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How spontaneous brain activity encodes the observation of grasping movements

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ABSTRACT

Spontaneous brain activity forms correlated networks resembling task-evoked activation patterns, yet its functional relevance remains debated. The representational hypothesis suggests that resting-state networks (RSNs) encode frequent behaviors, but whether these representations are motor-based or cognitive is unclear. Here, we used fMRI to examine RSNs activity during the observation of reach-to-grasp movements with either regular (common) or perturbed (uncommon) kinematics. We found that the dorsal attention network (DAN) exhibited greater similarity between rest and task patterns for common movements, whereas sensory networks showed no significant effects. While DAN is classically associated with attention mechanisms, these results suggest that it may also contribute to tracking the location or motion of the hand. Furthermore, uncommon movements elicited stronger activation in parietal and premotor areas, likely reflecting adaptive updating of internal models. Our findings support the role of spontaneous brain activity in maintaining cognitive representations of frequent behaviors, optimizing motor planning and perception.

1. Introduction

When the brain lies at rest, cortical activity exhibits temporal correlation across distributed regions (Biswal et al., 1995; Fox and Raichle, 2007). These discrete spatiotemporal patterns of activity, or resting state networks (RSNs), are intrinsically generated by the brain and not tied to specific inputs or outputs. Since their seminal observation, resting state becomes an experimental condition for investigating the large-scale organization of the brain (Fox and Raichle, 2007). RSNs are closely associated with task-evoked networks. The first systematic investigation revealed a striking similarity between the spatiotemporal structure of spontaneous activity and the topography evoked by finger tapping in the primary somatomotor cortex (Biswal et al., 1995). Since then, RSNs have been consistently observed across a variety of controlled cognitive, sensory, and motor paradigms (Cole et al., 2014; Krienen et al., 2014; Smith et al., 2009; Tavor et al., 2016). However, the role of spontaneous brain activity is debated, with hypotheses ranging from its involvement in offline plasticity and homeostasis (Laumann and Snyder, 2021) to its role in encoding abstract, low-dimensional representations that summarize large amounts of information underlying ecological stimuli and tasks (Betti et al., 2021; Pezzulo et al., 2021).

Recent studies provided support to the “representational” hypothesis, showing that resting state resembles the spatial distribution of activity evoked by natural stimuli in primary sensory and motor regions and in high-order association areas, e.g., attention networks. In visual regions, connectivity patterns observed at rest match with those evoked by natural stimuli compared with synthetic visual stimuli (Betti et al., 2018; Strappini et al., 2018). Such spatial correspondence is also category specific. For example, spontaneously emerging patterns at rest in face-specific regions were more likely to match face-activation patterns

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than other categories (Kim et al., 2020). Similarly, studies focusing on hand movements, whether observed or performed, have expanded these findings.

Although natural hand movements are extremely complex, the daily repertoire of human hand movements can be described using statistics highly consistent across subjects, even during everyday tasks (Ejaz et al., 2015; Ingram et al., 2008; Jeannerod, 1986; Jeannerod et al., 1995; Napier, 1956; Sili et al., 2023). A limited set of common postures or motor synergies, typically, from three to six, explains >80 % of the variability of hand movements recorded with kinematics or electromyography (Santello et al., 1998; Santello et al., 2002). Interestingly, this low dimensionality is also observed in brain activity. fMRI studies of brain activity show that the motor cortex encodes human hand movements in terms of motor synergies (Leo et al., 2016). Building on these findings, recent fMRI studies explored whether spontaneously emerging patterns of activity in the motor cortex align with those evoked by performing ecological movements, more than unusual ones (Livne et al., 2022; Zhang et al., 2023). These studies revealed a replay of evoked activity patterns not only in the primary motor cortex but also in the high-level association dorsal attention network. In Zhang et al., 2023 replay for common movements occurs in the more dorsal parcels of the DAN encompassing superior parietal cortices and frontal eyes fields. These regions are involved with spatial attention and motion processing. Hence other processes may regard tracking the location or motion of the hand.

Based on this evidence, an open question is whether the rest-task similarity within the associative cortex arises solely during the execution of hand movements or whether it extends to the observation of these movements. Another fundamental aspect is whether these representations are "sensorimotor "in nature, capturing kinematic features such as speed, trajectories, and dynamics or they are purely "cognitive" reflecting abstract processes like the meaning or processes regarding tracking the spatial location or motion of the hand. Our expectation is that this similarity also emerges during the observation of such gestures. This suggests that spontaneous activity within the DAN may play a broader role working in concert with action-related networks. Understanding whether spontaneous signals have a far-reaching impact is crucial for elucidating the behavioral relevance of spontaneous brain activity. Previous studies employing a motor execution paradigm could not disentangle between these aspects (Livne et al., 2022; Zhang et al., 2023). Building on this research, our study adopts a movement observation task. This approach allows us to probe internally generated sensorimotor activity in a more controlled fashion—minimizing the contribution of overt motor output and associated bottom-up sensory signals. It also enables us to investigate whether high-level association networks - specifically the dorsal attention network (DAN) and ventral attention network (VAN) - encode ecological and unusual movements, respectively. If this representation is purely cognitive, we do not expect a spatial match within the visual network (VIS) and the somatomotor networks (SMN).

2. Materials and methods

2.1. Participants

In this fMRI study, we enrolled healthy adults with normal or corrected-to-normal vision. All participants were right-handed according to the Edinburgh Handedness Inventory (EHI; (Oldfield, 1971); 10-item version). Inclusion criteria included compatibility with MRI exam and no history of neurologic or psychiatric diseases. Based on a previous analysis comparing ecological and control representational patterns (Zhang et al., 2023), we ran a power sample analysis. We considered average and standard deviation (SD) from the multivertex similarity analysis for grip ($\mu1 = 0.1014$; SD1 = 0.04298) and shake ($\mu2 = 0.0767$; SD2 = 0.0383) conditions. A sample size of 24 subjects is required for alpha=0.05 and a power of 80 %. Considering an attrition rate of 0.2 based on processing failure and/or MRI artifacts, the final sample size consists of 29.

The experimental protocol was approved by the ethics committee of IRCCS Fondazione Santa Lucia, Rome (protocol n. 1485/2017). Participants were provided with a detailed description of all the experimental procedures and were required to sign a written informed consent. They were compensated for participating. All methods were carried out in accordance with relevant guidelines and regulations of the ethical review board.

2.2. Visual stimuli

Before running the fMRI experiment, we defined two observational conditions: ecological (common) and unusual (uncommon) reach-to-grasp movements. To achieve this, a preliminary behavioral study was conducted with an independent sample of 25 healthy participants (mean age = 23.1 ± 3.7 years; 18 females). The two conditions involved observing videos of reach-to-grasp movements. In the ecological condition, participants observed movements with a regular, natural kinematic pattern of the upper limb. In the unusual condition, movements featured perturbed kinematics, with a medial arm rotation and wrist torque that swung the elbow upward. Each video began with a static prone hand position. The hand then grasped an object (a cup), turned back, and placed the cup in its original position. All videos were presented from a first-person perspective and lasted 3 s.

To minimize habituation effects, the videos included variations in several factors: hand used (right or left), cup position (left, right, or center), cup color (green, orange, or red), type of grasp (pinch or whole hand), gender of the model performing the movement (female or male). In total, 24 videos were shown: 12 depicting common movements and 12 showing uncommon movements. After each video, participants responded to three questions using a keyboard, rating their agreement on a scale from −3 to +3. The questions evaluated three key aspects of the movements: Frequency: "I use this grasp frequently in everyday life." Spontaneity: "I would spontaneously perform this grasp." Naturalness: "I consider this grasp as natural."

The instructions were provided in Italian, and all participants were native Italian speakers. The experiment stimuli were presented using PsychoToolbox in MATLAB. Participants were closely monitored throughout the study, and none reported any difficulties. The average scores across participants and the three questions were analyzed using a paired *t*-test, with significance at $p< 0.05$. Positive scores indicated that the movement was perceived as common, while negative scores indicated it was perceived as uncommon.

2.3. Experimental fMRI design

Participants first performed a 15-minute resting state scan, fixating a red cross on a black screen without any other motor, sensory, or cognitive task (Fig. 1A). Next, a block-design paradigm was used in which participants observed the same video clips from the behavioral study depicting reach-to-grasp movements. Videos were presented in three runs including 24 blocks, 12 depicting common and 12 uncommon movements, alternated with 24 epochs of rest. Blocks (C—C-U-U or U-U-C—C) were counterbalanced across participants, with each block containing 5 videos interspersed by 0.5 s of fixation (Fig. 1B). After each run, participants reported the number of red cups to ensure attentiveness.

The main task runs were alternated with three functional localizer runs, where participants viewed images of hands, chairs, and bodies. The task consisted of identifying repetitions of images (1-back task, (Perini et al., 2014)) via a button press with the dominant hand. The functional localizer run was designed to identify a region of interest (ROI) within the lateral occipitotemporal cortex. Each run of the localization task lasted 4.30 min and was structured into four blocks of static images interspersed by 15 s of fixation (Fig. 1C). Each block contained

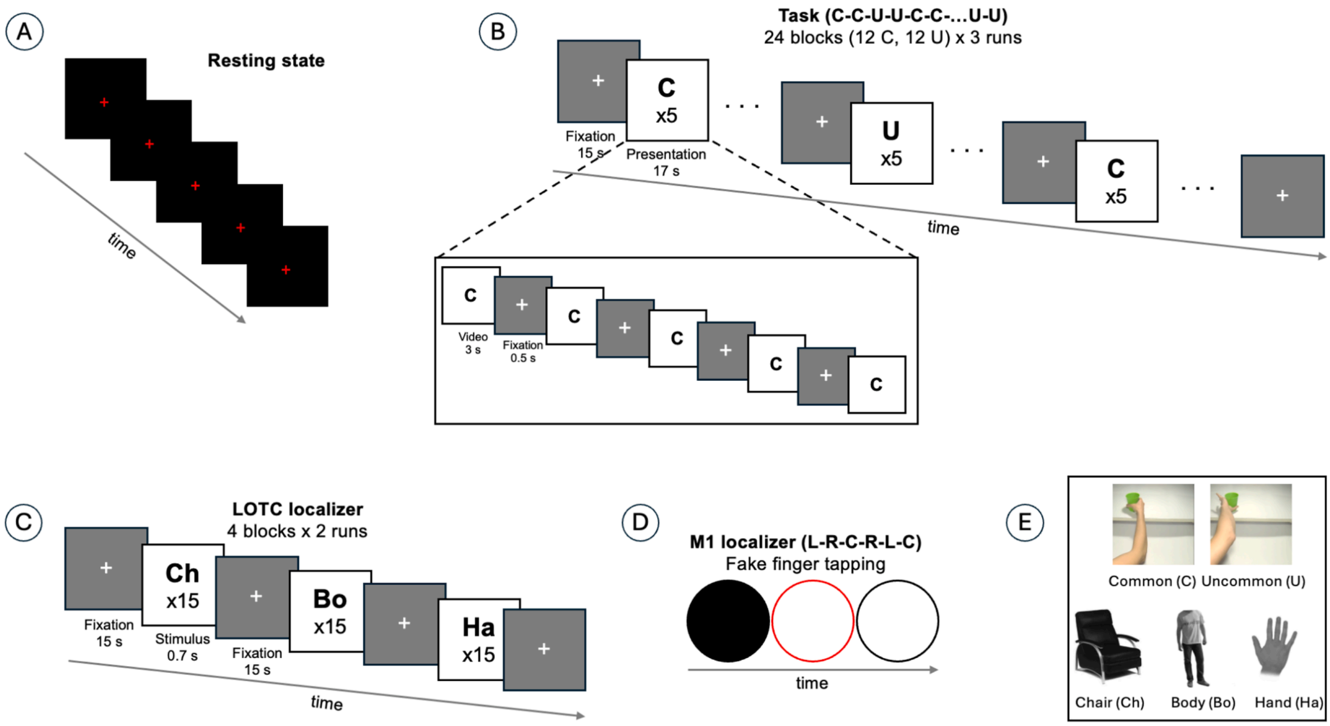

Fig. 1. ***fMRI protocol.*** **(A)** Prior to the task session, participants performed a 15-minute resting state scan (eyes-open with fixation cross). **(B)** In the task session, participants viewed 3-*sec* videos displaying either common (C) or uncommon (U) movements performed with the right or left hand. The videos were presented into 24 blocks - 12 C and 12 U movements - interspersed by 15-*sec* fixation. Series of two consecutive C or U movements (C—C-U-U or U-U-C—C) were counterbalanced across participants. The task session was repeated three times (runs) and lasted 39.15 min, with each run lasting 13.05 min; Each block within the task session comprised 5 videos, spaced by 0.5 s of fixation, lasting 17 s. A fixation cross was presented at the end of the session. **(C)** At the end of each task run, participants performed a localizer designed to detect the lateral occipitotemporal cortex (LOTC) activity. The LOTC localizer was repeated two times (runs). Each run was structured into four blocks and lasted 4.30 min. Each block lasted 45 s and included three random sequences, each lasting 15 s, and contained fifteen static pictures belonging to the same category: hands (Ha), chair (Ch), and body (Bo). Each image lasted 0.7-*sec* and was spaced by fixation 0.3-*sec* fixation. A fixation cross was presented at the beginning and the end of each run. **(D)** Following the task and LOTC sessions, participants performed a 3-minute finger-tapping task to localize the somatomotor regions. Specifically, subjects were shown three circles (left, center, and right). The circles were colored (filled) according to a specific sequence (L-R-C-R-l-C). Participants were instructed to perform a finger tapping task using either the left or right hand according to the filled sequence (i.e., left circle or right circle accordingly) or to rest in response to the filled centered circle. The finger tapping for each hand and the rest condition lasted 15 s for 3 min. **(E)** Representative pictures of both C and U movements (for the task session) and static pictures (for the localizer task).

three random sequences of fifteen stimuli (0.7 s each) belonging to the same category (hands/chairs/bodies), separated by fixation (0.3 s). Fifteen-second fixation blocks appeared at the beginning and at the end of each run.

Finally, a 3-minute finger-tapping task localized somatomotor regions (Fig. 1D). This task was performed with the right or left hand in a counterbalanced order. This order was based on the presentation of a colored circle, filled on the same side that indicated the hand to perform the movement (right vs left, 15 s each). The appearance of the filled circle at the center of the screen corresponded to the rest position (15 s). During this task, each finger opposed the thumb without actual contact to prevent tactile and sensory feedback.

Representative figures of videos and static images used for the experiment are depicted in Fig. 1E.

All the visual stimuli were projected on a translucent screen that participants saw through a mirror with the support of a PC running MATLAB (MathWorks Inc, Natick, MA, USA) and the Psychophysics Toolbox version 3.

2.4. MRI acquisition and imaging parameters

All MRI data were acquired using a Siemens 3-T Magnetom Prisma scanner with a 32-channel receive head coil and a 2-channel transmit coil. Functional images were obtained using whole-brain EPIs with TR= 1100 ms, TE = 30 ms, voxel size = 2.4 × 2.4 × 2.4 mm^3 isotropic, multiband acceleration factor = 4, field of view (FOV)=208 mm, and Flip angle = 65° (Feinberg et al., 2010; Moeller et al., 2010; Xu et al., 2012). The whole fMRI protocol lasted 70 min. Two spin-echo EPI volumes with opposite phase encoding directions and the same geometrical and sampling properties of functional runs, with no multiband acceleration, were acquired for field map generation (TE = 80 ms, TR = 7023 ms). Brain structural images (TR = 2500 ms; TE = 2 ms; TI=1070 ms; FOV=256 mm; Flip Angle 8°; 1 mm^3 isotropic voxel) were acquired using a T1-weighted MPRAGE (Magnetization Prepared Rapid Gradient-Echo) sequence incorporating perspective motion correction and selective reacquisition of corrupted data (Tisdall et al., 2012).

2.5. Imaging processing

All functional MRI (fMRI) data were preprocessed with a standard pipeline using SPM12 (http://fil.ion.ucl.ac.uk/spm/) and custom routines. The first seven TRs were discarded to allow for signal and scanner stabilization, and then EPI runs were simultaneously corrected for head motion and unwarped using the B_0 field derived from spin-echo scans. Slice timing correction was then applied to account for the differences in data acquisition timing for different slices. Epi series were normalized to a MNI template using the deformation field estimated in the T1 scan previously coregistered to the mean EPI. Epi intensities were normalized by dividing the intensity of each voxel over its mean over the time series and applied a multiple regression analysis (3dDeconvolve) to estimate the activation patterns for each category. We then spatially smoothed the data using a Gaussian kernel at 4.8 mm Full Width at Half Maximum

(FWHM).

For the resting state, additional steps were performed to reduce physiological noise (Mascali et al., 2021). Denoising included simultaneous frequency filtering in the band 0.09–0.1 Hz, regression of signals of no interest, and censoring motion-contaminated volumes via a single linear regression model. Regressors included 6 motion correction parameters, corrupted volume markers selected according to a Framewise Displacement threshold, and 10 tissue time courses, that were obtained by principal components analysis of EPI timeseries within cerebrospinal fluid (CSF) and white matter masks derived from the coregistered structural data, according to aCompCorr method (Behzadi et al., 2007). Finally, data were projected to the cortical surface using 164.000 vertices in the FSL-average space (Fig. 2A).

2.6. fMRI contrast analysis

Our first aim is to investigate the activation patterns elicited by the observation of common vs uncommon movements within specific RSNs, that is the dorsal attention network (DAN), ventral attention network (VAN), somatomotor network (SMN), and visual network (VIS). To do so, we calculated the mean activation patterns masks bilaterally for each condition using the Yeo's template (Yeo et al., 2011), as in (Livne et al., 2022; Zhang et al., 2023). For this reason, we do not consider the activity elicited by the localizer tasks in this study.

We first extracted activation maps for common and uncommon movements. For this purpose, a general linear model (GLM) was applied to task data for each participant. The GLM consisted of separate regressors for each stimulus category (e.g., common vs uncommon).

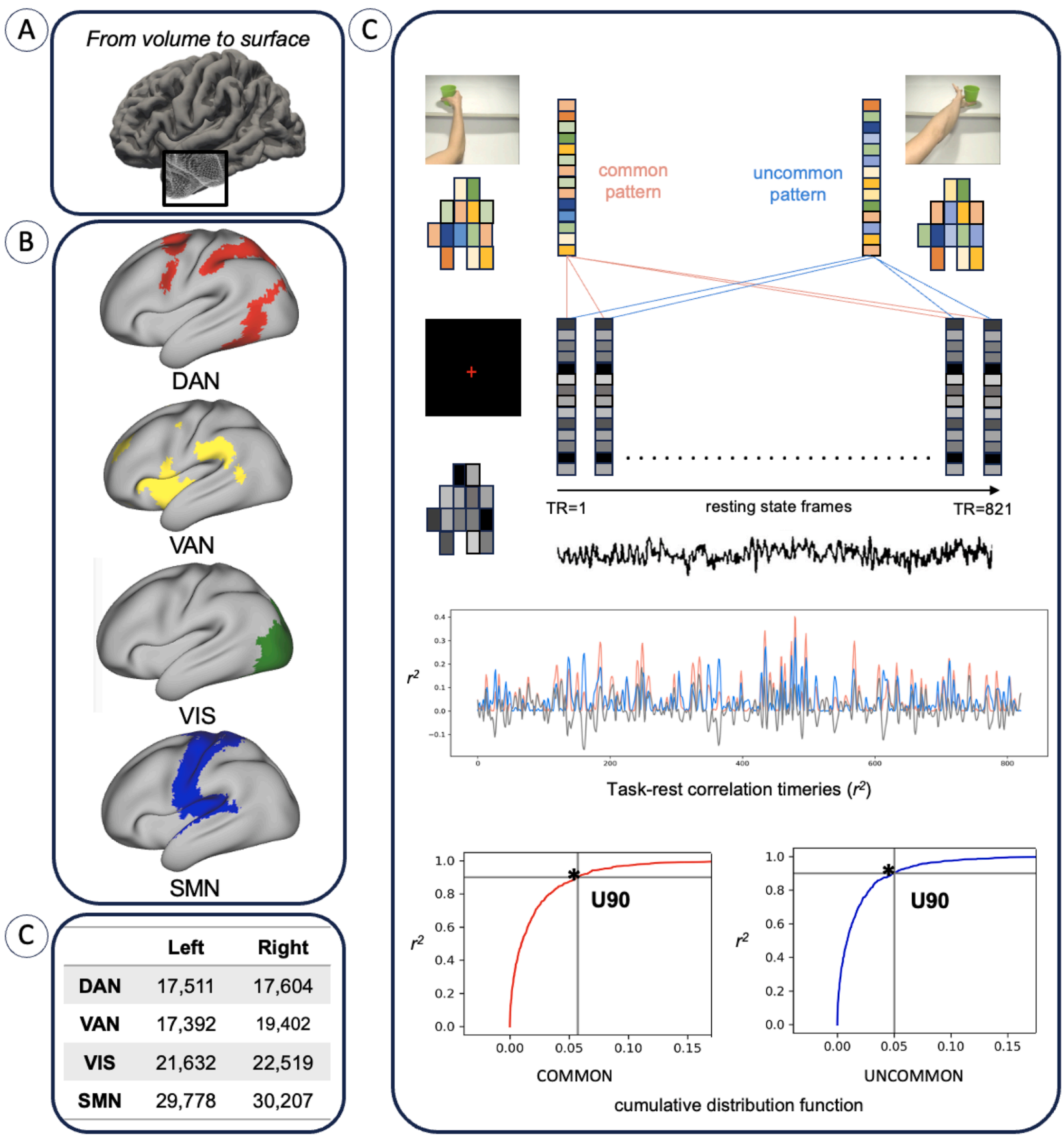

Fig. 2. ***Workflow of the methodology.*** (**A**) From volume to surface. All the data were projected from the volume to the surface level in *fsaverage* space with 164k vertices. (**B**) Networks selection. Four networks were selected: dorsal attention network (DAN, in red), ventral attention network (VAN, in yellow); visual network (VIS, in green); somatomotor network (SMN, in blue). Data were projected in the inflated template for visualization purposes. (**C**) The number of vertices for each network for both the left and the right hemisphere of the brain are reported. (**D**) analysis workflow for the computation of task-rest multi-vertex similarity. For each network and task condition (common/uncommon), we obtained an average of task-evoked activity patterns. For each participant, a total of two averaged task-evoked vectors were computed (one for common and one for uncommon), by averaging activation patterns, across the three runs. A vector of the same length was computed for each resting-state frame (n = 821, where n is TR). Then, we correlated the task-evoked vector with the resting-state data yielding n = 821 squared Pearson's values (r2) for each condition. We computed a cumulative distribution function on these r2 values and we identified the upper 90 % value of the distribution (U90 value).

Condition contrasts were formed to identify voxels showing a preference for common and uncommon categories during task activations: common preference (common > uncommon), uncommon preference (common < uncommon), and whole categories activation (common & uncommon). The mean averaged activation patterns were computed within this network and compared through analysis of variance (ANOVA). Separate ANOVA models were performed for the right and left hemisphere. In particular, two-way interaction ANOVAs investigated the activations for the two conditions (i.e., common vs uncommon) in the four networks (i.e., DAN, VAN, VIS, SMN). A p-value < 0.001 was considered significant.

Additionally, we explored voxel-wise differences between common and uncommon movements in the task activation. A paired-sample nonparametric inference based on FSL-randomise with n = 5000 permutations was used to compare the two groups, according to the established procedure (Winkler et al., 2014). Multiple comparisons were corrected using a $p < 0.025$ familywise error (FWE)-corrected based on permutation testing at a threshold-free cluster enhancement (TFCE).

2.7. Task and rest multi-vertex similarity analysis

To investigate the similarity between resting state and task patterns (common vs uncommon), we performed a multivertex linear analysis according to our previous publications (El Rassi et al., 2024; Kim et al., 2020; Livne et al., 2022; Zhang et al., 2023) using the same four RSNs of the contrast analysis (Fig. 2B). We obtained an average of task-evoked activity patterns for each network and task condition (common/uncommon). For each participant, these activation patterns were computed by averaging the signal of the frames within each visual stimulus across the three runs (Fig. 6C). The length of these vectors ($n = 2$, a map for each condition) represents the number of vertices for each network (Fig. 2D). A vector of the same length was computed for each resting-state frame (for a total of $n = 821$ vectors, where n is the number of EPI frames). Then, we correlated the task-evoked vector with each resting-state vector. This procedure yielded $n = 821$ squared Pearson's values (r^2) for each condition (i.e., common and uncommon), representing the degree of spatial similarity between the task-evoked and resting-state multi-vertex activity patterns. To compare the strength of the correlation between task-evoked and resting-state signals, we computed a cumulative distribution function on these r^2 values. According to previous studies (El Rassi et al., 2024; Kim et al., 2020; Livne et al., 2022; Zhang et al., 2023), we identified the upper 90 % value of the distribution (U90 value). These values obtained for the two experimental conditions (common vs uncommon) were then compared using a parametric paired t-test ($p < 0.008$ was considered significant; Bonferroni correction) for each RSN. We excluded data points above or below the 1.5 interquartile range to remove outliers in the analysis.

Finally, to assess whether the U90 values reported within the networks were significantly different compared to a null model, we shuffled the vertices within the mask from the activated map before computing the similarity analysis. U90 values from shuffled and unmanipulated activation images were compared through a paired t-test, independently for each network.

3. Results

From the original sample of 29 participants, we excluded two subjects due to gross artifacts in the images and three subjects after a visual quality check of the preprocessing due to misalignment. Results refer to a final sample of 24 right-handed participants (14 females; mean age ± standard deviation=27.08 ± 3.5 years).

3.1. Visual stimuli: behavioral results

The behavioral scores (ranging from −1 to 1) were summed and averaged across subjects and questions. Results showed a significant difference for all the three examined aspects between the two movements (natural: mean score = 1.6 ± 0.8, range +0.3:+2.4 SD) (wrist rotation: mean score = −2.4 ± 1, range −3:−0.3 SD) (all *p-values* <0.001). These results defined the two hand movements as "common" and "uncommon", used in the fMRI paradigm.

3.2. fMRI data: mean activation patterns

A significant main network effect was found for the left hemisphere (ANOVA $F(2,46)=442$, $p < 0.001$). Condition showed no significant effect ($p = 0.961$), as well as for the network × condition interaction ($p = 0.948$), suggesting an overall network effect. The same pattern was reported for the right hemisphere (network: $F(2,46)=438$, $p < 0.001$; condition: $p = 0.685$; interaction network × condition: $p = 0.988$).

A post-hoc analysis on networks revealed a significant gradient, with values decreasing in the order of VIS > DAN > SMN > VAN; all comparisons significant at $p < 0.001$ adjusted for FDR) (Fig. 3B) for both left and right hemispheres.

3.3. Differences between common and uncommon hand movements

Next, in the GLM contrast analysis, we explored potential differences between common and uncommon movements. Results showed stronger activation when observing uncommon movements than common ones ($p < 0.05$ FWE corrected) in the left superior parietal lobule (Fig. 4). By using a more lenient threshold ($p < 0.001$ uncorrected), we found significantly higher activation bilaterally. These regions encompass the superior parietal lobule and the precentral gyrus (i.e., dorsal premotor cortex), as emerged from the peak-search analysis. On the contrary, no significant higher activation was reported during the observation of common vs uncommon grasps ($p < 0.05$ FWE corrected). A more lenient threshold ($p < 0.001$ uncorrected) showed a bilateral higher activation encompassing the inferior frontal gyrus. Peak activation coordinates of the difference between the two conditions are reported in Table 1.

3.4. Similarity between task-evoked and spontaneous activity patterns

We performed a multi-vertex analysis to assess the similarity between the resting state and task fMRI patterns evoked. A paired t-test (significant *p-value* <0.008, Bonferroni correction) was performed to investigate task-rest similarity patterns between the view of common and uncommon movements. Results showed a higher similarity between the view of common movements and resting state signaling than uncommon movements for the left DAN (p value=0.004)(Fig. 5). In the right VIS, we found higher value during the view of common movements compared to uncommon movements, not surviving the multiple comparison correction ($p = 0.031$). All the remaining comparisons showed no significant results ($p > 0.05$).

Compared to the distribution from the shuffled activation data, similarity values were significantly higher in all the networks and hemispheres considered in the analysis ($p < 0.0001$ for all the comparisons).

3.5. Sensitivity analysis: activations across sub-parcels

Next, we assessed whether sub-regions within the DAN led to the higher similarity between common grasps and resting-state activity. The statistical analyses were repeated on 8 sub-parcels (Fig. 6A), defined based on the Schaefer atlas $n = 100$, (Schaefer et al., 2018). For visualization purposes, data were projected into the Conte69 surface cortex. Results showed similar activation between common and uncommon movements (Fig. 6B). A paired t-test run separately for each sub-parcels reveals no significant effects (Fig. 6C; $p < 0.05$ for all sub-parcels). This result suggests that the overall dorsal attention network is responsible for the encoding of common movements in spontaneous activity.

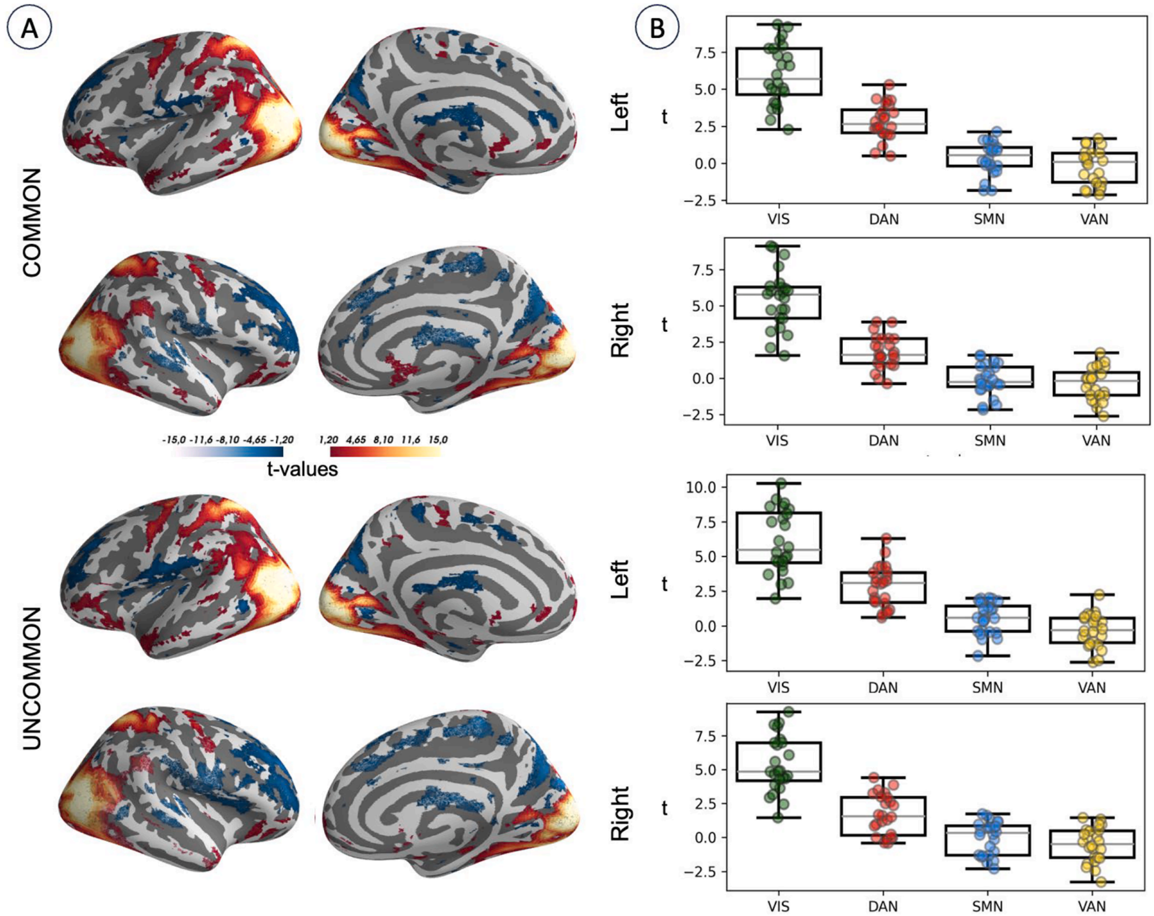

Fig. 3. ***Brain activation for common and uncommon hand movements.*** **(A)** Maps of mean activation patterns for each network (VIS, DAN, SMN, VAN), for common and uncommon hand grasps. **(B)** Significant network effect ($F(2,46)=442$, $p < 0.001$). Post-hoc analysis showed a significant gradient (VIS>DAN>SMN>VAN; all comparisons significant at $p < 0.001$) for common and uncommon hand grasps and for left and right hemispheres.

4. Discussion

Recent fMRI studies show that spontaneously emerging activity patterns in the motor cortex align with those evoked by performing ecological movements, more than unusual ones (Livne et al., 2022; Zhang et al., 2023). These studies revealed replays of evoked activity patterns also in the DAN for common movements and in the VAN for uncommon movements (Zhang et al., 2023). Whether the representational content of RSNs is sensorimotor or purely cognitive is still debated. Building on these findings, we aim to discern the nature of this representational content using an observation paradigm, thus minimizing the contribution of overt motor output and associated bottom-up sensory signals induced by motor execution. We used two reach-to-grasp movements characterized by regular and perturbed kinematics of the upper limb, to reproduce common vs uncommon movements, respectively. In line with these fMRI studies, we selected two high-level association networks (DAN and VAN) and two sensory networks (VIS and SMN). Before fMRI, a behavioral study was conducted to validate the two stimulus categories using an independent sample. Results showed that regular arm and hand movements are natural, frequent, and spontaneous, while movements with perturbed kinematics were the opposite. We referred to them as common or uncommon, respectively. Two functional results are worth discussing.

First, we show that spontaneous activity codes more frequently ecological manual behavior, as revealed by rest-task similarity in the high-order regions of the DAN (Fig. 5). It is not surprising that there is an encoding of visual stimuli in the resting human brain. Previous studies found spontaneous activity patterns within regions of the human visual cortex encoding information related to stimulus and category (Kim et al., 2020; Livne et al., 2022). For instance, Kim and coworkers (2020) found that resting-state multivertex patterns associated with a category (e.g., body) exhibited preferential fluctuations between regions that favor the same category and were largely uncorrelated with fluctuations of pattern for a disparate category (e.g., scene). They conclude that spontaneous patterns in the visual cortex mirrored those evoked by external visual stimuli, underlying a category specificity between rest and task. Furthermore, the spontaneous activity encodes natural hand pictures in the somatomotor regions as compared to other stimuli (El Rassi et al., 2024). However, here, we do not observe any significant effect in the sensory regions, including the VIS or SMN.

Why is the DAN involved? This result cannot be explained by stronger regional activation. As shown in Fig. 3, VIS exhibits greater activation than DAN, indicating a significant gradient. Moreover, the comparable activation levels observed for both "common" and "uncommon" conditions suggest that this region processes these stimuli similarly. Corbetta and Shulman (2002) showed that DAN regions are involved in establishing and maintaining preparatory signals for spatial attention. High-level association networks at rest maintain readiness for processing behaviorally relevant stimuli in space (Cole et al., 2014; Spadone et al., 2015) and time (Betti et al., 2021; Betti et al., 2018, 2013; de Pasquale et al., 2012; de Pasquale et al., 2018, 2021). The central role of the DAN in maintaining attentional readiness has been explicitly suggested by a MEG recent study using an attentional paradigm. Spadone and coll. (2015) showed that DAN maintains a relatively stable pattern of functional connections, even during rest. This could indicate that the DAN is inherently a *prior* or "tuned" for attention, even

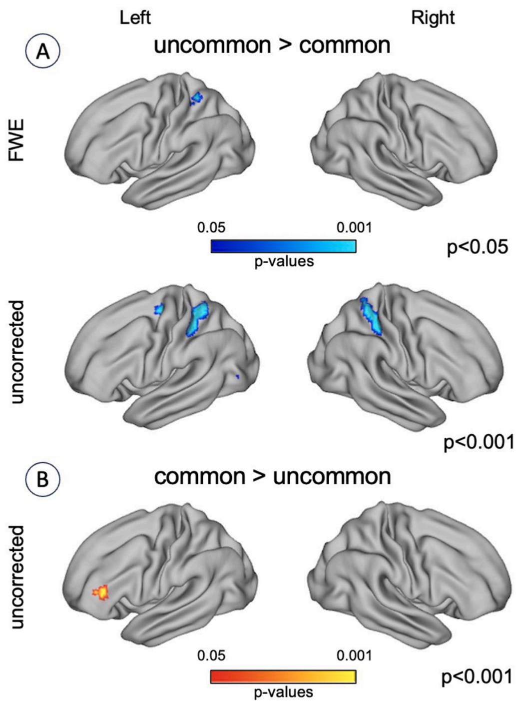

Fig. 4. ***Comparison between common and uncommon hand movements.*** **(A)** Left superior parietal cortex showed higher activation during the observation of uncommon hand grasps compared to common movements ($p < 0.05$ FWE corrected). Using an uncorrected threshold ($p < 0.001$), bilateral superior parietal cortex and the frontal eyes fields showed higher activity. **(B)** No significant higher activations for the comparison of common vs uncommon hand movements ($p < 0.05$ FWE corrected) were found. Using an uncorrected threshold ($p < 0.001$), bilateral inferior frontal gyrus showed higher activation. The two color bars represent p values.

Table 1

Peak activations of difference between common and uncommon. MNI coordinates (x, y, z) the difference of activations in common and uncommon conditions, right (R) and left (L) hemispheres. The view of uncommon hand movements activated the superior parietal lobule. With an uncorrected threshold, this activation became bilateral and also includes the precentral gyrus. While the view of common movements didn't show significant activation; an uncorrected threshold showed an activation in the frontal pole.

		uncommon > common					
		FWE			uncorrected		
		x	y	z	x	y	z
Superior parietal lobule (BA 5)	R				26	−52	74
	L	−37	−42	67	−35	−44	70
Precentral gyrus (dorsal premotor cortex)	R				33	−7	61
	L				−23	−14	57
		common > uncommon					
		FWE			uncorrected		
		x	y	z	x	y	z
Frontal pole	R				32	24	12
	L				−47	41	18

when no active attentional task is performed. In other words, it may be set up in an anticipatory way, as if it is always ready to engage attention when needed. The idea that the DAN might act as a *prior* means it could function as a preparatory network, waiting for new information to arrive and ready to act. This mechanism fits within the predictive coding framework, where the brain continuously generates top-down predictions (*priors*) from higher-order regions to lower sensory areas for faster and more efficient processing when new stimuli appear (Pezzulo et al., 2021; Schuck and Niv, 2019). Our findings align with this interpretation, however, they move further on the functional significance of the spontaneous activity. The fact that DAN codes more frequently common movements suggests that these preparatory signals are content-specific and tuned to interpret the meaning of movement. Existing literature suggests that motor planning representations for hand movements are located more in IPL. However, DAN contains regions in the frontoparietal cortex involved in motor control and action planning (Andersen and Cui, 2009). At rest replay of natural movements occurs in the more dorsal parcels of the DAN that have to do more with spatial attention and motion processing (Zhang et al., 2023). Hence other processes may regard tracking the location or motion of the hand. In light of the lack of a significant match between rest and task patterns in the SMN, our interpretation is that the representational content of RSNs is cognitive. This is especially evident when the motor-evoked component and the bottom-up sensory signals are minimized, as in our observational paradigm.

How do these content-specific representations emerge? During offline periods (rest or sleep), where external input is minimal, the brain reinforces existing *priors* by replaying learned spatiotemporal patterns from past experiences (Miall and Robertson, 2006). This maintains a flexible, efficient state, enabling quick responses to environmental demands, especially if those are regular or natural. This idea is supported by the observation that spontaneous brain activity during rest closely resembles the activity seen during task performance or sensory engagement (El Rassi et al., 2024; Kim et al., 2020; Livne et al., 2022; Raichle, 2011; Zhang et al., 2023), reinforcing the idea that the brain continuously rehearses its predictive framework (Fox and Raichle, 2007). Regular exposure to frequent behavior and sensory stimuli in daily activities produces internal models (Harmelech and Malach, 2013) that generate *prior* expectations stored in spontaneous activity patterns (Betti et al., 2021). This view is supported by studies in the ferret's visual cortex, where the tuning functions of neurons "*learn*" the statistics of natural stimuli as the animal grows (Berkes et al., 2011). Since in this and other studies (Kim et al., 2020; Livne et al., 2022; Zhang et al., 2023; El Rassi et al., 2024) the resting state condition is always at the beginning of the study, we can exclude reverberation of the task-evoked activity in the spontaneous activity. Thus, we assume a role of previous experience in shaping the brain response to stereotyped arm and hand movements. This may explain why we do not observe any significant effect for uncommon movement. Moreover, this encoding of common movements relies on the distributed network, as demonstrated through parcel-wise analysis (Fig. 6).

Deviations from regularity (e.g., sensory stimuli, body movements) force the adaptation of these internal models. Our second result is in line with this view. The increased activation for unfamiliar perturbed reach-to-grasp movements (Fig. 4A) may reflect the necessity of neural circuits to flexibly adjust to new behavioral or environmental demands. These circuits involve the superior parietal cortex and precentral gyrus. Previous studies show that the superior parietal cortex is crucial for maintaining an internal body representation, essential for perception and action (Wolpert et al., 1995). This area closely localizes in the vicinity of those areas classically reported as crucial for representing fingers and shoulder (Huang et al., 2012; Sereno and Huang, 2014). The superior parietal cortex (area 5) represents spatial information for limb movements and is involved in reaching arm movements (Andersen and Cui, 2009). It projects to the dorsal premotor cortex, or area F2 in monkeys (Wise et al., 1997), where an intertwined representation of fingers and wrist (Sanes et al., 1995) or fingers and elbow (Rao et al., 1995) is present. This activation may reflect the adaptation of kinematic parameters triggered by observing unfamiliar movements. Neurophysiological studies indicate that the dorsal premotor cortex and parietal area 5 encode positional or kinematic aspects of limb movement rather than the forces involved (Kalaska et al., 1990; Scott et al., 1997; Scott and Kalaska, 1995). In these studies, monkeys were trained to perform hand-reaching movements to fixed target locations with abduction,

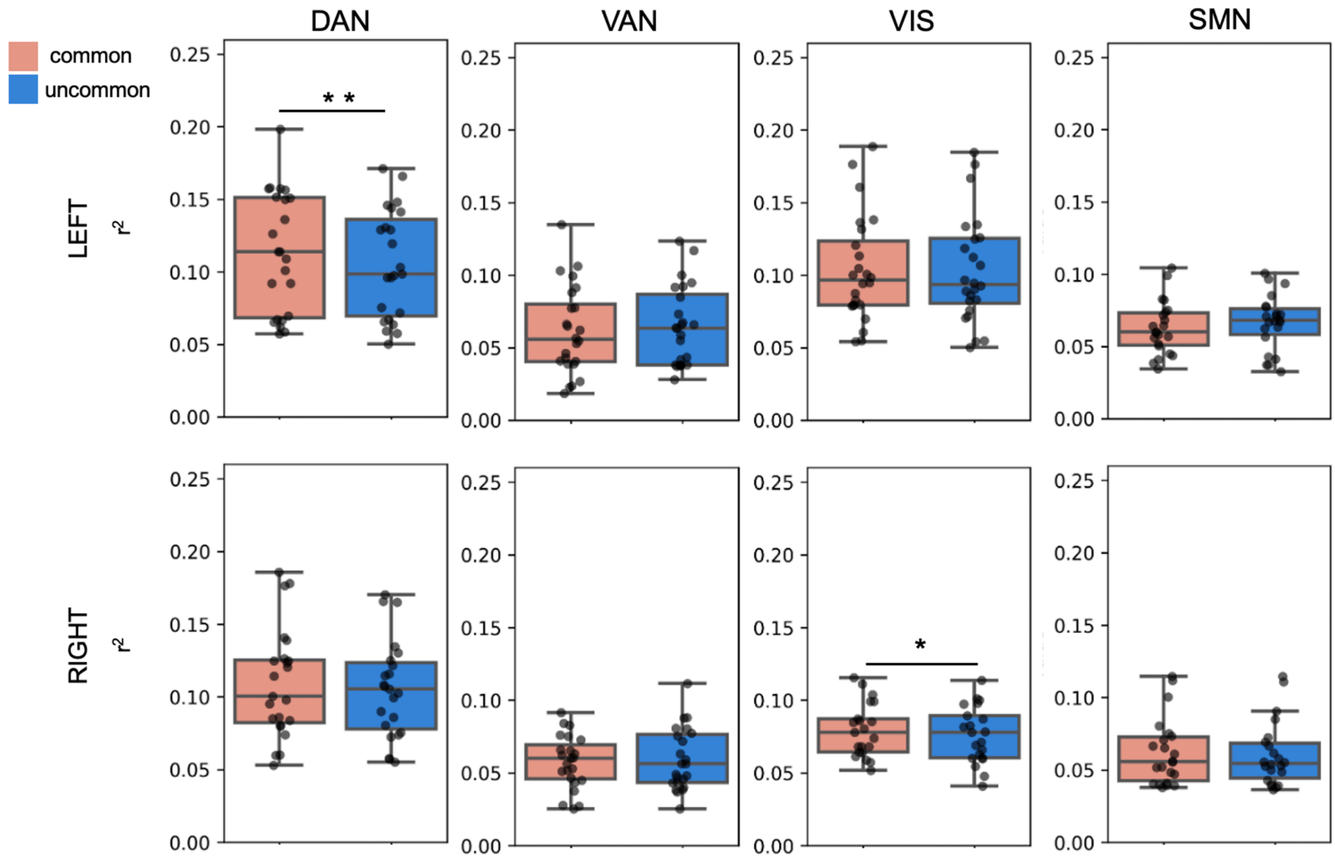

Fig. 5. ***Task-rest similarity patterns.*** A paired *t*-test (significant p-value <0.008; Bonferroni correction) was performed to investigate task-rest similarity patterns between the view of common and uncommon movements. Results showed a higher similarity between the view of common movements and resting state than uncommon movements within the left dorsal attention network (DAN) (p value=0.004). In the right visual network (VIS) we found higher value during the view of common movements compared to uncommon movements, not surviving the multiple comparison correction (p = 0.031). The remaining comparisons showed no significant results ($p > 0.05$). ** marks $p < 0.005$; * marks $p < 0.05$.

which was unnatural. Arm orientation showed increased neuron activation, which resembled our findings. Adaptation of internal models occurs through feedforward mechanisms, especially if behavioral adjustments are predictable (Fan et al., 2006). At the neural level, these feedforward mechanisms likely involve recurrent top-down interactions from parietal areas, which support visuomotor transformations, to prefrontal areas responsible for efficient motor control (Battaglia-Mayer and Caminiti, 2019). Our idea is that this fine-grained representation which includes the kinematic aspect of the movement pertains to the motor areas that implement the movement, when this is requested. The adaptation occurs in this circuit. By contrast, the meaning of movement and motion processing, consolidated through the experience (reach--to-grasp represents one of the most common movements occurring in our daily activities) and stored in the spontaneous activity, require a low dimensional representation. Indeed, the encoding of the kinematics details is computationally expensive for the brain to be maintained in the resting brain. Rather, one might expect a low-dimensional representation of behavior within spontaneous activity, possibly in the form of motor synergies, as observed in brain activity (Leo et al., 2016). However, further studies are needed to test this idea.

Two further considerations merit discussion. First, spontaneous activity results are mainly left-lateralized, likely due to the participants' right-handedness (Cabinio et al., 2010). Our interpretation is that the long-term hand preference experience not only affects neural correlates of motor execution and observation (Willems and Hagoort, 2009) but also shapes spontaneous activity. Recent Magnetoencephalography (MEG) evidence supports this, showing that interindividual variability in manual dexterity, a long-term motor skill, modulates the intrinsic connectivity (i.e., the strength of the connections) and functional brain architecture (i.e., segregation/integration and hub centrality) in right-handed individuals (Maddaluno et al., 2024). Neuropsychological observations on right-handed apraxic patients confirm the left hemisphere's role in upper limb control (Rounis and Binkofski, 2023).

A second final note is linked to the uncommon movement. Previous fMRI studies showed higher activity of the parietal regions for observing biologically impossible movements, which violate biomechanical constraints, as compared to possible hand movements (Costantini et al., 2005). However, the activation occurs in Brodmann's areas 40 and 7, in the posterior-ventral portion of the parietal cortex, unlike our study where stimuli are biomechanically possible but less ecological. Therefore, we exclude that our result may be due to similar mechanisms. Another possibility is that the observed movements were considered as wrong (Malfait et al., 2010; Pavone et al., 2016). Despite perturbed kinematics, our study does not include a missing grasp of the object toward which the hand is directed, but the object is always placed back in the starting position. Therefore, it is unlikely that higher activity of prefrontal and parietal regions is explained by mechanisms of detection of other's actions, as previously suggested for motor systems in expert observers (Aglioti et al., 2008; Pavone et al., 2016; Shimada, 2009). The observed motor act may imply unattended spatial and temporal aspects (Buccino et al., 2007). Still, no increased activity was found in the right temporal parietal junction (TPJ), linked to attentional reorienting (Corbetta and Shulman, 2002). Instead, our findings suggest that these areas with a stronger activity during the uncommon movement may update and store motor parameters, with statistical learning possibly shaping internal models in spontaneous activity.

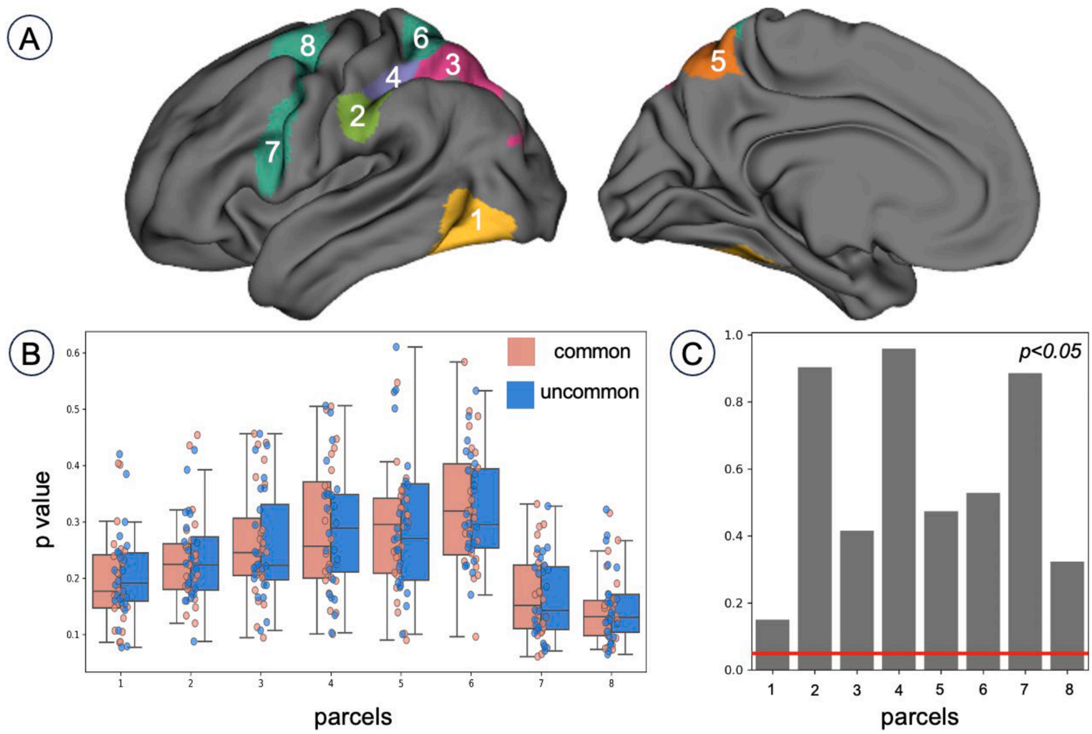

Fig. 6. ***DAN sub-parcels.*** (**A**) Left dorsal attention network parcels from Schaefer functional atlas ($n = 100$ parcellation) projected into the Conte69 surface cortex. 1: inferior temporal gyrus; 2: supramarginal gyrus, anterior division; 3: lateral occipital cortex, superior division; 4: postcentral gyrus; 5: precuneous cortex; 6: superior parietal lobule; 7: precentral gyrus; 8: superior frontal gyrus. (**B**) common vs uncommon activation values within the DAN sub-parcels with no significant difference (C; $p < 0.05$). (**C**) P-values are reported for all the parcels (red lines identify the significance threshold $p < 0.05$).

Several limitations must be noted. First, our study only examined a limited set of movements (e.g., reach-to-grasp actions with regular and perturbed kinematics). This restricts the generalizability of our findings to other movement types, such as whole-body actions or fine-motor tasks. Future studies should explore whether similar patterns of spontaneous activity emerge for different types of actions, such as tool use.

Second, investigating how spontaneous activity differs in individuals with motor impairments or atypical movement experience (e.g., amputees, athletes, musicians, or individuals with neurological conditions) could offer further insights into the plasticity of the selected networks.

Third, the time of day when fMRI data were collected may have influenced resting-state connectivity due to circadian fluctuations (Iester et al., 2023). However, in this study, participants were distributed between morning and afternoon, minimizing possible time-of-day effects on intrinsic brain activity.

Finally, our study was limited to a single resting-state scan at the beginning of the session. Future studies should incorporate multiple resting-state scans, including post-task resting-state measurements, to determine whether spontaneous activity patterns change following exposure to movement observation.

Author contributions

Conceptualization: YER, ER, VB
Methodology: YER, FG, ER, VB
Software: GH, FG
Validation: YER, FG, VB
Formal analysis: CP, LP, LZ
Investigation: YER, DS
Visualization: CP, VB
Supervision: ER, MC, VB
Writing—original draft: CP, LP, VB
Writing—review & editing: CP, LP, ER, MC, VB
Funding acquisition: VB.

CRediT authorship contribution statement

Cristina Perciballi: Writing – review & editing, Writing – original draft, Visualization, Formal analysis, Data curation. **Lorenzo Pini:** Writing – review & editing, Formal analysis. **Daniele Sili:** Investigation, Data curation. **Yara El Rassi:** Validation, Methodology, Investigation, Conceptualization. **Lu Zhang:** Formal analysis. **Giacomo Handjaras:** Software. **Federico Giove:** Writing – review & editing, Software, Methodology. **Emiliano Ricciardi:** Writing – review & editing, Methodology, Conceptualization. **Maurizio Corbetta:** Writing – review & editing, Supervision. **Viviana Betti:** Writing – review & editing, Writing – original draft, Validation, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no competing interests.

Data and code availability statement

All data needed to evaluate the conclusions in the paper are present in the paper. The fMRI data and the codes can be provided by Viviana Betti pending scientific review and a completed material transfer agreement. Requests for the data should be submitted to: viviana.betti@uniroma1.it.

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Data availability

Data will be made available on request.

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