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Spatiotemporal Brain Dynamics of Transitive and Intransitive Action Observation

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ABSTRACT

Observing another person's action recruits the action observation network (AON). Evidence suggests that distinct AON pathways are engaged depending on action features, such as their transitivity or the movement's target; however, the spatiotemporal dynamics of these circuitries remain unclear and debated. In the present study, to further explore this aspect, healthy participants completed two experiments involving the passive observation of distinct grasping actions: intransitive (isolated grasp), object-directed (hand grasping a bottle), and socially-directed (hand grasping another person's hand). In *Experiment 1*, using electroencephalography (EEG), we examined whole-brain temporal patterns of AON activation during the observation of these stimuli through event-related potentials and microstate analyses. In *Experiment 2*, informed by EEG results, we used transcranial magnetic stimulation (TMS) to assess the temporal dynamics of motor resonance, a corticospinal marker of AON recruitment. *Experiment 1* showed that observing transitive and intransitive grasping activates the same core circuit within the AON, albeit with distinct spatiotemporal dynamics emerging in two separate time windows, peaking at approximately 200 and 350 ms after action onset. Specifically, observation of object-directed grasping relies more on the engagement of posterior brain regions. In contrast, intransitive and socially-directed movements recruit anterior areas more quickly, with the activation pattern of the latter class of stimuli likely reflecting the additional visuo-tactile processing associated with the observed action. *Experiment 2* showed muscle-specific motor resonance at 200 ms only for intransitive and object-directed grasping, but no corticospinal facilitation at later latencies, where inhibitory patterns instead emerged, suggesting that EEG and TMS capture complementary dynamics underlying action observation and understanding. Overall, our findings suggest that observing transitive and intransitive movements modulates AON activity through shared pathways expressed in specific spatiotemporal gradients, corresponding to distinct cortical and corticospinal signatures that encode the features of the observed action.

1 | Introduction

Observing an action performed by another person activates a set of fronto-temporo-parietal regions in the observer's brain, known as the action observation network (AON; Rizzolatti and Craighero 2004). This high-order cortical network is believed to be involved in several cognitive processes, including action understanding, imitation, motor learning, social cognition, empathy, and language (for reviews, see Bonini et al. 2022; Rizzolatti et al. 2014; Rizzolatti and Sinigaglia 2016).

The activation of AON cortical nodes (e.g., ventral premotor cortex, inferior frontal, inferior parietal lobule—IPL, supramarginal gyrus—SMG, superior temporal gyrus) is modulated

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by the features of the observed action, as shown by several functional magnetic resonance imaging and electroencephalography (EEG) studies (e.g., Agnew et al. 2012; Caspers et al. 2010; Decety et al. 1997; Di Cesare et al. 2024; Hamilton and Grafton 2006; Hétu et al. 2011; Qin et al. 2023; Sadeghi et al. 2022; Savaki et al. 2022; Simonelli et al. 2024). Specifically, regions of the parietal cortex, like the IPL or the SMG, are more activated during the observation of goal-directed actions (e.g., Aberbach-Goodman and Mukamel 2023; Di Cesare et al. 2024; Newman-Norlund et al. 2010; Urgen and Orban 2021), while the observation of actions with social features (e.g., observing communicative gestures) consistently recruits more frontal and limbic regions than non-social actions (e.g., observing object-directed gestures; Zhao et al. 2024).

However, to date, most of these studies have focused on "how" and "where" observing actions with distinct features recruits AON nodes, leaving the question of "when" largely unexplored. Although the neuroimaging evidence demonstrates the existence of different specific AON activation patterns based on the characteristics of the observed action (e.g., Abdollahi et al. 2013; Ferri et al. 2015; Montgomery et al. 2007; Savaki et al. 2022; Simonelli et al. 2024; Urgen and Orban 2021; Zhao et al. 2024), less is known about the temporal dynamics and hierarchies of these cortical activations. A recent electrocorticography study in epileptic patients elegantly showed that observing manipulative movements recruits distinct parieto-temporo-frontal AON pathways that encode different temporal phases of the observed action, such as reaching or grasping (Del Vecchio et al. 2026). However, patients always observed manipulative actions with tools, leaving it unexplored whether these pathways are engaged differently depending on the characteristics of the observed action (e.g., its transitivity or whether it is directed toward another human being). Even AON studies using non-invasive brain stimulation techniques with high spatial and temporal resolution, such as transcranial magnetic stimulation (TMS), provide controversial evidence on the topic. The latter body of literature assesses peripheral indexes of AON recruitment, like the muscle-specific facilitation of corticospinal excitability during action observation (i.e., motor resonance; Craighero 2024), to investigate the chronometry of mirror phenomena, but they do not converge in providing optimal timings to detect these modulations or the extent to which observation of transitive and intransitive actions could influence these temporal patterns (e.g., Barchiesi and Cattaneo 2013; Cavallo et al. 2014; Donne et al. 2011; Gianelli et al. 2020; Guidali, Picardi, Franca, et al. 2023; Naish et al. 2014). Nevertheless, uncovering the chronometry of AON activation depending on the type of action observed is crucial to understand cortical and corticospinal AON dynamics and, in turn, to optimize state-dependent non-invasive brain stimulation protocols targeting this network (e.g., Chiappini et al. 2024; Guidali, Arrigoni, et al. 2025; Guidali et al. 2020; Guidali, Picardi, Gramegna, and Bolognini 2023; Picardi et al. 2025; Turrini et al. 2025) and clinical treatments based on action observation (e.g., Ciullo et al. 2026; Ertelt et al. 2007; Franceschini et al. 2012; Ryan et al. 2021; Tani et al. 2018; Zhang et al. 2023).

To better define the spatiotemporal patterns of AON activity, we conducted two experiments with healthy participants, utilizing the high temporal resolution of EEG (*Experiment 1*) and TMS (*Experiment 2*). In particular, we aimed to characterize the central (i.e., cortical) and peripheral (i.e., corticospinal) spatiotemporal fingerprints of AON recruitment while observing transitive and intransitive (simple) actions. In both experiments, we exploited an action observation paradigm with visual stimuli depicting intransitive (i.e., a grasping movement presented in isolation, without a target and, hence, a goal), object-directed (i.e., a hand grasping a bottle, which could be interpreted as a goal-directed movement), and socially-directed grasping (i.e., a hand grasping another hand, which could be construed as a social gesture to get in touch with another person) made with the right hand and in an egocentric perspective. The key feature of our visual stimuli, adapted from previous studies of our research group (Guidali, Franca, et al. 2025; Guidali, Picardi, Franca, et al. 2023), is that we solely modulate the target of the movement, always presenting the same effector, background, and grasping kinematics. We then used EEG and microstate analysis to investigate whole-brain patterns during grasping observation (*Experiment 1*) and, informed by the results of this investigation, TMS to assess the temporal profile of motor resonance (i.e., corticospinal excitability facilitation during the observation of the same grasping actions), a peripheral, covert marker of AON recruitment (*Experiment 2*).

2 | *Experiment 1*: Cortical Correlates of Transitive and Intransitive Grasping Observation

2.1 | Aims

In *Experiment 1*, we recorded event-related potentials (ERP) while participants passively observed the above-mentioned transitive and intransitive grasping movements. First, we compared ERPs time-locked to the onset of different grasping actions through cluster-based permutation testing (Maris and Oostenveld 2007), to highlight differences in whole-brain spatiotemporal dynamics evoked by action observation across experimental conditions. Here, we hypothesize that the degree of transitivity of the observed action, as well as the target depicted (i.e., an object or another human being), could strongly influence cortical patterns between conditions. Then, microstate analysis was used to decompose the ERP signal into quasi-stable topographical map configurations, whose activations and switching across time represent changes in brain network engagement and information transfer (Lehmann et al. 1987; Michel et al. 2009; Michel and Koenig 2018). In the last decade, ERP microstate analysis has gained traction in social and affective neuroscience (for reviews, see Michel et al. 2024; Schiller et al. 2024), but it has been scarcely adopted in the action observation literature, despite its potential to provide valuable whole-brain information. In fact, to the best of our knowledge, only three studies used microstate analysis to deepen understanding of AON functioning, investigating how distinct actors' intentions influenced cortical patterns during the observation of movements toward the same target (Avanzini et al. 2013; Ortigue et al. 2010; Zhang et al. 2018). We hypothesize that microstate features—such as duration, global field power (GFP), or map presence—vary among the observed action stimuli as a function of the movement's target,

shedding light on the whole-brain spatiotemporal patterns of AON recruitment. Crucially, such variations could reflect either distinct, stimulus-specific processing within the AON or the same core process expressed with different temporal and spatial gradients.

2.2 | Materials and Methods

2.2.1 | Participants

Twenty-five healthy participants took part in the first experiment of the study. One participant was excluded due to excessive signal noise during EEG recordings, resulting in a final analyzed sample of 24 participants (11 males; mean age ± standard deviation—SD = 25 ± 4.2 years; mean education ± SD = 16.1 ± 1.9 years). All participants were right-handed, as determined by the Edinburgh Handedness Inventory (mean score ± SD = 87.7% ± 12.2%; Oldfield 1971), and had no neurological problems. Given the difficulties of conducting an a priori power analysis with the variables employed here, we based our sample size on a previous study on action observation using microstate analysis (Zhang et al. 2018). Here, researchers found significant effects in a sample of 24 healthy participants, and we decided to recruit the same number of participants, also considering that the other two studies using microstate analysis during action observation had smaller sample sizes (i.e., $N = 10$ for Avanzini et al. 2013; $N = 20$ for Ortigue et al. 2010). The experiment adhered to the ethical standards outlined in the Declaration of Helsinki and was approved by the University of Milano-Bicocca's Ethical Committee (protocol number: 664-2022). Before participating in the study, participants provided their written informed consent.

The scripts, raw data, and analysis of this study are publicly available on the Open Science Framework (OSF): https://osf.io/x8v5e.

2.2.2 | Experimental Procedure

The experiment consisted of one EEG session, during which participants performed the action observation task described below. The session began with completing the written informed consent form and the Edinburgh Handedness Inventory. Then, after EEG preparation, participants underwent two recordings at rest (one with eyes closed, one with eyes open). Following these, blocks of the action observation task were administered. The session lasted about 2 h.

2.2.3 | Action Observation Task

Participants were seated in a chair in front of a PC screen, approximately 100 cm from their faces, with their hands relaxed on a table and out of view. The task consisted of passively observing whole-hand grasping movements presented on the PC screen while recording EEG to obtain event-related potentials (ERPs) during action observation. Throughout the task, three grasping conditions were randomized and counterbalanced, with the target of the grasping action varying across trials. The hand movement could be (i) intransitive, that is, a grasping action not directed to any target ("intransitive grasping"), (ii) object-directed, that is, the goal of the movement was the grasping of a bottle ("object grasping"), or (iii) a social action, consisting in the grasping of another person hand ("social grasping").

We used the same visual movement stimuli adopted and validated in previous works by our research group (Guidali, Franca, et al. 2025; Guidali, Picardi, Franca, et al. 2023). Every trial began with a red asterisk on a black background acting as a fixation cross (duration jittered between 1000 and 2000 ms). Following this, a frame depicting a static right hand (in an egocentric perspective and on the right side of the screen) appeared for 1000 ms. In the "object" and "social grasping" conditions, the target (i.e., the bottle or another hand, respectively) was also presented in this frame centrally on the screen and in the background concerning the static hand. Then, a third frame, showing the grasping movement of the right hand (i.e., "movement frame"), was presented with a fixed duration of 800 ms. The rapid succession of this frame gave rise to apparent motion, thereby allowing precise control over the timing of the participant's observation of the action. At the onset of the movement frame, a trigger was delivered via a parallel port to the EEG system for subsequent ERP analysis. Finally, the frame depicting the static right hand reappeared for 500 ms, marking the end of the trial (Figure 1a).

The action observation task comprised 480 trials (160 trials per condition, in random order). Trials were presented in 8 blocks of 60 trials each (i.e., 20 trials for each condition); each block lasted about 4 min, allowing a short break (30 s) and avoiding excessive fatigue for the participant.

To ensure that participants maintained an attentive focus on the task's stimuli, 48 trials out of 480 (i.e., 16 trials for each category) presented a small red dot (diameter: 20 pixels) that appeared on the back of the right hand at the onset of the task's third frame. Participants had to press one of the PC mouse keys with their left hand every time the dot appeared. We required participants to achieve a mean accuracy of at least 90% across these trials to avoid being considered outliers and excluded from subsequent analysis. All our participants met this criterion; on average, accuracy was 94.1% (SD = ±2.7%). ERPs were not recorded during these attentional trials.

The timing of the stimuli and trial randomization were controlled by a computer using the E-Prime 2.0 software (Psychology Software Tools Inc.).

2.2.4 | EEG Recording and Preprocessing

EEG data were continuously recorded using a 60-channel EEG cap (EasyCap, BrainProducts GmbH, Munich, Germany) with a Nexstim EEG system (Helsinki, Finland). Two electrodes were placed over the forehead as the ground and reference electrodes. Additionally, two electro-oculographic (EOG) channels were placed over the right eyebrow and the left cheekbone to detect and monitor ocular artifacts associated with eye movements and blinking. The electrodes' impedance was kept below 5 kΩ, and the EEG signal was acquired with a sampling rate of 1450 Hz.

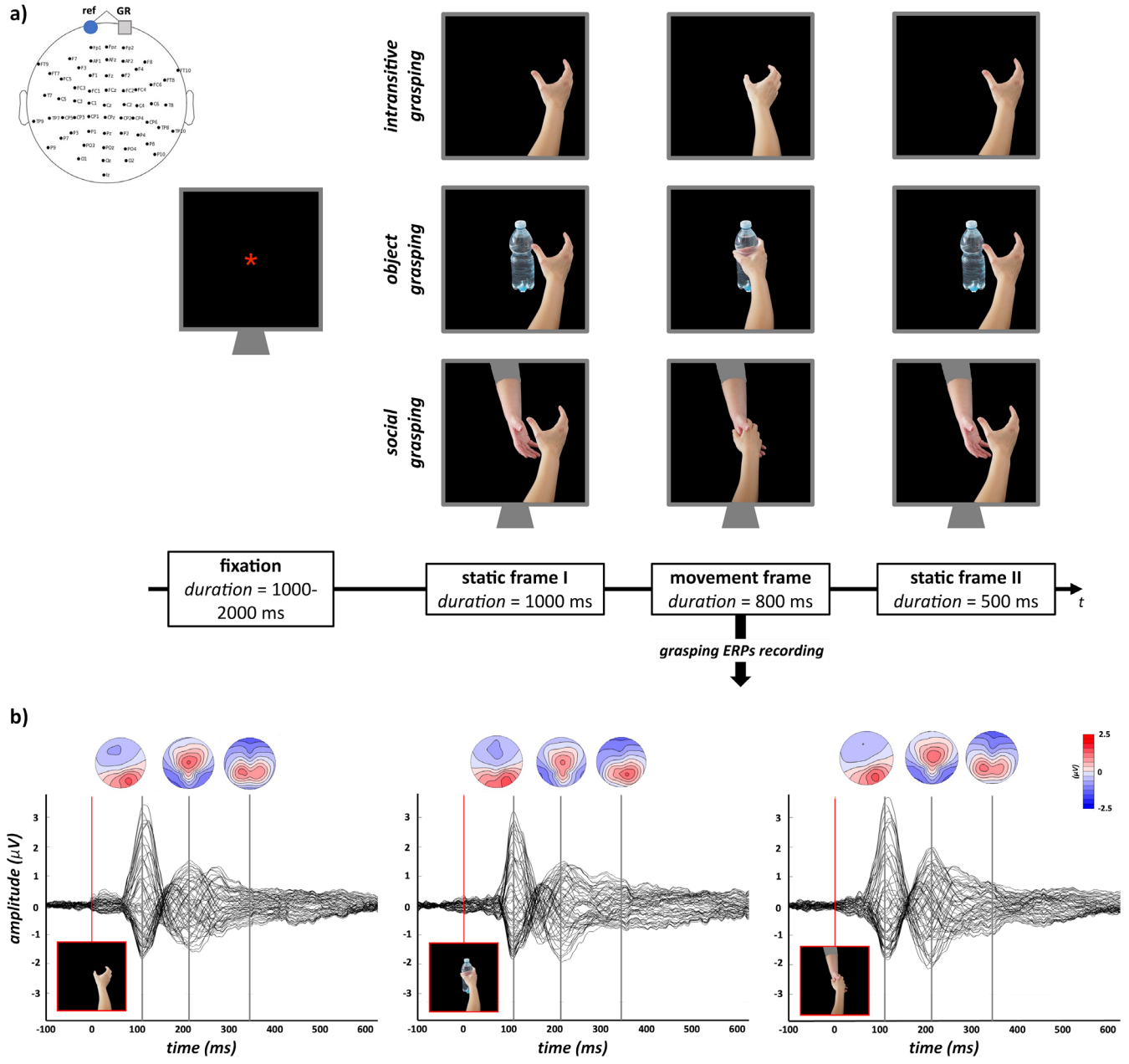

FIGURE 1 | Experiment 1: (a) Action observation task; (b) ERP grand averages and topographies of the main ERP components found during the three experimental conditions; ERPs were recorded from a 60-channel EEG cap at the onset of the movement frame.

EEG preprocessing was performed in MATLAB (MathWorks, Natick, MA, USA) using the EEGLAB (Delorme and Makeig 2004) and TESA toolbox (Rogasch et al. 2017) functions. Data were downsampled to 725 Hz and re-referenced using an average reference, segmented in epochs starting 800 ms before and ending 800 ms after the onset of the visual stimulus of movement (i.e., "movement frame", the third frame of the action observation task), and baseline-corrected in the pre-stimulus window from −200 to 0 ms. Then, trials with excessive artifacts were rejected by visual inspection. We applied the source-estimate-utilizing noise-discarding algorithm (SOUND), implemented in TESA, to attenuate extracranial noise from bad channels, utilizing a 3-layer spherical model with default parameters ($\lambda = 0.1$; Mutanen et al. 2018). Independent Component Analysis (FastICA, pop_tesa_fastica, "tanh" contrast) was performed after Principal Component Analysis (PCA) compression to 30 components (pop_tesa_pcacompress) to remove blinks, eye movements, residual electrical artifacts, and spontaneous muscular activity (as in Arrigoni et al. 2026). Epochs were band-pass filtered from 1 to 80 Hz and band-stop filtered from 48 to 52 Hz using a 4th-order Butterworth filter. Finally, trials were divided into the three experimental conditions (i.e., intransitive, object, and social grasping) and prepared for the subsequent statistical analysis. ERPs' grand averages during the three experimental conditions are reported in Figure 1b.

2.2.5 | Cluster-Based Analysis

To highlight differences in ERP spatiotemporal patterns across grasping conditions, we analyzed ERP amplitudes using a

whole-head, non-parametric, cluster-based permutation multivariate analysis of variance (MANOVA) implemented in Fieldtrip (Oostenveld et al. 2011). Analyses were performed on all 60 electrodes within the 0–600 ms time interval after the onset of the grasping action (i.e., movement frame). First, we conducted a cluster-based repeated-measures ANOVA using a multivariate F-statistic with the factor "viewed Grasping" (intransitive, object, social). This procedure accounts for the dependency structure of within-subject designs and controls for multiple comparisons across channels and timepoints (Maris and Oostenveld 2007). We identified spatiotemporal clusters when at least two neighboring electrodes exceeded a sample-level threshold of $p < 0.05$. Cluster-level statistics were evaluated using 5000 Monte Carlo permutations, with significance assessed against the permutation distribution. We applied a one-tailed test (right tail only), consistent with the F-statistic being defined only in the positive direction. Cluster-level significance was $p < 0.05$ (cluster alpha = 0.05).

We then performed post hoc pairwise cluster-based *t*-tests between each condition pair to further examine specific differences between conditions. These tests followed the same nonparametric Monte Carlo cluster procedure described above (two-tailed, dependent samples *t*-statistic, 5000 permutations, cluster alpha = 0.05).

2.2.6 | Microstate Analysis

We used the MATLAB-based open-source toolbox Randomization Graphical User software (RAGU; Koenig et al. 2011) to perform microstate analysis, following the guidelines published in previous works (Habermann et al. 2018; Koenig et al. 2014). Our experimental design was within-subject with one factor ("viewed Grasping") and three levels (intransitive, object, and social). We selected the following randomization options for all our analyses: normalization = L2 norm of raw data; runs = 5000; $p = 0.05$. We normalized our data, that is, each topography has all its values divided by its global field power (GFP) (Lehmann and Skrandies 1980), because this permits the detection of differences in the spatial distribution of the sources at the scalp level, eliminating differences due to scaling factors like the GFP (Habermann et al. 2018). Given the results of the MANOVA (see 2.3.1), we selected the first 500 ms after the onset of the visual movement stimulus for our analysis.

As a preliminary step, we conducted a topographical consistency test using GFP (Koenig and Melie-García 2010). Topographical consistency refers to the non-random, systematic recurrence of a specific scalp voltage configuration across observations, which serves as direct evidence for the activation of a common, stable set of underlying neural generators. Under the null hypothesis that scalp configurations are driven by independent noise, averaging across conditions would cause spatial configurations to cancel out, driving the grand-average GFP toward zero. By comparing our empirical data against a null distribution generated via non-parametric channel-shuffling, the topographical consistency test evaluates the stability of these voltage configurations (Koenig and Melie-García 2010). Results showed high topographical consistency across our three conditions ($p < 0.05$), confirming the presence of a reliable, shared neural signal and allowing us to perform subsequent microstates analysis on the entire epoch of interest (i.e., 0–500 ms) to classify dynamic changes in ERP topographies.

Since microstates analysis has been scarcely performed with ERPs on action observation directed to distinct targets, we were not able to a priori determine an expected number of maps from previous literature; therefore, we identified them using a cross-validation procedure, iterated for 50 times (for a similar procedure, see: Koenig et al. 2014; Lucarelli et al. 2025). Our dataset of 24 participants was randomly divided into a learning set, used to build microstate maps with the number of classes increasing from 3 to 12, and a test set to evaluate the resulting maps and quantify the variance explained by the model. The cross-validation procedure suggested a solution with 5 microstate maps for our data, as the explained variance from additional maps did not increase, indicating that this number was sufficient to achieve a high explained variance (i.e., 89.87%) without overfitting the model. Then, we used the k-means algorithm implemented in RAGU with 250 iterations to segment ERPs into microstates defined by the five previously defined topographic maps. In each iteration, the group-level data from all conditions were combined, and five scalp topographies were randomly sampled from this dataset. Each datapoint was then assigned a label corresponding to the topography with which it showed the highest correlation. The templates were refined by averaging the signals of all datapoints sharing the same label, and the set of template maps that maximized global explained variance was retained (Koenig et al. 2014).

We extracted five microstate features for each map, analyzing them using randomization statistics (run = 5000, $p < 0.05$, as implemented in RAGU): (i) onset; (ii) offset; (iii) duration; (iv) area under the curve (AUC), calculated as the integral of the GFP over the microstate's active lifespan, which represents the cumulative electrical energy (or total neural investment) allocated to that configuration; and (v) mean GFP, which reflects the average instantaneous signal strength and degree of simultaneous neural synchronization of the microstate independent of time (Habermann et al. 2018).

2.3 | Results

2.3.1 | Cluster-Based Analysis

The cluster-based repeated-measures MANOVA revealed a significant main effect of viewed Grasping, identifying two significant clusters (both $p < 0.001$), and suggesting that ERP activity differed across grasping conditions. For visualization purposes, the spatiotemporal extent of the clusters is shown in Figure 2a. The first cluster extended from 69 to 241 ms after action onset, whereas the second extended from 268 to 432 ms. To further characterize these differences, post hoc cluster-based pairwise *t*-tests were conducted.

The comparison between Object and Intransitive grasping identified three significant clusters (92–144 ms, $p < 0.001$; 99–192 ms, $p = 0.003$; 379–441 ms, $p = 0.034$; Figure 2b). Visual inspection of the scalp maps suggested that, at earlier latencies, a more bilateral distribution is observed during the Object grasping

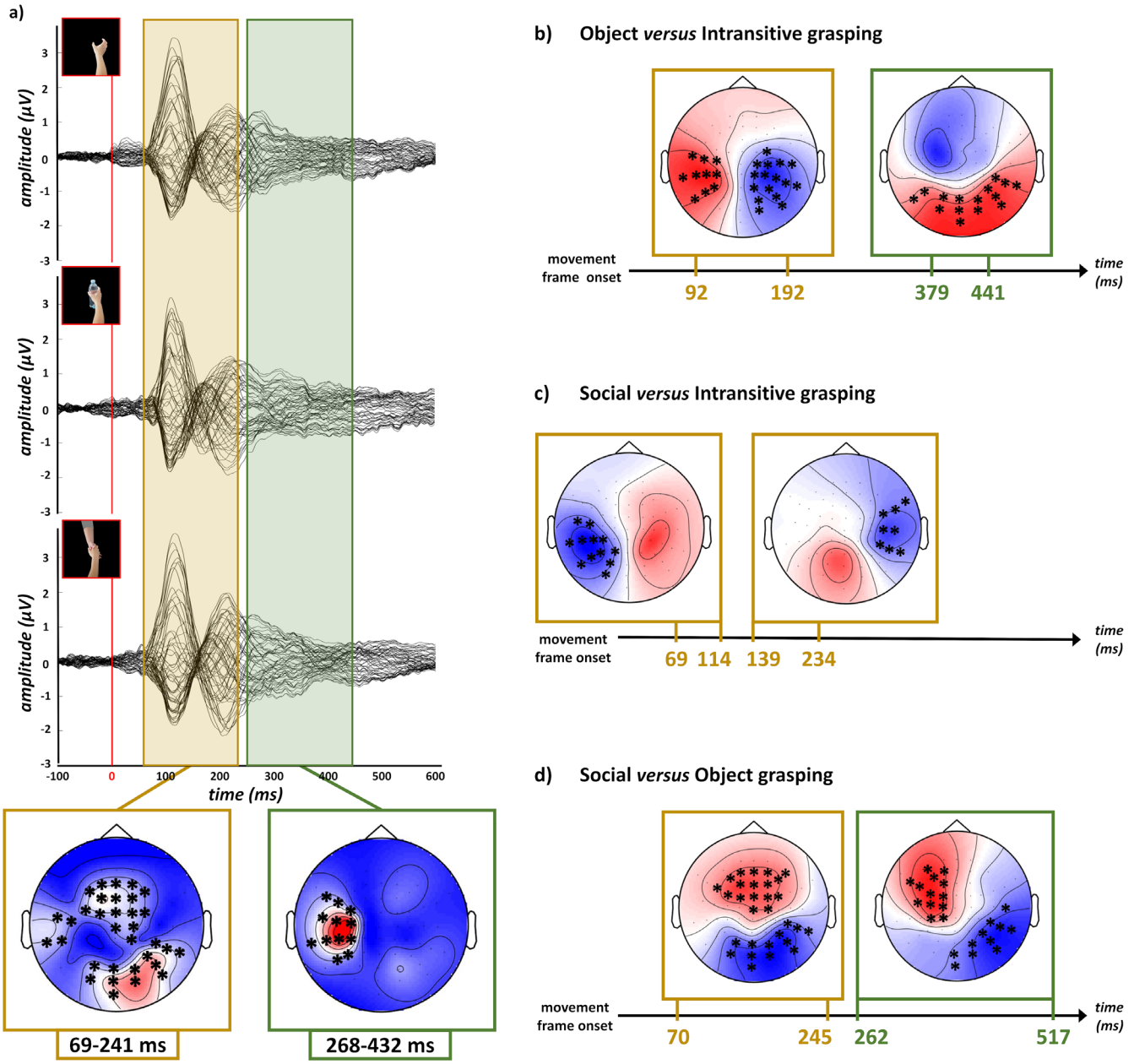

FIGURE 2 | Cluster-based permutation analysis. (a) The cluster-based repeated-measures MANOVA identified significant differences in ERP activity among the three grasping conditions. Two significant clusters were identified, with temporal extents of 69–241 ms (gold) and 268–432 ms (green) relative to movement onset. (b–d) Results of the post hoc cluster-based permutation *t*-tests comparing Object versus Intransitive (b), Social versus Intransitive (c), and Social versus Object (d) grasping observation. Scalp maps depict the spatial distribution of *t*-values for the difference between the two conditions at the latency corresponding to the maximum *t*-value within each significant cluster. For visualization purposes, in panel (d), the six significant clusters are summarized into earlier and later temporal windows. Gold and green frames indicate clusters whose temporal extents overlapped with the earlier and later significant clusters identified by the MANOVA, respectively. These maps visualize the spatial distribution of the cluster statistics and are not intended to support statistical inference regarding specific scalp locations or time points. Asterisks indicate electrodes belonging to the significant clusters identified by the permutation procedure ($p < 0.05$).

condition, whereas the Intransitive condition showed a more pronounced right-lateralized distribution. At later latencies, the scalp distributions differed, with Object grasping exhibiting relatively stronger posterior activity centered over parieto-occipital regions.

The comparison between Social and Intransitive grasping identified two significant clusters (69–114 ms, $p = 0.025$; 139–234 ms, $p = 0.047$; Figure 2c). At earlier latency, the scalp maps display a more right-lateralized distribution during Social grasping observation than during Intransitive grasping. At later latencies, the scalp distributions also differ, with Social grasping exhibiting relatively reduced activity over right parietal scalp regions.

Finally, the comparison between Social and Object grasping identified six significant clusters (spanning 70–245 ms and 262–517 ms; Figure 2d), comprising three positive ($p < 0.001$, $p < 0.001$, $p = 0.04$) and three negative clusters ($p < 0.001$,

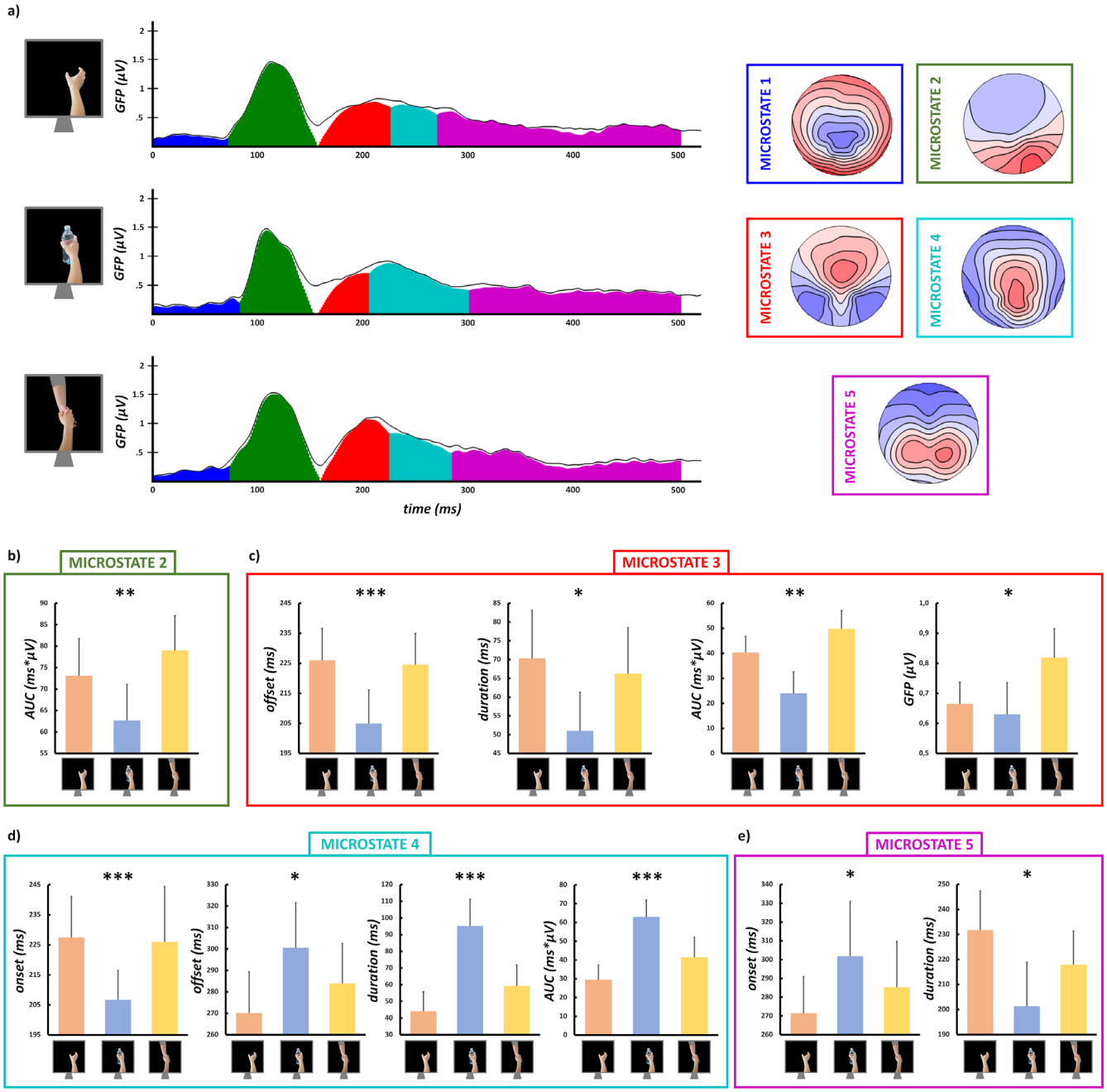

FIGURE 3 | Microstate analysis. (a) Temporal succession and topographies of the 5 microstates extracted during the observation of the different grasping conditions. Left panel: GFP of the three grasping stimuli plotted over the analyzed time window. The proportion of the signal variance explained by the model is colored by the microstate class that dominates each time interval. Right panel: Color-coded template maps of individual classes. (b–e) Statistically significant microstate parameters during the three grasping observations (Intransitive = orange bars; Object = blue bars; Social = yellow bars). Error bars depict standard errors. *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

$p = 0.02$, $p = 0.04$). Descriptive evaluation of the scalp topographies shows more right-lateralized activity during Social grasping observation at earlier latencies, whereas a more bilateral distribution emerged during Object grasping observation. At later latencies, Social grasping was featured by a more bilateral posterior activity.

Overall, the cluster-based permutation analyses confirmed significant differences in ERP activity between the three grasping conditions. On a descriptive level, Intransitive grasping exhibits an intermediate spatiotemporal profile, sharing features of both Social and Object grasping across early ERP response distributions and later posterior activity. This temporal evolution and topographic organization were further characterized by the microstate analyses presented in the following section.

2.3.2 | Microstate Analysis

Figure 3a depicts the topographies and temporal succession of the five microstates obtained from the cross-validation procedure. All microstates in the post-stimulus time window of

interest (0–500 ms) appear only once and are not specific to any experimental condition, that is, the different action stimuli involve the same brain functional states, differing primarily in their durations and activation strengths.

The first microstate in our epoch of interest showed pronounced negativity over central posterior electrodes and occurred within the first 80 ms after the presentation of the action stimulus. None of the first microstate parameters differed significantly between conditions (all $ps > 0.292$).

The second microstate's topography presented a right-lateralized positivity over occipito-parietal electrodes, reassembling the prototypical map associated with visual processing (Schiller et al. 2024). Analyses revealed that the AUC significantly differed between conditions ($p = 0.008$), with the Social grasping observation yielding a higher AUC (79 ms*μV) compared to the Intransitive (73.1 ms*μV) and Object conditions (62.7 ms*μV; Figure 3b).

The third microstate occurred within the first 200 ms (i.e., encompassing the P200 component in our ERP grand averages; Figure 1); its map showed a prominent positivity over centro-frontal and sensorimotor electrodes and a negativity over bilateral occipito-parietal electrodes. Microstate features primarily differed between conditions (Figure 3c). Offset, duration, and AUC values were significantly greater in Intransitive (offset = 226 ms, duration = 70.3 ms; AUC = 40.3 ms*μV) and Social conditions (offset = 224.6 ms, duration = 66.2 ms, AUC = 49.8 ms*μV) compared to Object grasping (offset = 205 ms, $p = 0.001$; duration = 51 ms, $p = 0.012$; AUC = 24 ms*μV, $p = 0.006$). At the same time, microstate GFP was lower in Intransitive (0.67 μV) and Object conditions (0.63 μV) compared to Social grasping (0.82 μV, $p = 0.047$). Overall, these patterns of results suggest that observing intransitive and social grasping stimuli activated brain's anterior regions for a more extended period than observing object-directed movements. Notably, in contrast to intransitive and object grasping, social grasping observation simultaneously recruited more neuronal resources during this time frame.

Similarly to the previous one, the fourth microstate, presenting a prominent positivity over central parietal electrodes and occurring within the first 300 ms, significantly differed between conditions (Figure 3d): Object grasping stimuli had an earlier microstate onset (206.7 ms, $p = 0.001$) and a later offset (300.5 ms, $p = 0.022$) than the other two conditions (Intransitive: onset = 227.4 ms, offset = 270.4 ms; Social: onset = 226 ms, offset = 283.9 ms). This pattern resulted in a longer overall microstate duration during Object (95.2 ms, $p < 0.001$) compared to Intransitive grasping (44.1 ms), with the Social condition showing an intermediate value (59.3 ms). The same gradient between conditions was also found for the AUC (Object: 62.9 ms*μV, Social: 41.5 ms*μV, Intransitive: 29.5 ms*μV; $p < 0.001$). These results indicate that the observation of object-directed movements activated posterior brain regions earlier and for a longer duration, recruiting more brain resources than the observation of intransitive and, to a lesser extent, social grasping stimuli.

Finally, the fifth microstate presented a map characterized by positivity over posterior parietal electrodes, more prominent in the right hemisphere, and covered the rest of the analyzed epoch. We found that its onset and duration differed between conditions, with a pattern likely driven by the one observed in the previous microstate map (Figure 3e). Namely, Object grasping stimuli had a later microstate onset (301.8 ms, $p = 0.022$) and a shorter duration (201.3, $p = 0.022$) than the other two conditions, with the Social grasping presenting intermediate values (Social: onset = 285.3 ms, duration = 217.9 ms; Intransitive: onset = 271.5 ms, duration = 231.7 ms).

2.4 | Interim Discussion

Cluster-based permutation analysis identified significant differences in ERP activity between grasping conditions. The significant clusters are presented as a visualization of the spatio-temporal distribution of the test statistics rather than as evidence of statistically localized effects within specific time intervals or scalp regions (Sassenhagen and Draschkow 2019). The interpretation of the temporal evolution and topographic organization of these condition-related differences is therefore based on a qualitative examination of the grand-average scalp topographies and on ERP microstate analysis.

This descriptive approach suggests that intransitive actions exhibit a dynamic, intermediate spatial profile between object- and socially-directed grasping. Around 100 ms, during the earliest positive ERP deflection, the topographic distribution for intransitive actions resembled the bilateral posterior organization of object-directed grasping, rather than the right-lateralized pattern of socially directed grasping. At later stages (peaking around 200 and 300 ms), this pattern shifted: the scalp distributions associated with intransitive actions progressively resembled those of social grasping, with a more pronounced right-lateralized parieto-occipital pattern. Thus, rather than reflecting a uniform intermediate state, intransitive grasping shares different aspects of the spatial organization of object- and social-directed actions across distinct processing stages.

The presence of early condition-related ERP differences aligns with neuroimaging evidence showing that nodes of the AON, such as superior and middle temporal gyri, exhibit target-sensitive responses during the initial stages of action observation (Caspers et al. 2010; Gatti et al. 2017; Kilintari et al. 2014; Schultz et al. 2004). Crucially, these early differences cannot be attributed solely to physical stimulus characteristics (e.g., the presence or absence of a target object). Indeed, the social condition also featured a target but elicited topographies more similar to those of the intransitive condition than to those of the object-directed condition. This pattern suggests that the AON is sensitive not only to the physical kinematics of an observed movement but also to its social and communicative meaning.

At later processing stages, the condition-related ERP differences co-occurred with distinct posterior scalp distributions, particularly during observation of object-directed grasping. This pattern is consistent with the involvement of processes related to action-goal understanding and contextual integration, which rely on the target object's semantic and physical features (Avanzini et al. 2013; Simonelli et al. 2024; Urgen and Orban 2021). In support, Avanzini et al. (2013) showed that perturbing occipital activity around 200 ms after action onset selectively impaired

the decoding of an observed object-directed grasping action (i.e., distinguishing movement from use; Avanzini et al. 2013). Furthermore, previous ERP studies associating stronger posterior responses at later processing with action-intention decoding (Ortigue et al. 2009, 2010; Zhang et al. 2018) converge with our microstate findings: *Microstate 4*, characterized by a posterior positivity over centroparietal electrodes, showed higher AUC, earlier onset, and longer duration specifically in this condition (Figure 3).

In contrast, socially meaningful grasping likely engages processes that represent the social relevance of the observed action (Amoruso and Finisguerra 2019; Guidali, Picardi, Franca, et al. 2023), as well as visuo-tactile mirroring mechanisms, given that participants observed both a grasping movement and physical contact between body parts. Observation of such tactile interactions is known to recruit bilateral somatosensory and parietal regions, with effects emerging within intermediate stages of visual processing (~150–200 ms; e.g., Bolognini et al. 2014; Lee Masson and Isik 2023; Maddaluno et al. 2020; Pihko et al. 2010; Pisoni et al. 2018; Schaefer et al. 2024; Streltsova and McCleery 2014). Accordingly, the enhanced fronto-parietal ERP activity observed during social relative to object-directed grasping may reflect the integration of tactile and social information conveyed by the observed action.

Finally, regarding intransitive grasping observation, descriptive evaluation of scalp maps suggests that this condition may engage a greater contribution from contralateral sensorimotor processes than object-directed movements. This pattern aligns with previous neuroimaging and neurostimulation studies showing lateralized recruitment of motor areas during the observation of simple unilateral movements, adhering to the somatotopic organization of the observed effector (e.g., Avenanti et al. 2007; Aziz-Zadeh et al. 2002, 2006; Borroni et al. 2008; Guidali et al. 2020; Guidali and Bolognini 2025; Sartori et al. 2013).

Importantly, these interpretations rely on the spatial configuration of the topographies and converging literature, rather than on the localization of significant electrodes identified by the cluster-based permutation analysis. Nevertheless, while our results suggest that action type modulates spatiotemporal ERP patterns across at least two temporal windows, they cannot definitively adjudicate between two interpretations: (a) the three conditions recruit qualitatively distinct cortical sub-processes, or (b) they engage the same sequential processes with differing temporal and spatial gain. The ERP microstate analysis was designed specifically to disentangle these two possibilities.

In fact, microstate results complement previous patterns, highlighting that the cortical elaboration of grasping movements is not characterized by distinct, stimulus-specific sub-processes (i.e., microstate maps appearing only during one of our conditions, or in different orders), but rather by different timing and magnitude of information elaboration (i.e., quantitative differences in microstate parameters). Microstate order of appearance is the same for all the different types of observed grasping actions: in the first 500 ms from the action onset, after the visual elaboration of the stimuli in posterior regions (*Microstate 2*, which map closely reassembles the prototypical one of visual processing, Schiller et al. 2024), positive activity is found over fronto-central electrodes (*Microstate 3*) before the posterior activation returns to prevail in the extracted maps (*Microstate 4* and *5*).

The two microstates exhibiting the greatest parameter differences among our stimuli (i.e., *Microstates 3* and *4*) occurred in an earlier window, between 170 and 300 ms after action onset. This time window is compatible with the visually driven activation of AON fronto-parietal nodes found in previous literature (e.g., Avanzini et al. 2013; Ortigue et al. 2010; Zhang et al. 2018).

Overall, the fact that the two transitive actions, despite both sharing the presence of a "target", show the greatest differences in *Microstates 3* and *4* parameters—with the socially-directed action presenting a modulation profile more similar to the intransitive condition—is not surprising. Previous literature suggests that spatiotemporal patterns of AON recruitment differ significantly when the observed, target-directed action conveys a social or communicative meaning (for a review, see: Zhao et al. 2024). Hence, microstate results effectively reflect the network's sensitivity to the social relevance and communicative intent of the observed movement, rather than its mere physical attributes (i.e., the presence of a target), in line with the pivotal role of the AON in action understanding (Rizzolatti and Sinigaglia 2016). In detail, considering *Microstate 3*, the observation of intransitive and social grasping induces longer and stronger activation of anterior electrodes than transitive, object-directed actions. Importantly, during socially-directed grasping observation, this third microstate is characterized by the simultaneous recruitment of more neural sources (i.e., GFP) than during the other two stimuli. One mechanism underlying this effect likely involves additional visuo-tactile mirroring elaboration in sensorimotor and parietal regions during this time window (e.g., Pisoni et al. 2018; Bolognini et al. 2014); cluster-based analysis results also support this proposal. In this regard, it is worth noting that the observation of social grasping already showed a higher AUC during *Microstate 2* than in the other two conditions, corroborating the idea that observing this movement led to more engaging cortical elaboration from the earliest stages of visual processing. Interestingly, *Microstate 3* exhibited the same topography as microstates reported in the literature between 150 and 200 ms when observing static stimuli depicting bodies, with cortical sources located within the temporo-occipital lobes (Thierry et al. 2006). Although we cannot entirely rule out that *Microstate 3* is partially modulated by cortical processing reflecting body perception, or that the greater GFP observed for social-directed grasping is influenced by the depiction of two interacting body parts, it is worth noting that the actor's hand was already visible during the preceding static frame of our paradigm. Consequently, the specific modulation of *Microstate 3* at this latency most likely reflects the spatiotemporal processing of movement dynamics and action observation, rather than the mere structural perception of static body parts. *Microstate 4* is characterized by posterior positivity over central electrodes and shows a higher AUC, earlier onset, and longer duration during object-directed grasping observation, suggesting that posterior elaboration occurred with greater magnitude, earlier, and for a longer duration for this latter stimulus. In line with the cluster-based findings, the predominant posterior activation during action observation of object-directed stimuli emphasizes that

goal-directed movement recruited parietal regions to a greater extent (e.g., Aberbach-Goodman and Mukamel 2023; Caspers et al. 2010; Handjaras et al. 2015; Newman-Norlund et al. 2010; Simonelli et al. 2024), also considering that these regions play a vital role in visually guided grasping interactions, grounding manipulative behavior (Di Caro et al. 2025; Del Vecchio et al. 2026).

Importantly, our microstate results also corroborate and extend findings from previous research using microstate analysis in action observation (Avanzini et al. 2013; Ortigue et al. 2010; Zhang et al. 2018). In contrast to our work, all these studies employed object-directed stimuli depicting the same target to investigate the cortical dynamics of action understanding, revealing a succession of microstates that roughly correspond to the temporal and topographical patterns observed in the present study. For instance, Zhang and colleagues found greater modulation among their different experimental conditions (i.e., different intention of the observed movement) for the microstate occurring between 160 and 240 ms from action onset, which was hypothesized to be indicative of mirror-matching processes that acquire information from action kinematics and thus could be sensitive to the decoding of immediate action goals by the AON (Zhang et al. 2018). Our *Microstate 3* occurred in a similar time window and presents the same topographic map. Avanzini et al. (2013) found similar temporal dynamics during object-directed action observation, which index forward processing from occipito-temporal regions to the anterior temporal lobes, followed by backward processing that reactivates the temporo-parietal regions. This pattern suggests that the reactivation of posterior areas is instrumental in understanding the conceptual properties of the observed movement within the AON (Avanzini et al. 2013).

Taking together the two analytic approaches, the results of *Experiment 1* highlighted that the observation of transitive and intransitive grasping movements likely recruited the same AON circuitry but with spatiotemporal gradients that are specific for the depicted movement.

3 | *Experiment 2*: Corticospinal Correlates of Transitive and Intransitive Grasping Movements Observation

3.1 | Aims

In *Experiment 2*, we extend our investigation to the motor resonance phenomenon, that is, the enhancement of motor-evoked potential (MEP) amplitude during biological action observation, which is considered a *gold standard* for non-invasive investigation of visuomotor mirroring properties (Craighero 2024). Here, we investigate whether this peripheral marker of AON activation is modulated by different transitive and intransitive grasping conditions, with temporal patterns that may mimic those observed in the previous experiment.

Corticospinal excitability facilitation during action observation (i.e., motor resonance) is thought to reflect activation of AON populations in the ventral premotor cortex. This region directly connects with M1, influencing its reactivity during action observation and leading to motor resonance (Rizzolatti et al. 2014). Importantly, the modulation of corticospinal excitability is detectable only in the muscles actually involved in the observed action, allowing for the disentangling of this phenomenon, and hence the recruitment of the AON, from non-specific changes of M1 reactivity during the sight of moving stimuli (Naish et al. 2014). Considering this, the mirror activation of M1 likely represents one of the last "extended AON" nodes recruited during action observation processing (Bonini 2017). In this regard, different studies showed that motor resonance could be reliably found between 150 and 350 ms from the observed action onset but with controversial results on the optimal timing to detect this modulation and even the direction of the effect, that is, MEP facilitation versus inhibition (e.g., Barchiesi and Cattaneo 2013; Cavallo et al. 2014; Dalla Volta et al. 2025; Donne et al. 2011; Gianelli et al. 2020; Guidali, Picardi, Franca, et al. 2023; Guidali and Bolognini 2025; Huntley et al. 2018; Makris et al. 2011; Matamala-Gomez et al. 2025; Naish and Obhi 2015; Nieto-Doval et al. 2025; Ubaldi et al. 2015). Despite these controversies, it is well established that the features of the viewed action (such as its goal, context, effector, or perspective) modulate the magnitude of motor resonance (for reviews, see Amoruso and Finisguerra 2019; Fadiga et al. 2005; Naish et al. 2014).

Given this premise, we hypothesized that motor resonance patterns during the observation of different grasping stimuli used in the first experiment should be, at least partially, superimposable to their cortical signatures found in *Experiment 1*, allowing us to better relate central and peripheral markers of AON activation at the sight of transitive and intransitive movements. In this second experiment, we delivered TMS pulses over M1 at three time points relative to action onset, selected based on the results of the previous experiment. Electrophysiological spatiotemporal patterns observed in *Experiment 1* during action observation revealed two distinct periods (between ~70 and 240 ms and ~270 and 430 ms) in which ERPs differed significantly among our grasping actions (Figure 2a). Notably, the first period also encompassed *Microstate 3* dynamics (i.e., the only microstate showing prominent positive activity over anterior electrodes), and the second period encompassed *Microstates 4* and *5*, suggesting feedback processing that reactivates posterior areas. Hence, we assessed motor resonance by delivering TMS over M1 at 200 and 350 ms from the onset of the grasping. We selected a third timing of 500 ms as a control. Following previous evidence using action observation tasks with similar frame-based movements (Guidali, Franca, et al. 2025; Guidali, Picardi, Franca, et al. 2023), we expect to find motor resonance at 200 ms while, during later timings (i.e., 350 and 500 ms), evidences from previous literature are more controversial and, besides not detecting motor resonance at all (Naish et al. 2014), MEP facilitation during action observation could also turn in MEP inhibition, especially for the two transitive actions (object- and socially-directed; see, e.g., Dalla Volta et al. 2025; Gianelli et al. 2020). Furthermore, we recorded MEPs from three muscles of the right hand (i.e., *first dorsal interosseus*—FDI, *abductor pollicis brevis*—APB, and *abductor digiti minimi*—ADM) to investigate motor resonance muscle-specificity (Craighero 2024). As previous evidence suggests, we expect to record motor resonance only in the muscles involved in the observed movement, and clearly depicted in the visual stimulus (i.e., FDI, APB), and not in the ADM, which serves as a control muscle (Naish et al. 2014).

3.2 | Materials and Methods

3.2.1 | Participants

Twenty-four healthy participants (10 males; mean age ± standard deviation—SD = 21.4 ± 2.3 years; mean education ± SD = 13.6 ± 1.8 years) took part in the second experiment of the study. None of them has participated in *Experiment 1*. All participants were right-handed (mean Edinburgh Handedness Inventory score ± SD = 81.5% ± 16.2%) and had no contraindications to TMS administration, as assessed using an ad-hoc questionnaire (Rossi et al. 2021). We estimated the sample size based on the effect size reported in a previous study of our research group, which investigated the temporal features of motor resonance using the same three visual stimuli of grasping as in the present work (partial eta-squared—$\eta p^2 = 0.11$; Guidali, Picardi, Franca, et al. 2023). We performed an a priori sample size estimation, accounting for a within-subject 3 × 3 × 3 repeated-measures ANOVA (rmANOVA), using the software G.Power 3.1 (Faul et al. 2009). We set the desired effect size to 0.35 (corresponding to $\eta p^2 = 0.11$), with an alpha level of 0.05 and statistical power of 0.95. The results suggest that a sample size of at least 23 participants is required to achieve sufficient statistical power.

The experiment adhered to the ethical standards outlined in the Declaration of Helsinki and was approved by the University of Milano-Bicocca's Ethical Committee (protocol number: 881-2024). Before participating in the study, all participants provided their written informed consent.

3.2.2 | Experimental Procedure

The second experiment consisted of a single TMS session, during which participants underwent the same action observation task as in *Experiment 1* to assess how different targets affected corticospinal enhancement via action observation (i.e., the motor resonance phenomenon). The session began with filling out the informed consent form and the Edinburgh Handedness Inventory. Then, the experimenters performed neuronavigation procedures and assessed the participants' resting motor threshold (rMT). Following these, the action observation task was administered. The session lasted about 1.5 h.

3.2.3 | Action Observation Task

The action observation task consisted of the passive observation of the same visual stimuli of grasping used in *Experiment 1* (i.e., "intransitive", "object", and "social" grasping) while recording right-hand MEPs, thus to obtain an index of corticospinal facilitation during action observation (i.e., motor resonance; for similar tasks, see: Guidali et al. 2020; Guidali, Picardi, Franca, et al. 2023). Participants were seated in a chair in front of a PC screen at approximately 100 cm, with their hands resting on a table out of view. As for *Experiment 1*, every trial began with a frame depicting a red asterisk, serving as a fixation cross, on a black background (with a duration jittered between 1000 and 2000 ms). A second frame depicting a static hand appeared for 1000 ms after this. Then, a third frame, showing the grasping movement of the right hand (i.e., "movement frame"), was presented with a fixed duration of 800 ms. From the onset of this frame, TMS over the left M1 could be delivered after 200, 350, or 500 ms. TMS intensity was set at 120% rMT. Finally, the frame depicting a static hand reappeared for 500 ms, ending the trial. Besides being delivered during movement observation, TMS pulses were also delivered during the observation of the asterisks (i.e., "rest" trials). In this further condition, throughout the trial, the frame on screen remained the one depicting the red asterisk and serving as a fixation cross (Figure 4).

The action observation task consisted of 3 blocks of trials, each corresponding to a different TMS timing (i.e., 200, 350, or 500 ms). Each block consisted of 80 trials (20 for each condition: "intransitive grasping", "object grasping", "social grasping", or "rest"), presented randomly to participants, and lasted approximately 8 min each. Similar to *Experiment 1*, participants had to press one of the PC mouse keys with their left hand when the task's trials presented a small red dot (diameter: 20 pixels) that appeared on the back of the right hand at the onset of the task's third frame. For the "rest" trials, the attentive cue was a red circle appearing around the asterisk. Twenty-four trials out of 240 (i.e., 8 trials for each category) presented these attentional cues. On average, the participants' accuracy was 95.2% (SD = ±3.4%), indicating attentive participation. MEPs during these attentional trials were not analyzed.

TMS timing, stimulus presentation, and trial randomization were controlled by the computer using E-Prime 3.0 software (Psychology Software Tools Inc.).

3.2.4 | TMS and EMG Recording

TMS pulses were delivered with a figure-of-eight coil (diameter = 70 mm) connected to a biphasic Magstim Rapid 2 stimulator (Magstim, Whitland, UK) over the motor hotspot of the right-hand FDI muscle. This was found by moving the TMS coil around the presumed hand area of the left hemisphere M1 and recording MEPs. The coil was placed tangentially to the scalp with the handle held backward and laterally at a 45° angle to the sagittal plane, inducing currents in the brain with an anterior-to-posterior (first phase) / posterior-to-anterior (second phase) direction. The stable TMS coil placement and position were monitored during the experimental sessions using the SofTaxic Optic 3.4 neuronavigation software and the standard brain template implemented in the software (EMS, Bologna, Italy). The individual rMT was calculated using the parameter estimation by sequential testing (PEST) procedure, a maximum-likelihood threshold-hunting method optimized for rMT detection (Awiszus 2003). On average, participants presented an rMT of 57.5% (SD = ±8.8%) of the maximum stimulator output (MSO). Considering that we used a single muscle (i.e., FDI) as a reference for the motor hotspot, we ensured that participants presented stable MEPs of at least 200 μV in all the target muscles at the stimulation intensity employed during the action observation task (i.e., 120% rMT, corresponding on average to 68.8% ± 10.1% MSO). All our participants respected this criterion.

We recorded MEPs from three muscles of the right hand: FDI, APB, and ADM. We placed active electrodes (15 × 20 mm

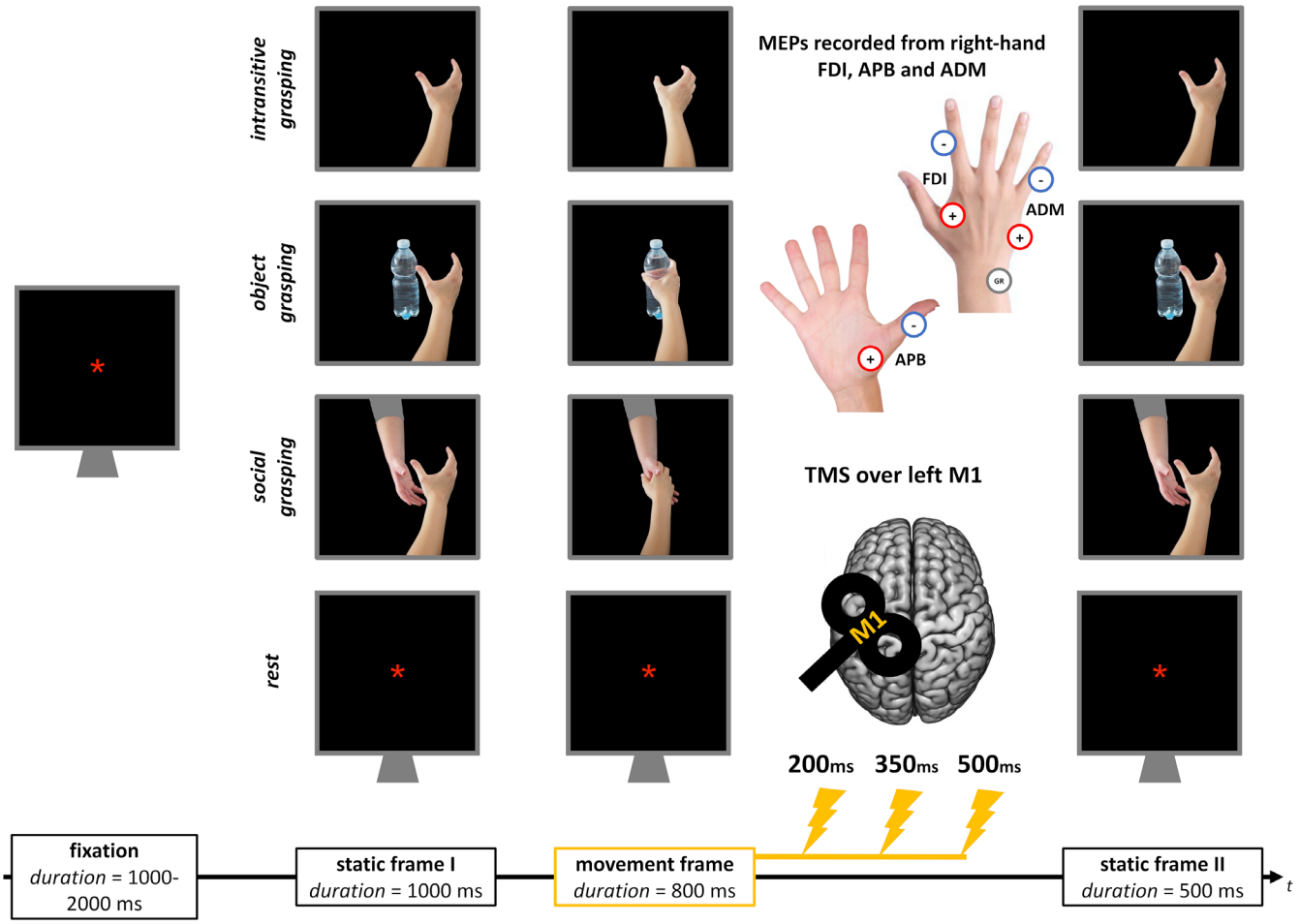

FIGURE 4 | Action observation task of *Experiment 2*. TMS over left M1 was delivered after 200, 350, and 500 ms from the onset of the movement frame, and MEPs were recorded from FDI, APB, and ADM muscles of the right hand.

Ag-AgCl pre-gelled surface electrodes, Friendship Medical, Xi'an, China) over the muscle bellies. Reference electrodes were placed over the metacarpophalangeal joint of the index finger (for FDI), thumb (for APB), and little finger (for ADM). The ground electrode was placed over the right head of the ulna.

Before data acquisition, we visually inspected the EMG trace to ensure that the background noise from the three channels was less than 50 μV. MEPs were recorded using Signal software (version 3.13, Cambridge Electronic Devices, Cambridge, UK) at a sampling rate of 5 kHz, with a Digitimer D360 amplifier (Digitimer Ltd., Welwyn Garden City, UK) connected to a CED micro1401 A/D converter (Cambridge Electronic Devices, Cambridge, UK). The signal was amplified, band-pass filtered (10–1000 Hz), notch-filtered, and then stored for offline analysis. We collected data from 100 ms before to 200 ms after the TMS pulse (time window: 300 ms).

3.2.5 | Statistical Analysis

We analyzed MEPs offline using Signal software (version 3.13), utilizing the standard preprocessing pipeline employed in our laboratory (e.g., Guidali, Arrigoni, et al. 2025). Initially, trials with muscular artifacts or background noise deviating by more than 100 μV from 100 μV within the 100 ms preceding the TMS pulse were automatically excluded from the analysis. Then, the MEP peak-to-peak amplitude was calculated for each trial between 5 ms and 60 ms after the TMS pulse. We excluded from the following analyses trials in which MEP amplitude was smaller than 50 μV. Then, for each participant, in every experimental block, trials where MEP amplitudes were ±2.5 SD from the mean of each condition (i.e., "intransitive grasping", "object grasping", "social grasping", and "rest" trials) were considered outliers and excluded from the following analyses. On average, across all our criteria, 6.3% (SD = ±2.3%) of MEPs recorded for a participant were discarded.

We computed a *motor resonance index* (e.g., Guidali, Arrigoni, et al. 2025) to assess corticospinal facilitation during action observation, defined as the ratio in MEP amplitude between movement and rest trials:

$$\text{motor resonance index (\%)} = \frac{\text{MEP amplitude in movement trials}}{\text{MEP amplitude in rest trials}} - 1$$

Namely, for every grasping condition (i.e., intransitive, object, or social), the mean MEP amplitude in trials depicting the movement was divided by the MEP amplitude from rest trials, which

served as the baseline condition for corticospinal excitability. The value "1" was subtracted from the ratio to express the percentage of the rest condition. Hence, positive values indicated facilitation of corticospinal excitability by action observation (and thus the presence of motor resonance). In contrast, negative ones indicated inhibition of corticospinal excitability by action observation. We report MEP raw values in the different experimental conditions in Table S1.

We then assessed motor resonance for the three grasping movements with a "TMS timing" (200, 350, 500) × "viewed Grasping" (intransitive, object, social) × "Muscle" (FDI, APB, ADM) rmANOVA. Statistical significance was set at $p < 0.05$ if not otherwise specified. The normality of the distributions was confirmed using the Shapiro–Wilk test and Q–Q plots. Significant main effects and interactions were explored with multiple Tukey's HSD post hoc comparisons. Partial eta-squared (ηp^2) was calculated in every rmANOVA and reported as an effect size value. The mean ± standard error is reported for each variable if not otherwise specified. Statistical analyses were performed using the software Jamovi (v. 2.7; The Jamovi Project 2025).

3.3 | Results

Results from the rmANOVA on the *motor resonance index* showed a significant "TMS timing" × "viewed Grasping" × "Muscle" interaction ($F_{8,184} = 4.09$, $p < 0.001$, $\eta p^2 = 0.15$), as well as the main effect of factors "TMS timing" ($F_{2,46} = 8.43$, $p < 0.001$, $\eta p^2 = 0.27$), "viewed Grasping" ($F_{2,46} = 12.5$, $p < 0.001$, $\eta p^2 = 0.35$), and interaction "viewed Grasping" × "Muscle" ($F_{4,92} = 3.14$, $p = 0.018$, $\eta p^2 = 0.12$). No other significant effect was found (all $Fs < 0.98$, all $ps > 0.423$). Muscle-specific corticospinal patterns were further explored with three separate rmANOVAs, one for each muscle.

For FDI, we found a significant effect of both factors "TMS timing" ($F_{2,46} = 7.87$, $p = 0.001$, $\eta p^2 = 0.25$) and "viewed Grasping" ($F_{2,46} = 11.84$, $p < 0.001$, $\eta p^2 = 0.34$) and of their interaction ($F_{4,92} = 3.62$, $p = 0.009$, $\eta p^2 = 0.14$). Post hoc highlighted that only during the observation of Intransitive grasping, and only when TMS is delivered after 200 ms from the onset of the movement, motor resonance emerged for this muscle (8.1% ± 4%). Furthermore, during Object grasping observation, motor resonance inhibition was significantly greater at 350 ms (−18.4% ± 3.4%) than at 200 ms (−3.1% ± 2.8%, $t_{23} = 3.81$, $p = 0.021$; see Table 1 for all significant post hoc comparisons; Figure 5a).

Considering APB, the pattern of results was similar to FDI with a statistically significant main effect of the two factors ("TMS timing": $F_{2,46} = 5.53$, $p = 0.007$, $\eta p^2 = 0.19$; "viewed Grasping": $F_{2,46} = 7.75$, $p = 0.001$, $\eta p^2 = 0.25$) and their interaction ($F_{4,92} = 2.79$, $p = 0.031$, $\eta p^2 = 0.11$). Crucially, post hoc analysis showed that for this muscle solely the observation of Object grasping stimuli led to the emergence of motor resonance, specifically at 200 ms from the onset of the movement

TABLE 1 | Significant Tukey-corrected post hoc comparisons for *motor resonance index*.

	Condition			Versus				
Muscle	TMS timing	Viewed grasping	Mean ± ES	TMS timing	Viewed grasping	Mean ± ES	t_{23}	p_{tukey}
FDI	200	Intransitive	8.1% ± 4%	200	Object	−3.1% ± 2.8%	3.6	0.033
					Social	−8.01% ± 3.6%	4.43	0.005
				350	Intransitive	−13.09% ± 3.4%	4.19	0.009
					Object	−18.4% ± 3.4%	4.63	0.003
					Social	−17.6% ± 4.2%	4.21	0.008
				500	Intransitive	−13.7% ± 3.5%	4.02	0.013
					Object	−16.3% ± 4.4%	4.05	0.012
					Social	−22% ± 4.5%	4.69	0.003
	200	Object	−3.1% ± 2.8%	350	Object	−18.4% ± 3.4%	3.81	0.021
APB	200	Object	10.4% ± 4.4%	200	Intransitive	−0.1% ± 4.8%	3.93	0.016
					Social	−6.1% ± 4.5%	4.43	0.005
				350	Intransitive	−9% ± 5.4%	3.35	0.047
					Object	−12.9% ± 4.7%	3.66	0.029
					Social	−17.6% ± 4.7%	4.54	0.004
				500	Intransitive	−12.3% ± 5%	4.1	0.011
					Object	−16.1% ± 5.2%	4.21	0.008
					Social	−18.3% ± 5.8%	4.26	0.007

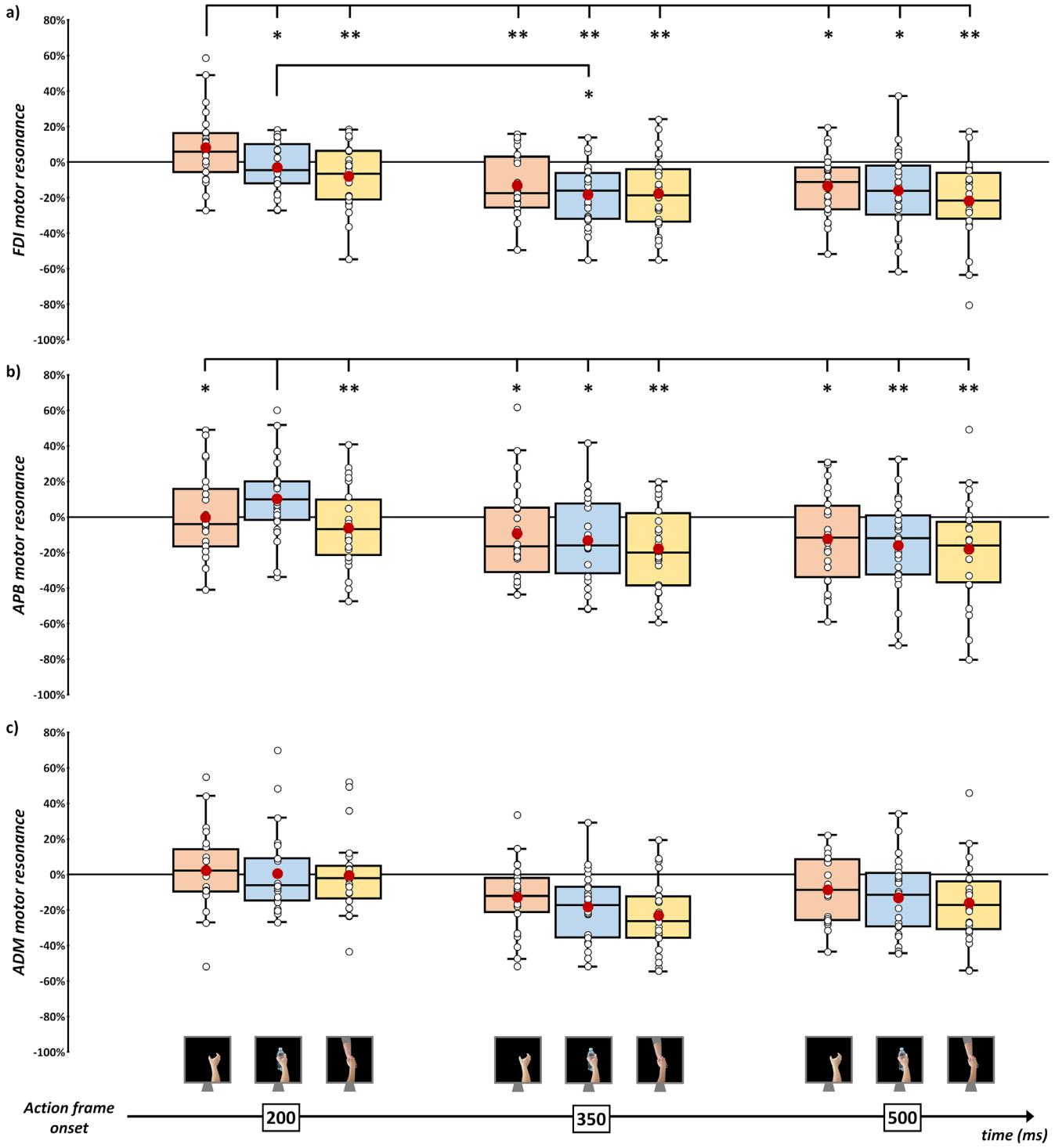

FIGURE 5 | Motor resonance index results (i.e., MEPs amplitude in movement trials divided by MEP amplitude during rest trials) for the three visual stimuli of grasping (intransitive = orange boxplots; object = blue boxplots; social = yellow boxplots) recorded from FDI (a), APB (b), and ADM (c) muscles during the three TMS timings (200, 350, and 500 ms). In the box-and-whiskers plots, red dots indicate the means of the distributions. The center line denotes their median values. White dots show individual participants' scores. The box contains the 25th to 75th percentiles of the dataset. Whiskers extend to the greatest observation falling within the 1.5*inter-quartile range from the first/third quartile. Significant p values of Tukey corrected post hoc comparisons are reported (*$p < 0.05$; **$p < 0.01$).

(10.4% ± 4.5%), compared to all other conditions (Table 1 for all significant post hoc comparisons; Figure 5b).

Finally, for ADM, the "TMS timing" × "viewed Grasping" interaction was not statistically significant ($F_{4,92} = 0.56$, $p = 0.693$, $\eta p^2 = 0.02$). Nevertheless, main effects of both "TMS timing" ($F_{2,46} = 6.4$, $p = 0.003$, $\eta p^2 = 0.22$) and "viewed Grasping" ($F_{2,46} = 6.43$, $p = 0.003$, $\eta p^2 = 0.22$) reached significance, showing that, regardless of the observed movements, motor resonance was higher when TMS is delivered 200 ms from the movement onset

(1% ± 4.2%), as compared to the 350 (−18.4% ± 3.3%, $t_{23} = 3.03$, $p = 0.018$) and 500 ms (−12.2% ± 3.7%, $t_{23} = 2.64$, $p = 0.041$) delays; regardless of TMS timing, Intransitive grasping stimuli (−6.3% ± 1.8%) exhibited a less pronounced inhibition of motor resonance than Social ones (−13.1% ± 2.3%, $t_{23} = 3.5$, $p = 0.006$; Figure 5c).

3.4 | Interim Discussion

Motor resonance patterns detected in *Experiment 2* support the presence of two distinct phases of corticospinal excitability modulation when observing the three kinds of grasping movements. In the first phase, around 200 ms after action onset, muscle- and stimulus-specific facilitation of corticospinal excitability is detected only for intransitive and object-directed movements. In a later phase, lasting at least 500 ms after action presentation, corticospinal excitability is no longer modulated, with an overall pattern suggesting MEP inhibition during observation of grasping movements.

Indeed, given the first TMS delivery timing (200 ms), we found that passive observation of intransitive and object-directed grasping led to MEP facilitation in the selective hand muscles (FDI and APB, respectively). Muscle-specificity is indeed a key feature of motor resonance (Craighero 2024), and it is modulated by the goal and effector properties of the depicted movement (e.g., Alaerts et al. 2010; Amoruso and Finisguerra 2019; Cattaneo et al. 2009; Perez and Rothwell 2015; Rens et al. 2021). Given the APB's role in the thumb's abduction, opposition, and stabilization, this muscle is fundamental for object manipulation (Nowak and Hermsdorfer 2009). We suggest that the observation of object-directed grasping had prioritized the mirror recruitment of APB motor regions relative to other hand muscles that may be involved in the depicted movement. In contrast, observing the intransitive movement facilitated motor resonance for the muscle primarily depicted in the viewed action (i.e., FDI) and where the observer's attention is put on, due to the fact that the (rare) attentional stimuli during the action observation task appeared on the back of the hand, near the FDI region (e.g., D'Innocenzo et al. 2017; Gangitano et al. 2001; Puglisi et al. 2017; Sriutaisuk and Franz 2026). Considering the lack of effects for ADM, it has to be noted that the movement of the hypothenar hand region (and thus of the little finger) is only suggested by the presumed kinematics of our grasping stimuli. This feature of our visual stimuli may have maximized motor resonance for FDI/APB (whose movements are clearly depicted in the action frame), hence detecting a stimulus-specific motor resonance effect confined to these two muscles (see Guidali, Picardi, Franca, et al. 2023, but also Picardi et al. 2025, for similar results). In this regard, our previous TMS study found that only intransitive grasping observations yielded a pattern of results suggesting muscle-specific motor resonance at 200 ms, with no modulation for object-directed movements (Guidali, Picardi, Franca, et al. 2023). Indeed, the difference between FDI and ADM motor resonance magnitudes during object-directed grasping observation reached statistical significance only with larger sample sizes (Guidali, Franca, et al. 2025). Crucially, we did not record MEPs from the APB muscle in our previous works. The results of the present experiment shed better light on these controversial findings (Guidali, Franca, et al. 2025; Guidali, Picardi, Franca, et al. 2023), suggesting that APB could be the optimal muscle to record corticospinal excitability facilitation during object-directed movement observation, requiring smaller samples to detect motor resonance patterns successfully.

Interestingly, we did not find statistically significant motor resonance effects for the social grasping. One possible explanation is that passively observing social actions engages stronger mechanisms for withholding automatic imitation (e.g., Cracco et al. 2018; Giesen et al. 2018). Control of shared action representations involves brain regions associated with self–other distinction and perspective-taking (e.g., taking a bodily third-person perspective, Brass et al. 2001; Brass and Heyes 2005). Since social actions carry more salient behavioral consequences than interactions with a neutral object or an intransitive gesture, such control is likely more necessary during the passive observation of grasping with a social goal. To substantiate this interpretation, we note that the commonly found and partially overlapping neural substrates of imitative control and social-cognitive functions, notably in the anterior frontal medial cortex and the right temporo-parietal junction (Brass et al. 2009), align well with the topographical patterns observed in *Experiment 1* (Figure 2). These regions can exert an inhibitory control over corticospinal output, keeping automatic activation of the motor system at bay (Derosiere and Duque 2020). This pattern is further intriguing, given that previous evidence has shown that observing social grasping movements was the only condition leading to a clear-cut, muscle-specific temporal pattern of motor resonance (Guidali, Picardi, Franca, et al. 2023). Nevertheless, it must be considered that the action observation paradigm used here (set to be as similar as possible to the one used in *Experiment 1*) is different from the one employed in our previous studies (Guidali, Franca, et al. 2025; Guidali, Picardi, Franca, et al. 2023). Indeed, in the latter, action observation tasks were divided into blocks that always depicted the same kind of grasping. In the present study, transitive and intransitive grasping stimuli were instead randomized within the same block. The block design used in our previous work may have led to cumulative effects that reversed the trend toward enhanced corticospinal facilitation. In contrast, the event-related design employed in the current investigation may have been better suited to capturing the early inhibitory nature of socially relevant action processing. However, this remains speculative, and future studies should further investigate the corticospinal patterns observed in response to socially directed stimuli.

Considering the later timings (i.e., 350 and 500 ms), no muscle-specific motor resonance effects were detected for grasping movements. Rather, corticospinal excitability seemed inhibited compared to observing a neutral stimulus (i.e., "rest" condition), as indicated by the significant main effect of "TMS timing" in all our rmANOVAs (see Section 3.3). In line with previous evidence and considering the passive nature of our action observation paradigm, this result suggests a suppression of motor activity in the hand muscles involved in the viewed action, likely to prevent imitation of the overt movement in the observer (e.g., Dalla Volta et al. 2025; Gianelli et al. 2020; Guidali, Picardi, Franca, et al. 2023; Hardwick et al. 2012; Nieto-Doval et al. 2025; Sartori et al. 2012; Villiger et al. 2011).

4 | General Discussion

4.1 | Cortical and Corticospinal Spatiotemporal Patterns During Transitive and Intransitive Action Observation

Our study investigated the spatiotemporal dynamics of AON recruitment during the observation of transitive (i.e., object-directed, social-directed) and intransitive grasping movements at the cortical (*Experiment 1*) and corticospinal (*Experiment 2*) levels using EEG and TMS, respectively.

Taking together the results of our two experiments, we show that the passive observation of similar movements but with distinct targets recruits the AON with different temporal and spatial gradients, with cortical and corticospinal activations framing complementary aspects of action observation mirroring, at least for simple actions, such as the ones exploited in the present study.

During the early processing stages, posterior regions are activated to varying degrees depending on the observed grasping content, likely reflecting spatiotemporal dynamics along visual elaboration pathways.

At around 150–200 ms, topographies and microstate analysis show predominant anterior activity, suggesting possible recruitment of temporo-frontal regions with stimulus-specific spatiotemporal patterns. Considering that the increased corticospinal output responsible for the motor resonance phenomenon is supposed to reflect the facilitation of AON premotor-to-M1 connectivity during action observation (Craighero 2024; Fadiga et al. 2005; Rizzolatti et al. 2014), the detection of motor resonance only at 200 ms (with stimulus- and muscle-specific patterns) fits well with the positive activity found around this timing over frontal electrodes (i.e., *Microstate 3*), as well as with findings from previous studies using electrocorticography, showing a rapid desynchronization of mu rhythm over motor and pre-motor cortices during action observation (Halje et al. 2015; Tremblay et al. 2004), coordinated with sensory activity over posterior temporo-occipital regions.

In the later stages of elaboration (i.e., from around 300 ms), topographic patterns indicate that cortical activity is localized over posterior electrodes (*Microstates 4* and *5*), likely mainly reflecting temporo-parietal activations, but with gradients that vary by action type. In this time window, motor resonance is no longer recorded. Paired-pulse TMS studies showed that parietal areas of the AON (like the IPL or SMG) have direct connections with M1, which are sensitive not only to the planning of grasping movements but also to their observation and, crucially, these connections could be either facilitatory or inhibitory according to the task's demand (e.g., Karabanov et al. 2013; Koch, Cercignani, et al. 2010; Koch et al. 2007; Koch, Versace, et al. 2010). Therefore, given the passive nature of our task, which does not require overt imitation of the observed grasping, we propose that following the initial facilitation of M1 reactivity—likely driven by transfer of visual information that encodes muscle-specific features of the observed action from posterior to more anterior AON nodes (*Microstate 3*)—the motor system is subsequently inhibited via AON parietal connectivity to prevent action imitation (e.g., posterior activity predominant in *Microstates 4* and *5*). As a result, corticospinal excitability facilitation during action observation becomes undetectable. Interestingly, this pattern of "facilitation/inhibition" is consistent with a seminal study using single-cell recording, which demonstrated that subsets of neurons in frontal and temporal cortices, presenting mirror-like patterns of activation (i.e., firing both during action observation and execution), can be excited but also subsequently inhibited during action observation, potentially to prevent (automatic) imitation (Mukamel et al. 2010). Considering the observation of social grasping, motor system inhibition seems to be already present in the early stages of cortical elaboration, during which we did not detect any motor resonance effects.

The absence of muscle-specific facilitation at 350 and 500 ms, combined with the general suppression of corticospinal excitability relative to the rest condition, does not license the conclusion that central (i.e., cortical) and peripheral (i.e., corticospinal) levels of the motor system are decoupled during action observation. Rather, the present data indicate that action-specific, effector-level motor resonance was not detectable at the sampled time points in the later epoch. Notably, qualitative convergence between the ERP topographic patterns and microstate transitions observed in *Experiment 1* and the timing-dependent MEP modulations of *Experiment 2* suggests that the two experiments capture related, rather than orthogonal, neural phenomena. Whether muscle-specific resonance is present but temporally precise, and thus missed by the discrete TMS timing approach, or genuinely absent in this epoch remains an open question. Resolving it will require a dedicated study employing a continuous, point-by-point TMS sampling strategy over this later time window, which remains crucial for action observation-related processing. At present, our evidence could explain why previous literature has not always succeeded in relating cortical and corticospinal signatures of AON activation, nor in identifying the same motor resonance patterns when slightly different action observation paradigms are employed (e.g., Kemmerer 2021; Naish et al. 2014).

4.2 | Limitations and Future Directions

In this regard, it must be acknowledged that the EEG (*Experiment 1*) and TMS (*Experiment 2*) investigations were conducted on independent samples. While this cross-sample convergence highlights the robustness and generalizability of the described action observation mechanisms across different cohorts, it precludes a direct, individual-level correlation between cortical dynamics and corticospinal excitability. Future research should implement within-subject designs, ideally employing EEG-informed TMS protocols. This would allow for a better evaluation of how specific cortical mechanisms directly gate and modulate corticospinal outputs during action observation within the same individual.

Furthermore, we stressed that, because our EEG investigation was restricted to the sensor space due to the absence of individual structural MRIs, speculations about the exact cortical sources of our effects should be interpreted with caution, and future studies using source analysis are recommended to better address this point.

Some important methodological aspects of our action observation paradigm should also be discussed. First, the effector (i.e., right

hand) and the movement's target already appeared in the static frame, presented 1000 ms before the "movement frame" depicting the actual grasping movement (Figure 1). Hence, we can state that differences in our ERPs are not given by the different complexity of the visual stimuli elaboration (i.e., the presence of an object or a hand in the action frame) but by the (apparent) movement elaboration and, in turn, action observation (Guidali, Picardi, Franca, et al. 2023). Second, participants already knew from the static frame which kind of grasping conditions would be presented. This could have facilitated AON elaboration (and hence the temporal pattern of AON activity detected at the cortical and corticospinal levels) at the sight of the actual movement, given that it could be successfully predicted in advance from the contextual information provided in the static frame (e.g., Betti et al. 2022; Bianco et al. 2024; Maddaluno et al. 2020). In this vein, the reactivation of occipito-parietal areas found after 200–250 ms from action onset could also underlie feedback monitoring processes from AON anterior regions to posterior ones (e.g., Avanzini et al. 2013; Cerliani et al. 2022; Kilner et al. 2007; Qin et al. 2023; Thomas et al. 2018). Future studies should explore whether, and to what extent, the predictability of our observed actions influenced the pattern found in the present study, for instance by presenting videos where the final part of the movement is truncated, and the action goal should be predicted (Ansuini et al. 2016; Fanghella et al. 2026). Third, it could be argued that a baseline condition for the *motor resonance index* based solely on fixation introduces spurious contributions due to differences in visual features and/or sustained attention. Although the fixation-only baseline differs from the action stimuli in terms of visual complexity, we preferred this choice over a baseline consisting of a static hand to avoid implicit motor simulation or affordance effects that could suppress motor resonance (e.g., Proverbio et al. 2009; Urgen and Orban 2021; Urgesi et al. 2006; Villiger et al. 2011). MEP recorded at rest while observing a neutral stimulus, like an asterisk, thus provides a more physiologically unbiased baseline. Furthermore, the distinct muscle-specific modulations observed between our three experimental conditions—which share nearly identical visual and attentional demands—rule out the possibility that our corticospinal patterns stem from low-level visual or attentional confounds, confirming the isolation of action-specific mirroring mechanisms, at least at 200 ms from action onset.

As a final note, given prior literature indicating that mu rhythm desynchronization during action observation is greater in females (Silas et al. 2010) and influenced by menstrual cycle phase (de Souza et al. 2022), participants' sex could have affected cortical patterns. Future studies with an appropriate experimental design that does not compromise statistical power should also explore whether sex differences affect the spatiotemporal dynamics of cortical and corticospinal activity during transitive and intransitive action observation.

5 | Conclusion

In conclusion, our findings demonstrate that observing transitive and intransitive grasping significantly modulates the spatiotemporal dynamics of the AON, already from the early stages of visual processing. Microstate results suggest that different kinds of grasping movements activate the same core circuitry with varying spatial and temporal gradients, particularly after 200 ms from action onset. Specifically, cortical elaboration of object-directed grasping relies more on posterior brain regions, whereas the observation of intransitive and socially-directed grasping engages more anterior regions. The latter stimulus recruited more cortical resources in the first 250 ms, likely due to additional social meanings conveyed and visuo-tactile mirroring processes (e.g., Schaefer et al. 2024; Zhao et al. 2024). At the same time, cortical and corticospinal signatures of AON activation frame distinct but complementary aspects of action observation, likely supporting different information processing in action understanding and preparation. The overall pattern of results found elegantly corroborates and integrates evidence from a previous retrospective study of our research group, where we showed that the magnitude of motor resonance during object- and socially-directed grasping observation was predicted by different individuals' empathic facets (cognitive versus affective empathy), whose respective cortical substrates are located in parietal and frontal regions (Guidali, Franca, et al. 2025).

Besides shedding further light on the spatiotemporal dynamics of (simple) transitive and intransitive action observation, our findings, if replicated with larger sample sizes, could help optimize action observation paradigms and state-dependent non-invasive brain stimulation protocols targeting AON dynamics. Similarly, clinical treatments based on action observation could also benefit from our findings, considering that the role of the movement's target and its cortical underpinnings are often neglected or underestimated during rehabilitation with such interventions (e.g., Garrison et al. 2010; Ryan et al. 2021).

Author Contributions

Giacomo Guidali: conceptualization, methodology, investigation, formal analysis, software, data curation, visualization, validation, writing – original draft. **Eleonora Arrigoni:** conceptualization, methodology, investigation, formal analysis, software, visualization, writing – original draft. **Angelo Maravita:** resources, funding acquisition, writing – review and editing. **Alberto Pisoni:** supervision, resources, writing – review and editing. **Nadia Bolognini:** supervision, resources, funding acquisition, writing – review and editing.

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Ethics Statement

The experiments reported in the present study have been approved by the Ethics Committee of the University of Milano-Bicocca (protocol numbers: 664-2022 and 881-2024).

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available on Open Science Framework (OSF) at the following link: https://osf.io/x8v5e.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** Mean ± standard error of raw MEP values (in mV) recorded in the different experimental conditions.