The Brain Encyclopedia Atlas Project (BEAP): A Literature-Derived Atlas of Human Functional Neuroanatomy

Oren Poliva

Department of Neuroscience, Washington University School of Medicine in St. Louis, St. Louis, MO, USA

ABSTRACT

The neuroscience literature contains thousands of studies that localize cognitive, sensory, and motor functions to specific brain regions, yet this knowledge remains fragmented across experimental modalities, naming conventions, and spatial reference systems. Consequently, relating reported activations, lesions, or stimulation sites to the broader functional literature often requires substantial manual synthesis by individual researchers. The Brain Encyclopedia Atlas Project (BEAP) was developed to make this synthesis explicit by serving as a spatially driven index of the functional neuroanatomy literature.

BEAP is an expert-curated neuroinformatics resource that organizes literature-defined cortical and subcortical functional entities within a common anatomical framework. Cortical fields are defined by manually aligning published figures from 1,453 research articles using functional methodologies (functional neuroimaging, intracranial electrophysiology, and invasive and non-invasive cortical stimulation) to a standard anatomical template and assigning them to parcels of an established reference atlas (HCP-MMP1). Inclusion criteria require: (i) at least five functional studies associating the same area with a shared function, (ii) at least one lesion study associating loss of that function with damage to the region, and (iii) evidence for a functional boundary relative to neighboring regions. Putative connectivity annotations were derived from 475 non-human primate tract-tracing studies and mapped to human anatomy under homology assumptions. Subcortical nuclei are delineated through comparison with published histological atlases.

The resource is publicly accessible at https://brainatlas.online/3d-brain/, where users can explore an interactive three-dimensional brain and navigate from anatomical locations to structured, reference-rich encyclopedia entries documenting functional profiles, boundary rationale, internal organization, alternative nomenclature, associated clinical manifestations, and connectivity. Each entry includes an open commentary interface that supports community feedback and versioned refinement.

At whole-cortex scale, BEAP not only indexes prior findings but also makes explicit recurring organizational structure implied across the functional neuroanatomy literature. In particular, the synthesis suggests an expansion of the set of primary-like sensory cortices, a graded parietal–temporal to frontal mapping of putative connectivity, and an integrative, literature-derived framework for frontal lobe architecture organized along partially parallel gradients. These resource-enabled summaries provide a tractable framework for generating and comparing global hypotheses about cortical organization.

INTRODUCTION

Since the advent of functional magnetic resonance imaging (fMRI) more than three decades ago, the neuroscience literature has accumulated thousands of reports describing functionally specialized regions of the human cerebral cortex. These include widely recognized territories such as the primary and extrastriate visual cortices, the frontal eye field, Broca's region, and the fusiform face area. The literature also describes less commonly referenced regions, including the inferior frontal face area, the dorsal precentral speech area, and Exner's area. Many of these regions recur across task-based imaging, lesion studies, stimulation experiments, and intracranial recordings. Collectively, this body of work has produced a rich but highly fragmented body of functional localization evidence distributed across experimental modalities, historical traditions, and naming conventions.

Despite this accumulation of evidence, many literature-defined functional fields are not explicitly represented in commonly used human brain atlases. Most widely adopted atlases are organized around anatomical landmarks (gyri and sulci), cytoarchitecture, or molecular features, and therefore often provide limited support for linking atlas labels to the functional boundaries emphasized in the experimental literature (Eickhoff et al., 2018). As a result, researchers frequently rely on informal expert knowledge or ad hoc literature searches to interpret how reported activations or lesions relate to previously described functional territories. This gap reflects a broader neuroinformatics challenge: functional knowledge is abundant, but rarely indexed in a way that enables systematic spatial comparison across studies and modalities.

A major exception is the Human Connectome Project's multimodal parcellation atlas (MMP1) (Glasser et al., 2016), which integrates classical anatomical maps (e.g., Brodmann, von Economo) with MRI-derived measures such as cortical thickness, relative myelin content, resting-state connectivity, and seven task-fMRI paradigms (Glasser et al., 2016). Using this multimodal approach, the neocortex was parcellated into 180 regions per hemisphere. Although HCP-MMP1 includes several well-established functional fields (e.g., the fusiform face complex and the frontal eye field), most parcel labels are not accompanied by explicit functional descriptions. When functional descriptions are provided, they are often supported by relatively few citations and limited discussion of how the underlying evidence motivates the assigned label (see Fig. 1 for an example). Given the widespread adoption of the MMP1 atlas (cited over 5,000 times at the time of writing), there remains a clear need to systematically relate its parcels to the functional cortices described across decades of empirical research.

The present project examines whether the existing literature is sufficient to support a structured, spatially grounded index of human cortical function. Specifically, it aims to clarify how previously reported functional fields relate to anatomically defined regions by organizing the literature within a common spatial reference framework, using MMP1 as an indexing system. Rather than testing new hypotheses or proposing a novel parcellation, this work focuses on synthesizing, contextualizing, and making explicit the evidentiary basis underlying reported functional localizations.

Importantly, the Brain Encyclopedia Atlas Project (BEAP) is designed as a neuroinformatics resource that organizes the functional neuroanatomy literature to support comparison, interpretation, and reuse across studies. Specifically, the present work contributes three elements: (i) a publicly accessible encyclopedia-style atlas of literature-defined cortical fields, (ii) a transparent methodology for translating heterogeneous localization reports into a common spatial reference framework, and (iii) a synthesis of large-scale organizational patterns suggested by the integrated literature.

The results of this effort are presented in an online platform, BEAP (https://brainatlas.online/3d-brain/), a freely available resource for research and education. The platform displays cortical fields on an interactive three-dimensional human brain that users can rotate, zoom, and explore. Each field links to a dedicated encyclopedia entry synthesizing putative function, boundary-defining evidence, lesion and stimulation correlates, internal organization, connectivity annotations, alternative nomenclature, and associated pathologies, all explicitly grounded in primary sources. In addition to cortical fields, the resource includes subcortical regions delineated from histology-derived atlases.

METHODS

Overview

The Brain Encyclopedia Atlas Project (BEAP) is a whole-brain, encyclopedia-style neuroinformatics resource designed to synthesize heterogeneous functional neuroanatomical evidence into a common spatial framework. BEAP was constructed by translating figure-based localization reports from the literature into a standardized cortical and subcortical reference space. Because figure-based localization necessarily involves expert judgment, curation decisions were guided by explicit predefined decision rules to promote internal consistency and transparency.

Published figure panels, and stereotaxic coordinates when available, were aligned to canonical volumetric and surface templates and matched to parcels of an established multimodal reference atlas (MMP1). Evidence was accumulated on an area-by-area basis to delineate literature-defined functional fields. Human functional and lesion evidence was supplemented with non-human primate tract-tracing studies to derive putative connectivity annotations, and with histological studies, including those from other mammals (e.g., rodents, cats), to delineate subcortical and brainstem nuclei. For each brain region, evidence from primary studies, reviews, and meta-analyses was aggregated into structured encyclopedia-style entries. All cortical and subcortical assignments were performed by a single expert curator following the predefined decision rules.

Area-by-area curation and evidence accumulation

Curation in BEAP proceeds by aggregating evidence for one candidate region at a time. Initial studies may implicate a single MMP1 parcel or a small cluster of adjacent parcels. As additional studies are incorporated, new evidence is evaluated relative to the full spatial extent of the candidate region rather than being forced into a single-parcel assignment. This iterative process allows regional boundaries and functional descriptions to evolve as evidence accumulates. The overall curation workflow is summarized in Fig. 2.

(1) Literature identification and eligibility

A systematic literature search was conducted using Google Scholar to identify studies reporting associations between behavior and cortical activity using functional brain mapping techniques, including functional MRI (fMRI), positron emission tomography (PET), transcranial magnetic stimulation (TMS), magnetoencephalography (MEG), stereotactic EEG (sEEG), electrocorticography (ECoG), and direct electrical cortical stimulation.

Studies were eligible for inclusion only if they contained figure panels depicting the spatial location of the reported activation, lesion, stimulation site, or recording location. Coordinate-only studies were excluded because stereotaxic coordinates alone lack sufficient anatomical context to reconstruct spatial extent or boundary relationships across heterogeneous reporting conventions. Initial searches used established cortical field names as keywords. Additional studies were identified through citation tracing and relevant reviews. The search strategy was iterative: newly encountered field names and alternative nomenclature were recorded during screening and reused as search terms to increase coverage across historically inconsistent naming conventions.

Because BEAP is a curation resource rather than a reanalysis of primary data, article screening focused on identifying (i) a clearly stated functional claim and (ii) spatially localizable evidence presented in figures. Methods sections were consulted as needed to verify experimental modality and anatomical plausibility, but full evaluation of acquisition or statistical pipelines was beyond scope.

(2) Figure selection and coordinate handling

For each eligible article, the figure panel that most clearly depicted the spatial location of the reported effect was selected. When stereotaxic coordinates were reported, they were extracted to supplement figure-based localization but were not used as a substitute for figures. When coordinates and figures referred to the same or immediately adjacent cortical territory, both sources informed localization; in cases of discrepancy, figure-based localization was prioritized. Reported Talairach coordinates were converted to MNI space using the BioImage Suite online converter (https://bioimagesuiteweb.github.io/webapp/mni2tal.html).

(3) Template matching

Spatial correspondence between published figures and standard templates was established using widely adopted neuroimaging visualization software (Fig. 2C,D). Volumetric figures depicting coronal, axial, or sagittal slices were compared to the T1-weighted MNI152 template using FSLeyes, guided by global brain outline and sulcal, gyral, ventricular, and cerebellar geometry. Surface-based cortical representations or three-dimensional volumetric renderings were matched by aligning figure orientation and viewing angle to anatomical landmarks of the template brain, including the frontal, occipital, and temporal poles, the central sulcus, and the sylvian fissure, using FreeView. Spatial correspondence was treated as approximate and parcel-level rather than voxel-precise.

(4) Tiered localization procedure

Once correspondence between the published figure and the template brain was established, MMP1 parcels were visualized using either the original surface-based annotation file (Glasser et al., 2016) or a volumetric NIfTI representation of the atlas, which was developed using a custom script (Fig. 2A,B). When the effect site was readily demarcated relative to clear anatomical landmarks, parcel identification was performed directly within the visualization software without manual image alignment (e.g., associating activation within posterior Heschl's gyrus with parcel A1). In cases requiring finer alignment, parcel identification proceeded through the manual registration procedure described below.

(5) Manual registration and parcel identification

To document correspondence between published figures and reference templates, selected figures and template images with visible MMP1 parcels were imported into a graphics editing application (Autodesk SketchBook). Published figures were manually scaled and aligned to match the orientation and size of the reference brain using overall brain contours and major anatomical landmarks as anchors. Activation or lesion extents were traced on a separate layer, and the underlying MMP1 parcel labels corresponding to the traced regions were identified and recorded. This procedure allowed each study to be associated with one or more parcels while preserving the spatial extent depicted in the original publication (Fig. 2E). As studies accumulated, footprints were combined to represent the candidate region. Subsequent findings were evaluated relative to this accumulated region rather than reduced to a single-parcel label.

Lesion evidence

For lesion studies, figures depicting lesion extent were inspected. Studies involving lesions spanning entire lobes or multiple lobes were excluded due to insufficient spatial specificity. For eligible cases, lesion location and reported deficits were recorded and associated with BEAP regions whose approximate spatial extent overlapped the lesion territory. Lesion–deficit associations were documented regardless of whether they aligned with the region's putative function, allowing entries to capture both convergent and contradictory lesion evidence. For voxel-based lesion–symptom mapping studies, statistically significant lesion overlap clusters were used as localization targets, and associations were assigned only to regions intersecting those clusters.

Expansion logic, merge–split rules, and stopping criteria

A functional field was designated an official cortical field if:
(i) at least five functional studies linked the same set of parcels to a common function;
(ii) for each boundary with a neighboring region, at least one functional study (preferentially fMRI-based) demonstrated functional separation between the regions, either through dissociation of task responses or through circumscribed activation within one region but not the adjacent region; and
(iii) at least one lesion study linked loss of that function to damage involving the region (Fig. 3).

Expansion, merge, and split decisions followed predefined rules:

1. Parcels that did not satisfy the minimal criteria to be designated as a cortical field, but were strongly supported by non-human animal anatomical evidence, were retained as provisional entries and noted as requiring additional human evidence in the *Notes* section.
2. If a study extended a cortical field into an adjacent MMP1 parcel lacking an existing functional assignment, the field was expanded to include that parcel.
3. If a study extended a cortical field into a neighboring cortical field with a distinct established function, the overlapping parcel was designated a transition region and documented in the *Internal Organization* sections.
4. If fewer than five functional studies assigned a novel function to a cortical field with an already established different function, and the functional description could not reasonably be generalized to encompass both, the novel function and supporting evidence were documented in the *Notes* section.
5. If at least five functional studies reported a functionally distinct subregion within a field with consistent spatial localization, the field was split into two distinct cortical fields.
6. If at least five studies reported a functionally distinct subregion but with inconsistent spatial arrangements across studies, the region was considered to contain multiple distinct cortices supporting different functions.
7. If fewer than five studies reported functionally distinct subregions whose functions reflected nuanced variants of the broader field function, this internal organization was documented in the *Internal Organization* section.
8. If fewer than five studies reported evidence directly contradicting the established function of a region, the conflicting evidence was documented in the *Notes* section.
9. If a study assigned a novel function to a region and the functional description could be generalized to encompass both existing and novel roles, the description was updated to a more inclusive formulation.
10. If at least five functional studies and at least 1 lesion study supported a novel function incompatible with the established function, the region was treated as containing more than one cortical field.

Putative connectivity annotations

Tract tracing is an anatomical method commonly used in non-human primates to delineate connectivity by identifying the regions that provide afferent input to a region of interest (retrograde tracing) and the regions that receive its efferent output (anterograde tracing) (Felleman & Van Essen, 1991; Markov et al., 2014). This level of cellular and directional specificity is not directly captured by human neuroimaging measures such as functional connectivity or effective connectivity, which infer statistical coupling or directed interactions rather than tracing physical axonal pathways (Friston, 2011; Van Dijk et al., 2010). Consequently, tract tracing is widely regarded as the gold-standard experimental approach for mapping anatomical connectivity.

In this study, the non-human primate tract-tracing literature was surveyed to compile putative connectivity profiles. A connection was annotated as present if it was reported in at least one tract-tracing study, even if other studies did not report that connection, reflecting differences in tracer type, injection site, and sampling across reports. Putative connectivity in humans was then hypothesized by assigning a macaque homologue to each human region based on established homologies (e.g., V1, AIP, FEF) or relative anatomical position with respect to regions with established homology. Each BEAP cortical field was compared to corresponding fields in two established macaque atlases, the Pandya atlas (Fig. 4-top) and the M132 atlas (Fig. 4-middle). When homology was uncertain, the rationale for the proposed mapping, including relevant references, was documented in the *Notes* section for that region. When available, human functional imaging or cortical electrophysiology studies reporting task-related co-activation or functional connectivity were also cited as supplementary context. These connectivity profiles are intended as qualitative reference annotations to support interpretation and hypothesis generation, not as direct evidence of human structural connectivity.

Subcortical and brainstem nuclei delineation

Unlike cortical fields, subcortical and brainstem nuclei were delineated primarily using histology-based atlases, reflecting differences in data availability and the greater anatomical stability of these structures. Primary delineation was based on cross-referencing two histology-based human brain atlases: *Atlas of the Human Brain* (Mai et al., 2015) and the *Allen Human Brain Atlas* (Ding et al., 2016). When atlases agreed, nuclei were manually delineated directly on the MNI152 template using FSLeyes. When atlases disagreed or coverage was incomplete, additional peer-reviewed histological studies were consulted as tie-breakers (see Table I).

For brainstem delineation, atlas plates from an established histological atlas (Mai & Paxinos, 2011-Chpater 10) were digitized and visually aligned to corresponding MNI152 template sections using ventricular and brainstem landmarks, and nuclei were manually traced in template space (Fig. 5 Top). Several structures not reliably visible on T1-weighted MRI were localized using the Big Brain Project, which is a histological atlas that is available directly in MNI152 space (Fig. 5 Bottom) (Amunts et al., 2013). Additional nuclei, which were not reported in any of the histological atlases, but are known from the literature, were delineated by integrating anatomical descriptions relative to known nuclei, from the mammalian literature (Table II). Due to the interpretive nature of this process, subcortical nuclei should be regarded as literature-anchored approximations intended to support cross-referencing rather than definitive neuroanatomical boundaries.

Table I: Literature used as tie-breakers for subcortical nuclei:

rhinencephalon	(Seubert et al., 2013)
amygdala	(Kedo et al., 2018)
entorhinal cortex	(Schultz et al., 2012)
hippocampus	(Palomero-Gallagher et al., 2020)
striatum	(Averbeck et al., 2014)

Table II: Brainstem field added to the atlas from the literature:

Region	Reference
Barrington's nucleus	(Blanco et al., 2013)
Bötzinger and pre-Bötzinger complexes	(Schwarzacher et al., 2011)
caudal and rostral respiratory groups	(Ellenberger & Feldman, 1990)
subcoeruleus and pre-coeruleus nuclei	(Lu et al., 2006; Peever & Fuller, 2017)
medullary inhibitory area	(Karlsson & Blumberg, 2005; Peever & Fuller, 2017)
nucleus retroambiguus	(Aydogdu et al., 2001; VanderHorst et al., 2001)
riMLF (rostral interstitial nucleus of the medial longitudinal fasciculus)	(Horn & Büttner-Ennever, 2008)
inhibitory and excitatory burst neuron regions controlling ocular saccades	(Strassman et al., 1986a, 1986b),
pretectal nuclei	(Hutchins & Weber, 1985)
terminal nuclei	(Cooper & Magnin, 1987)

Data access and intended use

BEAP is publicly accessible via an interactive three-dimensional brain viewer (Fig. 7; https://brainatlas.online/3d-brain/) and as a clickable atlas interface (https://brainatlas.online/encyc/). Clicking on each region leads the user to a dedicated encyclopedia entry, which aggregates the data collected for each cortical field, including human functional studies, monkey research and tracing, and related review articles, and meta-analyses. Each encyclopedia entry was formulated using the following entries (Fig. 8):

Description.

The first 1–2 sentences provide a concise summary of the main function(s) of the region, with references to review articles, meta-analyses, and/or key primary studies that clearly illustrate these functions. Subsequent paragraphs describe, in order: (i) the afferent inputs to the region (including the type of information they likely convey), (ii) how the region appears to process or transform this information, and (iii) the principal efferent targets.

This description reflects the author's interpretation of the available data. For some controversial regions, alternative interpretations are possible and may be favored by other authors. Readers are therefore encouraged to treat this section as a guided introduction rather than a definitive statement, to consult the primary literature, and to contribute their own perspectives in the comments section.

Alternative names.

This subsection lists alternative labels used for the region of interest. These may include commonly used subregions (e.g., a known subregion of the precuneus termed the "medial parietal eye field"), larger territories that encompass the region (e.g., "inferior frontal gyrus" for

Broca’s opercular area), or functional complexes (e.g., pFs as part of the “lateral occipital complex”). Commonly used acronyms are included alongside the full names.

Correspondence with other atlases.
Here, putative homologues of the region are listed across multiple atlases. These include macaque atlases such as the Pandya atlas (Yeterian et al., 2012) and the M132 atlas (Markov et al., 2014), as well as human atlases such as MMP1 and early cytoarchitectonic atlases (Brodmann, 1909; Flechsig, 1920; Sarkissov et al., 1955; von Economo & Koskinas, 1925). Next to these atlases is an “eye” icon that, when clicked, displays the full atlas for visual comparison.

Associated pathologies.
This section lists behavioral and clinical correlates associated with lesions or atypical development involving the region of interest. It includes both individual case reports and lesion-overlap findings from larger cohorts, as well as conditions related to abnormal development (e.g., autism, schizophrenia). Each medical condition is accompanied by a brief, lay-language description of its key symptoms.

Internal organization.
This subsection summarizes studies that report functional subdivisions within the region. These studies did not meet the full criteria for defining a separate cortical field (as specified in the Methods) but nonetheless provide evidence for internal functional differentiation. Topographic maps such as somatotopy, retinotopy, and tonotopy are also described here when applicable.

Notes.
The Notes section captures relevant information that does not fit neatly into the other categories. Examples include perceptual experiences elicited by electrical stimulation, speculative or evolutionary accounts of the region’s emergence, and studies that appear to contradict or qualify the dominant functional interpretation presented in the Description.

Border demarcation.
This section documents studies, preferably fMRI-based, that clearly demarcate each of the boundaries of the region of interest and the contrasts used to reveal it. The goal is to provide practical guidance for researchers seeking to replicate or refine the boundaries used in this atlas. Border information derived from cytoarchitectonic, or molecular (e.g., genetic marker) mapping is also included here.

Connectivity.
Connectivity is organized into several subsections. First, standardized target systems that are relevant for nearly all cortical regions are summarized (e.g., dorsal thalamus, striatum, basis pontis/pontine nuclei, claustrum). Additional subsections list region-specific afferent and efferent connections, highlighting inputs and outputs that are distinctive for the cortical field in question.

Peer review and comments.

Because it is beyond the scope of a single publication to fully vet every encyclopedia entry, this responsibility is shared with the broader community of users. Readers are invited to comment on each entry, suggest corrections or improvements, and highlight additional relevant references. Unlike static journal articles, this dynamic comment system allows entries to evolve incrementally as new data and perspectives emerge.

Integration into MRI analysis pipelines

In addition to its educational role, BEAP is designed to support research by aiding the interpretation of neuroimaging findings. To this end, the atlas can be directly integrated into standard MRI analysis pipelines. At https://brainatlas.online/for-researchers/, users can download regions of interest as NIfTI files (.nii.gz) for volumetric analyses in MNI space, and as annotation files (.annot) for surface-based analyses in the fsaverage template.

Using FSLeyes, users can also load a colored lookup table (.lut file) of the atlas. Within this environment, clicking on any voxel reveals the most likely associated cortical field along with a brief functional description and a link to the corresponding encyclopedia entry for more detail.

A key caveat for research use is that the atlas indicates which cortices are most likely to lie in the vicinity of a given voxel but should not be treated as defining exact borders or locations for individual cortices in any given dataset. Researchers are encouraged to use BEAP as a functionally informed interpretive aid, rather than as a definitive parcellation of their own data.

RESULTS

Contents and scope of the BEAP resource

BEAP was constructed from spatially localizable evidence extracted from 1,928 studies, comprising 1,453 human studies and 475 non-human primate tract-tracing studies. The human evidence base comprised figures from 678 fMRI, 62 PET, 44 TMS, 36 ECoG, 39 sEEG, 65 direct electrical stimulation, 16 MEG, and 513 lesion studies. Evidence relevant to border demarcation additionally included 81 post-mortem histological studies and MRI studies examining human anatomical features (e.g., cortical thickness, myelin-density imaging). Beyond figure-based localization, the BEAP resource cites 2,134 additional articles (including meta-analyses and reviews) to support functional summaries and network-level interpretations. In total, BEAP cites 3,587 manuscripts at the time of writing.

Because BEAP is a literature-derived resource rather than an experimental dataset, the results focus on characterizing the contents, coverage, and internal consistency of the resource rather than testing specific hypotheses.

Mapping literature-defined functional entities to a common reference framework

Using the figure-to-template localization workflow (Methods; Fig. 2), the 180 parcels per hemisphere of the MMP1 reference atlas were organized into 102 BEAP cortices in the left hemisphere and 101 in the right hemisphere (108 unique cortices across both hemispheres), collectively spanning the neocortex (Fig. 6). Each BEAP cortex is linked to one or more MMP1 parcels, enabling direct interoperability with standard neuroimaging workflows while preserving the literature-defined functional identity of the region. The median number of supporting functional studies was 12 (range 3–34). Entries supported by fewer than five functional studies were retained only when strong convergent non-human anatomical evidence justified provisional inclusion (see Methods).

Several organizational patterns emerged from this mapping. First, multiple BEAP cortices were associated with more than one distinguishable function within the same approximate territory, including the fusiform face complex (FFC), posterior, anterior, and ventral insular cortices (pIns, aIns, vIns), parietal ventral cortex (PV), anterior inferior temporal lobe (aITL), posterior and central orbitofrontal cortices (OFCp, OFCc), orbital part of Broca's area (orBroca), right posterior inferior frontal gyrus (R-pIFG), anterior supplementary motor area (aSMA), and primary gustatory and viscerosensory cortex (G1), reflecting repeated reports of functional heterogeneity within these cortices. Second, in a subset of cases, the functional profile differed across hemispheres relative to the nominal left–right homologue. Examples include the following hemispheric contrasts (right / left): right anterior temporal-parietal junction (R-TPJa) / left anterior temporal-parietal junction (L-TPJa), second vestibular cortex (2V) / parietal tool area (PTA), right posterior inferior frontal gyrus (R-pIFG) / opercular part of Broca's area (opBroca)+ triangular part of Broca's area (trBroca), inferior frontal face area (IFFA) / superior Broca's area (sBroca). These asymmetries reflect both known hemispheric lateralization and differences in how functions have been described across the literature. Third, mapping literature-defined functional cortices to the MMP1 atlas revealed that many BEAP cortices correspond closely to existing parcel boundaries. However, in several regions the literature suggested functional distinctions that did not align fully with the MMP1 segmentation, including territories within auditory cortex, orbitofrontal cortex, insula, fusiform cortex, supplementary motor area, and intraparietal cortex.

Regions lacking standardized nomenclature and borderline cases

BEAP identified several functional entities that recur across the literature but lack widely standardized labels. In many cases, these entries reflect regions whose existence and approximate location are well supported by convergent evidence, but whose nomenclature has remained inconsistent across studies. BEAP assigns stable labels to these entities to support indexing and cross-referencing, while retaining alternative names and citation provenance within each encyclopedia entry. These regions were therefore assigned standardized labels under the current framework. These include: the central orbitofrontal cortex (OFCc), quantity comparison cortex (QCC), extra-striate face area (EFA), parietal tool area (PTA), posterior superior frontal gyrus (pSFG), anterior superior frontal gyrus (aSFG), and the ventral insula (vIns) and posterior insula (pIns). Novel names were also assigned to several subcortices.

In two instances, the lateral and medial entorhinal cortices (ECl and ECm**)** did not fully meet the predefined inclusion criteria for cortical designation, lacking 1-2 functional studies relative to the required threshold. Nevertheless, these regions were retained as BEAP cortices due to strong convergent evidence from non-human mammalian studies and their consistent anatomical placement relative to surrounding regions. They are therefore explicitly labeled in the *Notes* section as requiring additional human evidence. This transparency allows users to distinguish between well-established entries and those that remain provisional in the current release.

DISCUSSION

The Brain Encyclopedia Atlas Project (BEAP) is a literature-derived neuroinformatics resource designed to consolidate spatially localizable evidence about human cortical functional organization into an online encyclopedia. In the current release, BEAP incorporates figures from 1,453 primary human studies and 475 non-human primate connectivity studies, together with more than 2,000 additional review, meta-analytic, perspective and research articles used to support functional summaries and broader interpretations. This synthesis yielded 108 literature-defined cortical fields distributed across both hemispheres. BEAP is deployed as an interactive three-dimensional atlas linked to structured encyclopedia entries, intended both as an educational reference and as a practical aid for interpreting neuroimaging findings. To facilitate research use, BEAP provides downloadable atlas files and lookup tables that can be loaded in commonly used MRI viewers such as FSLeyes and FreeView, enabling voxel- and surface-level lookup of cortical fields and the evidence supporting their functional interpretation.

Although BEAP does not constitute a hypothesis-testing dataset in the conventional experimental sense, the process of synthesizing spatially localizable findings across modalities inevitably generates interpretable patterns about cortical organization. Each curated entry therefore reflects a synthesis of the available literature and can be viewed as a provisional, evidence-anchored model of a cortical field whose interpretation may evolve as new data accumulate. The discussion below focuses on three aspects of the resource: the methodological contribution of the curation framework, its relationship to existing atlases and neuroinformatics tools, and broader organizational patterns that become visible when the literature is integrated within a common spatial reference system.

Methodological contribution: an evidence-anchored curation framework

A central contribution of BEAP is the adoption of an explicit and conservative strategy for synthesizing heterogeneous functional localization evidence. Rather than imposing parcel-level assignments a priori, BEAP treats cortical fields as literature-defined entities whose spatial extent and functional characterization emerge gradually as evidence accumulates. This area-by-area approach reflects the empirical reality that many studies lack the spatial precision required for single-parcel attribution and that functional boundaries are often reported inconsistently across modalities, tasks, and experimental paradigms.

This conservatism also guides how BEAP resolves conflicts between spatial proximity and functional differentiation. Functional territories are expanded only when multiple independent studies converge on the same adjacent regions, and neighboring fields are merged by default unless consistent evidence supports functional dissociation. Spatial overlap in one functional domain is therefore not treated as sufficient grounds for unification when reliable task-based or lesion-based dissociations are present.

Importantly, BEAP distinguishes between cortical fields and finer-grained internal organization. When evidence suggests subregional specialization but falls short of supporting an independent cortical field, that structure is documented as internal organization rather than promoted prematurely. This approach avoids excessive fragmentation while preserving information that may become relevant as the literature matures.

More broadly, BEAP treats boundary uncertainty as an informative outcome rather than a methodological shortcoming. Many cortical transitions, particularly in association cortex, appear graded or context-dependent. Enforcing sharp borders where the literature does not warrant them risks misrepresenting both biological organization and evidentiary limits. By making such uncertainty explicit, BEAP aims to provide a faithful representation of the current empirical landscape.

Relationship to existing atlases and neuroinformatics tools

BEAP is designed to complement existing atlases and neuroinformatics resources rather than replace them. In particular, BEAP uses the Human Connectome Project multimodal parcellation (MMP1) as its spatial indexing framework, allowing literature-defined functional fields to be mapped onto parcels already widely used in neuroimaging workflows. In this context, MMP1 functions primarily as a coordinate system rather than as a definitive ontology of cortical function.

BEAP also differs in scope and methodology from coordinate-based meta-analytic tools such as Neurosynth and NeuroQuery. Those platforms enable powerful term-to-activation inference across large fMRI corpora, but they are necessarily limited to coordinate-reported fMRI studies and to the semantic granularity of published keywords. BEAP instead performs the complementary operation by providing a curated region-to-function synthesis grounded in figures and incorporating evidence beyond coordinate-based fMRI, including lesion studies, intracranial recordings, direct electrical stimulation, PET, TMS, and MEG.

Figure-based localization also preserves spatial context that is often lost in coordinate-only databases, including the spatial extent of activations, relationships to sulcal landmarks, and boundary contrasts between neighboring regions. These elements are frequently critical for interpreting functional specialization but are rarely recoverable from coordinates alone.

As a result, BEAP occupies a distinct niche within the neuroinformatics ecosystem. Rather than estimating pooled statistical effects for specific contrasts, it aggregates heterogeneous evidence to document functional descriptions, boundary-defining contrasts, and lesion associations for literature-defined cortical territories.

BEAP in relation to the MMP1 atlas

BEAP is designed to operate within an established neuroimaging reference framework. For this purpose, the Human Connectome Project multimodal parcellation atlas (MMP1) was adopted as the spatial indexing system for the present resource (Glasser et al., 2016). The MMP1 atlas is one of the most widely used cortical parcellations in contemporary neuroimaging and integrates multiple MRI-derived measures, including cortical thickness, relative myelin content, resting-state connectivity, and task-fMRI data, to delineate 180 parcels per hemisphere. Using MMP1 as an indexing framework allows BEAP cortical fields to be directly related to parcels commonly used in neuroimaging analyses, facilitating interoperability with existing datasets and analysis pipelines.

Across much of the cortex, the literature-defined cortices identified in BEAP correspond closely to parcel boundaries proposed in the MMP1 atlas. In these regions, multimodal MRI-based parcellation and decades of functional localization studies appear to converge on similar cortical subdivisions. This correspondence provides an independent form of validation for many MMP1 boundaries and supports the use of MMP1 as a practical indexing framework for linking atlas parcels to the functional neuroanatomy literature.

At the same time, the present synthesis highlights several instances where the functional distinctions reported in the literature do not map neatly onto existing parcel boundaries. These cases do not necessarily imply errors in the MMP1 atlas but rather illustrate how different methodological approaches can emphasize different aspects of cortical organization.

One example concerns auditory cortex. In the MMP1 atlas, associative auditory cortex along the superior temporal gyrus is subdivided into ventral-to-dorsal strips labeled A4 and A5, based largely on reductions in myelin density observed with relative myelin content imaging. The literature synthesis conducted here suggests that functional distinctions within this territory are more commonly described along a posterior–anterior axis. In particular, posterior superior temporal gyrus regions are frequently implicated in sound localization (Van der Zwaag et al., 2011), whereas more anterior and middle portions of the superior temporal gyrus are associated with pitch and phoneme perception (Bendor & Wang, 2006; DeWitt & Rauschecker, 2012). The absence of this posterior–anterior functional distinction in the MMP1 atlas is understandable given that none of the seven task-fMRI paradigms used in its construction directly evaluated auditory spatial processing.

Another example involves the orbitofrontal cortex. In the present synthesis, the parcel corresponding to posterior orbitofrontal cortex (pOFC) is associated primarily with sensory-specific motivational signals such as food-related reward (Rolls, 2008), whereas the more anterior orbitofrontal cortex is more frequently associated with valuation of abstract stimuli, including monetary or aesthetic rewards (Rolls & Grabenhorst, 2008). Evidence from cortical stimulation studies reporting olfactory or somatosensory percepts following stimulation of posterior orbitofrontal sites (Fox et al., 2018), together with functional imaging studies examining valuation of food versus non-food items (McNamee et al., 2013), suggests that the functional boundary between these regions may lie anterior to the border suggested by the MMP1 atlas.

The synthesis also highlights cases in which a single MMP1 parcel appears to encompass more than one literature-defined cortical field. For example, the parcel labeled POI2 in the MMP1 atlas appears to include two functionally related but distinct territories: a dorsal region corresponding to a primary gustatory and viscerosensory cortex (G1) and a ventral region corresponding to a more associative gustatory–olfactory cortex (G2). This distinction is supported primarily by depth-electrode recordings and stimulation studies within the insula (Isnard et al., 2004; Li et al., 2023; Ostrowsky et al., 2000), modalities that are less readily captured by conventional fMRI paradigms.

Similarly, the parcel labeled fusiform face complex (FFC) in the MMP1 atlas encompasses two face-selective regions that are consistently distinguished in the literature: a posterior occipital face area (OFA), associated with recognition of individual facial features, and a more anterior fusiform face area (FFA), involved in processing spatial relationships among facial features (Nakamura & Kubota, 1996; Pinsk et al., 2009). In BEAP, the boundary between these territories was demarcated using a probabilistic functional atlas derived from fMRI contrasts between faces and objects (Zhen et al., 2015).

In the MMP1 atlas, the supplementary motor area (SMA) is primarily associated with the SCEF parcel (supplementary and cingulate eye fields), with possible extension into the neighboring SFL parcel (superior frontal language area). Applying the present curation methodology, however, these parcels were subdivided into anterior and posterior components corresponding to anterior SMA (aSMA) and posterior SMA (pSMA). Although both subregions are broadly implicated in sequential and bilateral premotor planning (Nachev et al., 2008), the functional implementation of these processes appears to differ across the two territories. Consequently, lesions to the anterior and posterior divisions are associated with distinct clinical manifestations. The posterior SMA is more frequently associated with control of trunk and limb movements, whereas the anterior SMA is more commonly linked to control of facial, ocular, laughter, and speech-related motor patterns. This distinction parallels a similar division of labor within the lateral premotor cortex, where dorsal premotor cortex (PMDc) is preferentially involved in body movement planning and ventral premotor cortex (PMv) in planning movements of the face and mouth.

The literature synthesis also motivates reconsideration of several parcel labels proposed in the MMP1 atlas. One example concerns the auditory parcel labeled MBelt, which the MMP1 atlas identifies as homologous to the medial belt region in monkeys based on high-field fMRI evidence (Moerel et al., 2020). In contrast, the broader human literature consistently associates the region located on anterior Heschl's gyrus with the rostral primary auditory cortex (core area R), corresponding to the PAC-R designation used in BEAP (Da Costa et al., 2015; Dick et al., 2012; Formisano et al., 2003; Humphries et al., 2010; Langers, 2014; Moerel et al., 2012; Petkov et al., 2006; Saenz & Langers, 2014; Striem-Amit et al., 2011; Talavage et al., 2004; van Dijk & Langers, 2013).

Another example involves the parcel labeled VIP in the MMP1 atlas, intended to imply homology with monkey area VIP based on a surface-based registration study (Van Essen et al., 2012). That study, however, did not explicitly address human–monkey homology. BEAP corroborates VIP-like motion sensitivity in this region, corresponding to the BEAP label dIPSm

(Bremmer et al., 1997; Colby et al., 1993; Orban et al., 2006). However, motion processing in dIPSm appears more complex in humans (Orban et al., 2006), suggesting possible human-specific specialization. Moreover, neighboring regions, including dIPSa (MMP1 parcels 7AL and 7PC) and QCC (MMP1 parcels IP1 and IP2), also exhibit motion sensitivity and additional VIP-related properties. Both monkey VIP and human dIPSa respond to visual stimuli near the body (Bremmer et al., 1997; Huang et al., 2012), and both monkey VIP and human QCC are implicated in quantity estimation (Cappelletti et al., 2007; Dastjerdi et al., 2013; Montojo & Courtney, 2008; Rusconi et al., 2007; Wang et al., 2015). The BEAP synthesis therefore raises the possibility that these regions represent human-specific derivatives of a VIP-like precursor, making a one-to-one homology assignment problematic.

Finally, based on an fMRI contrast between story comprehension and mental calculation, the MMP1 atlas proposed a language-related parcel labeled the perisylvian language area (PSL), which was described as a previously unreported cortical territory. The present synthesis, however, finds substantial convergence between PSL and the sylvian–parietal temporal area (Spt), a region extensively described in prior work as active during both speech perception and speech production (Hickok et al., 2003; Hickok & Poeppel, 2007; Wise et al., 2001) and strongly associated with speech repetition (Buchsbaum et al., 2011).

Taken together, these examples illustrate how BEAP can function as a bridge between multimodal MRI–based parcellations and the broader functional neuroanatomy literature. By mapping literature-defined cortices onto an established atlas framework, BEAP enables atlas parcels to be interpreted in relation to the experimental evidence from which functional neuroanatomical concepts have historically emerged.

Organizational patterns suggested by literature synthesis

Although BEAP was not designed to test specific hypotheses about cortical organization, synthesizing spatially localizable evidence across modalities makes several recurring patterns in the literature easier to recognize. These patterns should therefore be regarded as literature-enabled hypotheses rather than conclusions derived directly from the present methodology.

Expanded notion of primary-like sensory territories

One pattern concerns the scope of primary sensory cortex. Classical accounts emphasize a limited set of primary fields such as V1, A1, and S1. The literature synthesized in BEAP suggests a broader class of “primary-like” sensory territories characterized by early ascending input, dense or early myelination, and in some cases rapid response latencies.

Examples include the motion-sensitive middle temporal cortex (MT), the parieto-insular vestibular cortex (PIVC; a sub-region of cortical field PV), the planum temporale (PT), area prostriata (ProS), and even the parietal eye field (PEF) (see complete list with references and explanation in supplementary material S2). Although these regions differ in modality and function, they share architectural and functional properties often associated with early stages of sensory processing.

Posterior association cortex to frontal cortex as a graded axis

A second pattern concerns the organization of association cortex and its relationship to frontal systems (see Fig. 10). Across parietal and temporal association regions, the literature suggests a graded posterior-to-anterior mapping of connectivity and function.

Superior parietal regions preferentially interact with caudal premotor and caudal prefrontal territories associated with sensorimotor control. Temporo-parietal junction regions interact with more central prefrontal areas involved in attentional reorienting and contextual evaluation. Lateral temporal regions project toward more anterior prefrontal territories associated with conceptual and semantic processing.

This gradient suggests that different classes of information may be routed along distinct positions of the prefrontal rostro-caudal axis. By linking curated human cortical fields to putative connectivity patterns derived from nonhuman primate tract-tracing studies, BEAP makes these relationships easier to visualize across the posterior–frontal axis.

A literature-derived framework for frontal lobe organization

The synthesis of frontal lobe literature within BEAP also highlights recurring organizational themes that are often difficult to see when studies are considered in isolation. Rather than a set of discrete modules, the evidence suggests partially parallel gradients across orbitofrontal, medial, and lateral prefrontal cortex (see Fig. 10).

Within orbitofrontal cortex, many studies describe a medial–lateral gradient in which medial regions preferentially encode reward value and positive outcomes while lateral regions are associated with punishment and avoidance. The synthesis also highlights an intermediate territory that may integrate multisensory information and contribute to exploratory evaluation of novel stimuli.

Along the medial wall, evidence suggests a ventral–dorsal gradient extending from valuation-related ventromedial prefrontal cortex toward dorsal cingulate regions associated with conflict monitoring, pain processing, and cognitive control. Intermediate zones appear to integrate motivational, emotional, and social information.

Within lateral prefrontal cortex, the literature frequently describes a rostro–caudal hierarchy in which rostral regions operate over abstract goals and relational reasoning, whereas progressively more caudal regions operate over concrete action selection and motor planning. A complementary gradient within ventrolateral prefrontal cortex appears to support linguistic planning, transforming conceptual representations into syntactic and phonological structures during speech production.

Together these gradients suggest that frontal cortex may implement multiple parallel transformations of information along motivational, cognitive, and communicative dimensions.

Practical value for research and education

BEAP is intended primarily as an interpretive resource rather than as a definitive parcellation of the cortex. Its purpose is not to impose fixed borders on individual datasets but to help researchers and students contextualize observed activations, lesions, or stimulation effects within a literature-grounded functional framework.

Each cortical field in BEAP links directly to a reference-rich encyclopedia entry summarizing convergent functional evidence, documenting boundary-defining contrasts, and listing associated lesion and stimulation correlates. This structure allows users to move directly from an observed activation pattern to the supporting literature and to evaluate alternative interpretations when they exist.

For research workflows, BEAP integrates with commonly used neuroimaging tools through volumetric NIfTI files, surface annotation files, and interactive lookup tables. These features allow cortical fields to be queried directly within visualization environments while preserving explicit links to the underlying literature.

Reliability and robustness of the curation procedure

Because BEAP is a literature-derived expert-curated resource, its credibility depends on the reliability and robustness of the curation process. Two analyses were therefore performed to examine stability of figure-to-parcel assignments and sensitivity to aggregation order.

A subset of 100 studies was re-curated approximately one year after the initial annotation, with the curator blinded to the original assignments. Concordance was highest in primary sensory and motor cortices and slightly lower in association cortex, where boundaries are often graded and localization in published figures is less precise. Most discrepancies involved adjacent parcels rather than entirely different cortical systems.

A complementary analysis evaluated robustness to the order in which studies were incorporated. Five well-studied cortical regions were re-analyzed with the same pipeline but with contributing articles randomly permuted. Across all regions examined, the core parcels associated with each cortical field remained stable, with differences largely confined to marginal parcels supported by sparse evidence.

Together these analyses suggest that the principal organizational features of the atlas are robust to reasonable variations in curation decisions.

Limitations and intended use

Several limitations inherent to the construction of BEAP should be emphasized. Spatial localization relies primarily on published figures and reported coordinates, which vary substantially in spatial resolution, smoothing, and visualization practices across studies. Consequently, cortical field boundaries should be interpreted as approximate literature-derived estimates rather than precise anatomical borders.

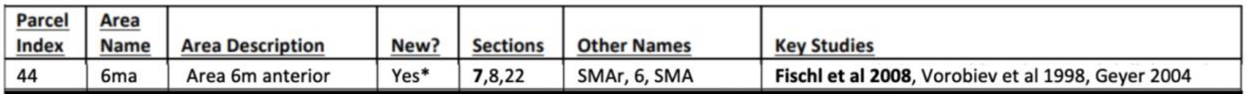
The evidence base also reflects asymmetries in the neuroscience literature. Functional domains such as vision, audition, motor control, and language are heavily represented relative to other systems, and lesion evidence is unevenly distributed across cortical regions. Study counts therefore reflect evidence density rather than functional importance.

BEAP should therefore be regarded as an interpretive aid rather than a definitive parcellation. Researchers are encouraged to combine BEAP with subject-specific analyses, task-specific localizers, and quantitative approaches when defining regions of interest.

Roadmap and versioning

BEAP is designed as a living resource that will evolve as new data emerge. The online platform supports versioned releases with stable region identifiers to maintain citability and reproducibility. Future updates will incorporate newly published studies, refine boundary annotations where evidence accumulates, and expand subcortical and brainstem coverage.

Each encyclopedia entry also includes a public comment interface that allows researchers to suggest corrections, highlight additional references, and contribute alternative interpretations. Through this combination of versioned updates and community feedback, BEAP aims to remain both stable for research use and responsive to the continuing development of the neuroscience literature.



Parcel Index	Area Name	Area Description	New?	Sections	Other Names	Key Studies
44	6ma	Area 6m anterior	Yes*	**7**,8,22	SMAr, 6, SMA	**Fischl et al 2008**, Vorobiev et al 1998, Geyer 2004

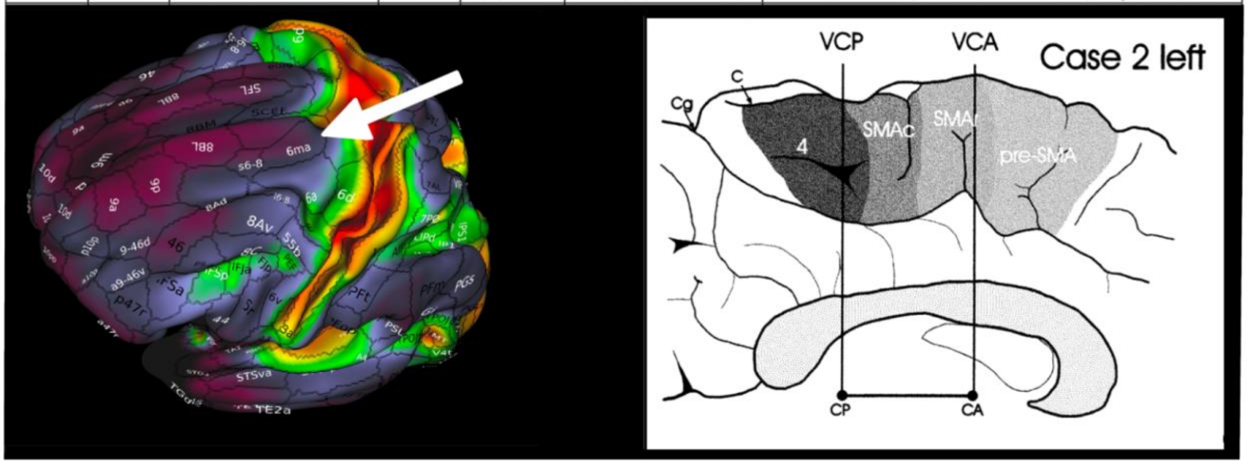


Figure 1. Example of the difficulty of linking atlas parcels to the functional neuroimaging literature.

The Human Connectome Project multimodal parcellation atlas (MMP1) divides the cortex into 180 parcels per hemisphere based on multimodal MRI measurements. However, linking these parcels to the functional neuroimaging literature is not always straightforward. An illustrative example is parcel 6ma, a small region located on the posterior portion of the superior frontal gyrus (left). In the supplementary material of Glasser et al. (2016), parcel labels are associated with supporting citations. In this case, parcel 6ma is described as part of the supplementary motor area (SMA) based on three references (top). Closer examination reveals that two of these sources (Fischl et al., 2008; Geyer, 2012) discuss the SMA only in general terms without specifying whether it extends to the lateral cortical surface. The third reference (Vorobiev et al., 1998) provides a detailed anatomical analysis of SMA boundaries but restricts its examination to the medial surface of the hemisphere (right). Consequently, the available citations do not clearly establish whether parcel 6ma should be considered part of the SMA, illustrating the broader challenge of linking atlas parcels to explicit functional evidence in the literature. Additional examples are discussed in the Discussion section.

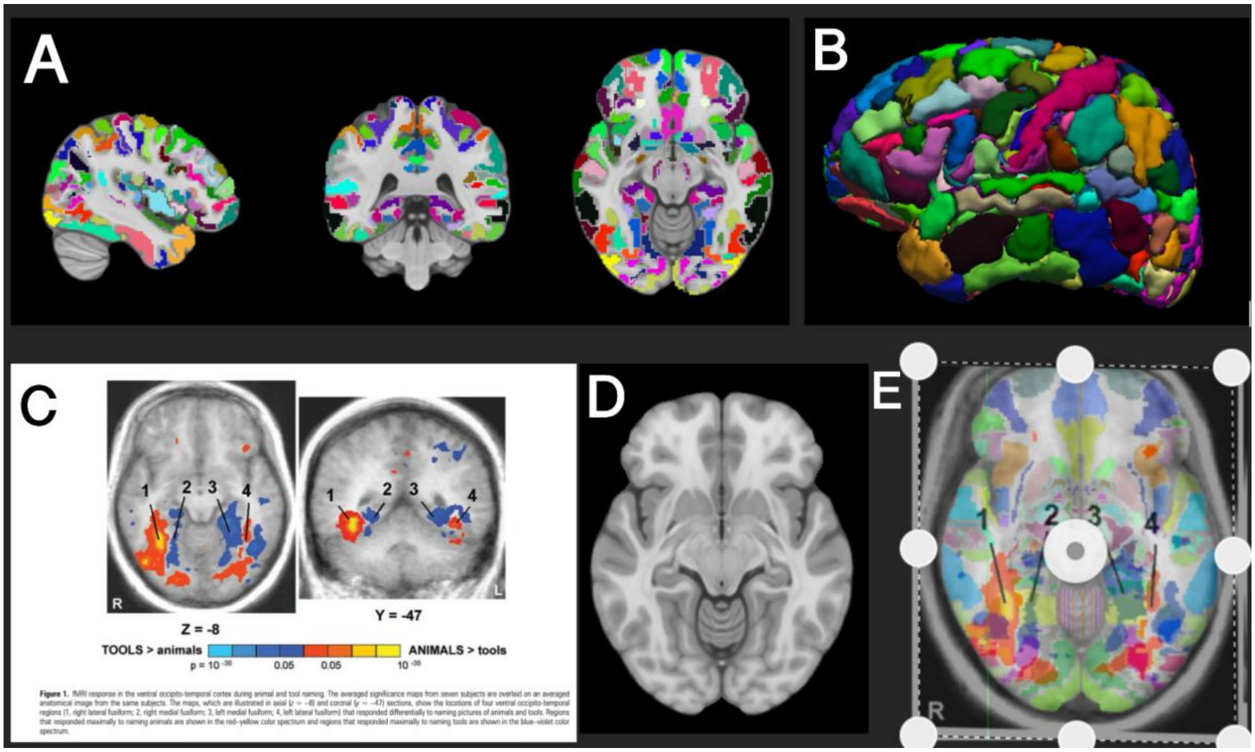


Figure 1. fMRI response in the ventral occipito-temporal cortex during animal and tool naming. The averaged significance maps from seven subjects are overlaid on an averaged anatomical image from the same subjects. The maps, which are illustrated in axial ($z = -8$) and coronal ($y = -47$) sections, show the locations of four ventral occipito-temporal regions (1, right lateral fusiform; 2, right medial fusiform; 3, left medial fusiform; 4, left lateral fusiform) that responded differentially to naming pictures of animals and tools. Regions that responded maximally to naming animals are shown in the red–yellow color spectrum and regions that responded maximally to naming tools are shown in the blue–violet color spectrum.

Figure 2. Workflow for associating MMP1 parcels with previously reported findings. Association of MMP1 parcels with previously published findings occurred in four stages. First, a custom script was used to convert the MMP1 atlas into volumetric space to enable comparison with slice-based figures from the literature (A,B). Second, figures from research articles reporting functional brain mapping results (fMRI, PET, ECoG, sEEG, MEG, TMS and cortical stimulation) were identified. As an example (C), we show a figure from Chao et al., (2002) who reported significant BOLD activation on axial and coronal slices when participants viewed animals in contrast to tools. To estimate the location of this activation, a corresponding axial slice from the MNI152 template was selected based on anatomical similarity (D). The published figure was then superimposed on the template brain and manually aligned so that major anatomical landmarks matched (E). The MMP1 parcels underlying the activation were then identified and recorded. Figure adapted from Chao et al. (2002) with permission.

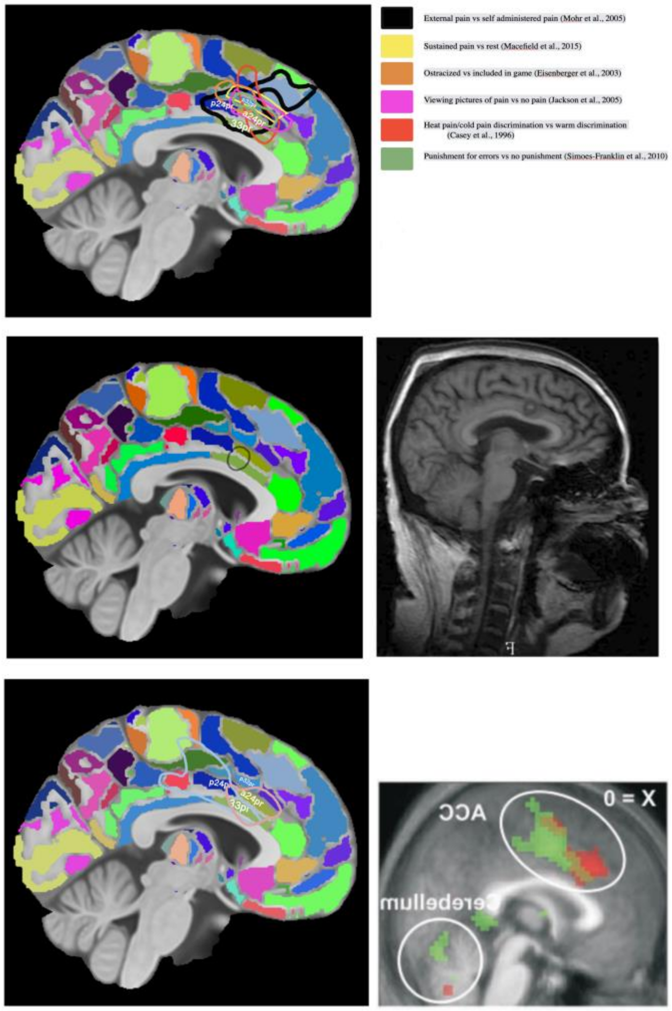


Figure 3. Criteria used to define a cortical field in the BEAP framework.
Three criteria were used to identify an MMP1 parcel, or group of parcels, as a cortical field. First, at least five functional studies using brain mapping methods (fMRI, PET, ECoG, sEEG, TMS, MEG, or cortical stimulation) had to report activation within the same parcel set associated with the same or closely related function. An example is shown for anterior middle cingulate cortex (aMCC). Using the figure-matching pipeline (Fig. 2), five fMRI studies and one PET study associated parcels a24pr and p32pr with the experience or anticipation of emotional and physical pain (top).

Second, at least one lesion study had to link damage within the same territory to disruption or loss of the same function. As an example (middle), Yen et al., (2009) reported chronic intractable pain in ten patients associated with tumors involving the middle cingulate cortex, with symptom improvement observed in six patients following tumor resection.

Third, for each of the region's borders there is at least one functional study, preferably fMRI because of its broader cortical coverage, which demonstrated a functional boundary with a neighboring region or circumscribed activation within one of the regions but not the other. In the example shown (bottom), Singer et al. (2004) reported differential activation between parcel p24p, associated with first-hand pain, and parcel a24pr, associated with empathic responses when participants observed their partner receiving a mild electric shock.

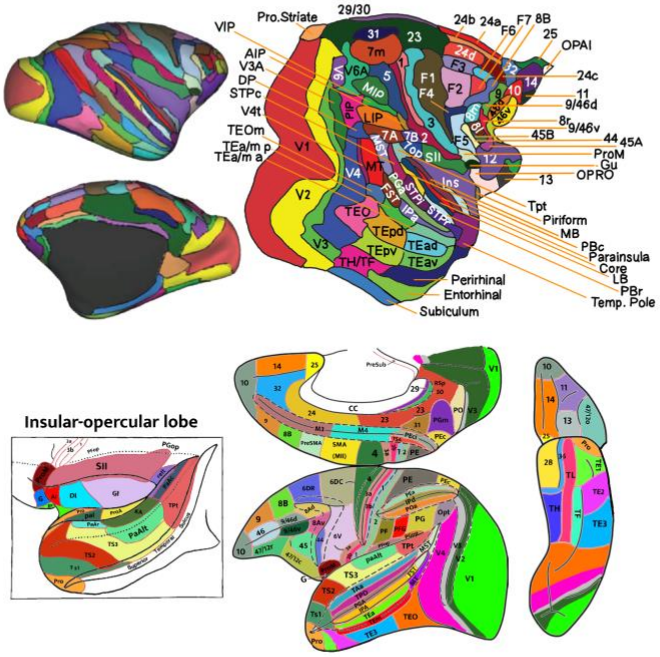


Figure 4. Assignment of putative connectivity through comparison with macaque atlases. Putative connectivity between human cortical fields was inferred by assigning candidate homologues in the macaque brain and examining their connectivity patterns in two macaque atlases commonly used in tract-tracing studies: the M132 atlas (top) (Markov et al., 2014) and the Pandya atlas (bottom) (Yeterian et al., 2012). Figures were adapted with permission from the original sources.

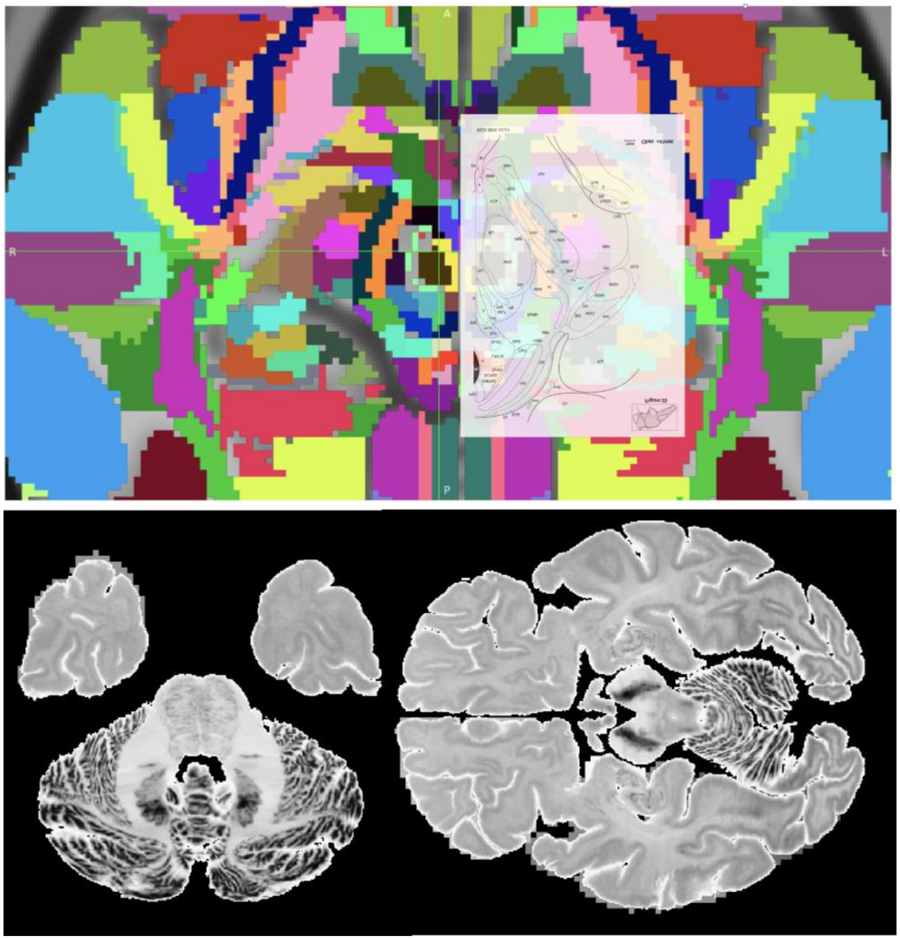


Figure 5. Delineation of brainstem and subcortical nuclei in template space.
Brainstem and subcortical nuclei were manually delineated on the MNI152 template using published illustrated atlases. **Top:** An axial section of the midbrain from a histological atlas was aligned to the corresponding MNI152 slice in FSLeyes and used to guide manual tracing of brainstem nuclei. **Bottom:** Several nuclei that are difficult to identify reliably on conventional MRI, including the substantia nigra, deep cerebellar nuclei, and the basis pontis (pontine nuclei), were delineated using the Big Brain Project (Amunts et al., 2013), which is available in MNI152 space.

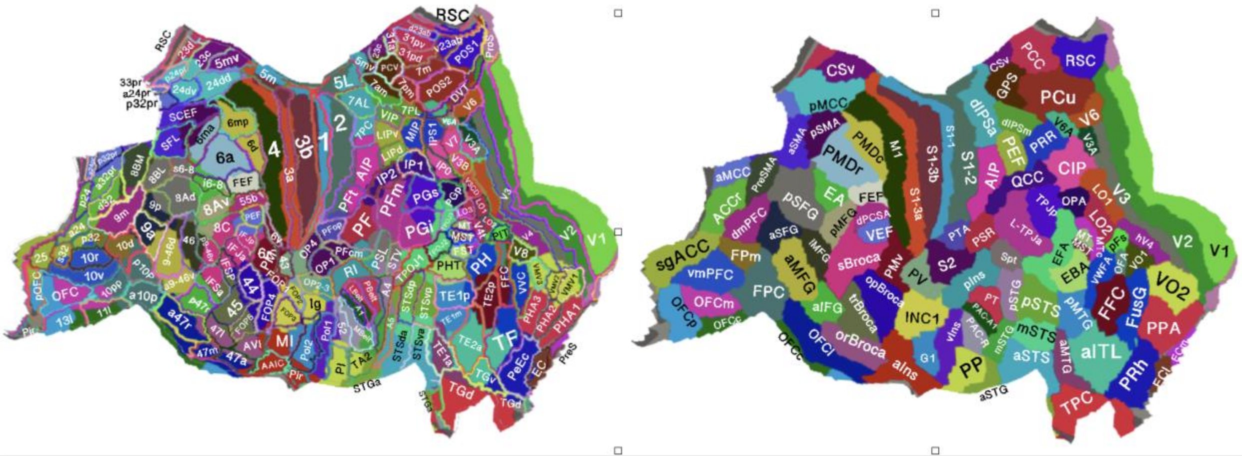
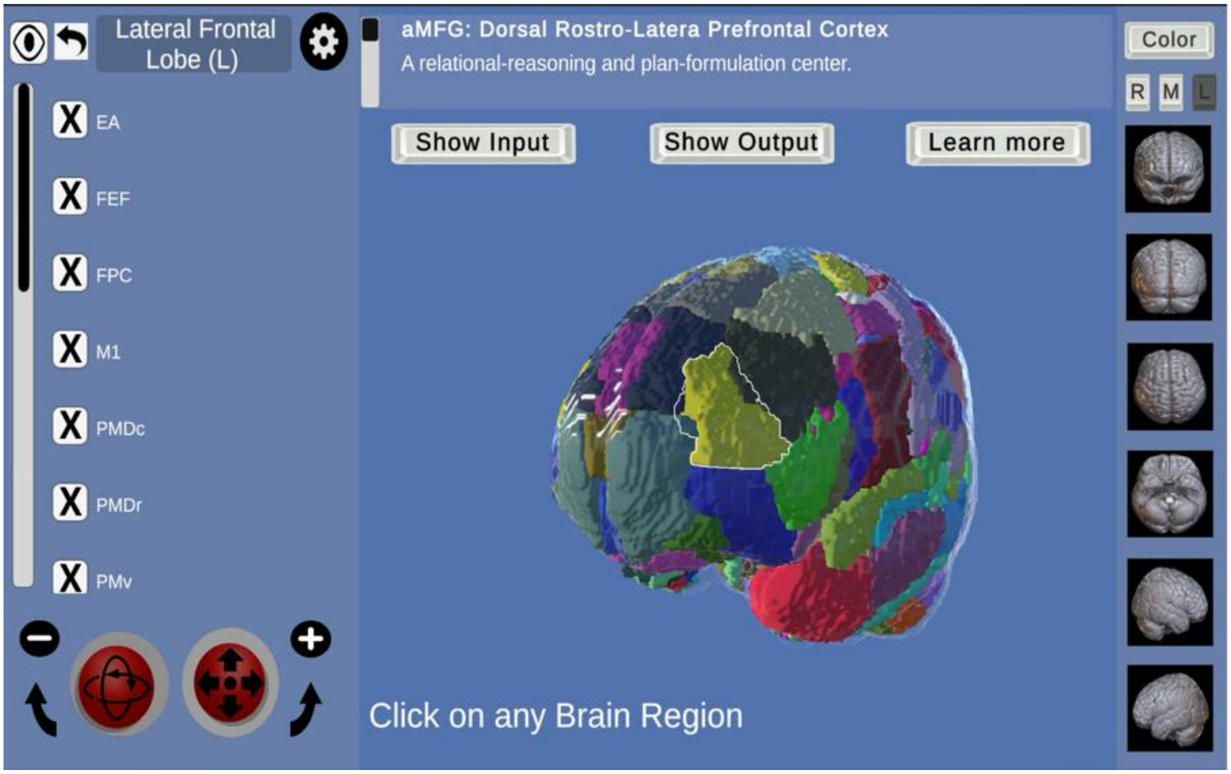


Figure 6. Correspondence between BEAP cortical fields and MMP1 parcels.
Map showing the relationship between BEAP cortical fields and MMP1 parcels in the left hemisphere, shown here as an example.

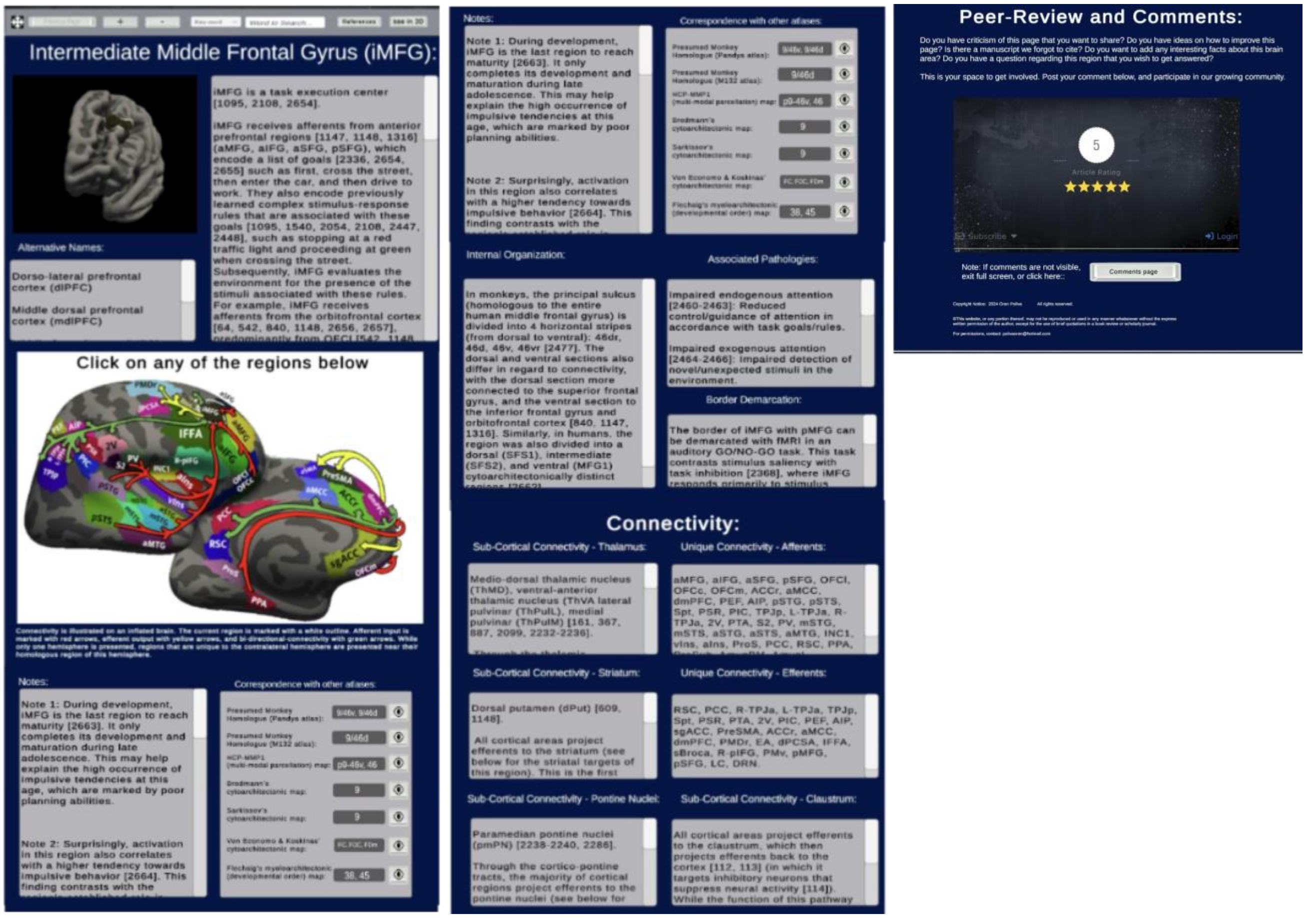


aMFG: Dorsal Rostro-Latera Prefrontal Cortex

A relational-reasoning and plan-formulation center.

Figure 7. Example of the interactive three-dimensional BEAP atlas.
Users can navigate the brain using the mouse or a virtual joystick (bottom-left panel). The right panel provides controls for selecting preset orientations, hiding the left, right, or midsagittal

portions of the brain (buttons “R,” “M,” and “L”), and toggling color labeling to display the brain in its natural appearance. The left panel allows activation or deactivation of individual brain regions. When a region with an associated encyclopedia entry is selected, a top panel appears that allows users to display regions providing input to the selected region (afferents), regions receiving output (efferents), or to open the corresponding encyclopedia entry by clicking the “Learn more” button (Fig. 8).



Intermediate Middle Frontal Gyrus (iMFG):

iMFG is a task execution center [1095, 2108, 2654].

iMFG receives afferents from anterior prefrontal regions [1147, 1148, 1316] (aMFG, aIFG, aSFG, pSFG), which encode a list of goals [2336, 2654, 2655] such as first, cross the street, then enter the car, and then drive to work. They also encode previously learned complex stimulus-response rules that are associated with these goals [1095, 1540, 2054, 2108, 2447, 2448], such as stopping at a red traffic light and proceeding at green when crossing the street. Subsequently, iMFG evaluates the environment for the presence of the stimuli associated with these rules. For example, iMFG receives afferents from the orbitofrontal cortex [64, 542, 840, 1148, 2656, 2657],

Alternative Names:

Dorso-lateral prefrontal cortex (dlPFC)

Middle dorsal prefrontal cortex (mdlPFC)

Connectivity is illustrated on an inflated brain. The current region is marked with a white outline. Afferent input is marked with red arrows, efferent output with yellow arrows, and bi-directional-connectivity with green arrows. While only one hemisphere is presented, regions that are unique to the contralateral hemisphere are presented near their homologous region of this hemisphere.

Notes:

Note 1: During development, iMFG is the last region to reach maturity [2663]. It only completes its development and maturation during late adolescence. This may help explain the high occurrence of impulsive tendencies at this age, which are marked by poor planning abilities.

Note 2: Surprisingly, activation in this region also correlates with a higher tendency towards impulsive behavior [2664]. This finding contrasts with the

Correspondence with other atlases:

Presumed Monkey Homologue (Pandya atlas):	9/46v, 9/46d
Presumed Monkey Homologue (M132 atlas):	9/46d
HCP-MMP1 (multi-modal parcellation) map:	p9-46v, 46
Brodmann's cytoarchitectonic map:	9
Sarkissov's cytoarchitectonic map:	9
Von Economo & Koskinas' cytoarchitectonic map:	FC, FDC, FDm
Flechsig's myeloarchitectonic (developmental order) map:	38, 45

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Internal Organization:

In monkeys, the principal sulcus (homologous to the entire human middle frontal gyrus) is divided into 4 horizontal stripes (from dorsal to ventral): 46dr, 46d, 46v, 46vr [2477]. The dorsal and ventral sections also differ in regard to connectivity, with the dorsal section more connected to the superior frontal gyrus, and the ventral section to the inferior frontal gyrus and orbitofrontal cortex [840, 1147, 1316]. Similarly, in humans, the region was also divided into a dorsal (SFS1), intermediate (SFS2), and ventral (MFG1) cytoarchitectonically distinct

Associated Pathologies:

Impaired endogenous attention [2460-2463]: Reduced control/guidance of attention in accordance with task goals/rules.

Impaired exogenous attention [2464-2466]: Impaired detection of novel/unexpected stimuli in the environment.

Border Demarcation:

The border of iMFG with pMFG can be demarcated with fMRI in an auditory GO/NO-GO task. This task contrasts stimulus saliency with task inhibition [2368], where iMFG

Connectivity:

Sub-Cortical Connectivity - Thalamus:

Medio-dorsal thalamic nucleus (ThMD), ventral-anterior thalamic nucleus (ThVA lateral pulvinar (ThPulL), medial pulvinar (ThPulM) [161, 367, 887, 2099, 2232-2236].

Unique Connectivity - Afferents:

aMFG, aIFG, aSFG, pSFG, OFCl, OFCc, OFCm, ACCr, aMCC, dmPFC, PEF, AIP, pSTG, pSTS, Spt, PSR, PIC, TPJp, L-TPJa, R-TPJa, 2V, PTA, S2, PV, mSTG, mSTS, aSTG, aSTS, aMTG, INC1, vIns, aIns, ProS, PCC, RSC, PPA,

Sub-Cortical Connectivity - Striatum:

Dorsal putamen (dPut) [609, 1148].

All cortical areas project efferents to the striatum (see below for the striatal targets of this region). This is the first

Unique Connectivity - Efferents:

RSC, PCC, R-TPJa, L-TPJa, TPJp, Spt, PSR, PTA, 2V, PIC, PEF, AIP, sgACC, PreSMA, ACCr, aMCC, dmPFC, PMDr, EA, dPCSA, IFFA, sBroca, R-pIFG, PMv, pMFG, pSFG, LC, DRN.

Sub-Cortical Connectivity - Pontine Nuclei:

Paramedian pontine nuclei (pmPN) [2238-2240, 2286].

Through the cortico-pontine tracts, the majority of cortical regions project efferents to the pontine nuclei (see below for

Sub-Cortical Connectivity - Claustrum:

All cortical areas project efferents to the claustrum, which then projects efferents back to the cortex [112, 113] (in which it targets inhibitory neurons that suppress neural activity [114]). While the function of this pathway

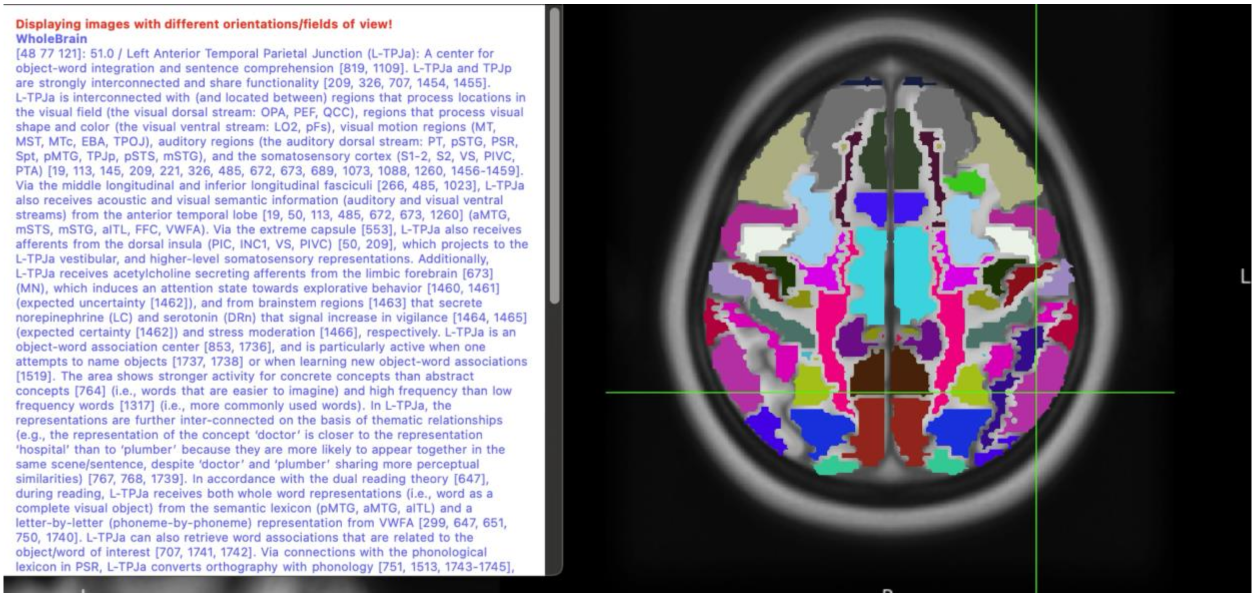
Peer-Review and Comments:

Do you have criticism of this page that you want to share? Do you have ideas on how to improve this page? Is there a manuscript we forgot to cite? Do you want to add any interesting facts about this brain area? Do you have a question regarding this region that you wish to get answered?

This is your space to get involved. Post your comment below, and participate in our growing community.

Note: If comments are not visible, exit full screen, or click here::

Figure 8. Example of a BEAP encyclopedia entry.
Selecting one of the 108 cortical fields in the three-dimensional atlas (Fig. 7) opens a dedicated encyclopedia page for that region. Each page presents a representative image and a brief functional summary, followed by sections describing alternative names, correspondence with other atlases, associated pathologies, internal organization, notes, border demarcations, and lists of connections with the dorsal thalamus, striatum, basis pontis, and region-specific afferent and efferent targets. A comment section at the bottom of the page allows users to provide feedback, suggest corrections, and recommend additional references.



Displaying images with different orientations/fields of view!

WholeBrain

[48 77 121]: 51.0 / Left Anterior Temporal Parietal Junction (L-TPJa): A center for object-word integration and sentence comprehension [819, 1109]. L-TPJa and TPJp are strongly interconnected and share functionality [209, 326, 707, 1454, 1455]. L-TPJa is interconnected with (and located between) regions that process locations in the visual field (the visual dorsal stream: OPA, PEF, QCC), regions that process visual shape and color (the visual ventral stream: LO2, pFs), visual motion regions (MT, MST, MTc, EBA, TPOJ), auditory regions (the auditory dorsal stream: PT, pSTG, PSR, Spt, pMTG, TPJp, pSTS, mSTG), and the somatosensory cortex (S1-2, S2, VS, PIVC, PTA) [19, 113, 145, 209, 221, 326, 485, 672, 673, 689, 1073, 1088, 1260, 1456-1459]. Via the middle longitudinal and inferior longitudinal fasciculi [266, 485, 1023], L-TPJa also receives acoustic and visual semantic information (auditory and visual ventral streams) from the anterior temporal lobe [19, 50, 113, 485, 672, 673, 1260] (aMTG, mSTS, mSTG, aITL, FFC, VWFA). Via the extreme capsule [553], L-TPJa also receives afferents from the dorsal insula (PIC, INC1, VS, PIVC) [50, 209], which projects to the L-TPJa vestibular, and higher-level somatosensory representations. Additionally, L-TPJa receives acetylcholine secreting afferents from the limbic forebrain [673] (MN), which induces an attention state towards explorative behavior [1460, 1461] (expected uncertainty [1462]), and from brainstem regions [1463] that secrete norepinephrine (LC) and serotonin (DRn) that signal increase in vigilance [1464, 1465] (expected certainty [1462]) and stress moderation [1466], respectively. L-TPJa is an object-word association center [853, 1736], and is particularly active when one attempts to name objects [1737, 1738] or when learning new object-word associations [1519]. The area shows stronger activity for concrete concepts than abstract concepts [764] (i.e., words that are easier to imagine) and high frequency than low frequency words [1317] (i.e., more commonly used words). In L-TPJa, the representations are further inter-connected on the basis of thematic relationships (e.g., the representation of the concept 'doctor' is closer to the representation 'hospital' than to 'plumber' because they are more likely to appear together in the same scene/sentence, despite 'doctor' and 'plumber' sharing more perceptual similarities) [767, 768, 1739]. In accordance with the dual reading theory [647], during reading, L-TPJa receives both whole word representations (i.e., word as a complete visual object) from the semantic lexicon (pMTG, aMTG, aITL) and a letter-by-letter (phoneme-by-phoneme) representation from VWFA [299, 647, 651, 750, 1740]. L-TPJa can also retrieve word associations that are related to the object/word of interest [707, 1741, 1742]. Via connections with the phonological lexicon in PSR, L-TPJa converts orthography with phonology [751, 1513, 1743-1745],

Figure 9. Integration of the BEAP atlas with FSLeyes.

The BEAP atlas can be loaded into FSLeyes using a color lookup table (.lut), enabling voxel-wise labeling. When a voxel is selected, the viewer displays the corresponding cortical field together with a brief summary of its associated function.

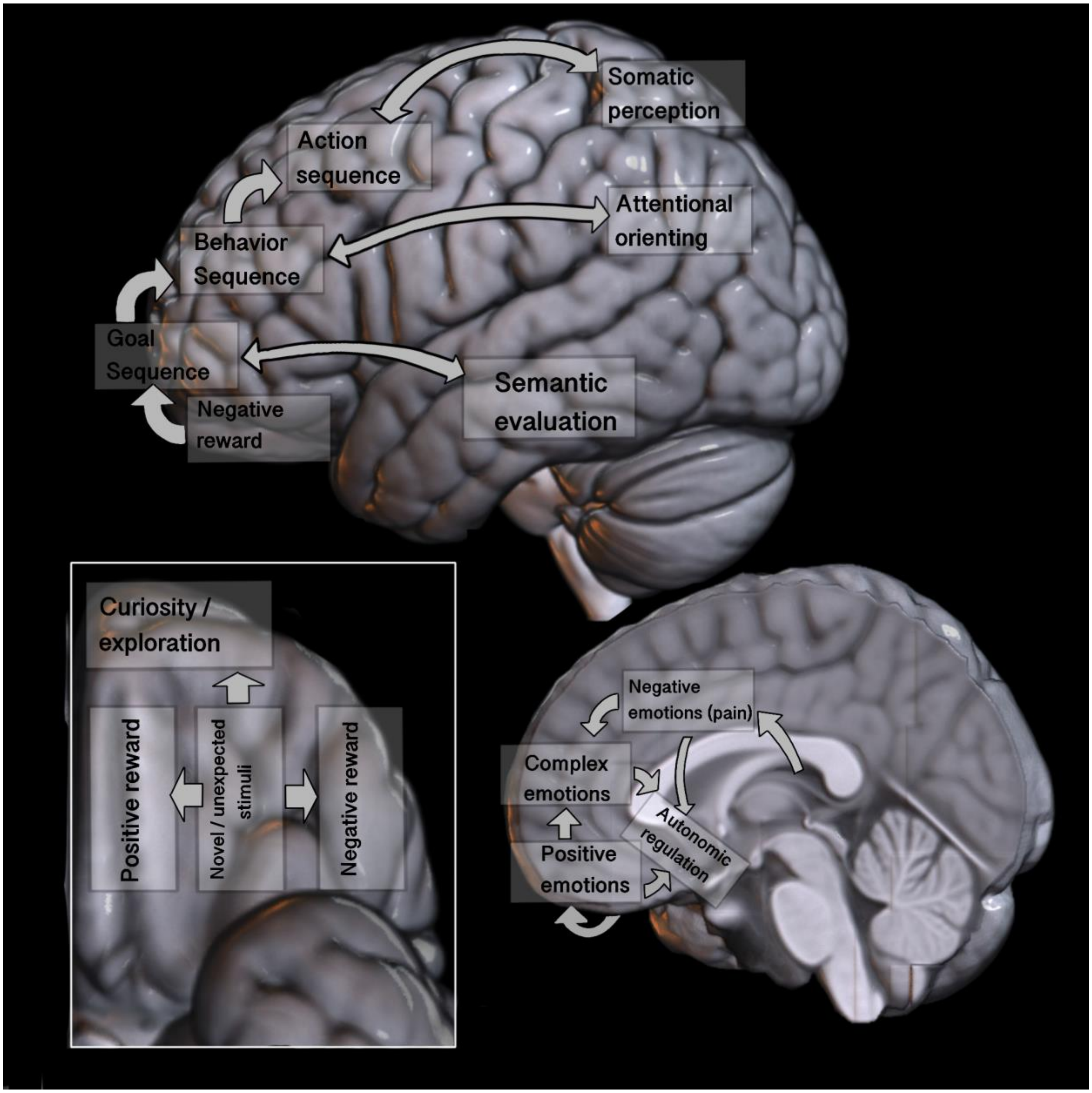


Figure 10. Parietal–frontal gradients
A visual depiction of the frontal model hierarchy as formulated by the present synthesis (see discussion for details).

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