (both grip and goal dimensions congruent) or dissimilar information (neither grip nor goal dimensions congruent). Black dots represent the mean of the distribution. Error bars represent standard errors. **: $p < .01$; *: $p < .05$; ns: $p > .05$.

does not always facilitate its subsequent processing: targets sharing the same information as the prime may be processed more slowly (i.e., slower RT) than targets not sharing the same information as the prime (D'Angelo, Thomson, Tipper, & Milliken, 2016; Frings, Schneider, & Fox, 2015; Hommel, 2004). In our case, this can be interpreted in terms of memory retrieval (Frings et al., 2015). While viewing the information in the prime, participants associated the grip configuration (e.g., typical) with the goal (e.g., atypical). However, if the target displayed another type of goal (i.e., a typical one), the reactivation of the prime's atypical goal would have disturbed the processing of the target's action goal, resulting in a cost (Bub, Masson, & Lin, 2015; Frings et al., 2015; Hommel, 2004). This effect has been consistently taken as an evidence that two pieces of information in the prime were associated with one another (Hommel & Zmigrod, 2013). In our experiment, this means that, if not integrated, grip configuration and goal dimensions were at least associated with one another. The fact that TMS affects the partial-repetition cost may indicate that the neurons responsible for this association are affected. Although TMS is generally thought of as being either inhibitory or excitatory, several sources of evidence suggest that TMS has different effects on neurons that are active and neurons that are not. In particular, TMS is thought to facilitate neurons that are less activated (Silvanto & Cattaneo, 2017; Silvanto et al., 2008), resulting, in a priming paradigm, in either a behavioral facilitation of the non-primed dimension (Silvanto & Cattaneo, 2017) or an overall increase in the noise level (Miniussi, Harris, & Ruzzoli, 2013) that can abolish the advantage of the primed dimension. This proposal has now been supported by a few TMS experiments (Cattaneo, 2010; Cattaneo et al., 2008; Ferrari et al., 2016; Kehrer et al., 2015; Mattavelli, Cattaneo, & Papagno, 2011; Soto, Llewelyn, & Silvanto, 2012; Taylor, Muggleton, Kalla, Walsh, & Eimer, 2011). Our data provide additional empirical evidence in this direction, suggesting that TMS during priming may cause cost reductions. By demonstrating that the partial-repetition cost between action dimensions is reduced after IFC and IPL stimulation in comparison to sham, this experiment hints at the presence of neuronal populations in the IFC and the IPL involved in the integration of grip configuration and goal information.

A fronto-parietal network is thought to link visual and motor formats of action representation (Hamzei et al., 2016; Hardwick, Caspers, Eickhoff, & Swinnen, 2018). Sensorimotor theories of action recognition argue that observers reactivate the same motor program they observe in another's action. The motor components of the action are "simulated" within the fronto-parietal network to allow recognition of the actor's goal (Decety & Grèzes, 2006; Gallese, 2005; Rizzolatti & Fogassi, 2014). Predictive theories of action recognition argue instead that the fronto-parietal network is fed by predictions of the actor's goal. The predictions are derived from non-motor sources of information, and are used by the fronto-parietal network to make sense of the observed motor components of the action (Amoruso, Finisguerra, & Urgesi, 2018; Bach, Nicholson, & Hudson, 2014; Donnarumma, Costantini, Ambrosini, Friston,

& Pezzulo, 2017; Kilner, 2011). The critical role of the fronto-parietal network in processing motor components and action goals has been repeatedly reported (Avenanti et al., 2018; Candidi et al., 2008; Cattaneo, 2010; Cattaneo et al., 2010, 2011; Jacquet & Avenanti, 2015; Koch et al., 2010; Michael et al., 2014; Pobric & Hamilton, 2006; Tidoni et al., 2013; Urgesi et al., 2007), but only indirect correlational evidence supports the roles of the IFC and the IPL in integrating goal-related information and motor components (Schubotz et al., 2014; Wurm & Lingnau, 2015). To the best of our knowledge, this is the first experiment to provide direct evidence of IFC and IPL involvement in the integration of motor components (or, at least, the grip configuration component) and action goals during action identification. Some authors previously argued that only motor components are represented within the fronto-parietal network after 200 msec, and that goals would be processed much later (Catmur, 2015; Naish, Houston-Price, Bremner, & Holmes, 2014). Our data demonstrate that, from about 280 msec, motor components (i.e., grip configuration) and goal-related information are fully integrated within the fronto-parietal network rather than processed independently. This is in line with similar evidence from cortico-spinal excitability studies in which motor resonance was affected by contextual information after 240 msec of visual processing of the action (Amoruso, Finisguerra, & Urgesi, 2016). It is interesting to note that timing may explain why our results differ from Cattaneo (2010). In his work, Cattaneo found that sharing the same hand posture decreased response times when categorizing hand posture photographs (i.e., facilitatory priming). When TMS was delivered at target onset over the ventral premotor cortex, the behavioral priming effects were reversed. This effect was not observed when TMS was applied over the dorsal premotor cortex or in the sham condition. Yet stimulation was applied at around 200 msec, as opposed to around 280 msec in our study. It is therefore possible to imagine two processing phases: (1) independent processing of grip configuration (and maybe goals; see Cattaneo et al., 2010) in the IFC at around 200 msec, and (2) later integration of grip and goal information within the IFC at around 280 msec. Targeting the IFC at around 200 msec would affect the independent processing of grip configuration and goals (e.g., facilitatory priming effects in Cattaneo's paradigm) whereas targeting the IFC at around 280 msec would affect their integration (i.e., partial-repetition cost in our paradigm). Overall, our data, while backing up previous sensorimotor and predictive accounts in the importance they give to the fronto-parietal network, also constrain future models of action recognition by providing a temporal landmark for the integration of information about the motor components[4] and action goals.

The fact that the effect of IFC and IPL stimulation on the partial-repetition cost was different for correct targets (i.e., yes-response items) and incorrect targets (i.e., no-response items) is a novel, interesting finding. Although we anticipated an influence of response type on the pattern of priming effects, a dissociation between IPL and IFC stimulation in interaction with response type was not specifically predicted and may invite several possible interpretations. One possibility is that grip configuration and goals are integrated in the IFC for correct targets and in the IPL for incorrect targets. This proposal may appear in line with prior studies reporting that the IFC is more engaged when processing actions belonging to the observer's motor repertoire, whereas the IPL and other parietal regions are more engaged for actions that violate human biomechanical constraints (Avenanti, Bolognini, Maravita, & Aglioti, 2007; Buccino et al., 2004; Candidi et al., 2008; Costantini et al., 2005). In contrast, however, other studies have reported greater frontal activations for incorrect observed actions than for correct observed actions (Aglioti, Cesari, Romani, & Urgesi, 2008; Koelewijn, van Schie, Bekkering, Oostenveld, & Jensen, 2008; Manthey, Schubotz, & von Cramon, 2003; van Schie, Mars, Coles, & Bekkering, 2004). It may thus be difficult to attribute our results to one or the other explanation. An alternative possibility is that the observed dissociation between the IFC and the IPL reflects temporal differences in processing correct and incorrect actions. In this case, both the IFC and the IPL would be involved in processing correct and incorrect actions. This explanation would nicely fit with the aforementioned mixed results, and further exploration of this possibility should be prioritized in future studies. It is indirectly supported by our finding of faster reactions to correct actions than to incorrect actions. Moreover, correct and incorrect action targets were differentially affected by priming. Furthermore, previous behavioral reports have found that the emergence of priming effects required a shorter prime duration for correct targets than for incorrect targets (Decroix & Kalénine, 2018). Different time courses may thus apply to processing correct and incorrect actions, and future work could further test this possibility using neurophysiological methods with high temporal resolution.

Finally, our data point towards the possibility of sneaking into the temporal dynamics of motor component and goal representation processing. Despite being recognized as a dynamic phenomenon (Catmur, 2015; Grafton & Hamilton, 2007; Kilner & Frith, 2008), action recognition is mainly investigated through methodologies with poor temporal resolution such as *f*MRI. As mentioned in the Introduction, this makes it difficult to clearly establish the roles of different brain regions in processing motor components and goal representations. TMS coupled with behavioral priming paradigms is an appealing method for establishing causal relationships between brain and the behavior while controlling the timing at which different pieces of information are processed. The present results demonstrated that both the left IFC and the left IPL are critically involved in integrating motor components (at least, the grip configuration component) and goal dimensions, with possibly different time courses for correct actions (e.g., drinking from an upright cup with a precision grip on the handle) and incorrect actions (e.g., drinking from an upside-down cup with a power grasp on the handle). They further highlight the relevance of using state-dependent TMS to study the neural substrates of action understanding, and reveal

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[4] One may also argue that our results remain limited to the grip configuration component, and we agree that future studies will have to evaluate the generalizability of our findings to the other motor parameters. However, grip configuration is an important component of many actions (Buxbaum, Shapiro, & Coslett, 2014) and there is currently no consensus on which motor components should be the most important for action understanding (Becchio, Koul, Ansuini, Bertone, & Cavallo, 2018).

exciting perspectives on investigating the dynamic involvement of fronto-parietal AON nodes in the recognition of others' actions.

Open practices

The study in this article earned Open Materials badges for transparent practices. Materials and data for the study are available at https://osf.io/cbq4y/.

We report how we determined our sample size, all data exclusions, all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study.

No part of the study procedures nor part of the analyses were pre-registered prior to the research being conducted.

Author contributions

Jérémy Decroix: Conceptualization, Methodology, Formal analysis, Data Curation, Writing - Original Draft, Visualization, Project administration. **Sara Borgomaneri**: Conceptualization, Methodology, Resources, Data Curation, Writing - Review & Editing, Visualization, Project administration, Funding acquisition. **Solène Kalénine**: Conceptualization, Methodology, Formal analysis, Writing - Review & Editing, Funding acquisition. **Alessio Avenanti**: Conceptualization, Methodology, Resources, Writing - Review & Editing, Visualization, Funding acquisition.

Declaration of Competing Interest

The authors declare no conflict of interest.

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Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cortex.2020.08.004.

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