







## As apparent as real: alpha and beta bands desynchronization unveils apparent motion perception dynamics

Marcella Romeo <sup>a,b</sup> , Francesca Genovese <sup>a</sup> , Monica Betta <sup>b</sup> , Alice Rossi Sebastiano <sup>a</sup>,  
Lorenzo Teresi <sup>b</sup> , Nicoletta Scanferlato <sup>a</sup>, Corrado Sinigaglia <sup>c</sup> , Emiliano Ricciardi <sup>b</sup>,  
Francesca Garbarini <sup>a,d,\*</sup> 

<sup>a</sup> Manibus Lab, Department of Psychology, University of Turin, Turin, Italy

<sup>b</sup> MoMiLab, IMT School for Advanced Studies Lucca, Lucca, Italy

<sup>c</sup> CIA Unit, PHILAB, Department of Philosophy, University of Milan, Milan, Italy

<sup>d</sup> NIT, Neuroscience Institute of Turin, Turin, Italy

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### ABSTRACT

It is well-known that real motion observation engages sensorimotor processes, so that when biological motion is presented, greater activation of the sensorimotor systems is measured in the observer compared to when non-biological motion is displayed. However, it remains unclear whether apparent motion, perceived from sequences of static images, relies on a similar neural mechanism. A typical blueprint of human action observation is illustrated by the electrophysiological recording of mu rhythm desynchronization, i.e., a power drop in alpha and beta frequency bands over sensorimotor cortices. In this study, by exploiting electroencephalography, we investigated whether apparent motion induces mu rhythm desynchronization when biological (but not non-biological) agents are observed, as usually recorded during real motion observation. Participants observed apparent rotations performed by biological (human hands) or non-biological (pseudo-hands) agents and reported the perceived direction of such rotations. In line with previous findings, our psychophysical results confirmed that only biological stimuli showed a preferential perceived direction of the rotation, compatible with biomechanical constraints that rule real movements. Electrophysiological data revealed significant mu desynchronization, with significantly greater drop for biological than non-biological agents. Taken together, our results suggest that apparent and real motion, when biological agents are involved, induce a similar motor resonance, as if the (real or apparent) action were performed rather than merely observed.

### 1. Introduction

The perception of motion, either biological or non-biological, is fundamental to interpreting the world around us. Understanding the motion dynamics of both humans and objects allows us to predict action consequences and to interact with the environment efficiently. Despite individuals usually observe actual actions, the human brain can recognize a motion even when embedded in a sequence of static images. Specifically, we can perceive a motion not only from real movement observation but also when it is suggested by the presentation of two stationary visual stimuli in alternating sequence [i.e., apparent motion (Shiffrar and Freyd, 1990, 1993; Yantis and Nakama, 1998)]. Indeed, an apparent motion occurs when a sequence of static images separated in time and space are perceived as a single moving stimulus.

Despite apparent motion perception can be elicited by both non-biological (e.g., points Yantis and Nakama, 1998) and biological images (e.g., human effectors Shiffrar and Freyd, 1990, 1993), psychophysical studies previously showed that they are constrained by different rules. While non-biological apparent motion is usually regulated by physical and geometrical rules, such as that of the minimum distance (Liu and Lourenco, 2021), when apparent motion regards human effectors, its perception is constrained by the biologically plausible range of movement, rendering it impossible to perceive a movement that does not belong to the observer's motor repertoire (Funk et al., 2005; Parmigiani et al., 2025; Shiffrar and Freyd, 1990, 1993). This evidence suggests a specific contribution of body knowledge and the possible role of sensorimotor processes in shaping the perception of biological apparent motion.

\* Corresponding author at: Department of Psychology, University of Turin, Via Verdi 10, Turin, 10124, Italy.

E-mail address: [francesca.garbarini@unito.it](mailto:francesca.garbarini@unito.it) (F. Garbarini).

Similarly, a growing body of evidence highlights that observation of human actions can engage sensorimotor simulation [motor resonance (Barchiesi and Cattaneo, 2013, 2015; Gallese and Goldman, 1998; Rizzolatti et al., 2001; Rizzolatti and Craighero, 2004)] by recruiting the same sensorimotor network as if the action were performed rather than merely observed. This mechanism, referred to as the mirror mechanism (Bonini, 2017; Rizzolatti and Craighero, 2004; Rizzolatti and Fogassi, 2014; Rizzolatti and Sinigaglia, 2010a), is particularly effective when observing the actions of others that fall within the observer's motor repertoire (Avenanti et al., 2013b; Calvo-Merino et al., 2005, 2006). Accordingly, when biological motion is presented, greater activation of the sensorimotor systems is measured in the observer compared to when non-biological motion is displayed (Buccino et al., 2004; Crescentini et al., 2011; Perry and Bentin, 2009). A typical blueprint of this motor resonance is illustrated by the electrophysiological recording of mu rhythm desynchronization, i.e., a power drop in alpha and beta frequency bands over sensorimotor cortices during action observation (Avanzini et al., 2012; Cochin et al., 1998, 1999). Consistently, it has been shown that biological motion elicits greater desynchronization of the mu rhythm than non-biological one (Altschuler et al., 2007; Oberman et al., 2005; Pfurtscheller and Scherer, 2007; Ulloa and Pineda, 2007).

Despite it is well-established that real motion observation is reflected in the above-mentioned mu rhythm desynchronization, whether a similar neural mechanism also accounts for apparent motion perception is yet to be demonstrated. Hence, in the present study, first we aimed to investigate whether apparent motion perception elicited mu rhythm desynchronization (i.e., alpha and beta bands power drop), as previously shown for real movement observation. Second, we tackled the hypothesis that, as already demonstrated for real motion, apparent motion relies on sensorimotor mu rhythm desynchronization when biological (but not non-biological) agents are observed, thus showing a specific modulation of mu rhythm reactivity depending on the nature of the stimuli.

Capitalizing on a previously devised task (Parmigiani et al., 2025), electrophysiological activity was recorded while participants observed a series of 180° apparent rotations performed by biological (i.e., human hands) or non-biological (i.e., pseudo-hands) agents, while psychophysical responses were collected (i.e., perceived direction of the rotation: clockwise or counterclockwise). At the psychophysical level, in line with previous studies (Funk et al., 2005; Parmigiani et al., 2025; Shiffrar and Freyd, 1990, 1993), we expected perceptual judgments to be ruled by biomechanical constraints only for human apparent motion. At the electrophysiological level, if apparent motion relied on similar mechanisms as those subserving real motion (Chatterjee and Mennemeier, 1996; G. Orgs et al., 2016; Parmigiani et al., 2025; Shiffrar and Freyd, 1990, 1993; Stevens et al., 2000), the former should show greater alpha and beta bands desynchronization for biological than non-biological movements over sensorimotor areas. On the contrary, if apparent motion resulted from a mere visual process (Muckli et al., 2002; Wibrall et al., 2009), no differential mu desynchronization should emerge in the sensorimotor areas, but a similar power drop between biological and non-biological motions should be observed over visual areas.

## 2. Materials and methods

### 2.1. Participants

Nineteen healthy subjects (age in years:  $26.15 \pm 3.28$ ; level of education:  $17.45 \pm 0.60$ ; female: 13) participated in the study. Nonetheless, due to technical issues during data collection, one subject was excluded from the study, resulting in a total sample size of eighteen subjects (age in years:  $26 \pm 3.4$ ; level of education:  $17.39 \pm 0.61$ ; female: 12). All participants were right-handed and had normal or corrected-to-normal sight. Before the experiment, participants signed the written informed consent, which conformed to standards required by the Declaration of

Helsinki and was approved by the Ethics Committee of the University of Torino (prot. n. 0290534, 07/06/2023).

The sample size was estimated on pilot behavioral data acquired on a sample of 10 subjects applying the method reported by Anderson et al. (2017) that returns the necessary sample size, correcting for publication bias or uncertainty. The effect of interest for the behavioral analysis is the interaction between stimulus and rotations. Thus, we employed the F value of such interaction for the a priori power analysis. The estimated sample size was 19 subjects (F value of the interaction=4.09;  $N = 10$ ; alpha planned=0.05; assurance=0.6, power=0.90, step=0.001). It is worth noticing that, despite sample size estimation was performed on pilot behavioral data, the resulting numerosity is coherent with those employed in previous electrophysiological data addressing the time-frequency dynamics of mu rhythm desynchronization during action observation task [i.e., real motion presentation; (Angelini et al., 2018; Avanzini et al., 2012; Duann and Chiou, 2016; Marshall et al., 2009; Thomas et al., 2018; Urgen et al., 2013)]

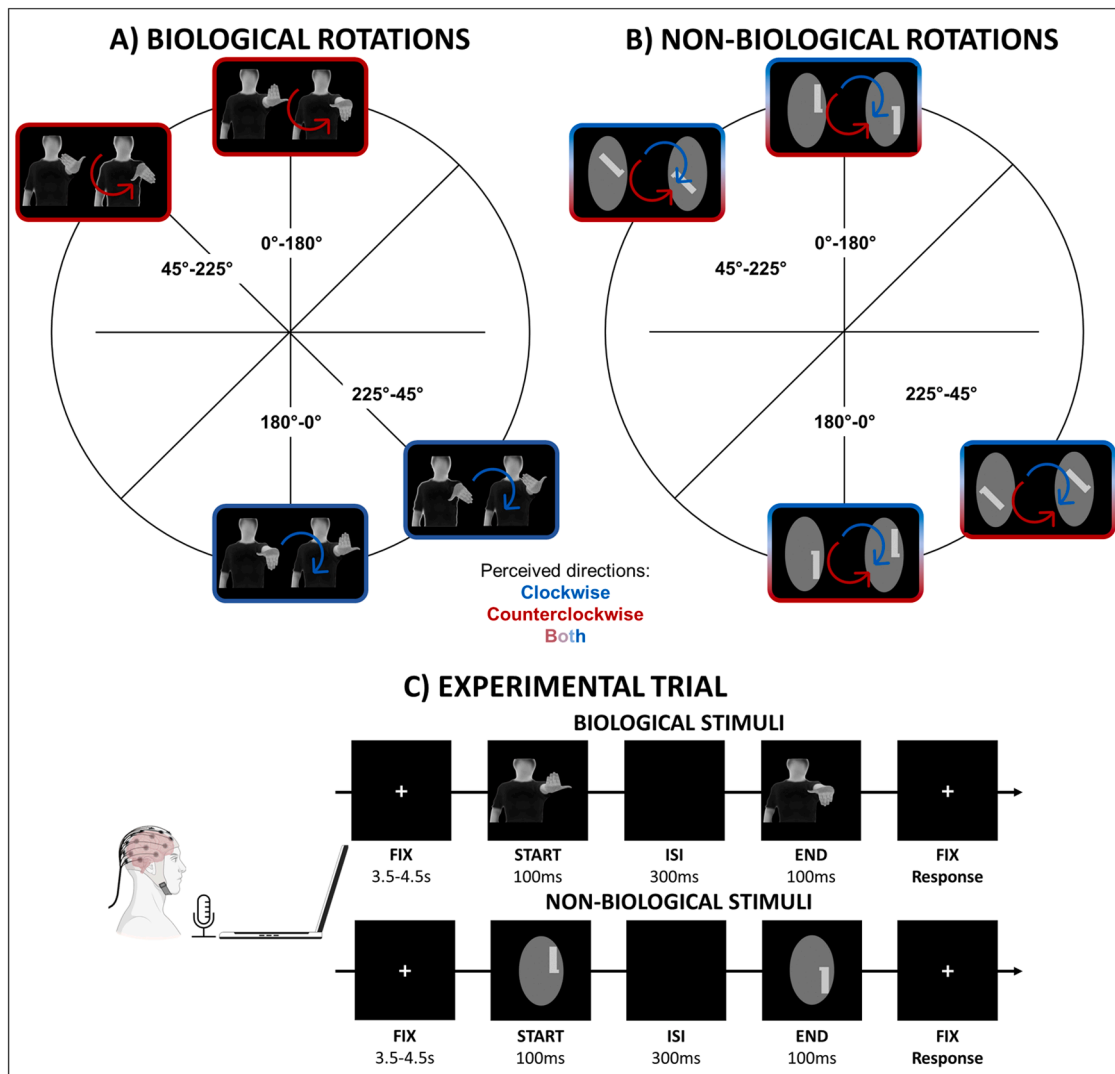
### 2.2. Experimental procedure

Participants underwent an apparent motion task, in which they observed both human (biological condition) and pseudo- (non-biological condition) hands apparent rotations (Fig. 1, panel A and B) displayed on a laptop screen. They were comfortably seated in a dimmed-lit room in front of the laptop, at a distance of 55 cm from the screen, with their arms resting on their lap, wearing the EEG cap. They were instructed to look at the fixation cross at the center of the screen and, on each apparent motion trial, to verbally report whether they perceived a clockwise or a counterclockwise rotation by saying "A" for "antiorario" (i.e., the Italian translation of counterclockwise) or "O" for "orario" (i.e., the Italian translation of clockwise). It is worth noticing that individuals were required to provide a rotation judgement in a force-choice task, requiring them to choose between one of the two possible responses. Participants were asked to be as precise as possible when making their rotation judgments, with no time constraint; therefore, response times data cannot be meaningfully analyzed. The experimental session comprised four 6-minute stimulation blocks, each composed of 48 trials, 6 per each of the four rotations, thus resulting in a total of 24 trials per rotation (Rossi Sebastiano et al., 2022) for both biological and non-biological conditions. Each trial comprised an apparent motion lasting 500 ms in total, and a response slide (Fig. 1, panel C). The inter-trial interval was jittered between 3.5 s and 4.5 s to avoid anticipation effects.

### 2.3. Stimuli

Visual stimuli consisted of images depicting either biological or non-biological agents. In the biological condition, stimuli represented the picture of a gender-neutral human being, displayed in third-person perspective, with their left hand in the foreground that could be oriented at 0°, 45°, 180°, 225°, according to the start and end point of the rotations. In the non-biological conditions, stimuli showed a grey oval over which another stylized shape (pseudo-hand) stood out, mimicking the L-shape formed by the hand and thumb, lateralized to the left as in the biological stimuli. The apparent motion was elicited by the presentation of two pictures (S1 and S2) that showed the start (S1) and the endpoint (S2) of the rotation, giving rise to four possible rotations, each of 180°, as follows: 0°–180°, 45°–225°, 180°–0°, 225°–45°. Each S1 and S2 lasted 100 ms and were separated by a 300 ms inter-stimulus interval as in previous studies (Funk et al., 2005; Parmigiani et al., 2025; Shiffrar and Freyd, 1990), giving rise to a 500 ms lasting motion. (see Fig. 1 panel B for a representation of the rotations).

The four rotations were chosen among those employed by Parmigiani and collaborators (Parmigiani et al., 2025). Specifically, we chose those rotations that, in the apparent motion framework, are preferentially perceived as clockwise or counter-clockwise due to the effect of



**Fig. 1. A-B)** Representation of the four biological and non-biological apparent rotations with start- ( $0^\circ$ ;  $45^\circ$ ;  $180^\circ$ ;  $225^\circ$ ) and end-points ( $180^\circ$ ;  $225^\circ$ ;  $0^\circ$ ;  $45^\circ$ ). Blue arrows indicate when a clockwise rotation is mechanically possible; red arrows indicate when a counterclockwise rotation is mechanically possible. In non-biological rotations, both arrows indicate that for pseudo-hand no biomechanical plausibility constrains the rotation. **C)** Example of an experimental trial of apparent motion with biological and non-biological stimuli. Each trial began with a fixation cross (duration jittered between 3.5 and 4.5 s), followed by the start point of the apparent motion (100 ms), the interstimulus interval (300 ms) and the end point of the apparent motion (100 ms). The trial ended with a fixation cross, and the subject verbally reported the perceived direction of the rotation (clockwise: "O"; counter-clockwise: "A").

biomechanical constraints that rule wrist rotations. Note that, when considering human-like apparent motion,  $0^\circ$ – $180^\circ$  and  $45^\circ$ – $225^\circ$  rotations are preferentially perceived as counter-clockwise, while  $180^\circ$ – $0^\circ$  and  $225^\circ$ – $45^\circ$  are primarily judged as clockwise.

Finally, stimuli were presented using E-prime V 3.0 software (Psychology Software Tools Inc., Pittsburgh, PA, USA) on a 15-inch Dell Latitude laptop.

#### 2.4. Behavioral analysis

Rotation judgments were coded by assigning a value of 1 for clockwise and a value of 2 for counter-clockwise perceived rotations and were analyzed through a generalized linear mixed model by means of Jamovi software version 2.3.28. The model comprised Stimulus (Biological; Non-Biological) and Rotation ( $0^\circ$ – $180^\circ$ ;  $45^\circ$ – $225^\circ$ ;  $180^\circ$ – $0^\circ$ ;  $225^\circ$ – $45^\circ$ ) as within-subject factors, including subjects as random intercept variable. Multiple comparisons were adjusted with the Holm post-hoc test.

#### 2.5. EEG acquisition, preprocessing, and analysis

EEG data were acquired employing 64 Ag-AgCl electrodes positioned on the scalp according to the International 10–20 system and referenced to Cz. The cap position was maintained stable by aligning it with the skull landmarks (i.e., nasion, ionion, periauricular points, and vertex). Electrode impedances were kept below 5 k $\Omega$ . The electro-oculogram (EOG) was recorded from a single electrode built-in with the cap and placed over the left lower eyelid. The signal was amplified and digitized at a sampling rate of 1024 Hz with the eego™ sports Ant Neuro recording system.

##### 2.5.1. EEG data preprocessing

EEG data preprocessing was performed with MATLAB (The MathWorks, Inc., Natick, Massachusetts, United States) and EEGLAB toolbox (Delorme and Makeig, 2004). Continuous data were high-pass (1 Hz) and low-pass (35 Hz) filtered and then segmented in single-trial epochs lasting 2.7 s. Each epoch was composed of 1.5 s of an inter-trial interval with a fixation cross, 0.5 s of stimulus presentation, and 0.7 s of

post-stimulus (see Angelini et al., 2018 for a similar approach). Epochs were merged according to stimulus kind, thus obtaining biological and non-biological conditions, each composed of 96 trials. Artifacts epochs were automatically detected and removed by applying the `pop_jointprob` EEGLAB function, which detects for each channel those trials whose probability exceeds 4 standard deviations from the mean of the other trials. For each condition, no more than 10 % of trials were marked as artifactual and removed. Then, noisy channels were detected (excluding electrooculogram) by combining probability, kurtosis and spectrum method of `pop_rejchan` EEGLAB function, again with 4 standard deviations as a cut-off. Specifically, the three noise identification methods implemented in the EEGLAB function detect noisy channels based on the standard deviation of the amplitude: those channels whose standard deviation exceeds four times the mean standard deviation of the other channels are considered artifactual and therefore marked for the exclusion (Delorme and Martin, 2021).

An Independent Component Analysis [ICA; (Galigani et al., 2021; Galigani et al., 2025a; Galigani et al., 2025b)] was performed on good channels only (also excluding the electrooculogram) to detect and remove artifactual activity. Since the aim in conducting the ICA was data cleaning, we opted to perform such analysis on good channels only, thus decomposing the signal in components already free from channel noise. Components were then labeled using `ICLabels` EEGLAB function, which computes the probability of each component to be composed by the brain, eye movements, cardiac, muscle, and electrical noise activity. Artifactual components, meaning those components whose first label was not either at least 25 % brain or in which the sum of the percentage of the labels was greater than the percentage of the brain one, were automatically rejected. Finally, noisy channels were interpolated with the nearest channels.

Each single-trial epoch was then time-frequency transformed for each channel applying a Morlet Wavelet convolution with a number of cycles that increased linearly with frequency (from 4 cycles at the lowest to 15.36 cycles at the highest frequency) in a frequency range from 5 to 32 Hz (frequency resolution 0.5 Hz) (Angelini et al., 2018). Each single-trial time-frequency transform was normalized with the full-epoch-length normalization method to minimize sensitivity to outlier and noisy trials. Then, data were expressed as an absolute ratio dividing averaged trials by averaged baseline period (−0.5 s to −0.1 s) (Angelini et al., 2018; Grandchamp and Delorme, 2011). In the end, absolute power values were transformed into decibel (dB). Thus, negative power values indicate a desynchronization, and positive power values indicate synchronization.

### 2.5.2. EEG data analysis

For each subject and each condition, mean power values in dB were extracted in alpha (8–13 Hz) and beta (15–20 Hz) frequency bands over sensorimotor and visual clusters (Angelini et al., 2018; Avanzini et al., 2012; Quandt et al., 2012; Shackman et al., 2010; Urgen et al., 2013). Specifically, according to previous studies (Angelini et al., 2018; Avanzini et al., 2012; Marshall et al., 2011; Muthukumaraswamy and Johnson, 2004; Quandt et al., 2012) and based on the nature of the task, we chose left and right fronto-central clusters (right FC: F2, F4, FC2, FC4; left FC: F1, F3, FC1, FC3), covering left and right sensorimotor areas, and left and right parieto-occipital clusters (right: PO4, PO6, PO8, O2; left: PO3; PO5; PO7; O1), corresponding to visual areas. Clusters were separated for left and right brain sides based on an a priori hypothesis on the hemispheric lateralization of action observation processing. It is important to point out that visual processes usually involve oscillatory activity in the alpha band (Chen et al., 2023; Xie et al., 2020), while sensorimotor processes are primarily represented in the beta band (Baker, 2007; Neuper and Pfurtscheller, 2001). Hence, grounding on this evidence and on previous studies in which mu rhythm was decomposed into alpha and beta frequency bands (Angelini et al., 2018; Avanzini et al., 2012), in the present study the activity elicited in each band was separately analyzed to reveal the specific contribution of the

desynchronization in the visual and sensorimotor natural frequencies in apparent motion perception.

First of all, the recording corresponding to each condition was divided into a pre-stimulus time-window (namely, the baseline: from −500 to −100 ms) and three post-stimulus time-windows, dividing the 500 ms of stimulus presentation in 166 ms segments, corresponding to early (0–166 ms), middle (167–333 ms) and late (334–500 ms) movement stages.

Second, we performed paired *t*-tests to check for significant desynchronization. Thus, we averaged power values across conditions and side of clusters, and, separately for alpha and beta frequency bands, and for fronto-central and parieto-occipital clusters, we compared each time-window to the baseline period (Angelini et al., 2018). Paired *t*-test were Bonferroni corrected dividing the *p* value ( $p = 0.05$ ) by the total of six multiple comparisons, thus resulting in a significance threshold of  $p = 0.0083$ .

Third, power values were entered in  $2 \times 3$  repeated-measure ANOVAs with Stimulus (biological; non-biological) and Time-window (early; middle; late movement stages) as within-subject factors, separately for right and left fronto-central and parieto-occipital clusters and for alpha and beta frequency bands. Bonferroni post-hoc test was applied to account for multiple comparisons.

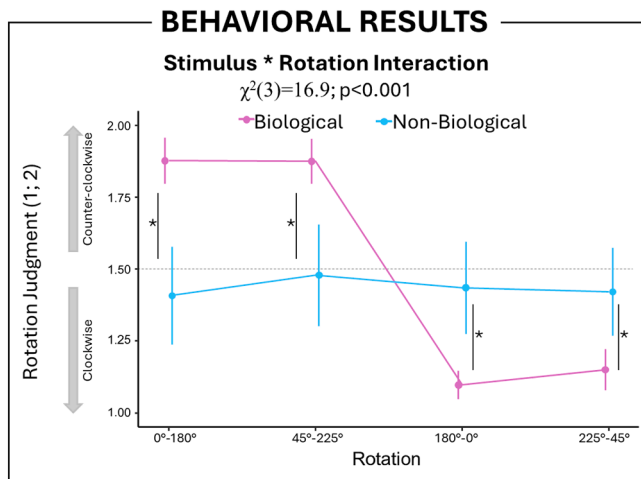
Finally, we performed an exploratory analysis to test the specificity of the effects observed in each cluster, as shown by the separate analyses. To do so, we adopted a multivariate approach allowing to compare all the four clusters in a single model. Hence, we performed a repeated-measures MANOVA with STIMULUS (2 levels: biological; non-biological) as within-subjects factor, while the four clusters (i.e., beta left fronto-central; beta right fronto-central; alpha left parieto-occipital; alpha right parieto-occipital) were entered as dependent variables. Since the main analysis demonstrated no significant interaction between time-windows and stimuli, in this exploratory analysis we averaged dB Power over time according to the stimulus type, thus reducing the factors of the analysis.

Statistical analyses for EEG data were performed by means of Jamovi Software (Version 2.3.28) and IBM SPSS Statistics.

## 3. Results

### 3.1. Behavioral results

The mixed model performed on the rotation judgment converged with all the random intercepts. We found a significant Stimulus\*Rotation interaction ( $\chi^2(3)=16.9$ ;  $p < 0.001$ ), with differences among rotations being significantly greater in biological than non-biological stimuli (Fig. 2). By further exploring the interaction with a *post hoc* test, we found that, in biological stimuli,  $0^\circ$ – $180^\circ$  and  $45^\circ$ – $225^\circ$  rotations were similarly judged ( $p > 0.99$ ) as counter-clockwise, but they significantly differed from  $180^\circ$ – $0^\circ$  and  $225^\circ$ – $45^\circ$  rotations ( $0^\circ$ – $180^\circ$  vs  $180^\circ$ – $0^\circ$   $p < 0.001$ ;  $0^\circ$ – $180^\circ$  vs  $225^\circ$ – $45^\circ$   $p < 0.001$ ;  $45^\circ$ – $225^\circ$  vs  $180^\circ$ – $0^\circ$   $p < 0.001$ ;  $45^\circ$ – $225^\circ$  vs  $225^\circ$ – $45^\circ$   $p < 0.001$ ), being  $180^\circ$ – $0^\circ$  and  $225^\circ$ – $45^\circ$  rotations similarly perceived ( $p > 0.99$ ) as clockwise. On the contrary no difference emerged when comparing non-biological stimuli across rotations ( $0^\circ$ – $180^\circ$  vs  $45^\circ$ – $225^\circ$   $p > 0.99$ ;  $0^\circ$ – $180^\circ$  vs  $180^\circ$ – $0^\circ$   $p > 0.99$ ;  $0^\circ$ – $180^\circ$  vs  $225^\circ$ – $45^\circ$   $p > 0.99$ ;  $45^\circ$ – $225^\circ$  vs  $180^\circ$ – $0^\circ$   $p > 0.99$ ;  $45^\circ$ – $225^\circ$  vs  $225^\circ$ – $45^\circ$   $p > 0.99$ ;  $180^\circ$ – $0^\circ$  vs  $225^\circ$ – $45^\circ$   $p > 0.99$ ). Further, coherently with the main effect of Stimulus, non-biological differed from biological stimuli in all four rotations ( $p_s$  always  $< 0.05$ ). To sum up, our psychophysical results confirmed that only biological stimuli showed a preferential perceived direction of the rotation compatible with biomechanical constraints that rule real movements, in line with previous studies (Parmigiani et al., 2025; Shiffrar and Freyd, 1990, 1993).



**Fig. 2.** Behavioral results with the Stimulus\*Rotation interaction. The rotation judgment (1=clockwise; 2=counter-clockwise) is reported on the y-axis. The four rotations are reported on the x-axis. Error bars represent the 95 % Confidence Interval. The dotted line at 1.50 represents the chance level at which participants perceived clockwise or counter-clockwise rotation.

**3.2. EEG results**

**3.2.1. Parieto-occipital clusters**

We found significant power desynchronization for the alpha frequency band in the late (334–500 ms) movement stage ( $t_{17}=-3.59; p = 0.001$ ). For the beta frequency band, we found significant power desynchronization in the middle (167–333 ms) ( $t_{17}=-8.35; p = 0.000001$ ) and late (334–500 ms) ( $t_{17}=-7.40; p = 0.000005$ ) movement stages (Fig. 3, panel A).

The  $2 \times 3$  repeated measures ANOVAs with Stimulus (biological; non-biological) and Time-window (early; middle; late movement stages) were performed in alpha and beta frequency bands over left and right parieto-occipital clusters with mean power values (dB) as the dependent variable.

For both frequency bands and clusters, we found significant main effects of Time-window (*Alpha band*: left cluster  $F_{2,34}=42.84, p < 0.001$ , partial  $\eta^2=0.72$ ; right cluster:  $F_{2,34}=41.22, p < 0.001$ , partial  $\eta^2=0.71$ . *Beta band*: left cluster  $F_{2,34}=53.17, p < 0.001$ , partial  $\eta^2=0.76$ ; right cluster:  $F_{2,34}=34.58, p < 0.001$ , partial  $\eta^2=0.67$ ), meaning that the power desynchronization increased gradually as the movements unfolded and reached their final stages (Fig. 4, panels A and B).

Interestingly, we found a significant main effect of Stimulus ( $F_{1,17}=5.49; p = 0.032$ ; partial  $\eta^2=0.24$ ) in the left cluster, only in the alpha band, with greater power drop for non-biological than biological stimuli (Fig. 4, panel C). Note that the left cluster lateralization of such an effect is coherent with the spatial localization of the human and pseudo-hands displayed primarily on the right portion of the laptop screen.

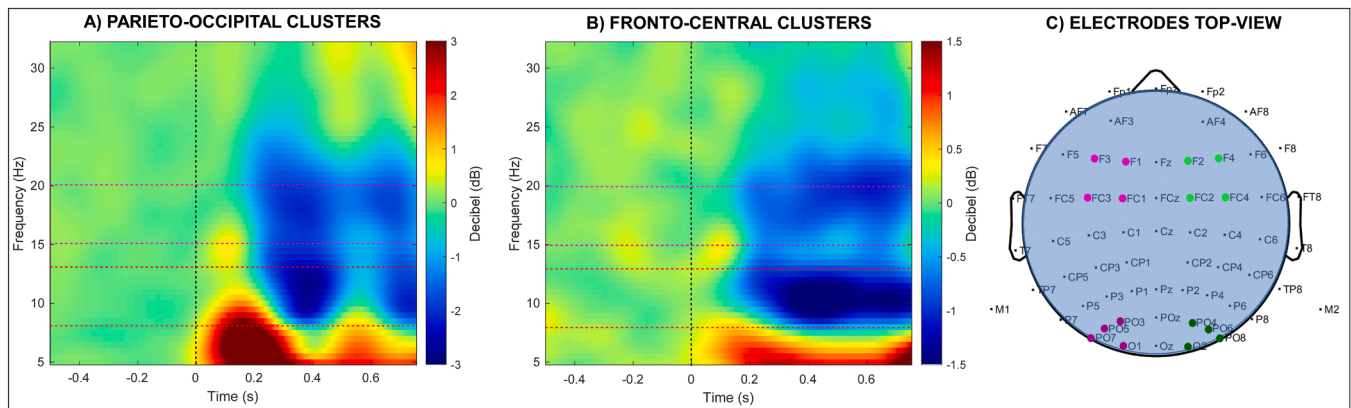
Altogether, these results highlight significant alpha and beta power desynchronization over visual areas, which increases as the apparent movement unfolds. Crucially, they also suggest greater alpha band desynchronization for non-biological stimuli in visual areas, especially in the hemisphere contralateral to the hemisphere primarily occupied by the observed stimulus.

**3.2.2. Fronto-central clusters**

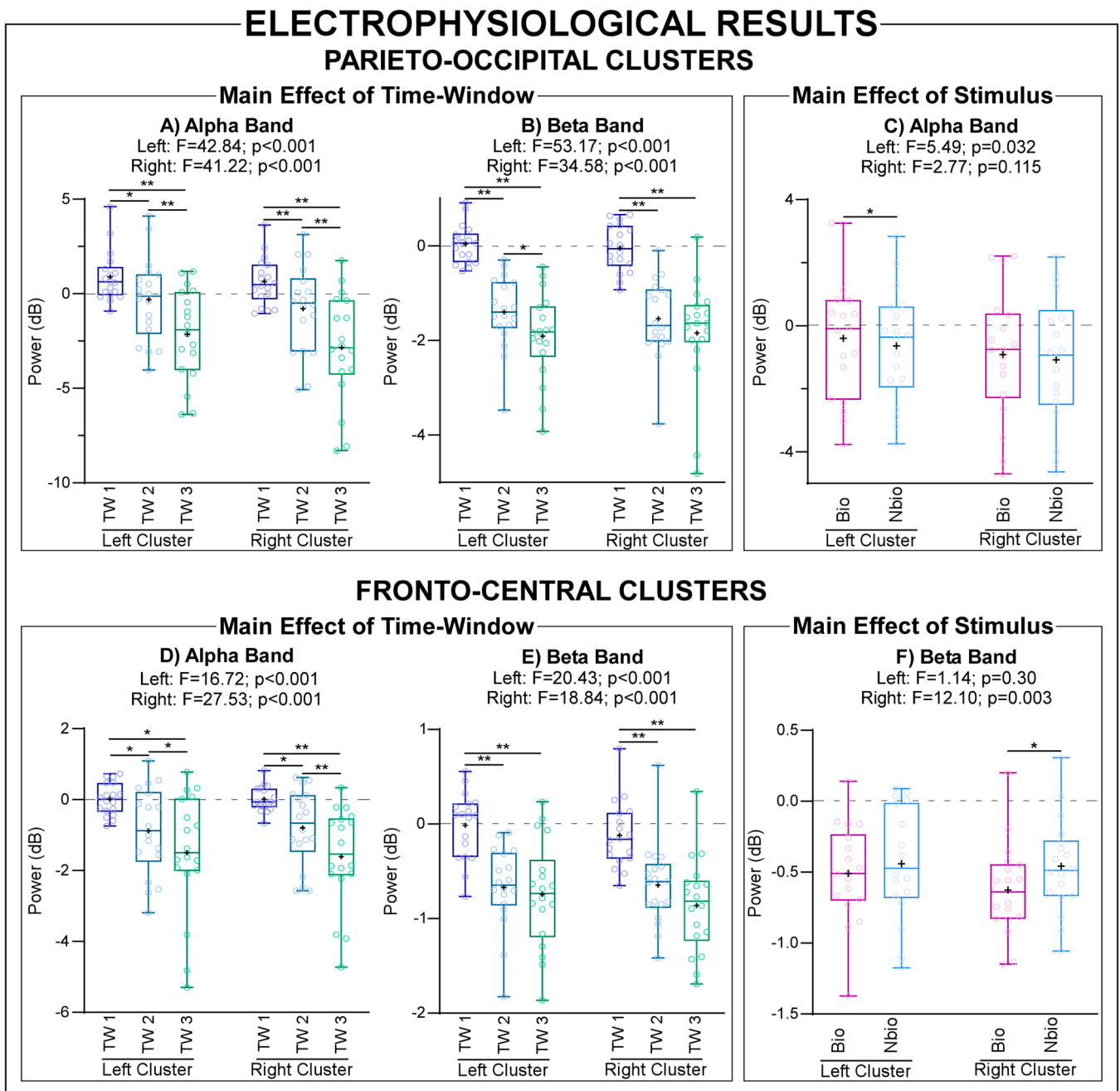
For alpha and beta frequency bands, we found significant power desynchronization in the middle (167–333 ms) (*Alpha band*:  $t_{17}=-2.92; p = 0.0048$ ; *Beta band*:  $t_{17}=-6.98; p = 0.000001$ ) and late (334–500 ms) (*Alpha band*:  $t_{17}=-4.02; p = 0.0004$ ; *Beta band*:  $t_{17}=-6.99; p = 0.000001$ ) movement stages. (Fig. 3, panel B).

The  $2 \times 3$  repeated measures ANOVAs with Stimulus (biological; non-biological) and Time-window (early; middle; late movement stages) were performed in alpha and beta frequency bands over left and right fronto-central clusters with mean power values (dB) as the dependent variable.

For both frequency bands and clusters, we found significant main effects of Time-window (*Alpha band*: left cluster  $F_{2,34}=16.72, p < 0.001$ , partial  $\eta^2=0.50$ ; right cluster:  $F_{2,34}=27.53, p < 0.001$ , partial  $\eta^2=0.62$ . *Beta band*: left cluster  $F_{2,34}=20.43, p < 0.001$ , partial  $\eta^2=0.55$ ; right cluster:  $F_{2,34}=18.84, p < 0.001$ , partial  $\eta^2=0.53$ ), meaning that the power desynchronization increased gradually as the movements unfolded and reached their final stages (Fig. 4, panels D and E). Crucially, we found a significant main effect of Stimulus ( $F_{1,17}=12.10; p = 0.003$ ; partial  $\eta^2=0.42$ ) in the right cluster only in the beta band, showing a diametrical effect to that observed over visual areas, namely with significantly greater power drop for biological than non-biological stimuli (Fig. 4, panel F). Further, we also found a significant Time-Window\*Stimulus interaction ( $F_{2,34}=6.03; p = 0.006$ , partial  $\eta^2=0.26$ ) again in the right cluster only in beta band (Fig. 4, panel G). The Bonferroni post-hoc test employed on such interaction described that the difference between biological and non-biological stimuli was significant in the early ( $p = 0.031$ ) and the middle ( $p = 0.048$ ) movement stages, while it did not reach the full significance in the late movement stage ( $p = 0.054$ ), even if the very same pattern of stimulus difference was observed. Importantly, in the beta band, we observed significant modulations of brain activity only in the right (i.e., the contralateral



**Fig. 3.** Averaged power ratio (dB), averaged across all experimental conditions and right and left parieto-occipital (A) and fronto-central (B) electrodes. The onset of movements is at 0 s. Frequency bands are highlighted by horizontal dotted lines: red lines delimit alpha band and pink lines delimit beta band. Electrodes top-view are represented in panel C: left fronto-central cluster in pink; right fronto-central cluster in green; left parieto-occipital cluster in dark pink; right parieto-occipital cluster in dark green.



**Fig. 4.** Results of the repeated-measures ANOVAs performed on left and right parieto-occipital and fronto-central clusters in alpha and beta frequency bands. Panels A and B show the main effects of Time-Window respectively for alpha and beta bands in the parieto-occipital clusters. Panels C report the main effect of stimulus in alpha band for the parieto-occipital clusters. Panels D and E report the main effects of Time-Window in alpha and beta for the fronto-central clusters. Panel F reports the main effect of stimulus and panel G the Time-Window\*Stimulus interaction in beta band for the fronto-central clusters. Mean power values in dB are reported in the boxplots, in which whiskers represent the minimum and the maximum value, the limits of the box represent the first and the third quartile, the median is depicted by the line that divides the box into two parts, the cross represents the mean value, and the circles represent single-subjects' values. \* $p < 0.05$ ; \*\* $p < 0.001$ .

hemisphere to the seen left hand), and not in the left cluster (Main effect of Stimulus:  $F_{1,17}=1.14$ ,  $p = 0.30$ , partial  $\eta^2=0.06$ ; Time-Window\*Stimulus interaction:  $F_{2,34}=0.23$ ,  $p = 0.79$ , partial  $\eta^2=0.01$ ).

In sum, these results highlight significant alpha and beta power desynchronization over sensorimotor areas, which increases as the apparent movement unfolds. Crucially, they also suggest greater beta band desynchronization for biological stimuli in sensorimotor areas contralateral to the displayed body effector, coherently with a motor resonance mechanism and the related sensorimotor simulation.

See Supplementary Materials for MANOVA's results that, by testing the four clusters identified in the separate analyses in a single model,

confirmed the specificity of the observed effects (i.e., preferential coding for biological than non-biological stimuli over the contralateral sensorimotor cluster and the opposite for the ipsilateral parieto-occipital cluster, with greater desynchronization for non-biological than biological agent/object).

#### 4. Discussion

The present study investigated whether apparent motion relies on neural mechanisms similar to those previously revealed during the observation of real motion, thus inducing sensorimotor alpha and beta

bands desynchronization when biological (but not non-biological) agents are observed. To this aim, we exploited an action observation paradigm in which we presented visual stimuli depicting apparent motions of either biological (i.e., human hands) or non-biological (i.e., pseudo-hands) agents. During EEG recording, participants observed sequences of static images of human hands and pseudo-hands rotations and had to judge the perceived direction of such apparent motions. Our behavioral results confirm that only biological stimuli showed a preferential perceived direction of the rotation, compatible with biomechanical constraints that rule real movements. As an important new finding, our electrophysiological data reveal that apparent motion perception induces significant mu desynchronization, with greater drop for biological than non-biological agents, as usually recorded during real motion observation.

Previous behavioural evidence (Funk et al., 2005; Orgs et al., 2011, 2013, 2016; Parmigiani et al., 2025; Shiffrar and Freyd, 1990, 1993) showed that biomechanical constraints rule human-like apparent motion. In line with this literature, we found that apparent movements performed by a human hand were perceived as clockwise or counter-clockwise accordingly to the biologically plausible wrist rotations. This suggests that human-like apparent motion is shaped by the constraints embedded in our body knowledge that govern real movement execution. Accordingly, when apparent motions were performed by non-biological agents, the biomechanical constraints did not have a role in driving the perceived directions of the rotations. When focusing on biomechanical constraints in apparent motion perception, a compelling parallel can be drawn with those constraints typically involved in tasks requiring engagement in motor imagery mechanisms, such as laterality judgement tasks (Conson et al., 2012; Jongasma et al., 2013). However, it is important to emphasize that, as previously demonstrated (Mibu et al., 2020), individuals can rely on either motor (i.e., motor imagery) or non-motor strategies in tasks in which biomechanical constraints are expected to modulate participants' responses. This latest finding points out that behavioral evidence alone is not sufficient to demonstrate that participants resorted to motor representation. For this reason, in our study, to disentangle between visual and motor processes, we combined a physiological measure to the behavioral one. In our case, however, the preferential perception of one direction over the other occurring only in the biological condition still suggests the use of different strategies for biological and non-biological motion. Finally, future studies could adopt experimental paradigms in which participants are required to provide speeded responses to address whether similar perceptual rotation approach is used with biological and non-biological agents/objects, as previously shown for the laterality judgement task (Mibu et al., 2020).

To the best of our knowledge, no previous studies investigated the electrophysiological dynamics of apparent motion perception, specifically addressing the presence of mu rhythm desynchronization. Our new electrophysiological findings showed that apparent movements elicited a significant alpha and beta bands desynchronization, which also increased in the middle and late movement stages. Importantly, we found that this desynchronization increased with the movements unfolding so that the late movement stage elicited the greater power drop. More crucially, we discovered a differential desynchronization according to the agent of the apparent motion (i.e., biological and non-biological) in both visual and sensorimotor clusters. Interestingly, the direction of such an effect was diametrical between the two.

Regarding the visual cluster, non-biological apparent rotations elicited a greater power desynchronization in the alpha band compared to the human rotations. Notably, such preference for non-biological apparent motion, although not expected, is consistent with previous studies highlighting greater activation in visual areas for object motion as compared to body motion observation (Handjaras et al., 2015; Kleinschmidt et al., 2002; Orgs et al., 2016). It is worth noticing that such differential power drop was specific for the hemisphere contralateral to the hemisphere primarily occupied by the visual stimulus, in

line with the recruitment of a mainly visual process.

Regarding the sensorimotor cluster, as expected, the apparent motion perception of human hands elicited overall a greater power drop in the beta band than pseudo-hands apparent rotations. Interestingly, such differential mu rhythm reactivity was specifically located in the right hemisphere, thus contralateral to the left hand presented in our study. Hence, the present electrophysiological findings point out that human-like apparent motion preferentially engages the contralateral sensorimotor network, which usually happens for actual actions. Indeed, this pattern resembles the typical motor resonance that indexes the activation of the mirror mechanism when observing and processing other people's actions (Fogassi et al., 2005; Gallese and Goldman, 1998; Perry and Bentin, 2009; Rizzolatti et al., 2001; Rizzolatti and Craighero, 2004; Rizzolatti and Fogassi, 2014; Rizzolatti and Sinigaglia, 2010a; G. 2016). This finding aligns with previous influential accounts showing the recruitment of a motor simulation mechanism during real movements observation (Fogassi et al., 2005; Gallese and Goldman, 1998; Perry and Bentin, 2009; Rizzolatti et al., 2001; Rizzolatti and Craighero, 2004; Rizzolatti and Fogassi, 2014; Rizzolatti and Sinigaglia, 2010a; G. 2016), and also extends them to the apparent motion perception, at least when it involves human body parts, as previously suggested by evidence deriving from the assessment of cortico-spinal excitability during apparent motion of tool-oriented hand actions (Gianelli et al., 2020).

Interestingly, our cluster-specific electrophysiological findings are in line with previous evidence of motor system engagement during the observation of implied actions (i.e., movements suggested by the presentation of static images). Indeed, an enhanced motor excitability related to the presentation of static images suggesting a biological movement has been extensively demonstrated exploiting both non-invasive brain stimulation alone (Avenanti et al., 2013a; Mattiassi et al., 2014; Mele et al., 2014; Urgesi et al., 2006, 2010) or combined with neuroimaging techniques (Proverbio et al., 2009; Urgesi et al., 2010). Altogether, these studies and ours, which employ different techniques yet pinpoint converging findings, seem to indicate a diametrical engagement of visual and sensorimotor networks depending on the type of stimulus (i.e., human vs. non-human).

In addition to an opposite preference between biological and non-biological stimuli, the results of the visual and sensorimotor clusters also differ in the involved frequency bands, namely the alpha and the beta bands, respectively. This differential result is in line with electrophysiological accounts showing that while visual processes mainly involves oscillatory activity in a frequency range compatible with the alpha band (Chen et al., 2023; Xie et al., 2020), the sensorimotor processes are primarily represented in the beta band (Baker, 2007), especially in its lower boundary (i.e., below 20 Hz) when it involves human hands processing (Neuper and Pfurtscheller, 2001).

Taken together, our behavioral and electrophysiological results showed that apparent motion can be assimilated to real motion, engaging both visual and sensorimotor processing. Thus, these findings may contribute to the ongoing debate regarding which networks support the processing of apparent motions. Specifically, some have hypothesized that apparent motion perception may rely solely on visual processes (Muckli et al., 2002; Wibral et al., 2009), as demonstrated by the activation of early and associative visual cortices during non-biological apparent motion tasks. On the other hand, other theories have proposed that sensorimotor mechanisms are also involved (Chatterjee and Menemeier, 1996; G. Orgs et al., 2016; Shiffrar and Freyd, 1990, 1993; Stevens et al., 2000), based on observations of sensorimotor cortices activation during the perception of biological apparent motion. By capitalizing on the systematic comparison between biological and non-biological apparent motion processing in visual and sensorimotor areas, we identified a preferential activation of both networks depending on the nature of the presented stimulus (i.e., non-biological; biological).

In sum, these findings align with the embodied cognition framework, which posits that cognitive processes, such as action understanding, are

grounded in the sensorimotor system (Gallese, 2007; Gallese and Sinigaglia, 2011; Rizzolatti and Sinigaglia, 2010b). Indeed, the ability to perceive actions from static cues, as pointed out in our and previous studies (Avenanti et al., 2013a; Parmigiani et al., 2025; Urgesi et al., 2006), supports the hypothesis that perceptual and motor systems do not merely react to external stimuli, but are intrinsically engaged in consolidating meanings and interpretations through embodied simulation. Particularly, the involvement of sensorimotor regions in processing biological apparent motion and implied actions supports the view that cognition is not dis-embodied but rather relies on the internal simulation of sensorimotor experiences (Rizzolatti and Sinigaglia, 2010b), thus suggesting a neural basis for understanding other's behaviors even from incomplete visual information. In this view, the results of the present study might extend embodied accounts of action understanding to the processing of apparent motion, wherein no physical movement is present, but the motion is instead inferred from static images.

## 5. Conclusions

In sum, in line with previous studies (Funk et al., 2005; Orgs et al., 2011, 2013, 2016; Parmigiani et al., 2025; Shiffrar and Freyd, 1990, 1993) we described that apparent motion of human limbs is perceptually judged according to the biomechanical constraints that typically rule human movements. Crucially, as an important new finding, our study showed that apparent motion, especially when human-like, is able to elicit sensorimotor mu rhythm desynchronization, considered as a blueprint of motor resonance during action observation. Interestingly, in the visual cluster a diametrical pattern was observed, with greater alpha band desynchronization for non-biological than biological apparent motion. In conclusion, we highlighted a neural mechanism subserving apparent motion perception comparable to that usually observed for real motion.

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## CRedit authorship contribution statement

**Marcella Romeo:** Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Francesca Genovese:** Writing – review & editing, Methodology, Investigation. **Monica Beta:** Writing – review & editing, Formal analysis, Data curation. **Alice Rossi Sebastiano:** Writing – original draft, Visualization, Conceptualization. **Lorenzo Teresi:** Writing – review & editing, Methodology. **Nicoletta Scanferlato:** Writing – review & editing, Methodology, Investigation. **Corrado Sinigaglia:** Writing – review & editing, Supervision, Conceptualization. **Emiliano Ricciardi:** Writing – review & editing, Supervision, Conceptualization. **Francesca Garbarini:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization.

## Declaration of competing interest

Authors declare no financial or personal competing interests.

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## Data availability

<https://data.mendeley.com/drafts/xs4zxfpm9> (Data will be available upon publication at this link:)

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