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Task-specific changes in connectivity between parietal and occipito-temporal areas following left hemisphere stroke

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Research Article

Keywords: Lateral occipitotemporal cortex, tool and body localiser tasks, functional connectivity, Limb Apraxia

Posted Date: May 25th, 2026

DOI: https://doi.org/10.21203/rs.3.rs-9376746/v1

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Additional Declarations: No competing interests reported.

Abstract

The lateral occipitotemporal cortex (LOTC) is crucial for action understanding, including the perception of tools and bodies, and has been implicated in gesture deficits after stroke. We investigated whether left hemisphere stroke alters LOTC activity and its connectivity within perceptuo-motor networks.

Twenty-nine chronic left hemisphere stroke patients and nineteen healthy controls underwent fMRI while observing pictures of tools, bodies, non-tools, and scrambled images during a one-back task. Whole-brain analysis revealed expected activity to tools and bodies in LOTC and fronto-parietal regions, with no significant group differences in activation levels.

However, psychophysiological interaction (PPI) analysis indicated increased functional connectivity between the left inferior parietal sulcus (IPS) and left LOTC in patients when viewing tools. This enhanced connectivity correlated with poorer performance on meaningless imitation tasks.

Our findings demonstrate that left hemisphere stroke is associated with altered connectivity between parietal and occipitotemporal regions. These changes suggest post-stroke functional reorganisation within networks critical for action perception and planning that persists even after good behavioural recovery in stroke.

Introduction

The human lateral occipitotemporal cortex (LOTC) is increasingly recognised as a critical hub for the representation of action (Lingnau & Downing, 2015). Evidence from functional neuroimaging studies indicates that this region integrates the representation of perceptual, semantic and motoric features of action supporting the perception of tools and bodies, the understanding of how they typically move and the retrieval of action knowledge (Mahon & Almeida, 2024). Recent work further demonstrates its specific role in encoding hand postures and the motor-affordance of objects, situating it at the intersection of perception and action planning (Bracci & Peelen, 2013; Zhang et al., 2021). The adjacent extrastriate body area (EBA) similarly contributes to this network by selectively processing human body parts (Downing et al., 2001, Zimmermann et al., 2018). These regions have been shown to play a role in motor planning (Astafiev et al., 2004; Kühn et al., 2011) by representing the desired postural configuration necessary for actions that anticipate future states (Zimmermann et al., 2012). The functional role of these regions has been effectively mapped using established localiser tasks that dissociate responses to tools, bodies, and other object categories (Gallivan et al., 2013).

Critically, the functional properties of the LOTC and EBA are supported by their integration within a distributed fronto-parietal action network. Despite their anatomical location within the ventral stream, these regions are densely connected to dorsal stream hubs, particularly within the inferior parietal cortex (Zimmermann et al., 2018). This parietal region is a key node for action, implicated in coding the spatial relationships between body parts and objects necessary for skilled tool use and gesture (Goldenberg, 2009; Orban & Caruana, 2014; Osiurak & Badets, 2016). It is crucial for maintaining a dynamic ‘body

schema'—an integrated representation of one's body in space that is continuously updated during action planning (Wolpert D, 2005). The necessity of cross-stream interplay (Weiller et al., 2011) is evidenced by findings that virtual lesions to the parietal lobe can disrupt task-driven responses in the intact LOTC, demonstrating that dorsal and ventral streams work interactively to support object-directed action (Lee et al., 2019; Mahon & Almeida, 2024). Conversely, lesions to the LOTC itself can cause deficits in body schema and impair both the production and recognition of gestures, underscoring the strength of investigating patient populations to understand this integrated network (Moro et al., 2008; Pizzamiglio et al., 2019; Vigliocco et al., 2020). Given the established role of the left intraparietal sulcus (IPS) in tool use, gesture, and visuomotor integration (Binkofski & Buxbaum, 2013), we predicted that connectivity changes involving LOTC would particularly involve this region.

Stroke affecting the left middle cerebral artery (MCA) territory provides a powerful model to study how focal damage disrupts this integrated action network, as it commonly impacts both frontal and parietal hubs. Patients with left MCA stroke often exhibit variable difficulties with gesture production and tool use, deficits historically attributed to parietal lobe dysfunction even though lesion symptom mapping studies often fail to reveal this critical hub (Goldenberg, 2009). However, the complex relationship between lesion location and functional impairment suggests that these clinical manifestations often stem from broader network disruptions. This can be explained by processes of 'diaschisis', where a focal lesion causes functional alterations in distant, but structurally or functionally connected, brain regions (Price et al., 2010; Carrera & Tononi, 2014). This intricate interplay, along with the brain's capacity to perform a function through multiple neural routes, means that different lesion patterns can cause similar functional impairments, hindering simple one-to-one structure-function mappings (Price et al., 2010; Talozzi et al., 2023; Metaireau et al., 2024). The variable patterns of recovery observed in patients further point towards large-scale neural network reorganization (Corbetta et al., 2015).

A compelling approach to address these complexities is to move beyond lesion location and directly study how neural function and connectivity are altered in response to simple, well-controlled tasks. In this study, we investigated whether chronic left MCA stroke leads to altered representations and functional connectivity of the LOTC within action-related networks. Using an established tool and body localiser task (Gallivan et al., 2013), we probed action-related processing in a cohort of left hemisphere patients with variable limb praxis abilities compared to healthy controls. We used Psychophysiological Interactions (PPI) to investigate whether chronic stroke affecting the left MCA leads to altered connectivity between LOTC and action-related parietal networks. We hypothesised that network changes would be detectable even in patients with good behavioural recovery, suggesting that fMRI methods can reveal subclinical network-level adaptations that persists beyond overt clinical deficits.

Material and Methods

Participants

Twenty-nine right-handed patients with chronic left hemisphere middle cerebral artery (MCA) stroke and nineteen healthy volunteers were recruited to participate in this study. Patients were recruited from NHS outpatient post-stroke clinics, selected based on the presence of a left MCA stroke confirmed on imaging, being in the chronic post-stroke stage (all patients were tested within 12-62 months of stroke onset) and their ability to provide informed consent. The healthy volunteer group had no history of stroke (as confirmed by MRI).

Participant sex was recorded as female or male. Among patients, there were 11 females and 18 males (mean age 59.5 years, range 29–79). Among healthy volunteers, there were 12 females and 7 males (mean age 60.5 years, range 28–79). All participants had normal or corrected-to-normal vision and no history of other neurologic or psychiatric disease. No sex-based analyses were conducted; results should therefore be interpreted with this limitation in mind.

Ethical Approval:

Full written consent according to the declaration of Helsinki was obtained from all participants. The study was approved by the Health Research Authority, South Central – Berkshire Ethics Committee.

Procedure:

Participants attended the Oxford Centre for Magnetic Resonance Imaging at the University of Oxford in 2015-2016, where they underwent neuropsychological testing and functional brain imaging on the same day. Participants were counterbalanced in terms of whether they completed neuropsychological testing before or after imaging. Specifically 15 patients and 10 controls were tested before imaging, while 14 patients and 9 controls were tested after imaging. No significant differences in apraxia scores were found between those tested before versus after imaging (patients: $t(27) = 0.42$, $p = 0.68$; controls: $t(17) = 0.37$, $p = 0.72$).

Neuropsychological assessments

Given the proposed role of object- and body-selective regions within LOTC in action planning, we sought to relate functional imaging findings to detailed behavioural assessments of limb apraxia gesture production and imitation tasks. To this end, both healthy participants and stroke patients completed a standardised battery of limb praxis tasks originally developed as part of the Birmingham Cognitive Screen (BCOS) (Bickerton et al., 2012), conducted using their unaffected, non-dominant hand. The BCOS was selected due to its clinical validation, use of age-related cut-offs, and its development in the late Glyn Humphreys' lab, where this study was conducted (2013–2015).

Participants completed a 'gesture production' task, involving three transitive (tool-use) and three intransitive (symbolic) gestures, and a 'meaningless gesture imitation' task using hand and finger postures (Rounis et al., 2016). All gestures were videotaped and scored for both accuracy and error type, aligning with evidence from prior studies that detailed error analysis can provide important diagnostic insights (Rothi et al., 1988; Buxbaum, 2001).

Accuracy scoring followed the BCOS protocol: two points were awarded for a correct response on the first attempt, one point if correct on the second, and zero for incorrect or missing responses. Total accuracy scores (out of 12 for gesture production and 20 for meaningless imitation, both scaled to 100) were used in group-level analyses. Additionally, we performed detailed error-type analyses (e.g., body-part-as-object, internal configuration, amplitude, sequencing) to explore patterns of gesture impairment more comprehensively. A summary of the total accuracy and error rates is provided in Online Resource 1.

Two independent coders (G.P., E.R.) who were blind to participant group, scored the videos for accuracy. Inter-rater reliability (Cohen's Kappa) was 0.76 for gesture production and 0.8 for meaningless imitation in patients (average= 0.78), and 0.88 for gesture production, 0.85 for meaningless imitation in controls (average 0.86), comparable to prior work (Buxbaum et al., 2005). This approach allowed for reliable, validated scoring within a smaller cohort, acknowledging the value of detailed error taxonomies while balancing practical considerations for clinical settings.

fMRI Localiser task

Participants performed a category 'Localiser' task, already described in Gallivan et al. (Gallivan et al., 2013). Each participant completed one run of the localiser scan that included stimulus blocks of colour photographs projected onto a 2D screen consisting of 4 image types: 1) familiar **tools** (87 different identities), 2) headless **bodies** (87 different identities, 44 of which were females), 3) non-tool objects (87 different identities) and 4) scrambled versions of these same stimuli. Each image subtended 15° of the subject's visual field. To provide a fixation point, a small black circle was superimposed at the centre of each image.

The whole run lasted 6 minutes 10 seconds and was composed of six blocks for each of the 'Tools', 'Bodies', 'Non Tools' conditions, and 'Scrambled' images, and one fixation/baseline block placed at the beginning and at the end of the run. Stimulus blocks (Tools, Bodies and Non Tools) were organised into sets of three, separated by a scrambled block, balanced for block order within a single run. Stimuli were organised into separate 14.4s blocks, with 18 photos per block, presented at a rate of 400ms per photo with a 400ms inter-stimulus interval.

To encourage participants to maintain attention throughout the localiser scans, subjects performed a one-back task throughout, whereby responses were made, via a button press, whenever two successive photos were identical. The frequency of these repetitions was less than 20% of the trials. Two types of response errors were recorded: false positives and misses. False positives indicate erroneous responses when participants pressed buttons that were not corresponding to a repeating trial. Missed responses indicate that participants did not respond when there was a repeated image. Though this task was not relevant for the perceptual fMRI study, participants were excluded if their error rates were above 3 standard deviations (SD) of the group's mean.

Image acquisition

MRI data were acquired on a Siemens 3T Trio MRI scanner with a 32-channel RF head coil at the University of Oxford Centre for Clinical Magnetic Resonance Research (OCMR). Structural T1-weighted MRI images were acquired using the MP-RAGE sequence (repetition time, 2040ms; echo time 4.7ms; field of view 174×192mm^2; 192 slices; voxel size, 1×1×1mm^3). Functional images were acquired using a whole brain echo planar imaging (EPI) sequence (repetition time, 2400ms; echo time, 30ms; flip angle, 87 degrees field of view, 192×192mm^2; 41 slices; voxel size, 3×3×3.5mm^3).

Imaging data preprocessing (BIDS and fMRI prep output):

The raw DICOM data was converted into BIDS format using heudiconv (v0.12.0) The data was then pre-processed using fMRIPrep 22.0.0 (full detail can be found in Online Resource 1) (Esteban et al., 2019; Gorgolewski et al., 2011).

Briefly, the following pre-processing steps were performed on the T1: 1) corrected for intensity non-uniformity; 2) skull-stripping; 3) tissue segmentation; and 4) non-linear normalisation to MNI152NLin2009cAsym space (using cost-function masking for the stroke lesion). The following pre-processing steps were performed on the fMRI data: 1) skull stripped reference volume; 2) estimate motion parameters; 3) slice time correction (middle slice); 4) co-registered to T1; and 5) mapping to MNI152NLin2009cAsym space using one transformation step. We estimated a B0 non-uniformity map using fmriprep's fieldmap-less approach, where a deformation field is produced by co-registering the EPI reference image to the T1 (intensity inverted) by constraining deformations only along the phase-encoding direction and modulated with an average fieldmap template.

Statistical Analyses

Behavioural data Analyses

Behavioural data from the apraxia assessments and the 1-back task were analysed using independent samples t-tests to compare performance between stroke patients and healthy controls. Participants whose performance fell beyond 3 standard deviations from the group mean were excluded as outliers.

Imaging data Analyses

GLM Analyses
For each participant, the fMRI time series were subjected to General Linear Model (GLM) analysis by using SPM12 (K. J. Friston, 2011) implemented on MATLAB 2019b (The MathWorks, Inc., US). Single subject models consisted of four regressors separately describing the main effect for each of the four conditions ('Bodies', 'Tools', 'Non Tools' and 'Scrambled'). These regressors were convolved with a canonical haemodynamic response function (HRF) without derivative terms. Head motion was accounted for by adding the six head motion parameters as additional 'nuisance' regressors (K. Friston, 1994). Slow signal drifts were removed by using a 1/128Hz high-pass filter. Serial correlations were accounted for with an autoregressive AR (1) model.

In order to obtain the activity maps for bodies and tools-related processing, the subject-level contrast images for 'Bodies' vs. all other conditions (contrast weights: 3, -1, -1, -1) and 'Tools' vs. all other conditions (contrast weights: -1, 3, -1, -1) were obtained and subjected to group-level one-sample t-tests, respectively. Furthermore, we assessed differences between patients and heathy volunteers by using two-sample t-tests at the whole-brain level. We applied cluster-wise family wise error (FWE) correction for multiple comparisons at $p < 0.05$, with a cluster-forming threshold of $p<0.001$ (uncorrected) across the whole brain. Anatomical locations of the activation were labelled according to the AAL3 atlas (Rolls et al., 2020).

ROI Definition:
For PPI analysis we combined literature-based and individual functional approaches because: (a) PPI requires subject-specific seed regions with adequate signal-to-noise; (b) the intersection method ensures both anatomical validity (based on prior literature) and functional relevance (active in the individual participant); and (c) this hybrid approach is standard practice in functional ROI and connectivity studies (Friston et al., 1997; Julian et al., 2012).

The literature-based coordinates for the left LOTC (-53, -57, -3) and left EBA (-49, -72, 1) were originally reported in Talairach space (Gallivan et al., 2013). We converted these to MNI coordinates (-56, -57, -10 for the left LOTC and -50, -73, -4 for the left EBA) using the MNI2TAL tool in BioImage Suite Web (https://bioimagesuiteweb.github.io/webapp/mni2tal.html). Contralateral right hemisphere ROIs were created by mirroring these MNI coordinates (LOTC: 56, -57, -10; EBA: 50, -73, -4).

We defined spherical ROIs with a 10mm radius, a common size in the literature that provides a sufficient number of voxels for multivariate and connectivity analyses while maintaining anatomical specificity (K. J. Friston et al., 1997). We identified that the ROIs for LOTC and EBA overlapped by two voxels. These overlapping voxels were excluded from both ROIs.

Psycho-Physical interactions (PPI)

Functional connectivity changes between patients and healthy volunteers within the networks engaged in representing 'Bodies' and 'Tools' were assessed using 'Psycho-physiological Interactions' (PPI), a method first described by K. J. Friston et al., (1997). The PPI analysis explains responses in one cortical area in terms of an interaction between activity in another cortical area and the influence of an experimental condition (O'Reilly et al., 2012). We used this to test the hypothesis that connectivity between the left and right LOTC and EBA may differ between healthy volunteers and stroke patients, during representation of tools and bodies, respectively. This hypothesis is based on previous literature reporting that LOTC areas are involved in representing hand postures in object use (Gallivan et al., 2013; Zhang et al., 2021) and EBA to be involved in hand postures (Zimmermann et al., 2012).

Following our hybrid approach described in the ROI Definition Strategy (above), we combined literature-based and individual functional ROIs to create seed regions. To define a LOTC seed ROI for each participant, we located the peak voxel from the subject-level contrast of 'Tools' vs. 'Scrambled' within the

literature-based 10mm sphere for LOTC. We then created a corresponding 10mm sphere around this individual-level peak. The intersection between the single-participant and literature-based spheres was used as the final seed ROI. A similar approach was applied for the EBA, using the contrast of 'Bodies' vs. 'Scrambled'.

Three variables were created for the PPI analyses in a generalised linear model:

1. A physiological variable, representing the BOLD signal in the seed region (LOTC, EBA on the right and left hemisphere).
2. A psychological variable, corresponding to the 'Tool' or 'Bodies' effect (compared to all other conditions, as in the main effects analyses reported above).
3. A psycho-physiological interaction variable, modelling the interaction between the physiological and psychological variables.

BOLD signal was extracted from each ROI and adjusted for the effects of the four task conditions. To derive brain interactions at the neuronal level, the BOLD signal was deconvolved through a haemodynamic function before multiplication with the psychological variable to derive the interaction variable. These three PPI variables (physiological, psychological, and interaction variables) were entered into a GLM analysis, together with six head motion estimates as nuisance regressors. Subject-level images for the interaction variable were then entered into two-sample t-tests to identify differences between patients and healthy volunteers.

PPI analysis examines interactions, which are inherently orthogonal to the main effects that contribute to them, including the main effects of the seed region. For a detailed discussion on the independence of interactions in PPI analyses, see Psychophysiological and modulatory interactions in neuroimaging (K. J. Friston et al., 1997; O'Reilly et al., 2012) and precedent using this technique in previous lesion studies (Rounis et al., 2005).

Sensitivity Analyses

Patient populations commonly exhibit greater head movement during fMRI acquisition compared to healthy controls, often correlating with disease severity and cognitive load (Van Dijk et al., 2012; Siegel et al., 2014). To ensure our connectivity findings were not confounded by systematic group differences in head motion, we repeated the main PPI analysis including mean framewise displacement (FD) as an additional covariate.

Mean FD was calculated for each participant using the motion parameters generated during preprocessing, providing a summary measure of head movement throughout the scan session. This approach tests whether connectivity differences persist when controlling for overall motion magnitude, thereby distinguishing genuine neural signals from motion-related artifacts.

Connectivity-behaviour relationships

Beyond establishing group differences in connectivity, we sought to determine whether these neural changes related to behavioural performance. We used linear regression to examine associations between PPI connectivity measures and gesture task performance, including both accuracy scores and error rates for meaningless gesture imitation and meaningful gesture pantomime (Table 1). Age and total lesion volume were included as covariates.

Results

Behavioural Results

Table 1 reports the respective patient and healthy volunteer group demographics and performance in gesture imitation and production tasks. There was a significant difference in performance between the groups in the meaningless gesture imitation ($t=-3.65$, $p=0.002$) and gesture production ($t=-2.35$, $p=0.03$) tasks, respectively. The same was true with regards to performance on the 1-back task localiser. Patients showed significantly higher miss rate ($t=2.63$, $p=0.012$) and false positive rate ($t=2.22$, $p=0.033$) than healthy volunteers. One patient with outlier performance (more than 3SD) on the one-back task was excluded from further analysis.

Two patients were excluded due to failed image acquisition (inability to tolerate scanning), and one additional patient was excluded due to poor performance on the one-back task, yielding a final sample of 26 patients for analysis. The lesion overlay map for the remaining 26 patients is shown in Figure 1. The lesions in this patient sample were located on the left hemisphere, concentrated in the white matter of the frontal cortex, extending to the insula, inferior frontal, precentral and postcentral gyri, and the inferior parietal lobule. The left temporal, occipital, and bilateral cerebellum were also affected, but to a lesser extent.

Main effects

A group-level analysis investigating effects of our task conditions was performed for each participant group separately: patients (N = 26) and healthy volunteers (N = 19). Activations for ‘Tools’ 'and 'Bodies, relative to all other conditions are reported in Figure 2 and Tables 2-3. Both groups showed similar patterns of activation in expected regions, with some differences in extent and magnitude. Results were whole-brain corrected at FWE $p<0.05$, cluster-wise.

Tools activated bilateral extrastriate and medial temporal gyri including inferotemporal and lateral occipito-temporal areas, extending to the superior and inferior parietal gyri and dorsal and ventral premotor cortices in both groups. Activations showed slight left lateralisation, particularly in the ventral LOTC and dorsal parietal regions. Bodies activated LOTC extending to the extrastriate body areas with stronger right-hemisphere predominance. Between-group comparisons using two-sample t-tests revealed no significant differences at the whole-brain level (cluster-level $ps > 0.05$).

Mixed-effects ANOVA within each ROI to further explore group-level differences in stimulus-specific activation, involving a 2 (Group: patients, controls) × 2 (Condition: tools, bodies) comparison revealed significant main effects of condition at all ROIs (all p<0.05), confirming that the brain activation reliably distinguished between tool and body stimuli. No significant main effects of the group (*p*s > 0.4) or group-by-condition interactions were found [right EBA (*p* = 0.21), left EBA (*p* = 0.48), left LOTC (*p* = 0.61), right LOTC (*p* = 0.79)].

[Tables 2 and 3 here]

PPI Connectivity

Main Analysis:

PPI analysis tested whether connectivity between LOTC and other brain regions differed between groups when viewing Tools. This comparison (26 patients vs. 19 controls) revealed increased coupling between left LOTC and left Intraparietal Sulcus in patients compared to controls (peak x = -28, y= -76, z= 37, cluster size = 106 voxels, cluster-level p_{FWE} = 0.019, Figure 3).

Sensitivity Analysis:

To ensure robustness of our connectivity findings we conducted a sensitivity analysis controlling for head motion. Head motion analysis showed that mean framewise displacement (FD) was significantly greater in patients than in controls (two-sample *t*-test: t = 2.60, *p* = 0.013; patients: Mean=9.32, SD=6.27; controls: Mean=5.71, SD=3.03). Therefore, we repeated the main PPI analysis including mean FD as an additional covariate. With motion control, the left LOTC-IPS connectivity difference did not survive whole-brain cluster-level correction (p_{FWE} = 0.147) but remained significant under small-volume correction (Worsley et al., 1996) using a 10mm sphere centered at the nearest local maximum to the peak IPS identified from the main effects activation of 'Tools 'vs 'Scrambled' (peak x = -28, y= -76, z= 37, t = 4.59, peak-level p_{FWE} = 0.001). This pattern reflects the common correlation between motion and disease-related factors in patient studies, while demonstrating that motion does not fully account for the observed connectivity differences. Small-volume correction is appropriate here as it represents hypothesis-driven analysis within anatomically-constrained regions of interest, based on our a priori predictions about LOTC-IPS connectivity changes following stroke. This approach balances sensitivity for detecting theoretically-motivated effects while controlling for multiple comparisons within the specified search volume.

Additional Connectivity Analyses: Further PPIs investigating connectivity changes with right LOTC or bilateral EBA ROIs for 'Bodies' revealed no significant results.

Connectivity-Behaviour Relationships

We examined whether LOTC-IPS connectivity changes related to gesture performance in patients. Using the left IPS cluster from the whole-brain PPI analysis as an ROI, we extracted mean connectivity values

for each patient. Enhanced LOTC-IPS connectivity showed significant negative correlation with meaningless gesture imitation accuracy (β=-0.46, t=-2.20, p=0.035) and positive correlation with total errors (β=1.55, t=3.11, *p*=0.0053), controlling for age and lesion volume (Figure 3B-C). These associations remained significant when mean FD of each subject was additionally controlled for (*p*s < 0.05). This indicates higher connectivity was associated with poorer gesture imitation performance. Notably, no significant associations emerged with gesture production scores (*p*s > 0.3), demonstrating specificity to imitation rather than production processes.

Discussion

In this study we investigated the neural correlates of tool and body perception in patients with chronic left hemisphere stroke compared with healthy participants, using an established localiser task (Gallivan et al., 2013). During scanning, patients maintained adequate attention to the task (1-back accuracy: 91–94% vs. 98–99% in controls), indicating that both groups engaged reliably with the stimuli. However, outside the scanner patients demonstrated measurable impairments in meaningless gesture imitation, providing an important behavioural context in which to interpret the neuroimaging findings. This combination of preserved task engagement but impaired gesture performance allowed us to examine whether functional neuroimaging could reveal network alterations associated with apraxia despite relatively intact perceptual processing during the localiser task.

Over recent years, the lateral occipitotemporal cortex (LOTC) has been increasingly recognised for representing various aspects of action, ranging from the perception of tools and bodies to their typical movements (Lingnau & Downing, 2015). LOTC activity is thought to form representational spaces capturing perceptual, semantic, and motor dimensions of actions, reflecting how actions alter the state of the world (Chen et al., 2017; Mahon & Almeida, 2024). Consistent with this framework, overall activation levels in LOTC and the extrastriate body area (EBA) were comparable between groups, suggesting preserved basic perceptual representations. However, psychophysiological interaction analyses revealed increased functional connectivity between LOTC and the left intraparietal sulcus (L-IPS) in patients when viewing tools. These findings point to subtle but functionally meaningful alterations in the action network despite relatively preserved performance during the perceptual localiser task.

Network-level connectivity changes

The left IPS is a key component of the dorsal visuomotor system supporting the transformation of visual information into action plans, particularly for reaching and grasping movements (Rossit et al., 2013;Gallivan et al., 2013). Beyond motor control, IPS activity is also modulated by visuospatial and semantic task demands (Humphreys & Lambon Ralph, 2017; Humphreys et al., 2022). LOTC contributes to perceptual and conceptual representations of objects and actions, particularly for manipulable objects and tools (Brambati et al., 2006; Kalénine et al., 2010; Buxbaum et al., 2014; Mahon et al., 2007 ; Tranel et al., 2003 ; Wurm et al., 2017 ; Wurm & Caramazza, 2022).

The increased LOTC-IPS connectivity observed in patients likely reflects post-stroke reorganization within the action network. Studies of stroke recovery show that functional connectivity changes can reflect both adaptive compensation and maladaptive network interactions (Grefkes & Fink, 2014; Siegel et al., 2016). Increased coupling between occipitotemporal and parietal regions may therefore reflect recruitment of additional dorsal stream resources following network disruption. However, such recruitment is not necessarily beneficial: increased connectivity may also reflect inefficient processing in which additional neural resources introduce noise or interference rather than improving performance (Humphreys et al., 2022).

Nevertheless the directionality of the relationship between altered connectivity and gesture performance remains to be tested. While enhanced LOTC-IPS connectivity correlates with poorer meaningless gesture imitation, this association does not establish causation. Several scenarios could account for this relationship. First, inefficient compensatory connectivity may contribute directly to behavioural impairment, whereby attempts to recruit additional parietal resources disrupt rather than facilitate processing. Second, underlying network damage may simultaneously drive both connectivity alterations and behavioural impairments, with connectivity changes serving as a marker rather than a cause of dysfunction. Third, the cognitive demands of gesture imitation may trigger compensatory recruitment that remains insufficient for the precision required by the task. Longitudinal studies tracking connectivity from acute to chronic stages, alongside causal interventions such as targeted neuromodulation, will be necessary to clarify whether these connectivity changes represent adaptive plasticity, maladaptive reorganisation, or epiphenomena of stroke-related damage.

Clinical Implications: diaschisis and gesture impairment

These connectivity alterations can be interpreted within the framework of functional diaschisis, whereby focal lesions disrupt activity in distant but functionally connected regions within distributed networks(Carrera & Tononi, 2014). Our findings suggest that parietal damage may influence occipito-temporal representations involved in action perception, thereby affecting higher-order motor planning even when basic perceptual processing remains relatively intact.

Meaningless gesture imitation is particularly sensitive to such disruptions and is considered a more demanding measure of gesture performance than tool-use pantomime (Goldenberg, 2009 ; Achilles et al., 2016). Successful performance requires flexible selection among alternative postural configurations and the ability to represent body-part relationships independent of familiar object associations (Rounis et al., 2021). Parietal lesions disrupt both the motor planning and perceptual mechanisms necessary for anticipating and representing actions (Buxbaum et al., 2014; Sperber et al., 2019; Pizzamiglio et al., 2019; Vigliocco et al., 2020).

The parietal cortex plays a central role in encoding spatial relationships between body parts and objects and maintaining a dynamic body schema for action planning (Arbib et al., 2009; Orban & Caruana, 2014; Osiurak & Badets, 2016; Osiurak et al., 2021;Wolpert D, 2005; Gallagher & Brøsted Sørensen, 2006; Zimmermann et al., 2012). Within the perception-action framework proposed by Goodale and Milners

(1992), the dorsal occipito-parietal stream supports visuomotor transformations for action, whereas the ventral occipito-temporal stream supports object recognition. LOTC and EBA contribute to this ventral pathway by representing manipulable objects and body parts respectively (Lingnau & Downing, 2015; Zimmermann et al., 2018). The parietal cortex acts as a hub integrating these perceptual representations with motor planning and body state estimation (Shadmehr & Krakauer, 2008, Astafiev et al., 2004; Zimmermann et al., 2012; Zhang et al., 2021) and disruption of this distributed network in limb apraxia may impair both movement execution and the internal simulation of actions.

Recent studies demonstrate that connectivity patterns shape category selectivity in occipitotemporal cortex (Osher et al. 2016, Chen et al. 2017, Amaral et al., 2021, Walbrin & Almeida 2021), providing a potential mechanism through which parietal damage may alter perceptual representations via diaschisis. In our study, the association between LOTC–IPS connectivity and meaningless gesture imitation performance—replicated across both accuracy-based and error-based measures—suggests that such alterations may specifically reflect the demands of body schema representation and higher-order motor planning rather than object manipulation alone.

Beyond its theoretical implications, this work also highlights a translational aspect of network-level analyses in stroke research. Behavioural assessments of gesture and apraxia often rely on heterogeneous scoring systems and qualitative classifications that vary across studies and clinical settings. In contrast, functional connectivity measures provide quantifiable metrics that may capture subtle alterations in distributed action networks. Combining targeted localiser paradigms with connectivity analyses may therefore offer a complementary approach for tracking how action representations evolve during stroke recovery. As localiser tasks for body, hand, and tool representations become increasingly refined, they may provide a useful framework for probing representational changes longitudinally and for developing network-based markers of recovery or treatment response. Future studies incorporating more selective hand-localisers alongside larger and more heterogeneous patient samples will be important to disentangle these contributions more precisely.

Limitations

Several limitations should be considered when interpreting these findings. First, the sample size was modest (N = 26 patients), which may limit statistical power and the generalizability of the results. Second, the cohort was restricted to individuals with chronic left-hemisphere stroke, and therefore the findings may not extend to patients with right-hemisphere lesions or to earlier stages of stroke recovery. Future studies should examine how different subtypes of gesture impairment and lesion locations, including right-hemisphere strokes, influence neural tuning and connectivity within action networks. Larger and more heterogeneous cohorts will be important for determining whether the connectivity patterns observed here represent general mechanisms of post-stroke reorganisation or are specific to particular clinical profiles. Nevertheless, our results remained robust across sensitivity analyses and provide important insights into network-level changes associated with chronic stroke

Conclusion

In conclusion, our findings highlight disruptions in distributed visuomotor networks during the chronic stages following stroke. Increased functional connectivity between the lateral occipitotemporal cortex (LOTC) and the left intraparietal sulcus (L-IPS) suggests altered functional dynamics within networks linking action perception and visuomotor planning. These results support the view that gesture impairments in apraxia may arise not only from focal parietal damage but also from changes in interactions between parietal and occipito-temporal regions within distributed action systems.

More broadly, this work illustrates how network-level measures derived from functional connectivity analyses can complement behavioural assessments of gesture performance, which are often heterogeneous and partly qualitative. Combining targeted localiser paradigms with connectivity analyses may therefore provide a useful framework for tracking how action representations reorganise during stroke recovery and for identifying network-level targets for future rehabilitation research.

Declarations

Acknowledgements

We would like to thank the participants taking part in this study. We would also like to thank our funders (see below) as well as Karl Friston and Peter Zeidman for her valuable input in the PPI analyses.

Funding

This study was supported by grants from the British Medical Association and Oxford University Graduate Programme for Clinical Lecturers to Dr Elisabeth Rounis, who also currently holds a UKRI Clinical Academic Partnership with Professor Lambon Ralph and Dr Ajay Halai.

Author contributions

ZZ and ER conceived the study. ZZ performed the imaging analyses. GP and ER scored behavioural data. AH contributed to data preprocessing methodology. MLR and ER supervised the work. All authors contributed to manuscript preparation and approved the final version.

Ethics approval

Full written consent according to the Declaration of Helsinki was obtained from all participants. The study was approved by the Health Research Authority, South Central – Berkshire Ethics Committee.

Consent to participate

Informed consent was obtained from all individual participants included in the study.

Consent for publication

Participants provided consent for publication of the study findings as part of the informed consent procedure.

Competing interests

The authors have no competing interests to declare.

Data availability

The data generated and analysed during the current study are not publicly available because they include potentially identifiable participant information and ethical approval for open data sharing was not obtained. Reasonable requests for access to appropriately de-identified data may be considered by the corresponding authors, subject to institutional and ethical approvals.

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Tables

Table 1 and 2 are available in the Supplementary Files section.

Figures

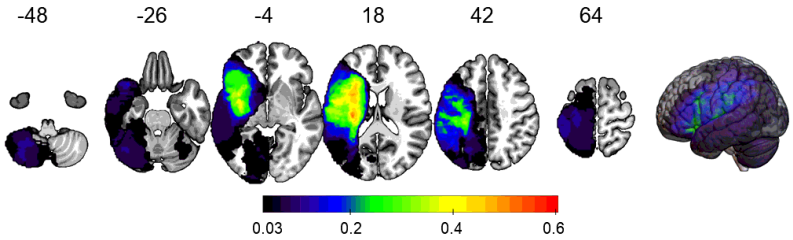

Figure 1

Lesion overlay map. The colour bar indicates the number of patients having lesions at a given voxel. The labels represent the z coordinate in the MNI space.

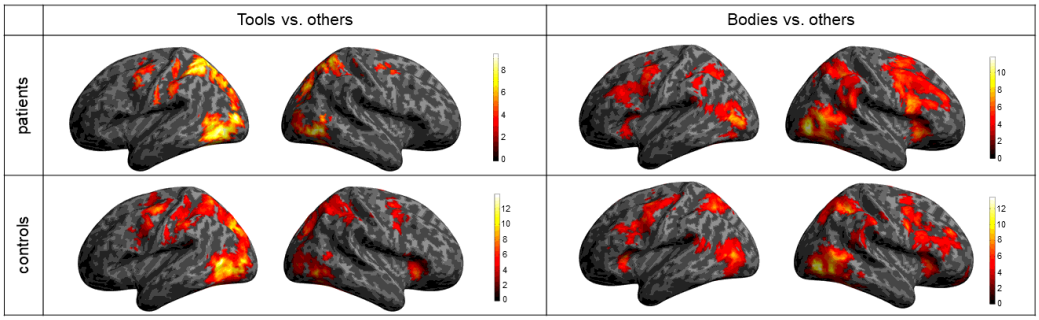

Figure 2

Lesion overlay map. The colour bar indicates the number of patients having lesions at a given voxel. The labels represent the z coordinate in the MNI space.

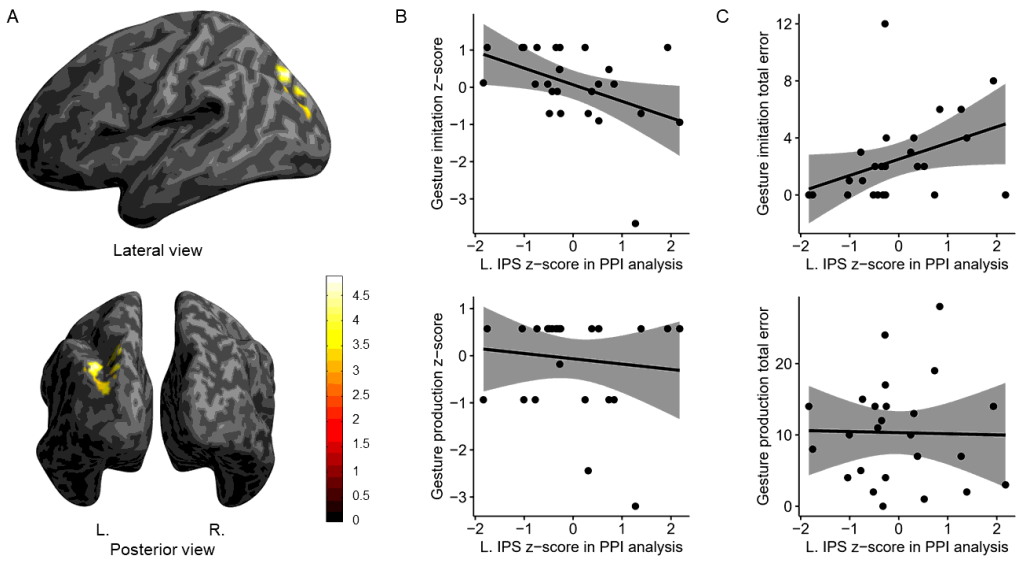

Figure 3

Results for the PPI analysis. The left lateral occipitotemporal (LOTC) was used as the source region. A cluster in the left Intraparietal sulcus (IPS) showed significantly higher connectivity with the left LOTC in patients than in healthy volunteers (A). A voxel-level threshold of $p < 0.001$ (uncorrected) and a cluster-level threshold of $p < 0.05$ (family-wise error corrected) was applied. The colour bar represents tvalues. The left IPS cluster was involved in a region-of-interest-based analysis to associate its values with patients' scores (B) and total errors (C) in the meaningless gesture imitation and gesture production tasks performed outside the scanner. Multiple regression models were applied to the patient sample, involving age and total lesion size as covariates.

Supplementary Files

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