Voxel Sensitivity to Kinematic and Object-related Features During Action Observation

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Introduction

To explain how the brain represents action, a hierarchical model of action organization has been proposed [1], according to which action-related information is represented by different brain areas from the concrete level of specific motor features to the abstract levels of goal and meaning. Evidence suggests that the functional organization of action relies on distributed overlapping representations, encompassing voxels that are tuned to specific features and carry discriminative information, while still participating in multiple representations [2,3].

Performing Representational Similarity Analysis (RSA) [4] on two independent experimental datasets, we aimed at determining the cortical organization of action features: after selecting voxels encoding transitive actions, we investigated their tuning to different stimuli dimensions and tested the generalizability of voxel responses to other stimuli and features; we also examined representational geometries at a cluster level, to highlight dominant dimensions driving stimulus representation.

Methods

Dataset 1

- 14 subjects (4 M, mean age: 37 ± 6 ys)
- **fMRI**: 3T, TR 2.5s, TE 35 ms, 3 mm isovoxel
- **Stimuli**: 120 clips of hand actions (grasp, push or putdown), on 20 objects (animate, i.e. animals or body parts, and inanimate, i.e. natural or artificial)
- **Feature space:** kinematic-based (i.e. action type), animacy, object category

Dataset 2

- 25 subjects (11 M, mean age 26 ± 4 ys)
- **fMRI**: 3T, TR 2.5s, TE 34ms, 3.8x3.8x4.6 mm
- **Stimuli**: continuous video of 72 hand actions, transitive (grasp or touch) or intransitive (symbolic or nonsense), 18 different objects, no repetition
- **Feature space:** kinematic (i.e. action type), meaning, object identity/goal-object

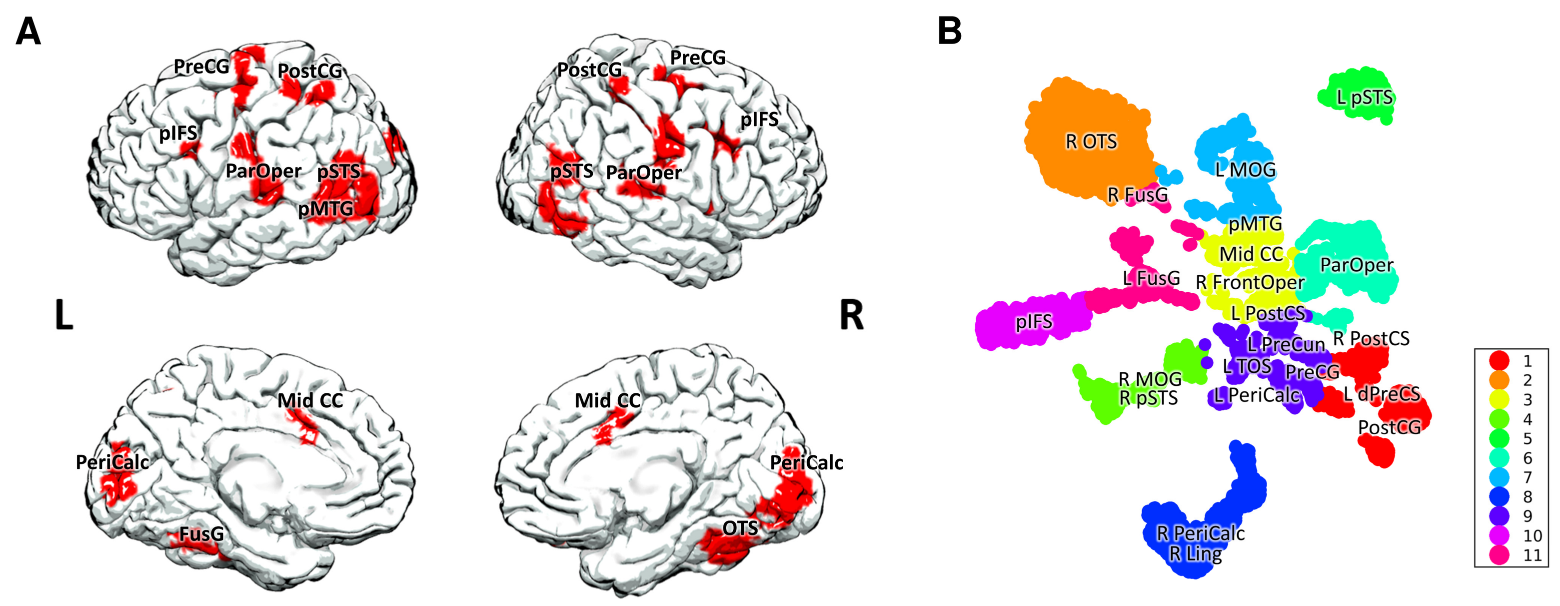
Data Analysis

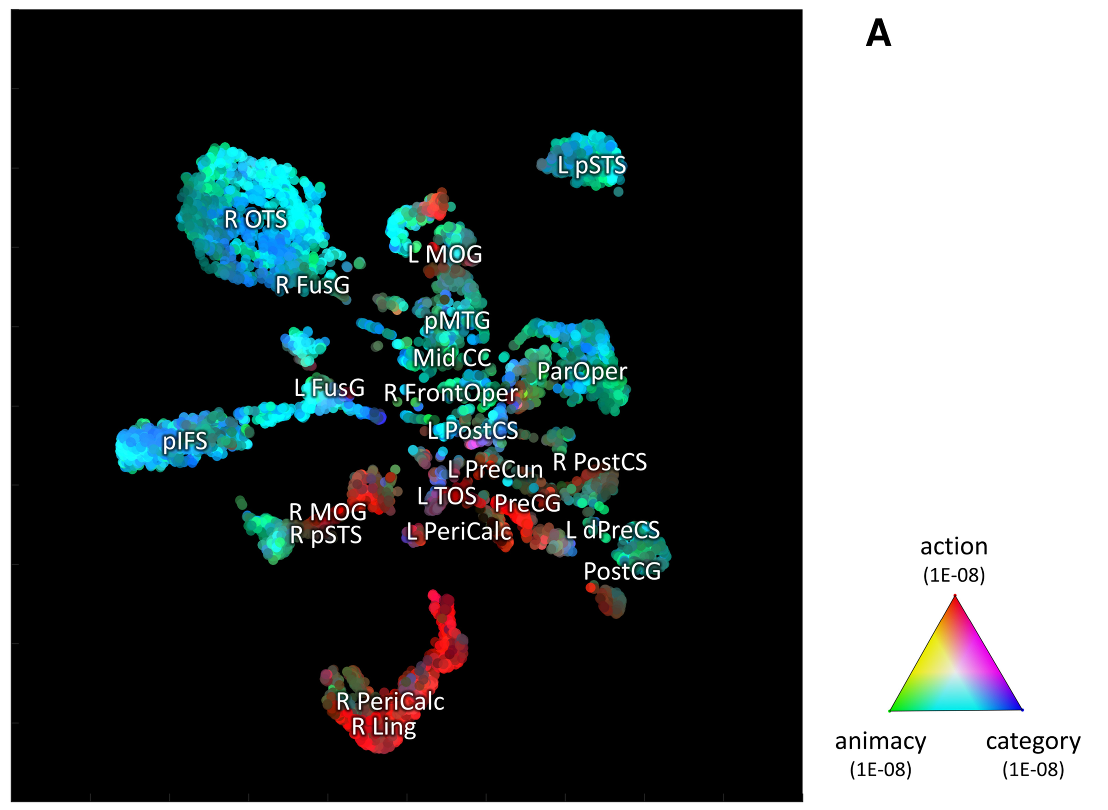
- fMRI standard preprocessing (slice timing correction, motion correction, 6 mm FWHM smoothing, signal normalization, anatomical-functional alignment, spatial normalization)
- **GLM**: separate regressors for each unique stimulus, motion parameters and outliers as nuisance regressors
- **RSA**: dissimilarity matrix (1 – r Pearson) on *t-scores* maps (median across subjects), using a volume-based searchlight approach; sensitivity index *d'* was used as a measure of discriminability between categorical dimensions of the stimuli feature space and statistical significance was tested through a Permutation test
- **Clustering**: selection of voxels with significant sensitivity for both kinematic- and object-related dimensions in dataset 1 and projection onto a 2D space using t-distributed stochastic neighbour embedding (t-SNE); *kmeans* clustering was performed to obtain a functional parcellation based on similarity of representational space
- **Voxel tuning**: mapping of p-values associated with sensitivity index *d'* onto the t-SNE space
- **MDS** to visualise representational geometry at the cluster level

Results

Voxels identified by their response to action stimuli in the first dataset match areas commonly recognized as part of the Action Observation Network (AON; fig 1A). Based on voxels functional similarity, clustering procedure identified 11 clusters, spanning anatomically distant brain regions (fig 1B).

Figure 1A. Areas showing significant sensitivity (q<0.01, FDR corrected) for both kinematic- and object-related features. **1B.** Projection of selected voxels onto a 2D embedding space: spatial distance between voxels reflects similarities in the representational space; *kmeans* algorithm identified a total of 11 clusters. *FrontOper*: frontal operculum; *OTS*: occipito-temporal sulcus; *dPreCS*: dorsal precentral sulcus; *PostCS*: dorsal postcentral sulcus; *FusG*: fusiform gyrus; *Ling*: lingual gyrus; *Mid CC*: middle cingulate cortex; *MOG*: middle occipital gyrus; *ParOper*: parietal operculum; *PeriCalc*: pericalcarine cortex; *pIFS*: posterior inferior frontal sulcus; *pMTG*: posterior middle temporal gyrus; *PostCG*: postcentral gyrus; *PostCS*: postcentral sulcus; *PreCS*: precentral sulcus; *PreCun*: precuneus; *pSTS*: posterior superior temporal sulcus; *TOS*: transverse occipital sulcus.





Mapping the relative contribution of action, animacy and category dimensions, revealed a dissociation between kinematic-based and object-based features at voxel level (fig 2A).

The same voxels were also tuned to kinematic features of a different set of stimuli (fig 2B) and showed a high specificity in their representational content as they carried information about object identity (fig 2C).

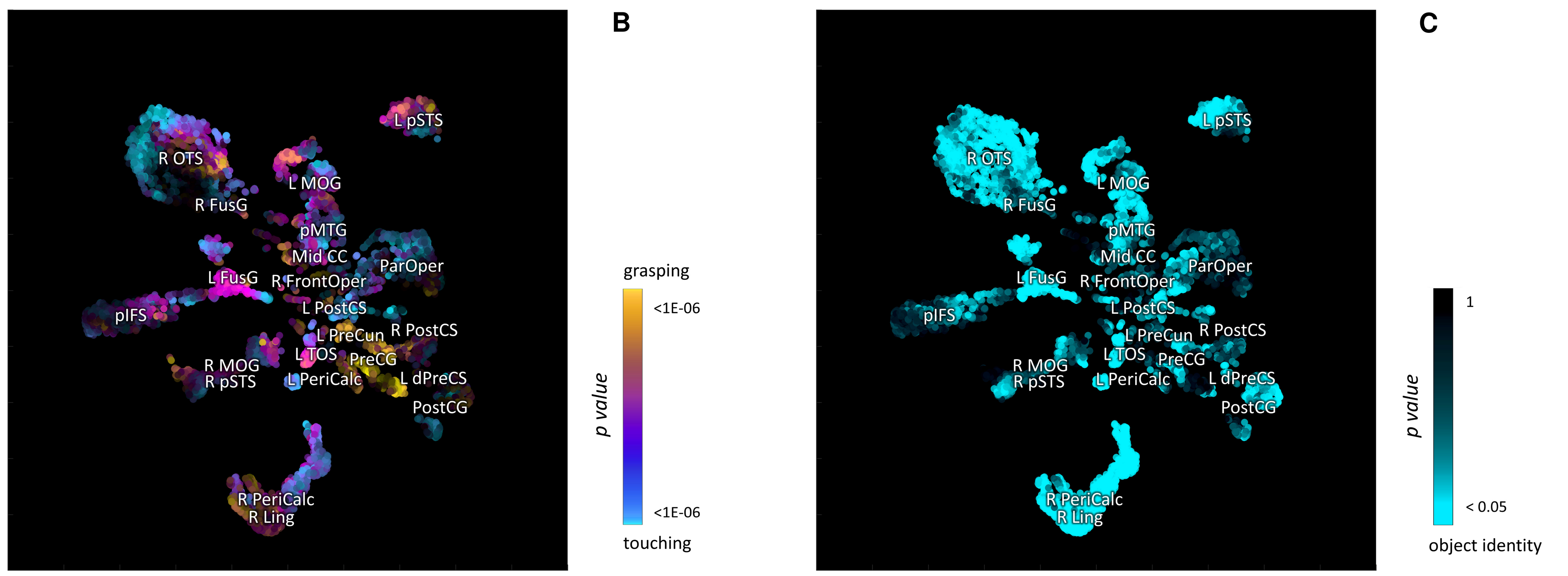
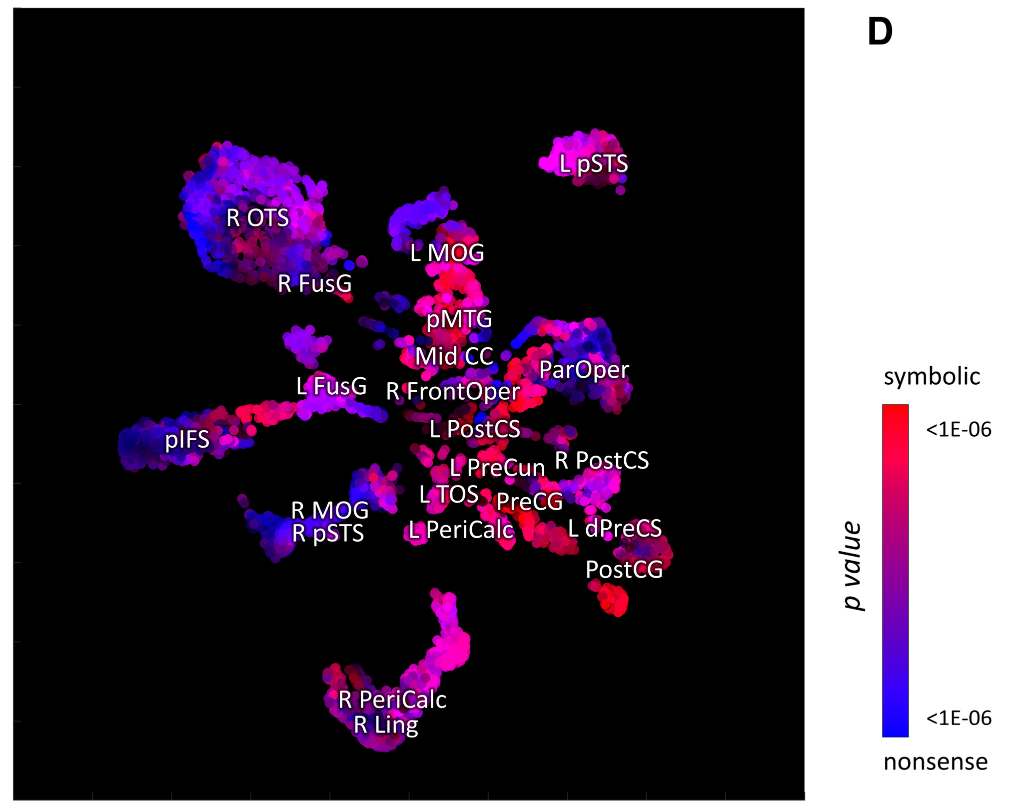


Figure 2. *p-values* associated to *d'* for each categorical dimension of the two datasets were mapped onto the same 2D space defined by the t-SNE. **A.** For dataset 1, action dimension was coded in red, animacy in green and object category in blue; maximal saturation of each channel reflects a p < 1E-08. **B**. Voxels tuning to transitive actions was further tested using the second dataset: the relative contribution of action features from grasping to touching was mapped with a colour scale ranging from yellow to magenta to cyan; maximal saturation of each channel reflects a p < 1E-06. **C**. Sensitivity to object-identity, rather than category, was also mapped and voxels associated with *p-values* < 0.05 were coloured in cyan. **D.** Sensitivity to other action dimensions (meaning of intransitive actions) was also tested and the relative contribution of from symbolic to nonsense was mapped with a colour scale ranging from red to magenta to blue; maximal saturation of each channel reflects a p < 1E-06.



Selected voxels were not specific for transitive actions but were also tuned to the feature space of intransitive actions.

Multidimensional scaling revealed the same dissociation between object- and kinematic- based features at the cluster level (fig 3).

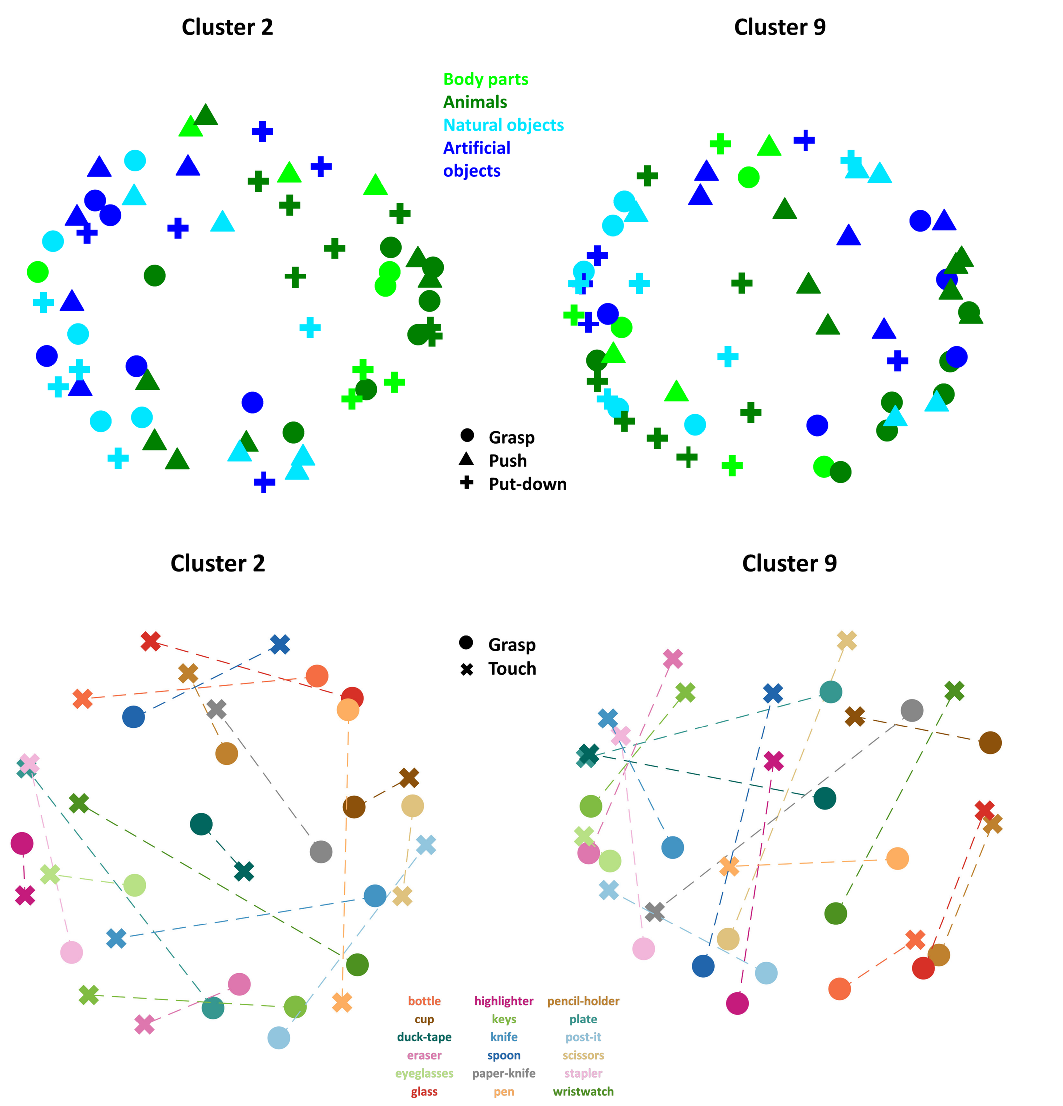


Figure 3. Multidimensional scaling performed on the RDM constructed using data from the cluster; action type is coded by symbols, while object-related information is color-coded. Euclidean distances between stimuli reflect pattern similarity. Only the two clusters with the highest *d'* for kinematic and object-related features are reported: the first row shows the representational organization of the first dataset stimuli in clusters 2 and 9, which is driven by animacy dimension (same-color markers grouped together) and action type dimension (lower spatial distance between identical symbols), respectively. In the second row, dissimilarity structure between stimuli from the second dataset is displayed: again, cluster 9 is organized primarily around kinematic-based features, as revealed by the separation in the Euclidean space between different symbols, while in cluster 2 shorter lines connecting same-object stimuli can be observe.

Conclusions

Using representational similarity analysis to explore the organization of action representation, we found that representational content similarity of voxels did not depend on their anatomical vicinity, as spatially distant cortical areas showed similar tuning to the same stimuli features. The same functional organization was present both at the voxel level and at the cluster level.

Voxels showed heterogenous tuning, encoding different features characterizing different actions; importantly, voxels selected based on their ability to discriminate transitive actions also encoded dimensions related to intransitive gestures, confirming the existence of overlapping functional representation.

Our results provide support for a hierarchical and distributed representation of action, whereby representations at different levels of the action hierarchy coexist at different spatial scales in the same brain areas.

References

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