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Accepted for publication in the Journal of Neural Engineering

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<https://doi.org/10.1088/1741-2552/ae302b>

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# Decoding Semantic Categories: Insights from an fMRI ALE Meta Analysis

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## Abstract:

*Objective:* The human brain organizes conceptual knowledge into semantic categories; however, the extent to which these categories share common or distinct neural representations remains unclear. This study aims to clarify this organizational structure by identifying consistent, modality-controlled activation patterns across several widely used and frequently investigated semantic domains in fMRI research. By quantifying the distinctiveness and overlap among these patterns, we provide a more precise foundation for understanding the brain's semantic architecture, as well as for applications such as semantic brain–computer interfaces (BCI).

*Approach:* Following PRISMA guidelines, we conducted a systematic review and meta-analysis of 75 fMRI studies covering six semantic categories: animals, tools, food, music, body parts, and pain. Using Activation Likelihood Estimation (ALE), we identified convergent activation patterns for each category while controlling for stimulus modality (visual, auditory, tactile, and written). Subsequently, Jaccard-based overlap analyses were performed to quantify the degree of neural commonality and separability across concept-modality pairs, thereby revealing the underlying structure of representational similarity.

*Main Results:* Distinct yet partially overlapping activation networks were identified for each semantic category. Tools and animals showed shared activity in the lateral occipital and ventral temporal regions, reflecting common object-based visual processing. In contrast, food-related stimuli primarily recruited limbic and subcortical structures associated with affective and motivational processing. Music and animal sounds overlapped within the superior temporal and insular cortices, whereas body parts and pain engaged occipito-parietal and cingulo-insular networks, respectively. Together, these findings reveal a hierarchically organized and modality-dependent semantic architecture in the human brain.

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1 *Significance:* This meta-analysis offers a quantitative and integrative characterization of how semantic  
2 knowledge is distributed and differentiated across cortical systems. By demonstrating how conceptual  
3 content and sensory modality jointly shape neural organization, the study refines theoretical models of  
4 semantic cognition and provides a methodological basis for evaluating conceptual separability. These  
5 insights have direct implications for semantic neural decoding and for the development of BCI systems  
6 grounded in meaning-based neural representations.

7 Keywords: Semantic Categories, fMRI Meta-Analysis, Activation Likelihood Estimation, Neural  
8 Representation, Brain-Computer Interfaces

## 9 1. Introduction

10 In everyday life, the human mind continuously deals with a vast array of semantic categories which play  
11 a fundamental role in shaping perception, reasoning, and decision-making. These categories encompass  
12 a diverse range of concepts, including but not limited to food, music, emotions, places, objects, and  
13 body-related sensations. The ability to classify and process these concepts efficiently allows humans to  
14 navigate their environment, interpret social interactions, and make informed choices. Neuroscientific  
15 research suggests that each of these concepts is encoded within specific neural networks distributed  
16 across the brain, enabling their retrieval and interpretation when needed(1).

17 Modern theories of semantic representation propose that conceptual knowledge is not stored in a  
18 single, centralized region of the brain, but rather distributed across multiple areas, including sensory and  
19 motor-related areas. Information related to perception, such as visual, auditory, and gustatory  
20 properties, is stored in the respective sensory cortices, while action-related knowledge is encoded in  
21 motor and premotor areas. For instance, visual properties such as shape and color are processed in the  
22 visual cortex; action-related features like movement are encoded in motor-related areas; and sensory  
23 properties such as taste or smell are processed in gustatory or olfactory areas, respectively(2, 3). This  
24 distributed nature of semantic representations allows the brain to activate and retrieve conceptually  
25 relevant information from multiple modalities. Consequently, encountering a word, image, or sound  
26 related to an object can trigger the activation of its corresponding semantic network, facilitating  
27 recognition and comprehension(4-6).

28 A key question in cognitive neuroscience is how different semantic categories are functionally mapped  
29 onto distinct brain regions. Research using functional magnetic resonance imaging (fMRI) has provided  
30 valuable insights into this question by revealing distinct patterns of neural activation associated with

1 specific categories(7-9). fMRI enables researchers to observe and analyze neural responses across  
2 various brain regions as participants process different types of semantic information. These studies have  
3 demonstrated that different conceptual domains elicit activity in distinct cortical and subcortical regions,  
4 supporting the idea of a distributed, yet functionally organized, neural system in the human brain that  
5 enables the encoding and representation of semantic knowledge(7, 10). Borghesani *et al.*(11) identified  
6 distinct neural activations for different semantic categories using fMRI. When comparing tools and  
7 animals, tools elicited greater activation in the bilateral fusiform gyrus, with peak coordinates at MNI (-  
8 27, -63, -12) in the left hemisphere and (30, -60, -9) in the right hemisphere. In contrast, animals  
9 produced stronger activations in a widespread occipital–parietal network. Notable peaks included the  
10 right inferior occipital gyrus (45, -75, -6), left middle occipital gyrus (-21, -99, 6), right inferior occipital  
11 gyrus (42, -51, -21), left inferior occipital gyrus (-45, -81, -6), and right precuneus (6, -51, 42). Moreover, a  
12 region-of-interest analysis in the left inferior parietal lobule (IPL) demonstrated a significant preference  
13 for tools over animals, consistent with the role of the left IPL in action-related and tool-specific semantic  
14 processing. These results support the notion that semantic category modulates cortical activation  
15 patterns, particularly in visual and sensorimotor associative regions. Charbonnier *et al.*(12) found that  
16 food choices compared to non-food choices elicited stronger activation in a network of left-lateralized  
17 brain regions. Specifically, significant clusters were observed in the left insula (-34, 12, -14), left superior  
18 temporal sulcus (-42, 12, -18), posterior cingulate gyrus (-2, -44, 22), precuneus (-6, -56, 14), and cuneus  
19 (-6, -68, 26). These regions are commonly associated with salience detection, attention, and value-based  
20 decision-making. The activation pattern suggests that food stimuli, even in the absence of hunger,  
21 engage neural systems involved in stimulus evaluation and relevance processing more strongly than non-  
22 food stimuli.

23 Understanding the neural basis of semantic categories is essential for advancing neurocognitive  
24 language processing models, refining conceptual models, and improving experimental paradigms in  
25 brain research. By systematically reviewing fMRI studies on semantic processing, our work aims to map  
26 out the neural activation patterns associated with various concepts and provide a comprehensive  
27 mapping of the brain regions involved in their processing. Identifying consistent activation patterns  
28 across studies can contribute to a more precise understanding of how the human brain organizes and  
29 retrieves semantic knowledge. Moreover, these findings have important implications for applied  
30 neuroscience, including the development of neural decoding technologies and cognitive-based  
31 applications. They can inform the design of experimental paradigms for various applications, such as BCI

1 systems, where selecting distinct and meaningful semantic concepts is crucial for optimizing  
2 performance.

3 **1.1. Rationale and Novelty of Current Work**

4 Over the past two decades, coordinate-based meta-analyses using ALE have substantially advanced our  
5 understanding of the neural architecture of semantic and conceptual representation. From the seminal  
6 synthesis by Binder *et al.*(13), which aggregated more than one hundred studies to delineate a  
7 distributed semantic system, to more focused ALE investigations of individual domains such as action  
8 concepts(14), semantic and phonemic fluency(15), or abstract versus concrete word meaning(16),  
9 research has progressively refined how conceptual knowledge is organized in the brain. Yet, despite their  
10 valuable insights, most prior ALE studies share several methodological and conceptual limitations that  
11 constrain the generalizability of their findings.

12 A first limitation concerns the restricted conceptual scope of many prior analyses. Studies reported by  
13 Watson *et al.*(14). or Wagner *et al.*(15) examined single conceptual or linguistic domains, leaving unclear  
14 how far their conclusions generalize across distinct categories. Second, and more critically, previous  
15 meta-analyses have rarely controlled for stimulus modality, that is, whether conceptual information was  
16 conveyed visually, auditorily, linguistically, or tactually. Comprehensive syntheses provided by Binder *et*  
17 *al.*(13) and Enge *et al.*(17) combined experiments employing diverse modalities and tasks, thus  
18 potentially conflating representational differences with perceptual or task-related confounds. This issue  
19 was later highlighted explicitly in methodological commentaries (e.g., Derderian *et al.*(18); Kuhnke *et*  
20 *al.*(19)), which emphasized that modality and task effects can systematically bias convergence patterns in  
21 ALE maps.

22 A third limitation lies in the domain specificity of most existing meta-analyses. For instance, Pando-  
23 Naude *et al.*(20) synthesized 130 experiments on music processing, Duerden & Albanese(21) mapped  
24 pain perception across hundreds of contrasts, and Rice *et al.*(22) explored multimodal semantics focused  
25 on the anterior temporal lobe. Each provided a detailed account of one conceptual field, yet none  
26 quantitatively compared cross-category overlap between conceptual domains. Likewise, models of  
27 semantic hierarchy proposed in recent large-scale reviews (e.g., Kuhnke *et al.*(19)) advanced integrative  
28 frameworks linking modality-specific and amodal representations, but they remained largely theoretical  
29 and did not yield actionable, discriminative mappings for applied use.

30 Methodologically, earlier work often relied on outdated ALE implementations or liberal voxel-wise  
31 thresholds, predating current best-practice recommendations emphasizing cluster-level family-wise error

1 (FWE) correction and sufficient sample size for statistical power (Eickhoff *et al.*(23); Turkeltaub *et al.*  
 2 (24)). Furthermore, few prior studies included systematic robustness or sensitivity assessments, leaving  
 3 uncertainty about the reliability of reported convergence.  
 4 The present study addresses these gaps through a comprehensive, modality-controlled ALE meta-  
 5 analysis that simultaneously expands the conceptual range and tightens methodological rigor. We  
 6 synthesized 75 fMRI experiments published up to September 2024, encompassing six distinct conceptual  
 7 domains: animals, tools, food, music, pain, and body parts. To eliminate confounding modality effects,  
 8 we conducted independent ALE analyses for each concept–modality pair (e.g., Animals-Visual, Music-  
 9 Auditory, Pain-Tactile), following PRISMA guidelines for systematic search and screening. Analyses  
 10 employed GingerALE 3.0.2, with cluster-level FWE correction ( $p < 0.05$ ), an additional voxel-level  
 11 threshold ( $p < 0.01$ ), and MNI-to-Talairach coordinate conversion, ensuring alignment with the most  
 12 stringent methodological standards.  
 13 Beyond replication of canonical semantic clusters, we introduced a novel quantitative measure of inter-  
 14 domain similarity using the Jaccard overlap coefficient applied to ALE maps. This analysis revealed  
 15 remarkably low cross-category convergence, such as the near-zero overlap of Food-Visual with other  
 16 visual categories, and modest auditory overlap ( $\approx 0.14$ ) between Music and Animal concepts. By  
 17 explicitly quantifying spatial distinctiveness, our approach moves beyond descriptive meta-analysis  
 18 toward a metric evaluation of conceptual separability, yielding data directly relevant for conceptual  
 19 decoding and BCI applications.  
 20 Table 1 situates the current work within the broader ALE literature, highlighting methodological scope  
 21 and conceptual focus relative to representative studies.

22 Table 1. Comparative Overview of Representative ALE Meta-Analyses on Conceptual/Semantic Processing

Study	Focus / Conceptual Scope	Stimulus-modality Control	Quantitative Inter-category Analysis	ALE Implementation	Main limitation Relative to Current Study
Binder <i>et al.</i> , 2009(13)	Landmark ALE meta-analysis of 120 studies defining the distributed semantic system; multimodal tasks, no modality control.	×	×	Pre-GingerALE	Combined heterogeneous tasks; no modality or category control

Watson <i>et al.</i> , 2013(14)	ALE of action-related concepts; embodied motor network emphasis.	Limited	✗	Early ALE	Single-domain; modality-confounded
Wagner <i>et al.</i> , 2014 (15)	ALE of semantic vs phonemic fluency; identifies distinct activation clusters for task types.	Limited	✗	Early ALE	Task-driven, not concept-driven
Bucur & Papagno 2021(16)	ALE of abstract vs concrete words; segregated anterior IFG vs posterior occipito-temporal.	✗	✗	GingerALE 2.x	Lexical only; no multimodal coverage
Enge <i>et al.</i> , 2021(17)	ALE of semantic cognition in children; shows early maturation of semantic network; mixed modalities.	✗	✗	Mixed	Broad but modality-heterogeneous
Pando-Naude <i>et al.</i> , 2021(20)	Large ALE (130 studies) on music perception/production/imagery; auditory vs sensorimotor dissociation.	✓	✗	GingerALE 3.0	Single conceptual field
Kuhnke <i>et al.</i> , 2023(19)	Review/meta-analysis (212 experiments) proposing a hierarchical semantic model across sensory dimensions.	Partial	✗	CBMA (non-ALE)	Theoretical; lacks discriminative mapping
Derderian <i>et al.</i> , 2021(18)	ALE meta-analysis of living vs non-living; shows strong dependence on imaging mode, task demand, and stimulus modality.	Partial	✗	GingerALE 3.0 (no FWE)	Limited scope; lenient thresholds
Duerden & Albanese, 2013,(21)	ALE meta-analysis (~140 studies) of pain-related activation; core nociceptive network (ACC-insula-thalamus)	✗	✗	ALE (pre-GingerALE 3.x)	Single-domain (pain); lacks cross-domain comparison and full modality control
Rice, Lambon Ralph & Hoffman, 2015(22)	ALE meta-analysis of 97 fMRI studies testing left vs right ATL roles in conceptual knowledge; evaluates competing accounts (verbal vs non-verbal, retrieval, social content) vs bilateral hub-and-spoke.	Partial	✗	GingerALE 2.x	Regional (ATL) focus; not a cross-domain conceptual comparison; limited modality control.
<b>Current study</b>	Six conceptual domains (animals, tools, food, music, pain, body parts)	✓ (Separate ALE for)	✓ (Jaccard coefficient)	GingerALE 3.0.2 FWE p < .05	-

		each concept– modality pair)			
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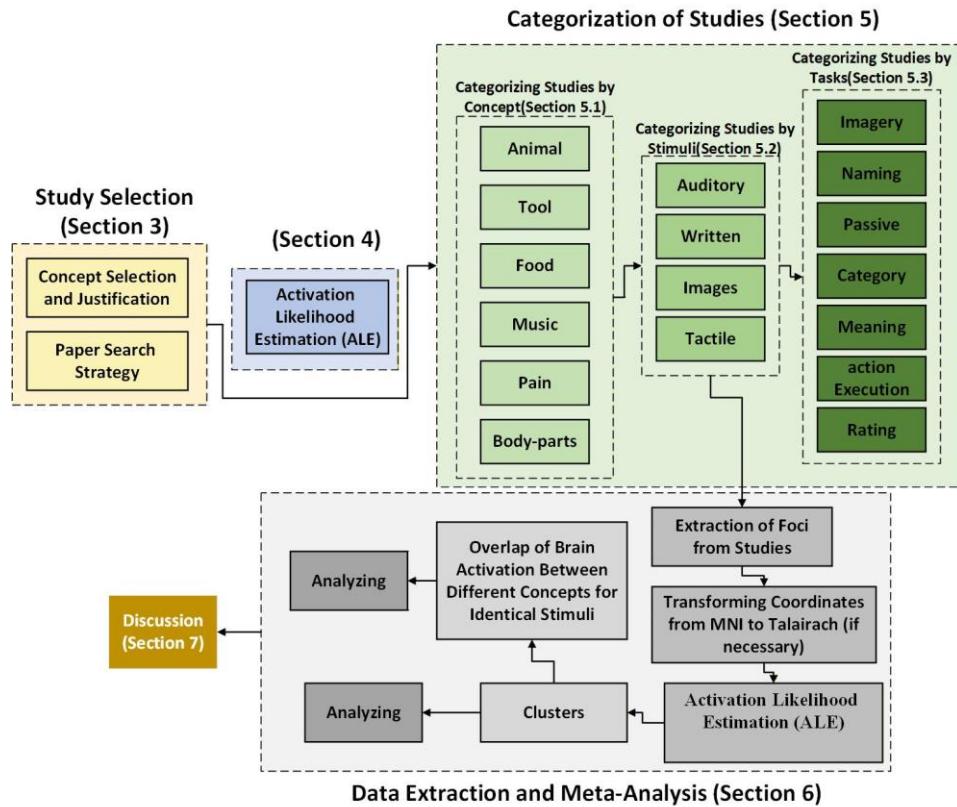
1

2 In contrast to earlier meta-analyses that either aggregated heterogeneous paradigms or targeted a  
 3 single conceptual category, the present work provides a systematically balanced and quantitatively  
 4 validated map of conceptual representations in the human brain. By combining a wide conceptual range  
 5 with strict modality control, this study delineates representational differences that are genuinely  
 6 semantic rather than perceptual or task driven. The inclusion of an explicit inter-domain overlap metric  
 7 establishes, for the first time, an empirical scale of conceptual separability, enabling the selection of  
 8 minimally overlapping categories for neural decoding. Methodologically, the pipeline adheres to current  
 9 best practices, enhancing reproducibility and statistical precision. Conceptually, it bridges theoretical  
 10 and applied neuroscience: the resulting low-overlap conceptual maps not only refine the neurocognitive  
 11 taxonomy of meaning but also provide actionable frameworks for semantic decoding and BCI  
 12 development.

## 13 2. Overview of Study Structure and Analytical Workflow

14 Following the PRISMA guidelines(28), the structure of this paper reflects the systematic methodological  
 15 workflow adopted for the meta-analysis, as illustrated in the color-coded diagram in Figure 1. The  
 16 process began with the selection of relevant studies (section 3, Yellow), which involved two sub-steps:  
 17 concept selection and justification, followed by a structured literature search strategy. The meta-  
 18 analytic method, Activation Likelihood Estimation (section 4, Blue), is then described in detail, outlining  
 19 the approach used to identify consistent activation patterns across studies. In the next phase (section 5,  
 20 Green), studies were categorized according to three dimensions: by semantic concept (e.g., animals,  
 21 tools, food, music, pain, and body parts, (section 5.1)), by stimulus type (auditory, written, image-based,  
 22 or tactile, (section 5.2)), and by task type (e.g., imagery, naming, passive viewing, (section 5.3)).  
 23 Although task type was documented, the ALE analysis focused exclusively on differences in stimulus type  
 24 within each concept. Following this, peak activation coordinates (*foci*) were extracted from each study  
 25 and transformed from MNI to Talairach space when necessary(25) (section 6, Grey). Separate ALE meta-  
 26 analyses were conducted for each concept-stimulus pair using GingerALE 3.0.2, and overlap analyses  
 27 were performed to assess shared activations across different concepts presented via the same stimulus

1 modality(26). Finally, the findings are discussed in relation to previous literature and theoretical  
 2 frameworks on semantic representation (section 7, Brown).



3

4 Figure 1. Methodological workflow of the meta-analysis conducted in this study.

### 5 3. Study Selection

#### 6 3.1. Concept Selection and Justification

7 To maintain focus and manage the scope of the review, we selected the top 10 semantic categories  
 8 reported in section 3.4 of Rybar *et al.*(27), which reflect the most frequently studied concepts across  
 9 neuroimaging modalities. Additionally, we included two concept categories, music and pain, that, while  
 10 less frequently studied, offer distinct semantic domains of interest. This selection allowed us to explore  
 11 how a diverse range of conceptual categories are represented in the brain.

12 The selection and exclusion of specific concepts were guided by predefined criteria. These criteria  
 13 included selecting only one representative concept from each major category (e.g., man-made objects)  
 14 to ensure a balanced and systematic approach. For instance, vegetables and fruits were omitted from  
 15 the final selection, as both belong to the broader category of food, rendering their distinction

1 unnecessary within the scope of this review. Likewise, tools and vehicles fall under the general  
2 classification of man-made objects. However, due to the vast diversity of concepts within this category,  
3 only tools were retained as a representative subset in this study.  
4 Based on these selection criteria and the information summarized in Table 2, the final set of semantic  
5 concepts analyzed in this review includes the following categories: Animal, Body-parts, Tools, Food,  
6 Music, and Pain.

7 Table 2. Selected semantic concepts and justification for inclusion or exclusion

Concept	Include/Exclude	Reasons for Excluding
Animal	Included	-
Tool	Included	-
Food	Included	-
Vegetables	Excluded	Similarity to the 'food' category and being considered a subcategory of 'food'
Insects	Excluded	Similarity to the 'animal' category
Fruit	Excluded	Similarity to the 'food' category and being considered a subcategory of 'food'
Music	Included	-
Body-parts	Included	-
Pain	Included	-
Vehicles	Excluded	Similarity to the 'tool' category (both of them are man-made)
Kitchen-items	Excluded	Similarity to the 'tool' category (both of them are man-made)
Man-made	Excluded	The concept 'man-made' encompasses a broad range of subcategories, such as tool, kitchen item, and more. Among these, 'tool' was selected as the representative concept for this category in the present study.

8

9 **3.2. Paper Search Strategy**

10 To identify relevant studies, we conducted a systematic literature search following PRISMA guidelines(28)  
11 using PubMed and Google Scholar. The search was performed in September 2024 using the keywords  
12 listed in Table 3, with the automated search restricted to studies published from 2010 onward to ensure  
13 a manageable scope and maintain a focus on recent findings. Including earlier years in the automated  
14 search would have generated an impractically large number of irrelevant records. To ensure that key  
15 foundational work predating 2010 was not missed, we complemented the keyword-based search with a  
16 targeted backward snowballing procedure, in which the reference lists of eligible post-2010 articles were  
17 screened for relevant earlier studies. This approach preserved methodological rigor while maintaining  
18 feasibility and ensuring coverage of both recent and foundational contributions. The search focused on  
19 titles and abstracts to maximize the relevance of retrieved records.

20 Following the initial retrieval of articles, a screening process was carried out to remove duplicates and  
21 exclude irrelevant studies. Articles that contained redundant content or did not meet the eligibility

1 criteria (Table 4) were excluded. This exclusion of unrelated studies was based on an initial review of  
2 paper titles and abstracts.

3 In next step, the reference lists of the initially selected articles were examined to identify additional  
4 relevant studies published before 2010. Only articles that were directly related to the research topic and  
5 met the inclusion criteria were incorporated into the final selection.

6 Table 3. Keywords used for systematic literature search

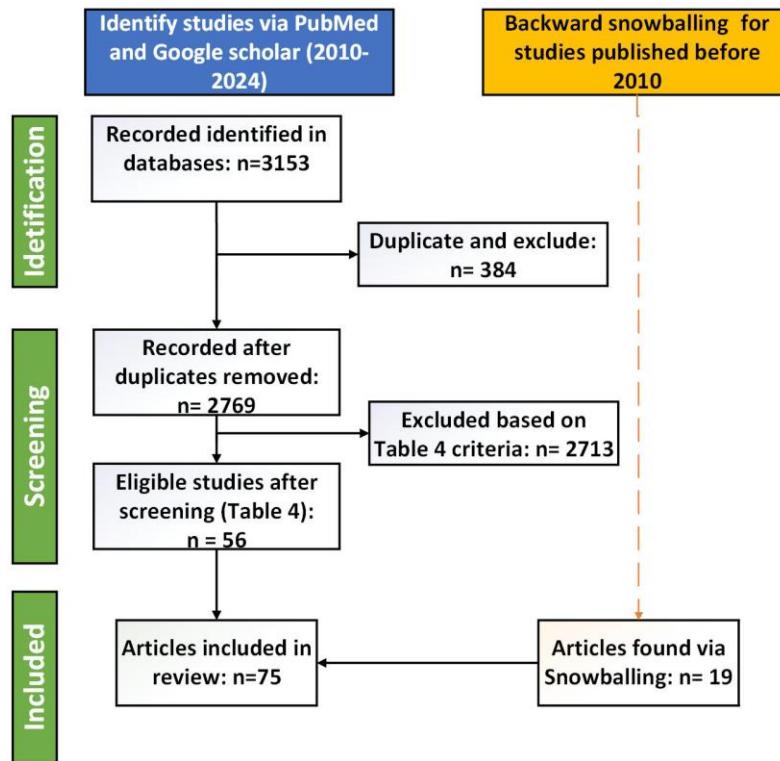
PubMed, Google scholar	First group	(fMRI) <b>or</b> (functional magnetic resonance imaging) <b>or</b> (functional MRI) <b>or</b> (neuroimaging) <b>or</b> (brain Imaging) <b>or</b> (brain mapping)
		<b>AND</b>
	Second group	(Semantic) <b>or</b> (concept) <b>or</b> (conceptual) <b>or</b> (category) <b>or</b> (decoding)

7  
8 To ensure comprehensive study coverage, two keyword categories were used (Table 3). The "OR"  
9 operator retrieved articles containing at least one term from each group, while the "AND" operator  
10 ensured the selection of articles containing keywords from both groups, enhancing search recall.

11 Table 4. Screening criteria for study selection

	<b>Screening Criteria</b>
1	Studies conducted on healthy participants
2	Studies that include the semantic concepts of animals, tools, food, music, pain, and body parts
3	Studies reporting precise brain activation coordinates

12  
13 Table 4 presents the screening criteria used for paper selection. Studies that met these criteria were  
14 included in the review. This screening process was conducted based on an initial evaluation of the paper  
15 titles and abstracts. Exclusion criteria included review papers, studies with insufficient or unclear results,  
16 and articles not written in English.



1

2

Figure 2. Study selection flowchart.

3     **4. Activation Likelihood Estimation (ALE)**

4     The ALE method is a meta-analytical approach used in neuroimaging to identify brain regions that show  
 5     consistent activation across multiple fMRI studies(26). Instead of treating reported activation *foci* as fixed  
 6     points, ALE models them as probability distributions, accounting for spatial variability between studies.  
 7     By aggregating these distributions across multiple datasets, ALE generates statistical maps that highlight  
 8     regions with the highest likelihood of activation, providing a robust means of identifying functional brain  
 9     areas(29).

10    Meta-analyses were performed using GingerALE 3.0.2, which included modifications to the ALE  
 11    algorithm described by Eickhoff *et al.*(26) and Turkeltaub *et al.*(29) with the following steps:

12    1) Modeling activation *foci* (peak activation coordinates): Each reported activation focus was  
 13       modeled as a three-dimensional Gaussian probability distribution, where the full-width at half-  
 14       maximum (FWHM) was adjusted based on the spatial uncertainty inherent in fMRI data(29). This  
 15       probabilistic modeling ensures that activation patterns are appropriately smoothed, facilitating  
 16       cross-study convergence while maintaining anatomical specificity. All *foci* were analyzed in  
 17       Talairach space; if originally reported in MNI space, they were converted using the Lancaster  
 18       transform implemented in GingerALE.

1        2) Computation of ALE scores: An ALE map was generated by computing, for each voxel in Talairach  
2        space, the weighted sum of Gaussian probabilities from all activation *foci* contributing to that  
3        voxel. The weights were determined based on the number of participants in each study,  
4        assigning greater influence to studies with larger sample sizes. This weighting enhances the  
5        statistical power of the meta-analysis and ensures that findings reflect robust patterns across  
6        studies.

7        3) Statistical thresholding: To control for false positives, cluster-level family-wise error (FWE)  
8        correction was applied at  $p < 0.05$ , using a permutation-based approach with 1000 iterations to  
9        estimate the null distribution of ALE scores. This process establishes a significance threshold by  
10       comparing observed activation patterns to a random spatial distribution. Furthermore, clusters  
11       were considered significant if they survived an additional threshold of  $p < 0.01$ , ensuring a  
12       stringent control for type I errors.

13       4) Cluster identification and anatomical labeling: Contiguous clusters exceeding the statistical and  
14       size thresholds were extracted from the ALE map. The anatomical labeling of significant clusters  
15       was performed using the Talairach map, allowing for functional interpretation of the observed  
16       activation patterns.

17       In the following section, the experimental design of each selected study will be examined.

## 18       5. Categorization of Studies

19       Experimental design is a fundamental aspect of neuroimaging studies, especially in fMRI research, as it  
20       critically determines how different factors influence brain activation patterns. The choice of studied  
21       concepts, the type of stimuli presented, and the tasks performed by participants during the experiment  
22       all play a significant role in shaping research outcomes. Careful consideration of these factors is essential  
23       to ensure valid and interpretable results.

### 24       5.1. Concepts

25       For this review, the final set of selected concepts included animals, tools, music, food, pain, and body  
26       parts. These categories were chosen based on their relevance to previous neuroimaging research. Table  
27       5 outlines the concepts and associated papers that we investigated. By examining these concepts, we  
28       aim to provide a comprehensive meta-analytical perspective on how different semantic categories are  
29       processed at the neural level.

30       Table 5. Overview of selected studies investigating semantic concepts in fMRI research

Concepts	Selected Studies
Animal	(11, 30-52)
Tool	(11, 31, 38, 41, 48, 53-67)
Food	(12, 68-75)
Music	(76-85)
Pain	(86-96)
Body-parts	(60, 68, 97-102)

1

## 2 5.2. Stimulus/Cue

3 Stimuli, or cues, are crucial in fMRI studies as they directly influence brain responses in cognitive,  
 4 emotional, and sensory processing. Their selection and presentation ensure targeted neural activation,  
 5 aligning with specific experimental tasks. Different stimulus types, such as words for memory studies or  
 6 facial expressions for emotional research, engage distinct brain networks. Key characteristics including  
 7 modality, intensity, and duration, shape neural activation patterns, making careful stimulus design  
 8 essential for reliable results. Poorly designed stimuli can introduce variability and affect  
 9 interpretability(103, 104). Table 6 summarizes the stimuli used across studies and the number of  
 10 participants in each experimental condition.

11 Table 6. Stimulus presentation modalities used in studies identified in our review.

Stimuli	Specific Stimuli	Animals	Tools	Food	Music	Pain	Body-parts	Total Number of Participants for each Stimulus
Auditory	Auditory (natural sounds)	(30-36)	(31)					143
	Auditory (name)		(53)					11
	Auditory (music)				(76-85)			238
Written	Written word	(37-43)	(38, 41, 54)	(68, 69)		(86, 87)	(68)	260
	Written sentences	(39)						24
Images	Images	(11, 44-51)	(11, 48, 55-66)	(12, 70-75)			(60, 97-102)	804
	Video Clip	(52)	(67)					35
Tactile						(88-96)		127

12

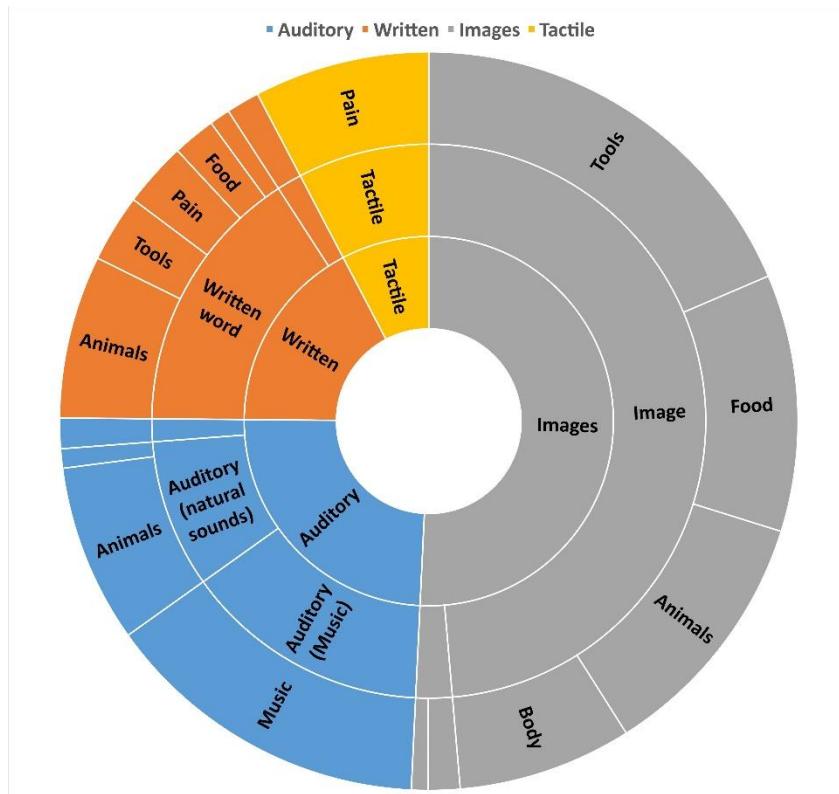


Figure 3. Stimulus presentation modalities used by the semantic decoding studies.

Figure 3 illustrates the distribution of participants across the selected studies in this review based on the type of stimuli used in fMRI experiments.

#### 5.2.1. Images

Image-based stimuli are widely used to present conceptual categories (e.g., food, animals, tools) in a visually consistent format. Using images ensures controlled and standardized concept presentation across trials. The characteristics of fMRI images vary based on study objectives. Some use black-and-white images(11, 44, 49) to reduce color-related confounds and emphasize shape details, while others use colored images(46, 62, 105). Stimuli may also be presented in 2D(64, 106) or 3D(105), depending on task complexity. For example, Garcea *et al.*(59) employed black-and-white 2D images to study neural processing of tools and animals. Their stimuli included 128 real-world images (32 per category, with two exemplars each). Scrambled images served as controls, disrupting structure while preserving low-level visual features.

#### 5.2.2. Auditory

Auditory stimuli are frequently categorized into natural sounds(30-32), spoken names(53), and music (Table 6). In the natural sounds category, participants hear real-world sounds linked to concepts, such as a dog barking for animals or a drill sound for tools. In contrast, the name category presents spoken labels

1 instead of actual sounds. For example, Doehrmann *et al.*(31) investigated neural processing of animal  
2 vocalizations and tool sounds, using 15 distinct samples per category. Animal sounds included species-  
3 specific vocalizations (e.g., dogs, cows, birds), while tool sounds featured mechanical noises (e.g., drill,  
4 saw, hammer)

5           5.2.3. Written

6 Written stimuli are classified into written words(37-43) and written sentences(39) (Table 6). In the word  
7 category, participants see a written name related to the target concept (e.g., banana). For example,  
8 Carota *et al.*(68) used 96 words from six semantic categories, including action-related verbs and nouns  
9 for animals, food, and tools, ensuring linguistic control over factors like length and frequency.

10           5.2.4. Tactile

11 Tactile stimulation, involving sensations like pressure, texture, vibration, and temperature, is widely used  
12 in neuroimaging to study sensory processing. For example, Cardinale *et al.* (91) applied mechanical sharp  
13 pain using a 4-mm blunt blade, while Kong *et al.* (89) applied heat pain stimuli with two intensity levels  
14 (low and high) to the right forearm of participants.

15           5.2.5. Challenges in the Use of Stimuli

16 A major challenge in cognitive and neuroimaging research is the influence of stimulus characteristics on  
17 study outcomes. Stimuli can affect cognitive processing, leading to potential biases if participants rely on  
18 low-level perceptual features (e.g., color, brightness) rather than conceptual meaning. For instance,  
19 differences in contrast between categories may drive neural distinctions unrelated to semantic content.  
20 To minimize such confounds, researchers can control physical properties of images(107) or use mental  
21 imagery to shift focus toward cognitive mechanisms(108, 109). Proper stimulus design, control  
22 measures, and advanced analysis techniques are essential for improving the reliability of findings and  
23 distinguishing perceptual from semantic influences.

24           5.3. Tasks

25 In fMRI studies, cognitive and behavioral tasks are used to engage specific brain regions, helping isolate  
26 neural activity and improve result reliability. These tasks also maintain participant attention, preventing  
27 distraction or drowsiness that could affect data quality. Proper task selection enhances both  
28 experimental control and engagement(110, 111). Table 7 summarizes the tasks used in the selected  
29 studies.

30           Table 7. Cognitive and behavioral tasks performed by participants in the selected studies.

		Category					
Task Type	Specific Task	Animals	Tools	Food	Music	Pain	Body-parts
Imagery	Imagined grasping		(53, 55, 57, 67)				
	Pain recall					(90)	
Naming	Silent naming task	(41, 51)	(41)	(68)			(68)
	Aloud naming task	(44, 45, 49)					
Passive	Passive task	(31, 33, 34, 47)	(31, 54, 55, 58, 59, 61)	(12, 70, 71, 73-75)			(98, 99)
	Passive viewing	(35, 46, 48)	(48, 65)				(100, 102)
	Passive auditory	(36)			(76-78, 82)		
Category/Property	Pain-related words					(86, 87)	
	Auditory decision task	(30)			(79)		
	Concept similarity	(43, 45)	(60)				(60, 97)
	Semantic categorization task	(11, 32, 37, 40, 42, 50, 52)	(11, 66)	(69)			(101)
	Visuomotor		(56)				
	Liked high- and low-calorie foods			(12)			
	Familiarity rating				(83-85)		
Meaning	Silent word reading	(38)	(38)				
	Sentence semantic judgment	(39)					
Action Execution	Actual tool use		(57, 67)				
	Gesturing tool use		(62, 63)				
	Tool learning		(64)				
Rating	Pain intensity rating					(88, 89, 91, 92, 94-96)	
	Emotional neurofeedback				(80, 81)		
	Food rating task			(72)			

## 1 6. Data Extraction and Meta-Analysis

2 We reviewed the selected studies based on predefined criteria, categorized by stimulus type and  
3 participant tasks. Section 5 provided detailed examples, highlighting the diversity of experimental  
4 paradigms in cognitive neuroscience. To identify brain regions associated with each semantic concept of  
5 interest (e.g., tools, animals, food, etc.), a meta-analysis using ALE was conducted separately for each  
6 stimulus type. This approach ensures greater precision by independently analyzing modalities like  
7 images, written words, and auditory stimuli, offering a clearer understanding of concept-specific neural  
8 activation patterns.

### 9 6.1. Animal

10 Based on the results presented in Table 6, studies that investigated the animal concept predominantly  
11 used three types of stimuli: written, auditory, and images. In the following sections, studies within each  
12 of these categories are examined separately in greater detail, and the results of the ALE analysis for each  
13 stimulus type are presented independently.

#### 14 6.1.1. Animal (Stimuli Type: Image)

15 Table 8 provides a summary of the selected studies that investigated the animal concept using image-  
16 based stimuli. This table includes key details such as the type of images presented to participants (Color  
17 or Grayscale), the number of participants in each study (which serves as a weighting factor in the ALE  
18 analysis to give greater influence to studies with larger sample sizes), the types of animals used as  
19 stimuli, the non-animal stimuli included as controls, and the reported *foci* from each study.

20 Table 8. Summary of studies using image-based animal stimuli in fMRI research.

Study Number	Ref	Stimuli	Number of Participants	FOCI	Type of Animals	Non-animal Stimuli
1	(44)	Grayscale	12	1	62 different animals	Artefacts
2	(45)	Grayscale	25	6	-	Radiological lesions
3	(46)	Color	21	10	Fearful and non-fearful types	Inanimate objects
4	(47)	Color	30	31	Dogs, cats, birds, etc.	Nature photographs
5	(11)	Grayscale	13	10	Domestic and wild animals	Tools
6	(48)	Grayscale	20	17	Mammals, birds, insects	Tools
7	(49)	Grayscale	38	8	Various	-
8	(50)	Color	14	9	Land animals, aquatic animal	Manipulable artifacts
9	(51)	Grayscale	12	4	-	Tools

22 As shown in Table 8, the total number of participants in experiments utilizing the animal concept with  
23 image-based stimuli is 185, and the number of *foci* extracted from these studies is 96.

1 Table 9 presents the results of the ALE meta-analysis for the Animals category based on studies that  
2 employed visual (image-based) stimuli. The table reports all significant activation clusters that emerged  
3 consistently across experiments, thereby capturing the convergent neural patterns associated with the  
4 visual processing of animal-related concepts. Each cluster is indexed numerically and includes its spatial  
5 volume (in mm<sup>3</sup>), along with the peak activation coordinates (x, y, z) in Talairach space, indicating the  
6 voxel with the highest convergence within the cluster. The associated z-scores reflect the statistical  
7 strength of these peaks under the ALE model.

8 To facilitate anatomical interpretation, the table specifies the hemisphere and cortical lobe associated  
9 with each cluster, followed by the distribution of contributing gyri and corresponding Brodmann areas.  
10 These anatomical breakdowns provide finer-grained insight into the functional roles of the identified  
11 regions, enabling a clearer understanding of the cortical networks that support category-specific visual  
12 processing of animals.

13 The results summarized in Table 9 reveal three consistent activation clusters associated with the visual  
14 processing of animal-related stimuli. These clusters were primarily located across occipito-temporal  
15 regions and adjacent cerebellar areas in both hemispheres, reflecting the engagement of higher-level  
16 visual cortices commonly implicated in object and category recognition. Overall, the convergence of  
17 these clusters indicates that the perception of animal images recruits a distributed network centered on  
18 regions specialized for processing complex visual features, with additional contributions from cerebellar  
19 structures.

20 Table 9. Summary of ALE results for the image-based animal stimuli.

Cluster #	Volume (mm <sup>3</sup> )	x	y	z	z-score	Hemisphere Distribution	Lobe Distribution	Main Gyrus	Cell Type
1	5552	-40	-74	-14	5.66	54.2% Left Cerebellum, 45.8% Left Cerebrum	36.6% Posterior Lobe, 34.4% Occipital lobe, 17.6% Anterior Lobe, 11.4% Temporal Lobe	35.8% Declive, 20.3% Fusiform Gyrus, 17.6% Culmen, 9.5% Middle Occipital Gyrus	24.4% Brodmann area 19, 13.3% Brodmann area 37, 6.8% Brodmann area 18
2	4928	42	-70	-6	5.3	88.6% Right Cerebrum, 11.4% Right Cerebellum	68% Occipital Lobe, 20.5% Temporal Lobe, 11.4% Posterior Lobe	4.2% Middle Occipital Gyrus, 21.5% Fusiform Gyrus, 17.4% Inferior Occipital Gyrus, 11.9% Inferior Temporal Gyrus	36.5% Brodmann area 19, 28.3% Brodmann area 37, 19.2% Brodmann area 18
3	3192	38	-48	-20	6.56	81% Right Cerebellum, 19% Right Cerebrum	62.1% Anterior Lobe, 19% Posterior Lobe, 19% Temporal Lobe	62.1% Culmen, 19% Fusiform Gyrus, 11.4% Tuber	14.1% Brodmann area 37, 4.9% Brodmann area 20

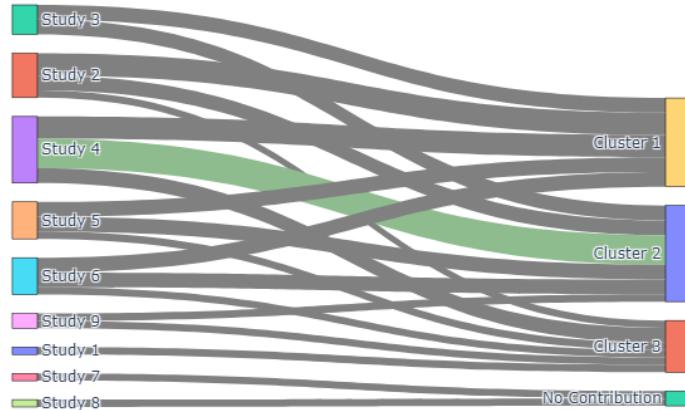


Figure 4. Contribution of studies to clusters (concept: animal, stimuli: image).

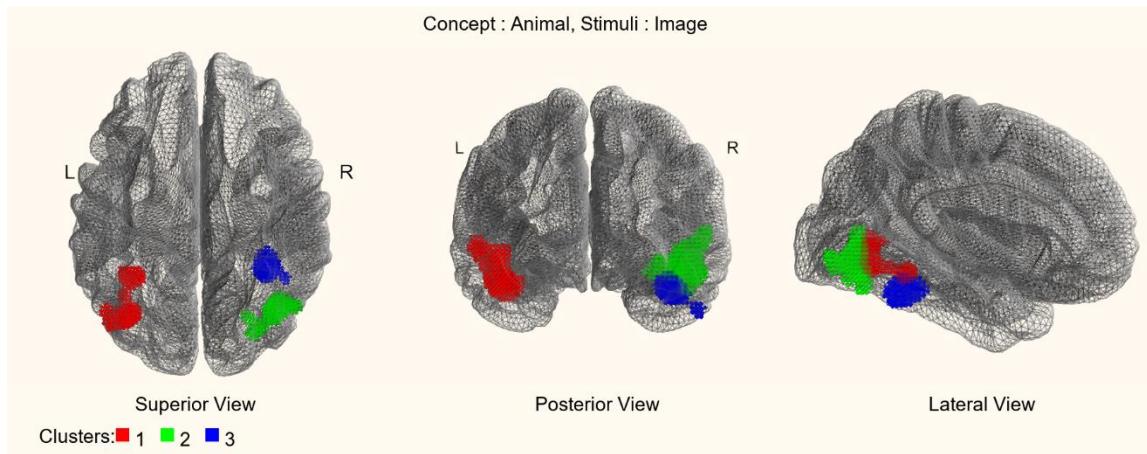
Figure 4 visualizes the contribution of studies from Table 8 to each cluster based on the number of *foci* provided. Thicker connections indicate higher contributions, with studies contributing more than three *foci* highlighted in green. For example, Study 4 significantly contributed to Cluster 2 with four *foci*. Some studies, like Studies 7 and 8, did not contribute to any clusters, while Study 4 had the highest overall impact on activation patterns.

The meta-analysis conducted in this study examined the neural representation of animals using image-based stimuli and identified three significant activation clusters, primarily located in the occipital, temporal, and cerebellar regions. These clusters correspond to well-established neural networks involved in high-level visual processing, particularly in category-specific perception(18, 112):

• Cluster 1: This cluster, spanning the left occipital lobe, fusiform gyrus, and cerebellum, is primarily associated with visual object recognition (BA19, BA37)(113, 114). The fusiform gyrus, known for its role in category-specific perception, has been extensively linked to the visual processing of animate objects, including animals. The involvement of the cerebellum suggests possible contributions to visuomotor integration or implicit processing of biologically relevant stimuli(115-117).

• Cluster 2: This cluster, predominantly in the right occipital and temporal lobes, reinforces the bilateral nature of object perception, with a stronger lateralization towards the right hemisphere. Activation in BA19, BA37, and BA18 indicates engagement in shape, motion, and identity recognition, essential for differentiating animate from inanimate objects(118, 119). The involvement of the inferior temporal gyrus suggests a role in conceptual and semantic processing of animals(112, 113).

1 • Cluster 3: Situated in the right cerebellum and adjacent to the fusiform gyrus, this cluster highlights the  
 2 interaction between higher-order visual processing and cerebellar functions. Given the cerebellum's  
 3 role in predictive coding and fine-tuning of perceptual processes, its activation may indicate an implicit,  
 4 experience-driven component of visual categorization(120-122).



6 Figure 5. Brain activation (clusters) in response to animal image stimuli: superior, posterior, and lateral Views.

7 Figure 5 illustrates the spatial distribution of the three significant activation clusters identified for the  
 8 animal concept under image-based stimuli, shown from superior, posterior, and lateral perspectives. The  
 9 clusters appear as distinct and non-overlapping regions situated within occipito-temporal cortices and  
 10 adjacent cerebellar areas. As visualized in the figure, two clusters are located in the right hemisphere and  
 11 one in the left, forming a bilateral pattern that aligns with the distributed nature of high-level visual  
 12 processing. Their relative positions and separation across views highlight consistent convergence across  
 13 studies, reflecting stable neural topography associated with viewing animal images. The figure thus  
 14 provides a clear anatomical depiction of how these clusters are organized within posterior cortical regions.

#### 15 6.1.2. Animal (Stimuli Type: Auditory)

16 Table 10 summarizes studies on the animal concept using auditory stimuli, including onomatopoeic  
 17 sounds, animal vocalizations, and action sounds. It also details the animal types used in each study. A  
 18 total of 129 participants were included, contributing 34 *foci* for the meta-analysis.

19 Table 10. Summary of studies using the animal concept and auditory stimuli.

Study Number	Ref	Stimuli	Number of Participants	FOCI	Type of Animals	Non-animal Stimuli
2	(30)	Animal vocalizations	26	8	Skylark, Owl, Crow, etc.	Pure tones, white noise
3	(31)	Animal vocalizations	14	6	Cat, Chicken, Chimp, etc.	Tool sounds
4	(32)	Animal vocalizations	17	7	Bear, Bull, Camel, etc.	-
1	(33)	Animal vocalizations	15	1	Bird, Camel, Frog, etc.	Mechanical sounds

5	(34)	Animal action sounds	20	3	-	Mechanical
6	(35)	Animal vocalizations	20	3	Mammals, Birds, etc.	Tool Sounds
7	(36)	Animal vocalizations	17	6	Mammals, Birds, etc.	-

1 Table 11 presents the ALE meta-analysis outcomes for the Animals category based on auditory stimuli,  
 2 highlighting brain regions consistently activated across studies investigating animal sounds. The results  
 3 reveal robust convergence within the superior temporal gyrus and adjacent auditory cortices, reflecting  
 4 the neural basis of animal sound perception.

5 Table 11. Summary of ALE results for the animal concept and auditory stimuli.

Cluster #	Volume (mm <sup>3</sup> )	x	y	z	z-score	Hemisphere Distribution	Lobe Distribution	Main Gyrus	Cell Type
1	6288	52	-15	4	5.86	100% Right Cerebrum	67.4% Temporal Lobe, 26.2% Sublobar, 6.4% Frontal Lobe	58.2% Superior Temporal Gyrus, 22% Insula, 9.2% Middle Temporal Gyrus, 6.7% Precentral Gyrus	45.7% Brodmann area 22, 22.3% Brodmann area 13, 12.8% Brodmann area 21
2	3584	-58	-13	0	5.55	100% Left Cerebrum	99.4% Temporal Lobe	59.4% Superior Temporal Gyrus, 35.8% Middle Temporal Gyrus	47.9% Brodmann area 21, 38.2% Brodmann area 22, 3% Brodmann area 41
3	2456	-49	-36	9	4.57	100% Left Cerebrum	94% Temporal Lobe, 6% Parietal Lobe	72% Superior Temporal Gyrus, 20% Middle Temporal Gyrus, 6% Inferior Parietal Lobule	36% Brodmann area 41, 26% Brodmann area 13, 24% Brodmann area 22, 6% Brodmann area 40

6 Figure 6 illustrates the contribution of individual studies (Table 10) to the significant ALE clusters identified  
 7 for the Animals category using auditory stimuli. As shown, Studies 2, 3, and 7 made the greatest  
 8 contributions to the formation of Cluster 1, which represents the strongest and most extensive activation  
 9 pattern within the right superior temporal region. Study 7 also exerted the highest influence in shaping  
 10 Cluster 3, located in the left temporal-areal area. Study 5 contributed exclusively to Cluster 1, whereas  
 11 Study 1 was solely involved in the formation of Cluster 2. Overall, the distribution of study contributions  
 12 highlights that Cluster 1 emerges as the most robust and consistent convergence zone across the auditory  
 13 studies of animal concepts.

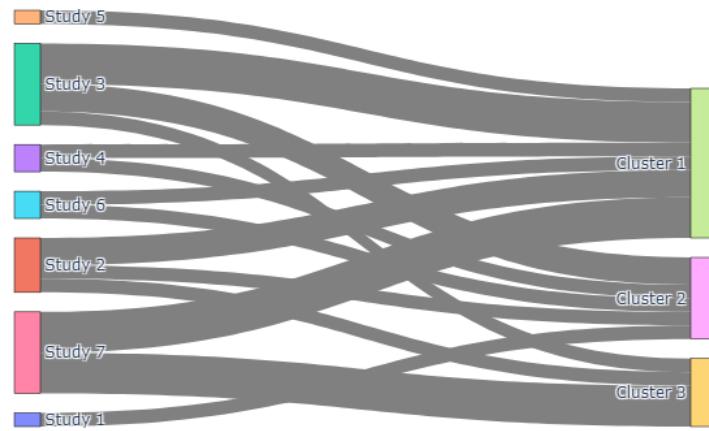
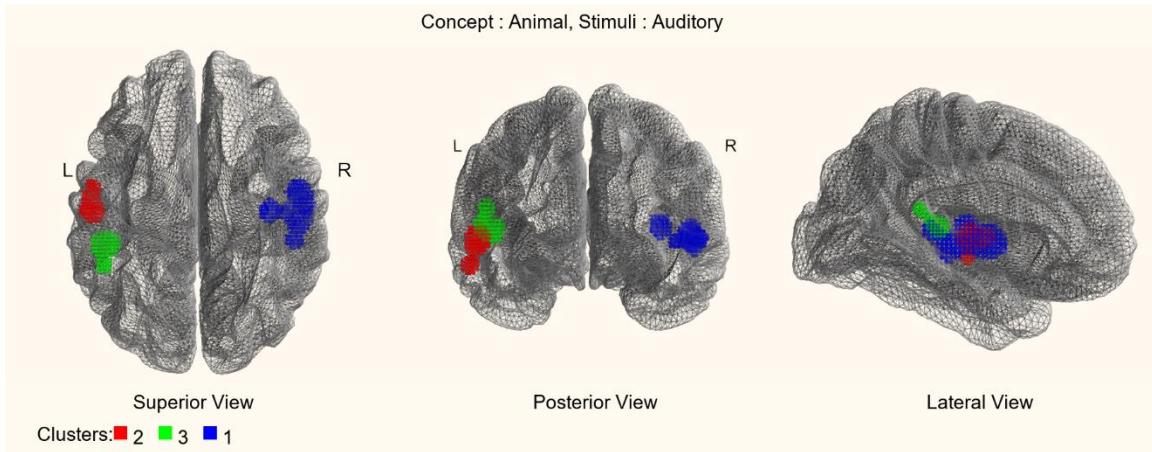


Figure 6. Contribution of studies to clusters (concept: animal, stimuli: auditory).

The ALE meta-analysis for the animal concept using auditory stimuli identified three statistically significant clusters. These clusters are primarily located in the superior temporal gyrus, insula, and adjacent auditory processing areas, all of which are known to play key roles in the perception and interpretation of non-verbal sounds, including animal-related auditory stimuli(123-125). Below is a concise interpretation of each cluster:

- Cluster 1: Primarily located in the right superior temporal gyrus, this cluster is crucial for processing complex auditory stimuli, particularly in Brodmann area 22, which has been shown to be involved in spectrotemporal patterns in sounds. Its role is essential for distinguishing animal vocalizations and environmental sounds. Additionally, insula involvement suggests a role in affective and salience processing, enhancing the emotional and behavioral significance of these sounds(126-128).
- Cluster 2: Located in the left superior and middle temporal gyri, this cluster supports auditory categorization and semantic processing of non-verbal sounds. The superior temporal cortex differentiates speech from non-speech stimuli, while the middle temporal gyrus links auditory inputs to conceptual knowledge, aiding in animal sound recognition(128, 129).
- Cluster 3: Located in the left superior temporal gyrus and inferior parietal lobule, this cluster supports multimodal sensory integration. Activation in Brodmann area 41 suggests early auditory processing, while the inferior parietal lobule links sounds to learned behaviors and contexts, aiding in the interpretation of biologically relevant sounds(124, 129, 130).



1  
2 Figure 7. Brain activation (clusters) in response to animal auditory stimuli: superior, posterior, and lateral views.

3 Figure 7 displays the three significant activation clusters obtained from the ALE meta-analysis for the  
4 Animals category using auditory stimuli. Among these, the blue cluster (Cluster 1) represents the largest  
5 and most extensive activation area, located in the right hemisphere, primarily within the superior  
6 temporal gyrus (STG). This cluster resulted from the combined contributions of Studies 5, 3, 4, 6, 2, and  
7 7, (figure 6) indicating strong convergence across auditory-temporal regions involved in processing  
8 animal sounds. In contrast, Clusters 2 and 3 are situated in the left hemisphere, extending into the  
9 middle temporal and inferior parietal areas, reflecting higher-order semantic and associative processing  
10 of auditory information.

11 6.1.3. Animal (Stimuli Type: Written)

12 Table 12 provides a summary of studies that investigated the animal concept using written stimuli. A  
13 total of 118 participants were included across these experiments, and 59 *foci* were reported.

14 Table 12. Summary of studies using the animal concept and written stimuli

Study Number	Ref	Stimuli	Number of Participants	FOCI	Type of Animals	Non-animal Stimuli
1	(37)	Single words	15	16	-	Concrete objects
2	(38)	Single words	19	2	Cow, Duck, Horse, Kitty, Monkey, etc.	Hand tools
3	(39)	Sentences	24	5	Dogs, Deer, Dolphins, Cats, etc.	People, places, objects
4	(40)	Single words	16	4	40 animals	Artificial objects
5	(41)	Single words	10	26	-	Tools
6	(42)	Single words	12	4	-	Vehicles, fruits, tools

7	(43)	Single words	22	2	-	Tools
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1 The ALE meta-analysis for the animal concept using written stimuli did not identify significant clusters,  
 2 indicating high variability in activation patterns across studies. This may stem from differences in  
 3 experimental design, stimulus presentation, or cognitive tasks. Unlike auditory or visual stimuli, written  
 4 words engage broader linguistic and semantic networks, leading to more distributed activation and  
 5 weaker spatial overlap. Additionally, the limited number of studies may have reduced statistical power.  
 6 Future research with larger datasets and standardized tasks could clarify whether specific regions  
 7 consistently process written representations of animals. This highlights the complexity of conceptual  
 8 processing in the orthographic Modality and the need for further investigation.

## 9 6.2. Tools (Stimuli Type: Image)

10 As shown in Table 6, studies investigating the tool concept primarily utilized image-based and written  
 11 stimuli. However, since only three studies employing written stimuli were identified, this sample size is  
 12 not sufficient for conducting a reliable ALE meta-analysis. Due to this limitation, the ALE analysis for the  
 13 tool concept was performed exclusively on studies that used image-based stimuli.  
 14 Table 13 presents a summary of studies that investigated the tool concept using image-based stimuli.  
 15 Across these studies, a total of 307 participants were included, and 156 *foci* were extracted and utilized  
 16 in the meta-analysis.

17 Table 13. Summary of studies using the tool concept and image stimuli

Study Number	Ref	Stimuli	Number of Participants	FOCI	Type of Tools	Non-tools Stimuli
1	(55)	3D Gray	12	30	Hammer, Screwdriver, etc.	Scrambled
2	(56)	Grayscale	16	7	Common tools	Animals
3	(57)	3D Gray	16	32	Graspable	Neutral shapes
4	(58)	Full-color	12	1	Common manipulable tools	Scrambled
5	(59)	Grayscale	25	5	Manipulable tools	Scrambled
6	(60)	Grayscale	16	3	Common manipulable tools	Scrambled
7	(61)	Grayscale	16	7	Common manipulable tools	Scrambled
8	(66)	Full-color	18	9	Common tools	Scrambled
9	(62)	Grayscale	33	5	Eight common tools	Scrambled
10	(11)	Grayscale	13	2	Common manipulable tools	Animals
11	(48)	Grayscale	20	5	16 common tools,	Animals
12	(63)	3Dprinted	19	5	3D-printed graspable tools	Objects
13	(64)	Full-color	19	22	14 known and 14 unknown tools	-
14	(65)	Grayscale	72	23	10 common tools	Chairs

1 Table 14 presents the results of the ALE meta-analysis for the Tools category using visual (image-based)  
 2 stimuli. The analysis identified five significant activation clusters, reflecting consistent neural patterns  
 3 across studies investigating the visual perception of tools. The clusters are primarily distributed in the  
 4 left hemisphere, encompassing regions within the inferior parietal lobule, middle temporal gyrus, and  
 5 lateral occipital cortex, areas traditionally associated with visuomotor integration, object manipulation,  
 6 and semantic representations of tool-related knowledge. The reported volumes, peak coordinates, and  
 7 z-scores describe the spatial extent and statistical strength of each cluster, while the hemisphere, lobe,  
 8 and Brodmann area information provide detailed anatomical localization. Overall, these findings  
 9 highlight a robust left-lateralized network supporting the recognition and conceptual processing of tools  
 10 in the visual modality.

11 Table 14. Summary of ALE result for the tool concept and image stimuli

Cluster #	Volume (mm <sup>3</sup> )	x	y	z	z-score	Hemisphere Distribution	Lobe Distribution	Main Gyrus	Cell Type
1	9152	-42	-39	42	7.14	100% Left Cerebrum	100% Parietal Lobe	64.4% Inferior Parietal Lobe, 15.7% Postcentral Gyrus, 10.9% Superior	73.2% Brodmann area 40, 14.2% Brodmann area 7
2	4720	-48	-62	-3	4.62	100% Left Cerebrum	54.3% Temporal Lobe, 45.7% Occipital Lobe	37% Middle Temporal Gyrus, 32.4% Inferior Temporal Gyrus, 21.4% Middle Occipital Gyrus	62.4% Brodmann area 37, 23.1% Brodmann area 19
3	3480	-48	1	25	4.68	100% Left Cerebrum	100% Frontal Lobe	61.3% Precentral Gyrus, 35.6% Inferior Frontal Gyrus	60.7% Brodmann area 6, 29.4% Brodmann area 9
4	2112	-34	-42	-18	4.29	73.6% Left Cerebellum, 26.4% Left Cerebrum	73.6% Anterior Lobe, 25.9% Temporal Lobe	73.6% Culmen, 25.4% Fusiform Gyrus	13.2% Brodmann area 37, 12.7% Brodmann area 20
5	2088	45	-60	-5	4.65	100% Right Cerebrum	69.7% Temporal Lobe, 30.3% Occipital Lobe	39.4% Inferior Temporal Gyrus, 30.3% Middle Temporal Gyrus, 24.2% Fusiform Gyrus	75.8% Brodmann area 37, 15.2% Brodmann area 19

12

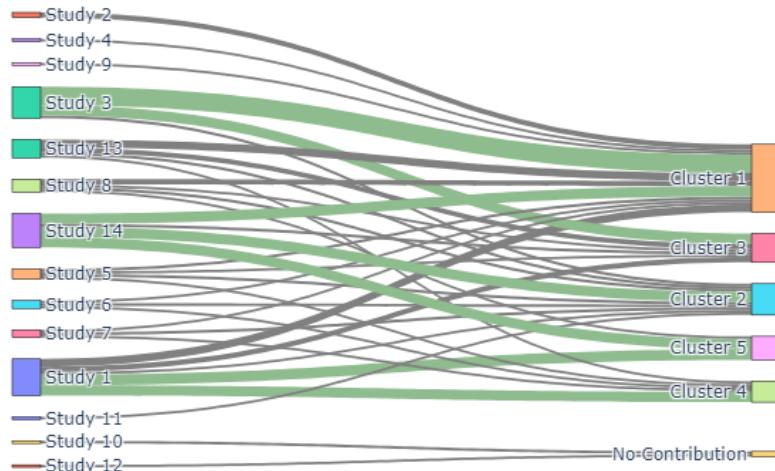


Figure 8. Contribution of studies to clusters (concept: tool, stimuli: image)

As illustrated in Figure 8, Cluster 1 represents the strongest and most extensive activation cluster obtained from the ALE meta-analysis for the Tools category using visual (image-based) stimuli. This cluster was formed through contributions from 11 studies, indicating a high level of cross-study convergence. Among these, Study 3 and Study 14 made the largest contributions, suggesting that their experimental paradigms strongly influenced the spatial distribution of this dominant activation pattern. In contrast, Studies 10 and 12 did not contribute to the formation of any cluster, highlighting variability in the localization or strength of tool-related activations across datasets. Overall, the figure emphasizes the central role of Cluster 1 in capturing the most consistent neural response associated with visual processing of tools.

The results of the ALE meta-analysis for the tool concept using image-based stimuli revealed five significant clusters, each associated with distinct brain regions:

- Cluster 1: Located in the left inferior parietal lobule, this cluster is involved in tool-related action representation and object manipulation. Activation in the postcentral gyrus suggests integration of visual and tactile information, while the superior parietal lobule (BA7) supports visuomotor coordination for guiding hand movements. This aligns with research on affordance processing, where the brain encodes tool functionality to facilitate their use(113, 116, 131).
- Cluster 2: Located in the left temporal and occipital cortices (BA37), this cluster is involved in object recognition and semantic memory retrieval. The inferior temporal gyrus supports visual category processing of tools, while the middle occipital gyrus contributes to early-stage visual analysis(132). This suggests that tools are processed as a distinct semantic category with specialized neural mechanisms.

- Cluster 3: Located in the precentral and inferior frontal gyri, this cluster is involved in motor planning and action execution. BA6 (premotor cortex) supports motor preparation for tool use, while BA9 and BA44 contribute to higher-order motor control. These findings suggest that perceiving tools activates motor-related brain regions, even without direct interaction(116, 133).
- Cluster 4: Involving the cerebellum and fusiform gyrus (BA37), this cluster plays a role in coordinating tool-related actions and object recognition. The cerebellum supports fine motor control and movement planning, while the fusiform gyrus helps distinguish tools from other objects. This highlights the integration of perceptual and motor systems in tool processing(116, 134).
- Cluster 5: Located in the right hemisphere, this cluster is involved in high-level visual processing and semantic categorization of tools. The inferior and middle temporal gyri (BA37) support semantic retrieval, while the fusiform gyrus aids in object recognition. Its presence suggests that tool perception engages both hemispheres, depending on task demands(115-117).

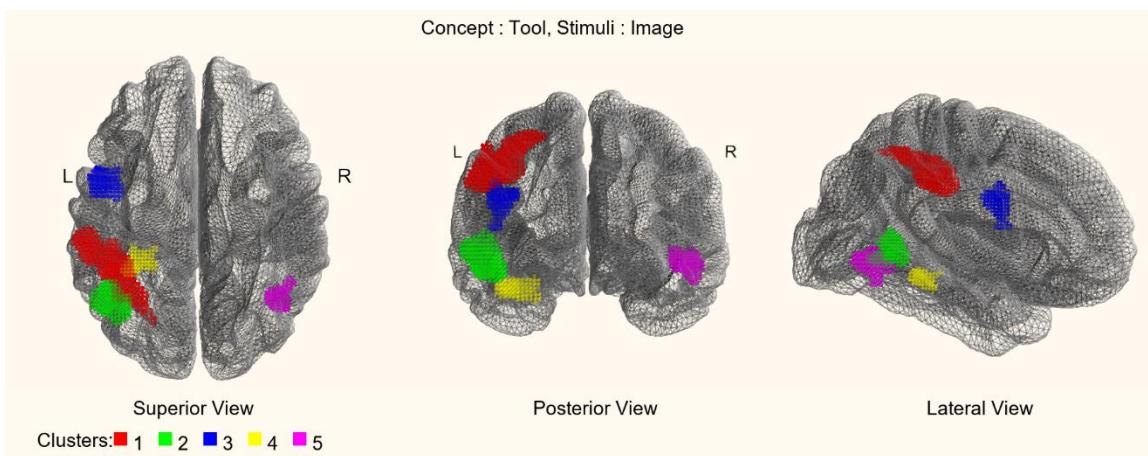


Figure 9. Brain activation (clusters) in response to tool image stimuli: superior, posterior, and lateral Views

Figure 9 illustrates the significant activation clusters obtained from the ALE meta-analysis for the Tools category using visual (image-based) stimuli. The figure depicts the spatial distribution of these clusters across the brain, revealing that four clusters are located within the left hemisphere. These clusters are primarily situated in regions associated with visuomotor and conceptual processing of tools, including the inferior parietal lobule, middle temporal gyrus, and lateral occipital cortex. The visualization highlights the left-lateralized organization of neural activations underlying tool recognition and demonstrates the convergence of results across multiple studies within the visual modality.

### 1 6.3. Food (Stimuli Type: Image)

2 As shown in Table 6, only two studies in the selected dataset investigated the food concept using  
 3 written stimuli. Given this limited sample size, conducting an ALE meta-analysis on these studies would  
 4 not yield meaningful results. Therefore, the ALE analysis for the food concept was conducted exclusively  
 5 on studies that used image-based stimuli.

6 Table 15 presents a summary of the selected studies in this review that investigated the food concept  
 7 using image-based stimuli. Across these studies, a total of 186 participants were included, from which 95  
 8 *foci* were extracted for the meta-analysis.

9 Table 15. Summary of studies using the food concept and image stimuli

Study Number	Ref	Stimuli	Number of Participants	FOCI	Type of Food	Non-food Stimuli
1	(70)	Colored	10	23	Fattening food, non-fattening food	Objects
2	(71)	Both	30	5	High-calorie, palatable foods	Office utensils
3	(12)	Colored	19	5	High-calorie foods, low-calorie foods	Office utensils
4	(72)	Colored	22	11	Junk food	-
5	(73)	Colored	20	19	Sweet, sour, salty	Familiar objects
6	(74)	Colored	53	25	Palatable foods	Neutral objects
7	(75)	Colored	32	7	High-calorie foods, low-calorie foods	-

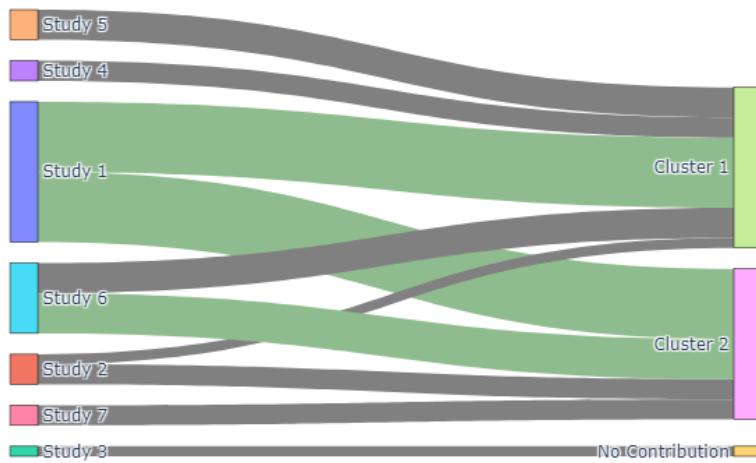
10 Table 16 presents the ALE meta-analysis results for the Food category using visual (image-based) stimuli.  
 11 The analysis identified two significant activation clusters of comparable size, located in opposite  
 12 hemispheres. Cluster 1, situated in the right hemisphere, is centered mainly within sub-lobar and limbic  
 13 regions, including the lentiform nucleus, parahippocampal gyrus, claustrum, and putamen, indicating  
 14 the involvement of reward-related and affective processing areas. Cluster 2, located in the left  
 15 hemisphere, shows a similar volumetric extent and encompasses sub-lobar and limbic structures such as  
 16 the lentiform nucleus, parahippocampal gyrus, amygdala, and globus pallidus. Together, these bilateral  
 17 clusters reflect a balanced engagement of emotional-motivational and associative networks during the  
 18 visual perception of food-related stimuli.

19 Table 16. Summary of ALE result for the food concept and image stimuli

Cluster #	Volume (mm <sup>3</sup> )	x	y	z	z-score	Hemisphere Distribution	Lobe Distribution	Main Gyrus	Cell Type
1	4736	21	-1	-7	3.62	99.5% Right Cerebrum	76.2% Sub-Lobar, 17.5% Limbic Lobe, 5.8% Frontal Lobe	59.2% Lentiform Nucleus, 17.5% Parahippocampal Gyrus, 11.7% Claustrum	48.5% Putamen, 14.1% Brodmann area 34, 6.3% Amygdala

2	5256	- 15	- 2	- 7	4.66	100% Left Cerebrum	56.8% Sub-Lobar, 43.2% Limbic Lobe	45.4% Lentiform Nucleus, 36.2% Parahippocampal Gyrus	29.9% Amygdala, 19.6% Medial Globus Pallidus, 18.5% Lateral Globus Pallidus, 12.5% Brodmann area 34
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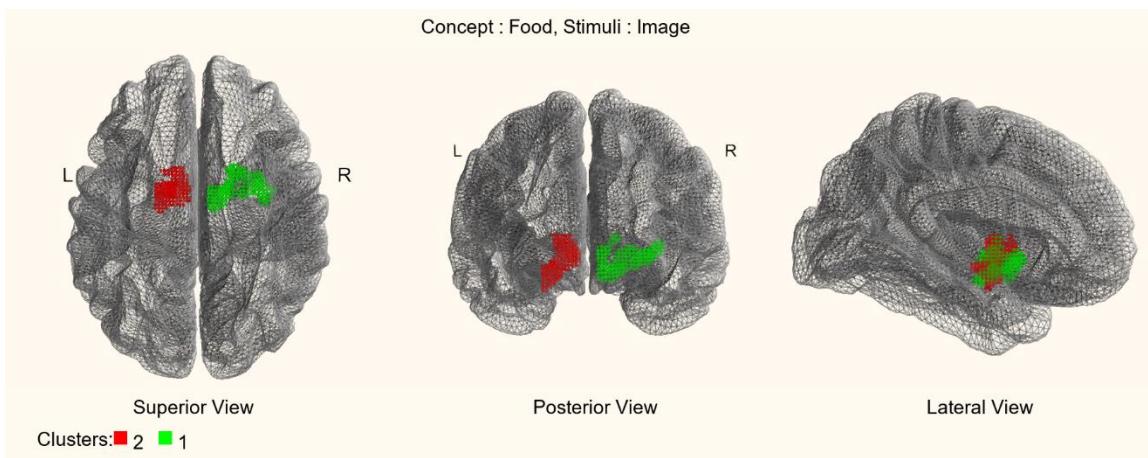
1 As shown in Figure 10, Study 1 demonstrates the highest contribution to the formation of both Cluster 1  
 2 and Cluster 2, indicating its strong overall influence on the ALE results for the Food category with visual  
 3 (image-based) stimuli. Study 6 shows the next largest contribution, primarily affecting Cluster 2, while  
 4 Study 3 did not contribute to the formation of any significant cluster. This distribution highlights the  
 5 differential weight of studies in shaping the final convergence patterns observed across the analysis.



6  
 7 Figure 10. Contribution of studies to clusters (concept: food, stimuli: image)  
 8 The ALE meta-analysis for the food concept using image-based stimuli revealed two significant clusters,  
 9 both of which are located within key subcortical and limbic structures. These regions are functionally  
 10 associated with reward processing, motivation, and memory encoding, all of which are integral to food-  
 11 related cognitive and emotional responses(135-137):

12 • Cluster 1: Located in the putamen, this cluster is involved in reward-based learning and motor control  
 13 of food-related behaviors. Activation in the parahippocampal gyrus links food stimuli to memory, while  
 14 the insula processes taste, craving, and sensory-emotional integration. The claustrum may support  
 15 multisensory integration of food cues, highlighting its role in appetite regulation and decision-  
 16 making(135-137).  
 17 • Cluster 2: Located in the left hemisphere, this cluster involves the putamen and parahippocampal  
 18 gyrus, similar to cluster 1, but with strong amygdala engagement for emotional salience and reward-

1 based learning. The uncus links food perception to olfactory-driven memory, while caudate activation  
2 suggests cognitive control in food-related behaviors. This highlights the role of deep limbic structures  
3 in integrating emotion, memory, and motivation in food perception(138, 139).



4

5 Figure 11. Brain activation (clusters) in response to food image stimuli: superior, posterior, and lateral views.

6 Figure 11 displays the spatial distribution of the two significant activation clusters identified for the Food  
7 category using visual (image-based) stimuli, shown from superior, posterior, and lateral views. As  
8 illustrated, Cluster 1 (green) is in the right hemisphere, while Cluster 2 (red) is situated in the left  
9 hemisphere. Both clusters occupy homologous regions within sub-lobar and limbic areas, including  
10 portions of the parahippocampal gyrus, amygdala, and lentiform nucleus. The visualization highlights a  
11 bilateral and nearly symmetrical activation pattern, indicating that both hemispheres contribute  
12 comparably to the neural processing of visually presented food-related concepts.

#### 13 6.4. Music (Stimuli Type: Auditory)

14 Table 17 presents a summary of the selected studies in this review that investigated the concept of  
15 music using auditory stimuli. Table 17 also provides details on the specific type of music used in each  
16 study. Across these studies, a total of 238 participants were included, and 154 *foci* relevant to the  
17 investigated concept and stimulus modality were extracted for analysis.

18 Table 17. Summary of studies using the music concept and auditory stimuli

Study Number	Ref	Stimuli	Number of Participants	FOCI	Type of Music	Non-music Stimuli
1	(76)	Auditory	15	30	America the beautiful, the star-spangled banner, chariots of fire	Random tones
2	(77)	Auditory	21	15	Frédéric chopin's etude in E major	-
3	(78)	Auditory	20	20	Simple novel piano melodies	Jabberwocky sentences

4	(79)	Auditory	18	6	60 excerpts of symphonic film music	-
5	(80)	Auditory	23	24	pleasant, classical, instrumental, and tonal,	-
6	(81)	Auditory	56	7	Film music	-
7	(82)	Auditory	26	13	Amateur rock	Spoken word condition
8	(83)	Auditory	21	10	Instrumental pop, rock, and classical genres	Pseudo-songs
9	(84)	Auditory	27	15	Pure tones	Visual stimuli
10	(85)	Auditory	11	14	Rhythmic stimuli	Isochronous sequences

1 Table 18 summarizes the ALE meta-analysis results for the Music category using auditory stimuli. The  
 2 analysis revealed three significant activation clusters, with Clusters 1 and 2 showing comparable  
 3 volumes and representing bilateral activations in the superior temporal and insular regions of the right  
 4 and left hemispheres, respectively. Cluster 3, a smaller right-hemisphere cluster, was primarily located  
 5 within the insular and frontal areas. Overall, the results indicate a largely bilateral organization of  
 6 auditory and associative regions involved in music processing.

7 Table 18. Summary of ALE result for the music concept and auditory stimuli

Cluster #	Volume (mm <sup>3</sup> )	x	y	z	z-score	Hemisphere Distribution	Lobe Distribution	Main Gyrus	Cell Type
1	8312	50	-13	4	5.22	100% Right Cerebrum	55.9% Temporal Lobe, 29.6% Sub-lobar, 8.9% Parietal Lobe	46.5% Superior Temporal Gyrus, 29.6% Insula, 8.4% Postcentral Gyrus	32% Brodmann area 13, 28.9% Brodmann area 22, 12.8% Brodmann area 41, 9.4% Brodmann area 40
2	7056	-49	-16	2	4.72	100% Left Cerebrum	63.4% Temporal Lobe, 36% Sub-lobar	55.1% Superior Temporal Gyrus, 36.6% Insula, 7.4% Middle Temporal Gyrus	44.9% Brodmann area 22, 37.5% Brodmann area 13, 4.9% Brodmann area 21
3	1880	35	15	8	3.54	100% Right Cerebrum	87.5% Sub-lobar, 12.5% Frontal Lobe	70% Insula, 17.5% Claustrum, 11.3% Precentral Gyrus	70% Brodmann area 13, 11.3% Brodmann area 44

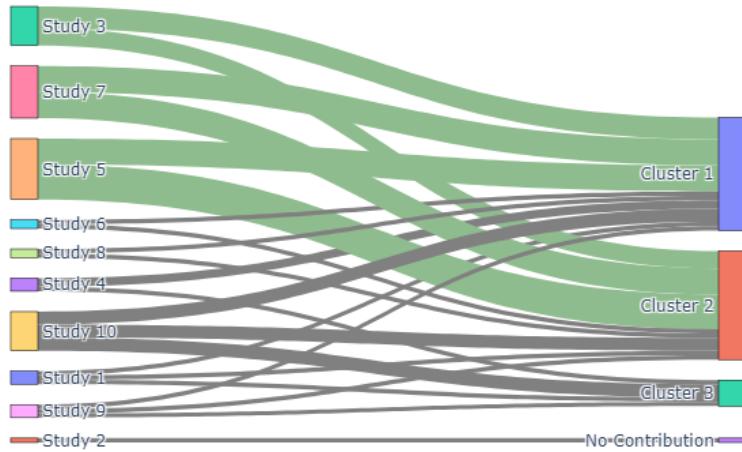


Figure 12. Contribution of studies to clusters (concept: music, stimuli: auditory)

Figure 12 illustrates the contribution of individual studies to the formation of the three significant ALE clusters identified for the Music category using auditory stimuli. As shown, Cluster 1 received contributions from the largest number of studies, with Studies 3, 7, and 5 having the strongest influence on its formation. Cluster 2 was supported by a smaller group of studies, while Cluster 3 received limited input, primarily from Study 1. Notably, Study 2 did not contribute to the formation of any cluster. This visualization highlights the relative weight and distribution of study contributions across clusters, demonstrating that most datasets converge toward the right-hemisphere temporal–insular network represented by Cluster 1.

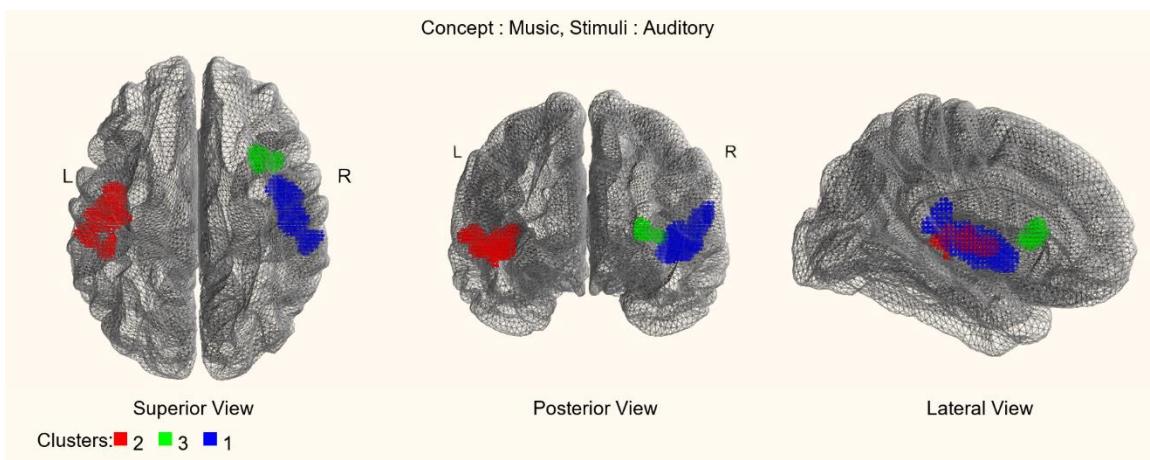
The ALE meta-analysis for the music concept using auditory stimuli revealed three statistically significant clusters. These clusters are primarily located in the superior temporal gyrus, insula, and precentral gyrus, all of which are well-established regions involved in auditory perception, music processing, and emotional responses to sound(140-142):

- Cluster 1: Primarily in the right superior temporal gyrus, this cluster is involved in higher-order auditory processing, pitch discrimination, and musical feature analysis. Activation in Heschl's gyrus supports early-stage acoustic processing, while the insula contributes to the emotional and sensory integration of music. This aligns with research highlighting the right superior temporal cortex's key role in melody perception and harmonic structure processing(113, 141, 142).
- Cluster 2: Located in the left superior temporal gyrus, this cluster parallels right-hemisphere activation but is more involved in rhythmic and structural aspects of music(113, 143). The insula's activation suggests bilateral engagement in emotional and interoceptive processing of music, while the middle temporal gyrus (BA21) contributes to retrieving auditory representations and integrating music with

1 memory. This supports the idea of hemispheric specialization, with the left hemisphere focusing on  
2 temporal structure and the right on pitch and harmony(142, 143).

3 • Cluster 3: Centered in the insula and claustrum, this cluster is involved in sensory integration,  
4 emotional responses, and attention modulation in music perception. The insula (BA13) is linked to  
5 emotional experiences like pleasure and arousal, while the claustrum facilitates cross-modal  
6 integration of auditory, motor, and emotional aspects of cognition. Activation in the precentral gyrus  
7 (BA44/45) suggests a role in rhythm processing and movement synchronization to music.

8 • Cluster 3: Centered in the insula and claustrum, this cluster is involved in sensory integration,  
9 emotional responses, and attention modulation in music perception. The insula (BA13) is linked to  
10 emotional experiences like pleasure and arousal, while the claustrum facilitates cross-modal  
11 integration of auditory, motor, and emotional aspects of cognition. Activation in the precentral gyrus  
12 (BA44/45) suggests a role in rhythm processing and movement synchronization to music(113, 142,  
13 143).



14

15 Figure 13. Brain activation (clusters) in response to music auditory stimuli: superior, posterior, and lateral views.

16 Figure 13 depicts the spatial distribution of the three significant activation clusters identified for the  
17 Music category using auditory stimuli, shown from superior, posterior, and lateral views. The results  
18 reveal a bilateral but asymmetric activation pattern, with Clusters 1 (blue) and 3 (green) located in the  
19 right hemisphere, while Cluster 2 (red) appears in the left hemisphere. The right-hemisphere clusters  
20 extend along the superior temporal and insular regions, whereas the left-hemisphere cluster  
21 encompasses homologous temporal areas. This lateralized yet coordinated configuration suggests that  
22 the processing of music engages both hemispheres, with a subtle dominance of right-hemisphere  
23 auditory and associative regions involved in melodic and tonal analysis.

## 1 6.5. Pain (Stimuli Type: Tactile)

2 Table 19 presents a summary of the selected studies in this review that investigated the concept of pain  
 3 using tactile stimuli. These studies employed two types of tactile stimulation: thermal and mechanical.  
 4 Across these experiments, a total of 127 participants were included, and 194 *foci* were extracted for the  
 5 meta-analysis.

6 Table 19. Summary of studies using the pain concept and tactile stimuli

Study Number	Ref	Stimuli	Number of Participants	FOCI	Type of Pain	Non-pain Stimuli
1	(88)	Tactile	13	13	Thermal	Baseline
2	(89)	Tactile	12	21	Thermal	Baseline
3	(90)	Tactile	15	29	Thermal	Baseline
4	(91)	Tactile	19	28	Mechanical	Baseline
5	(92)	Tactile	12	22	Thermal	Baseline
6	(93)	Tactile	12	16	Thermal	Baseline
7	(94)	Tactile	17	31	Mechanical	Baseline
8	(95)	Tactile	11	22	Thermal	Baseline
9	(96)	Tactile	16	12	Thermal	Baseline

7 Table 20 summarizes the ALE meta-analysis results for the Pain category. The analysis identified five  
 8 significant activation clusters, with Clusters 1 and 2 emerging as the largest and most prominent ones.  
 9 These clusters encompass bilateral subcortical and limbic regions, consistent with the affective–  
 10 motivational components of pain processing. The remaining clusters are distributed mainly across  
 11 parietal and insular areas, reflecting somatosensory and interoceptive aspects of pain perception.  
 12 Overall, the results indicate a broad and integrated pain network that bridges cortical and subcortical  
 13 structures to support the multidimensional nature of pain experience.

14 Table 20. Summary of ALE result for the pain and tactile stimuli

Cluster #	Volume (mm <sup>3</sup> )	x	y	z	z-score	Hemisphere Distribution	Lobe Distribution	Main Gyrus	Cell Type
1	8040	9	-7	8	4.2	64.8% Right Cerebrum, 35.2% Left Cerebrum	100% Sub-lobar	78.5% Thalamus, 12.5% Lentiform Nucleus, 5.8% Insula	23.9% Medial Dorsal Nucleus, 10.6% Putamen, 5.2% Brodmann area 13, 5.2% Pulvinar, 5.1% Ventral Lateral Nucleus
2	7232	1	6	41	4.78	56.1% Right Cerebrum, 43.9% Left Cerebrum	63.7% Limbic Lobe, 36.3% Frontal Lobe	70.7% Cingulate Gyrus, 14.3% Medial Frontal Gyrus, 13.3% Superior Frontal Gyrus	46.3% Brodmann area 24, 23.5% Brodmann area 32, 18.7% Brodmann area 6, 8.7% Brodmann area 8

3	4128	49	-32	31	3.92	100% Right Cerebrum	81.9% Parietal Lobe, 15.9% Sub-lobar	69.2% Inferior Parietal Lobule, 16.5% Insula, 12.1% Postcentral Gyrus	70.3% Brodmann area 40, 15.9% Brodmann area 13, 11.5% Brodmann area 2
4	3840	-55	-29	21	5.14	100% Left Cerebrum	62.5% Parietal Lobe, 25% Temporal Lobe, 12.5% Sub-lobar	40.3% Inferior Parietal Lobule, 22.2% Postcentral Gyrus, 20.5% Superior Temporal Gyrus, 12.5% Insula	62.5% Brodmann area 40, 14.8% Brodmann area 42, 12.5% Brodmann area 13, 10.2% Brodmann area 41
5	2624	-33	11	6	4.08	100% Left Cerebrum	100% Sub-lobar	66.7% Insula, 25% Caudate, 7.3% Lentiform Nucleus	65.6% Brodmann area 13, 7.3% Putamen

1 Figure 14 visualizes the distribution and overlap of study contributions across the five significant ALE  
2 clusters identified for the Pain category. The diagram highlights a complex and highly interconnected  
3 pattern, in which multiple studies contribute simultaneously to more than one cluster. Cluster 1  
4 emerges as the principal convergence zone, receiving input from nearly all datasets, followed by Cluster  
5 2, which also shows substantial multi-study involvement. In contrast, Clusters 3, 4, and 5 exhibit more  
6 selective participation, reflecting localized or study-specific activation patterns.

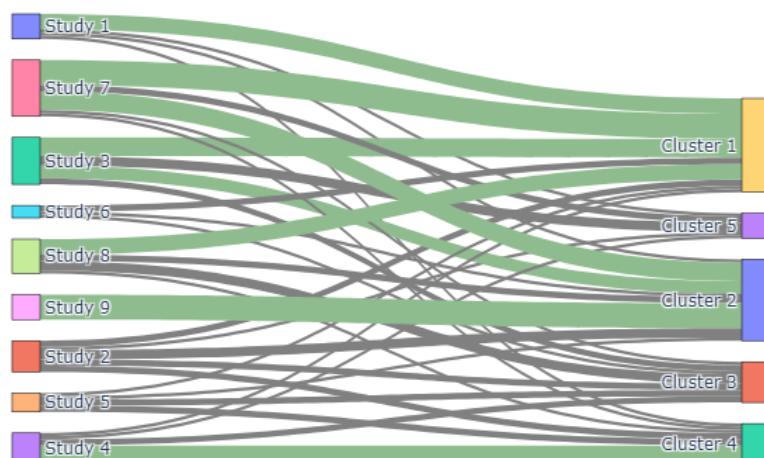


Figure 14. Contribution of studies to clusters (concept: food, stimuli: image)

9 The ALE meta-analysis for the pain concept using tactile stimuli identified five statistically significant  
10 clusters. These clusters are primarily located in key regions associated with sensory, affective, and  
11 cognitive aspects of pain processing:

- Cluster 1: Centered in the thalamus, this cluster is involved in transmitting pain signals and modulating affective aspects of pain. Activation in the putamen suggests integration with motor responses, while the insula contributes to interoceptive awareness and pain perception(144, 145).
- Cluster 2: Located in the anterior cingulate cortex (ACC), this cluster is involved in the emotional and cognitive modulation of pain, including anticipation and regulation. Activation in the medial prefrontal cortex suggests a role in top-down control, such as attention and cognitive appraisal of pain. These findings support the ACC's function in integrating sensory and emotional aspects of pain(144, 145).
- Cluster 3: Localized in the inferior parietal lobule and postcentral gyrus, this cluster is involved in processing somatosensory aspects of pain. Activation in the primary somatosensory cortex (S1) encodes pain intensity and location, while the inferior parietal lobule integrates nociceptive input with other sensory modalities for cognitive evaluation of pain(116, 145).
- Cluster 4: Located in the left inferior parietal lobule and superior temporal gyrus, this cluster is involved in sensory and perceptual aspects of pain processing. The superior temporal gyrus suggests an interaction between pain and auditory processing, while the postcentral gyrus contributes to encoding tactile and nociceptive information.
- Cluster 5: Centered in the insula and claustrum, this cluster is involved in the affective and interoceptive dimensions of pain. The insula integrates pain intensity, unpleasantness, and autonomic responses, while the claustrum may contribute to cross-modal sensory integration, linking pain perception with attention and emotion(145, 146).

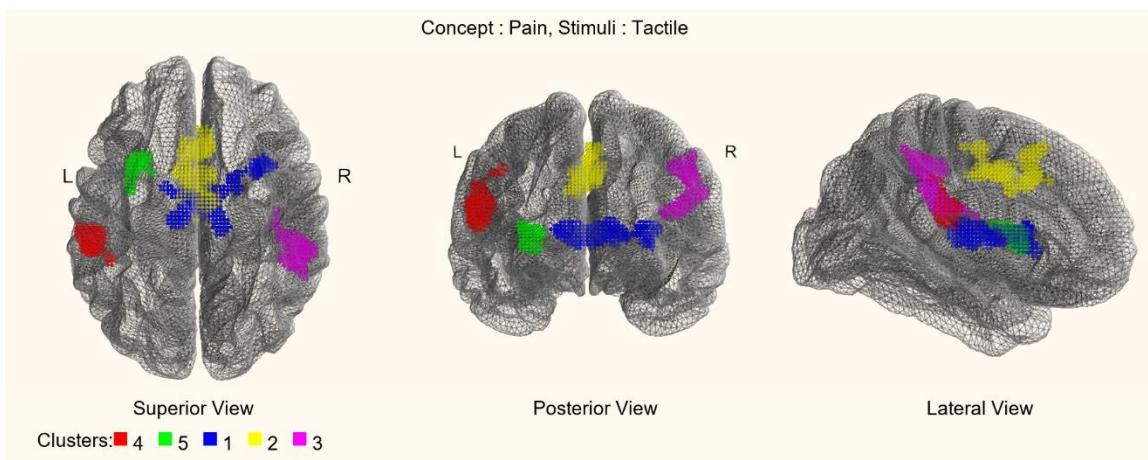


Figure 15. Brain activation (clusters) in response to pain (tactile stimuli): superior, posterior, and lateral views

Figure 15 illustrates the spatial distribution of the five significant activation clusters obtained for the Pain category using tactile stimuli, shown from superior, posterior, and lateral views. The pattern reveals a bilateral but functionally differentiated organization, with clusters distributed across both

1 hemispheres. The largest clusters occupy midline and parietal regions, extending into areas commonly  
 2 associated with somatosensory and cingulate cortices, while smaller clusters appear in lateral temporal  
 3 and insular regions. This configuration suggests that tactile pain engages a broad cortical network  
 4 integrating sensory, affective, and associative components, rather than a single localized area of  
 5 activation.

## 6 6.6. Body-parts (Stimuli Type: Image)

7 Table 21 presents a summary of the selected studies in this review that investigated the concept of body  
 8 parts using image-based stimuli. These studies examined the neural representation of body-related  
 9 visual processing through various experimental paradigms. Across these experiments, a total of 126  
 10 participants were included, and 73 *foci* were extracted for the meta-analysis.

11 Table 21. Summary of studies using the tool concept and image stimuli

Study Number	Ref	Stimuli	Number of Participants	FOCI	Type of Body Part	Non-body Part Stimuli
1	(60)	Greyscale	15	3	Hand, bodies	Scrambled objects
2	(97)	Greyscale	28	3	Body parts	Outdoor scenes
3	(98)	-	16	20	Hands	-
4	(99)	colored	18	5	Body parts	Scrambled
5	(100)	-	18	7	Body parts	Non-body Part
6	(101)	Greyscale	16	24	Feet, hands	Bottles
7	(102)	Greyscale	15	11	Body parts	Chairs

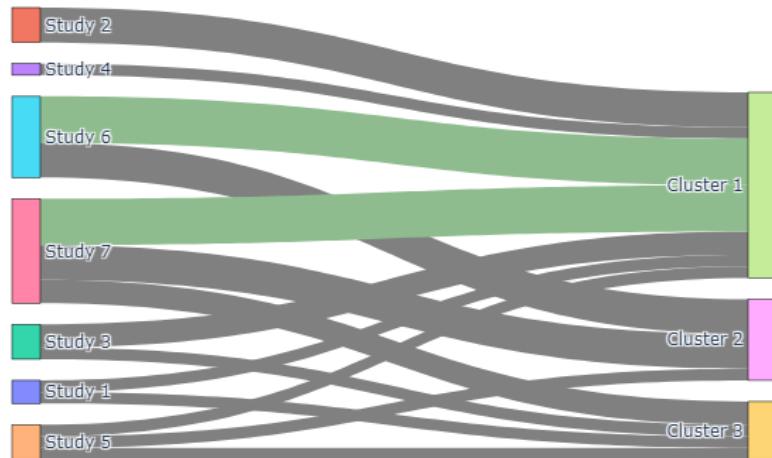
12 Table 22 presents the results of the ALE meta-analysis for the Body Parts category. The analysis yielded  
 13 three significant activation clusters, with Cluster 1 emerging as the largest, approximately twice the size  
 14 of the other clusters, and located predominantly in the left hemisphere. This cluster spans occipital and  
 15 temporal regions, particularly within the middle occipital and middle temporal gyri, suggesting a strong  
 16 visual-perceptual component in body-part representation. Cluster 2, found in the right hemisphere,  
 17 mirrors a similar occipito-temporal pattern, while Cluster 3 is smaller and extends into the left cerebellum  
 18 and adjacent fusiform regions. Collectively, these clusters reveal a left-lateralized yet bilateral network  
 19 supporting visual and sensorimotor aspects of body-part processing.

20 Table 22. Summary of ALE result for the body-part concept and image stimuli

Cluster #	Volume (mm <sup>3</sup> )	x	y	z	z-score	Hemisphere Distribution	Lobe Distribution	Main Gyrus	Cell Type
1	5784	-45	-68	-2	7.65	99.1% Left Cerebrum	70.1% Occipital Lobe, 29% Temporal Lobe	38.1% Middle Occipital Gyrus, 22.9% Middle Temporal Gyrus, 21.6% Inferior	42% Brodmann area 19, 35.5% Brodmann area 37, 12.1%

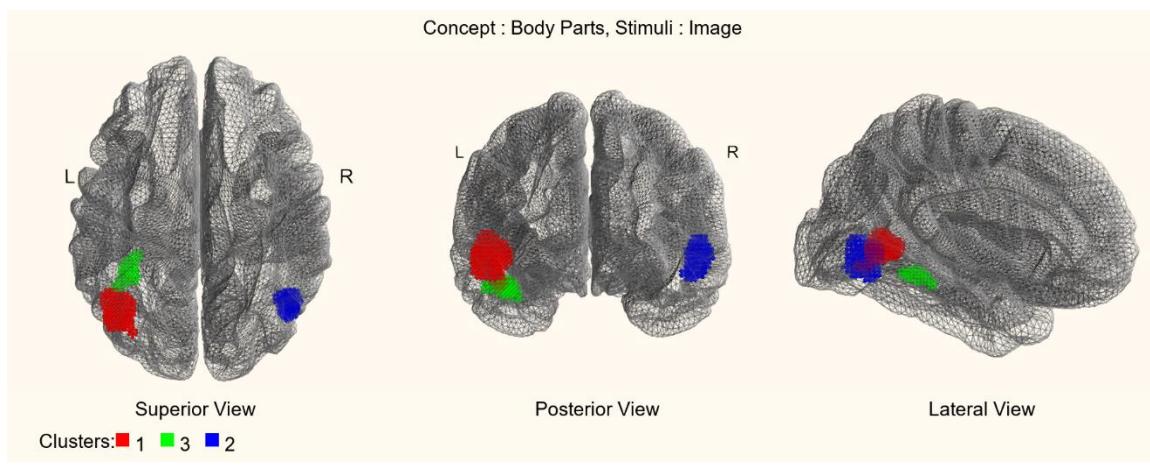
							Temporal Gyrus, 10.8% Inferior Occipital Gyrus	Brodmann area 18	
2	2920	49	- 64	-2	5.43	100% Right Cerebrum	35.5% Inferior Temporal Gyrus, 35.5% Middle Temporal Gyrus, 25.8% Middle Occipital Gyrus	66.1% Brodmann area 37, 21% Brodmann area 19	
3	1840	- 41	- 47	- 18	4.1	54% Left Cerebellum, 46% Left Cerebrum	51.1% Anterior Lobe, 46% Temporal Lobe	51.1% Culmen, 43.8% Fusiform Gyrus	41.6% Brodmann area 37, 4.4% Brodmann area 20

1 Figure 16 illustrates the relationship between individual studies and the three significant activation  
 2 clusters identified for the Body Parts category. The visualization shows a dominant convergence toward  
 3 Cluster 1, which integrates contributions from several datasets, principally from, with additional input  
 4 from Studies 2 and 7. In contrast, Clusters 2 and 3 received fewer and more selective contributions,  
 5 reflecting region-specific activations observed in only a subset of experiments. This pattern indicates that  
 6 body-part representation is supported by a central, highly consistent network (Cluster 1), complemented  
 7 by smaller clusters capturing study-specific variability across visual and sensorimotor regions.



8  
 9 Figure 16. Contribution of studies to clusters (concept: body parts, stimuli: image)  
 10 This meta-analysis identified three main clusters in the occipital, temporal, and cerebellar regions,  
 11 reflecting the neural basis of body part concept processing through visual stimuli.  
 12 • Cluster 1: This cluster is located in the left occipital and temporal cortex, involving the middle occipital  
 13 gyrus, middle temporal gyrus, inferior temporal gyrus, and fusiform gyrus. These regions, particularly

1 Brodmann areas 19, 37, and 18, are associated with high-level visual processing and object recognition  
2 (116), making their activation in response to body part concepts expected(147).  
3 • Cluster 2: This cluster is found in the right occipital and temporal cortex, showing a similar but slightly  
4 different activation pattern compared to cluster 1. The presence of Brodmann area 37 suggests a  
5 strong role in visual category processing, while right-hemisphere dominance may reflect holistic visual  
6 perception of body parts(113, 148).  
7 • Cluster 3: This cluster includes parts of the left temporal lobe and the cerebellum, with activation in  
8 the fusiform gyrus and culmen. While the temporal lobe's involvement aligns with visual object  
9 processing, the cerebellar contribution is less expected but could indicate sensorimotor integration  
10 related to body part perception(113, 149).



11  
12 Figure 17. Brain activation (clusters) in response to body part (image stimuli): superior, posterior, and lateral views  
13 Figure 17 shows the spatial distribution of the three significant activation clusters identified for the Body  
14 Parts category using visual (image-based) stimuli. The largest cluster (Cluster 1, red), almost twice the  
15 size of the others, is in the left occipito-temporal cortex, encompassing the occipital, temporal, and  
16 inferior temporal gyri (Brodmann areas 19 and 37). Cluster 2 (blue) appears in the right hemisphere,  
17 covering homologous occipital and temporal regions, whereas Cluster 3 (green) lies mainly in the left  
18 cerebellum, extending toward the fusiform gyrus. Together, these clusters indicate a left-lateralized but  
19 bilaterally organized network that supports the visual and perceptual representation of body parts.

20

## 6.7. Overlap of Neural Activations Across Concepts with the Same Stimuli

As summarized in Table 6, the distribution of stimulus modalities across conceptual domains is far from uniform. For instance, studies exploring animals have commonly used visual, written, and auditory stimuli, whereas investigations of tools, body parts, and food have relied primarily on visual paradigms.

In previous sections, ALE meta-analyses were conducted separately for each concept-stimulus pair, identifying consistent activation patterns associated with specific sensory and semantic characteristics.

To extend this analysis beyond isolated concept mappings, the current section employs a cross-concept comparative approach, examining overlaps in neural activations among different conceptual categories that share the same type of stimulus (e.g., image-based or auditory). By holding the stimulus modality constant, this approach effectively controls for perceptual variance and isolates concept-driven neural components, allowing for a more refined investigation of how the brain organizes conceptual knowledge across shared perceptual conditions.

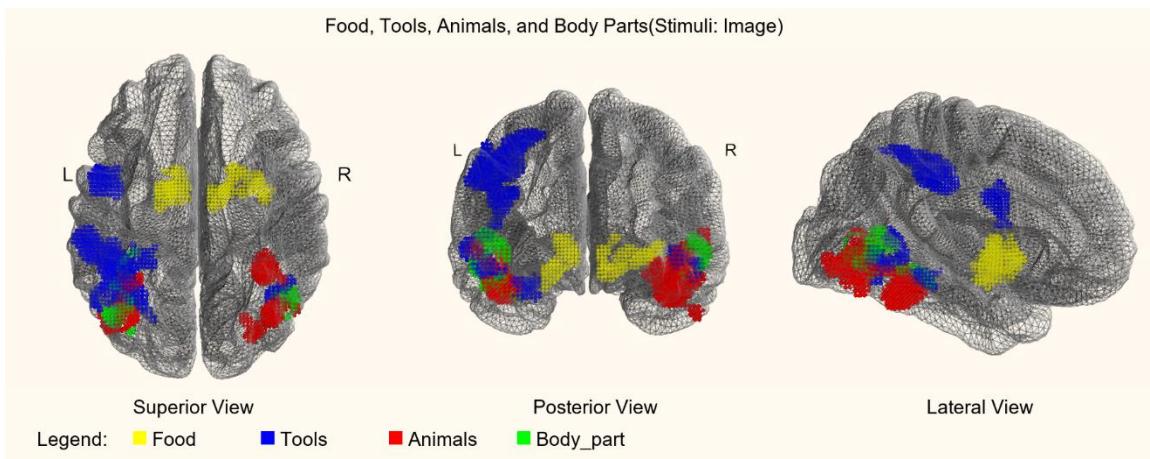
This methodological extension provides not only a deeper understanding of semantic representation but also a novel integrative perspective on how distinct conceptual domains may converge within common neural frameworks. For example, image-based stimuli allow direct comparison of animals, tools, body parts, and food, while auditory paradigms reveal shared and distinct neural bases for music and animal sounds. These overlap analyses uncover both the common representational substrates and the specialized networks supporting category-specific processing, bridging the gap between sensory perception and higher-order conceptual understanding.

Beyond their theoretical significance, these findings may also contribute to the optimization of concept selection for semantic BCI systems, where identifying distinct yet stable neural activation patterns across conceptual categories is essential. Understanding how conceptual representations overlap, or diverge, under the same stimulus modality can inform the design of more accurate and generalizable decoding models for semantic BCI applications, advancing efforts toward intuitive and concept-based neural communication systems.

#### 6.7.1. Overlap of Brain Activation Between Concepts for Image-Based Stimuli

The goal of this section is to identify and characterize the neural regions of overlap among conceptual categories that share visual (image-based) stimuli. By focusing exclusively on image-driven paradigms, the analysis aims to dissociate conceptual commonalities from perceptual confounds and to determine

1 whether distinct semantic domains recruit shared or segregated cortical networks under comparable  
2 visual conditions.  
3 For image-based stimuli, four conceptual categories were analyzed in this meta-analysis: animals (section  
4 6.1.1), tools (section 6.2.1), food (section 6.3.1), and body parts (section 6.6.1). The brain activation  
5 patterns associated with each concept were examined in detail, identifying distinct clusters of activation  
6 across studies. Figure 18 illustrates all activated brain regions corresponding to each concept when  
7 processing image-based stimuli.



9 Figure 18. Brain activation for food, tools, animals, and body parts (stimuli: images)

10 Figure 19 illustrates the overlap maps among all possible pairs of visual conceptual categories, with each  
11 overlapping region rendered in a distinct color to highlight the spatial intersections between concepts  
12 such as animals, tools, body parts, and food. This visual representation enables a direct assessment of  
13 how strongly the neural systems supporting these categories converge or remain functionally distinct.

14 As shown in Figure 19, overlap is observed among animals, tools, and body parts, primarily within  
15 regions known to mediate visual recognition and semantic integration, namely occipito-temporal and  
16 parietal cortices. In contrast, the food category exhibits no significant overlap with any of the other  
17 image-based concepts, indicating a functionally distinct neural profile. This lack of overlap may reflect  
18 the unique affective and interoceptive components associated with food-related processing, which  
19 engage regions beyond classical visual-semantic pathways (e.g., insular and limbic structures).

20

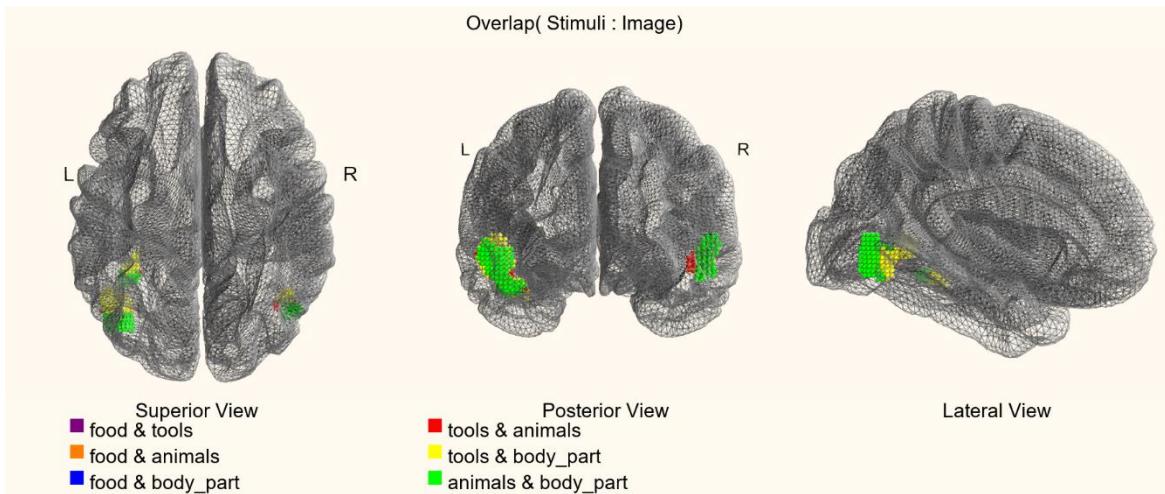


Figure 19. Overlap between concepts (stimuli: images)

Figure 20 presents the Jaccard overlap coefficient matrix depicting the degree of neural overlap among conceptual categories associated with image-based stimuli. Each cell in the matrix quantifies the proportion of shared activation between two concepts relative to their combined activated regions, where lighter colours indicate greater similarity. This quantitative representation complements the spatial overlap maps shown previously by providing a numerical index of cross-concept neural convergence.

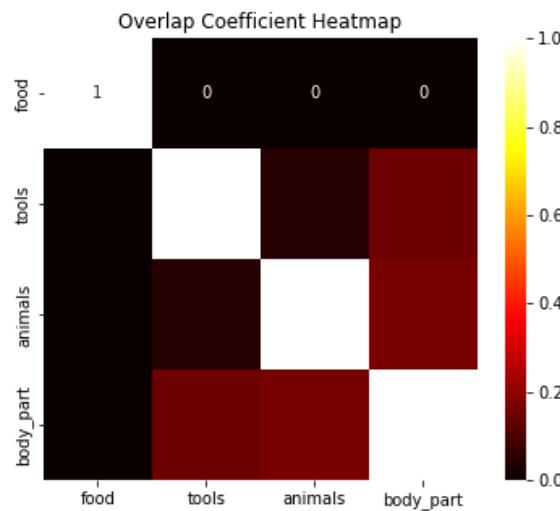
As illustrated, the food category shows no measurable overlap with any of the other visual concepts, underscoring its distinct neural profile and possible reliance on affective and interoceptive systems rather than classical visual-semantic circuits. In contrast, animals, tools, and body parts display moderate pairwise overlaps, suggesting partially shared cortical representations, particularly within occipito-temporal and parietal regions involved in object perception and semantic association.

By incorporating the Jaccard Index, this analysis allows for an objective comparison of neural similarity across conceptual domains, reducing the subjectivity of purely visual assessments. The resulting heatmap thus not only visualizes the degree of commonality but also highlights the functional separability of conceptual networks under identical stimulus conditions.

From an applied perspective, these findings bear relevance to the development of semantic BCI systems. Concept categories that exhibit minimal or no overlap, such as food, are more likely to produce distinct and non-redundant neural activation patterns, thereby enhancing the discriminability of signals and improving the robustness of concept decoding algorithms. Conversely, categories with higher overlap may represent semantically integrated or perceptually linked neural representations, providing insight into how conceptual similarity translates into cortical organization.

1 From an application-oriented perspective, the outcome of this overlap analysis provides practical  
2 guidance for the selection of optimal conceptual categories in semantic BCI systems. Since the food  
3 concept demonstrates minimal or no overlap with the other image-based categories, while animals,  
4 tools, and body parts share moderate but distinguishable neural patterns, this combination represents  
5 an ideal balance between separability and representational diversity. Therefore, selecting food together  
6 with one of the other three concepts (animals, tools, or body parts) could enhance classifier accuracy  
7 and improve concept decoding performance by maximizing inter-category distinctiveness in neural  
8 activation patterns.

9



10

11 Figure 20. Overlap coefficient heatmap (stimuli: image)

#### 12 6.7.2. Overlap of Brain Activation Between Concepts for Auditory Stimuli

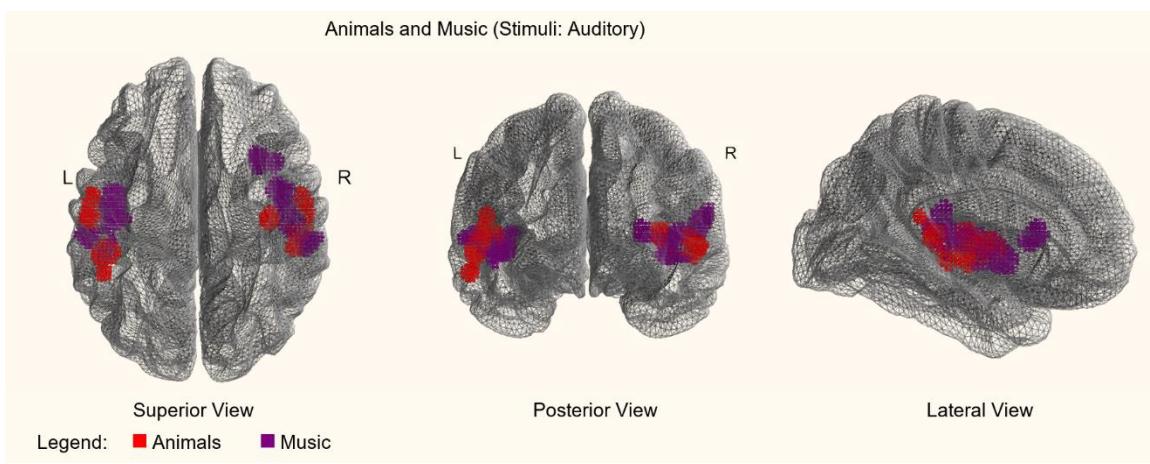
13 For auditory stimuli, two conceptual categories were analysed in the meta-analysis: music (Section 6.4.1)  
14 and animals (Section 6.1.2). Both domains engage the auditory system but differ in their semantic,  
15 perceptual, and emotional processing demands. The analysis aimed to determine whether these two  
16 auditory-based concepts rely on overlapping or distinct neural substrates when processed through  
17 sound-related stimuli.

18 Figure 21 illustrates the activation clusters corresponding to each concept, while Tables 11 and 18  
19 summarize their peak coordinates and anatomical localization.

20 For the music category, three distinct clusters were identified. The largest cluster (Cluster 1) was located  
21 in the right superior temporal gyrus (STG) and extended into the insula and postcentral gyrus, reflecting  
22 auditory integration and sensorimotor coupling during rhythm and melody perception. Cluster 2, in the

1 left STG and insula, demonstrated bilateral auditory engagement, consistent with pitch and harmonic  
2 processing. Cluster 3, centered in the right insula and inferior frontal regions, likely reflects the  
3 emotional and cognitive appraisal of musical structure.  
4 Similarly, animal sounds produced three significant clusters. The largest cluster (Cluster 1) was situated in  
5 the right superior temporal gyrus and insula, partially overlapping with music-related regions, indicating  
6 shared auditory perception mechanisms. However, the animal concept exhibited stronger activation in  
7 the posterior temporal cortex, particularly in Brodmann areas 21, 22, and 41, associated with voice and  
8 biologically relevant sound recognition. The left-hemisphere clusters (Clusters 2 and 3) extended along  
9 the superior and middle temporal gyri, suggesting left-dominant semantic and linguistic processing of  
10 animal sounds.

11



13      Figure 21. Brain activation for animal and music (stimuli: auditory)

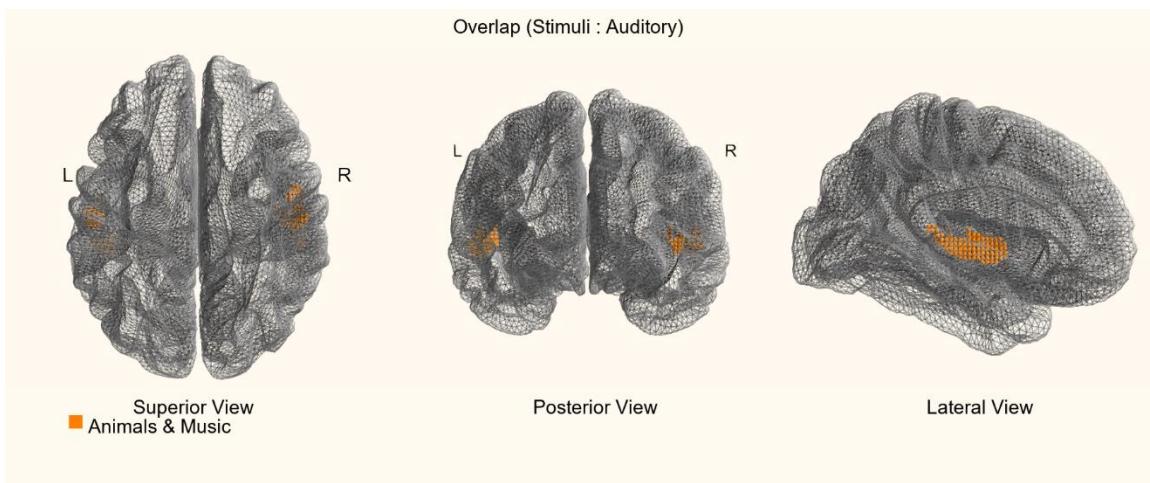
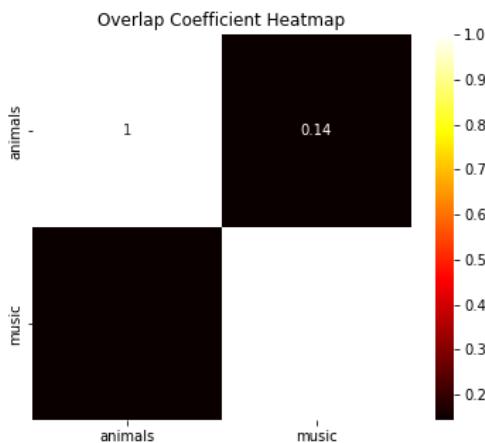


Figure 22. Overlap between concepts (stimuli: auditory)

2 Figure 22 illustrates the overlap between the concepts of music and animals when processed using  
3 auditory stimuli. This figure shows that, as expected, these concepts exhibit overlap in the auditory  
4 regions, reflecting their shared processing within the brain's auditory system.

5 Comparing these two auditory concepts reveals limited but systematic overlap within bilateral temporal  
6 cortices, primarily in regions supporting early auditory perception. Beyond this shared core, music  
7 uniquely engages limbic and multimodal networks, whereas animal sounds preferentially recruit  
8 temporal-parietal association areas involved in identifying biologically meaningful cues.

9 This pattern underscores the functional differentiation of auditory conceptual representations: both  
10 categories share low-level auditory processing pathways but diverge in higher-order semantic and  
11 emotional dimensions. From an applied standpoint, this distinction is particularly valuable for semantic  
12 BCI systems. Selecting auditory concepts such as music and animals which exhibit partially overlapping  
13 but separable activation profiles may enhance neural discriminability, enabling more robust decoding  
14 and classification performance in auditory-based semantic BCI paradigms.



15

Figure 23. Overlap coefficient heatmap (stimuli: Auditory)

17 Figure 23 presents the Jaccard overlap coefficient heatmap illustrating the degree of neural overlap  
18 between the two auditory-based conceptual categories: animals and music. Each cell in the matrix  
19 represents the proportion of shared activation relative to the total activated voxels of both categories.  
20 The diagonal value of 1.0 reflects within-category consistency, while the off-diagonal value of 0.14  
21 indicates a very limited overlap between these two auditory concepts.

22 This low overlap coefficient suggests that, although both music and animal sounds engage bilateral  
23 auditory cortices, they rely on functionally distinct neural circuits. Specifically, music activates extended

1 regions within the superior temporal, insular, and frontal cortices. These areas are associated with  
2 rhythm, harmony, and emotional appraisal, whereas animal sounds are primarily represented in the  
3 superior and middle temporal gyri, involved in the recognition of biologically relevant acoustic cues.  
4 The modest overlap (Jaccard = 0.14) thus captures shared engagement of early auditory processing  
5 regions, while highlighting clear divergence in higher-order semantic and affective processing networks.  
6 This finding supports the view that semantic differentiation can emerge even within a single sensory  
7 modality, reflecting concept-specific encoding in the auditory cortex.

## 8 7. Discussion

9 We moved beyond cataloguing studies by combining modality-controlled ALE with a quantitative overlap  
10 metric to test how separable semantic categories are in the brain. Across 75 fMRI experiments covering  
11 six domains (animals, tools, food, music, body parts, pain), we ran independent ALEs per concept–  
12 modality pair and then quantified inter-category similarity with Jaccard overlap maps. This revealed  
13 minimal visual overlap for Food with other visual categories and only modest auditory overlap between  
14 Music and Animals (Jaccard  $\approx$  0.14), establishing an empirical scale of conceptual separability rather than  
15 a purely descriptive classification.

### 16 7.1. Neural Representation of Semantic Concepts

17 Our findings reinforce the concept of a distributed yet functionally specialized network for semantic  
18 processing in the brain. Beyond confirming earlier evidence, the observed category-specific activation  
19 patterns highlight how distinct neural systems cooperate to represent meaning, indicating that semantic  
20 knowledge emerges from the interaction of modality-specific sensory regions and higher-order  
21 associative hubs.

#### 22 7.1.1. Animals

23 Image-based representations of animals elicited significant activation in the occipital cortex, fusiform  
24 gyrus, and cerebellum, highlighting the role of visual processing areas in object recognition and category-  
25 specific perception. Auditory animal stimuli, on the other hand, engaged the superior temporal gyrus  
26 and insular regions, supporting the role of these areas in processing biologically relevant sounds.

#### 27 7.1.2. Tools

28 The perception of tools primarily activated the left inferior parietal lobule, premotor cortex, and inferior  
29 temporal gyrus. These regions have been previously implicated in action planning and object  
30 manipulation, reinforcing the close link between tool perception and motor representations.

1           7.1.3. Food

2   Food-related stimuli predominantly engaged subcortical and limbic structures, including the putamen,  
3   amygdala, and parahippocampal gyrus. These findings align with the established role of these regions in  
4   reward processing, motivation, and memory encoding related to food stimuli.

5           7.1.4. Music

6   Auditory music stimuli activated bilateral superior temporal gyri, the insula, and precentral gyrus,  
7   confirming the involvement of these regions in auditory processing, pitch discrimination, and emotional  
8   responses to sound.

9           7.1.5. Pain

10   Tactile pain stimuli resulted in significant activation within the thalamus, anterior cingulate cortex, and  
11   insula, reflecting the sensory, affective, and cognitive aspects of pain perception.

12           7.1.6. Body Parts

13   The processing of body-related visual stimuli was primarily associated with activation in the middle  
14   occipital gyrus, inferior temporal gyrus, and fusiform gyrus, confirming their role in high-level visual  
15   categorization of human body parts.

16   Taken together, these results reinforce and refine the view that semantic knowledge is represented  
17   across a distributed but functionally specialized network in the brain. The activation patterns we  
18   observed for each conceptual category reflect both modality-specific processing demands and domain-  
19   level organization, extending prior neuroimaging findings and meta-analytic evidence.

20   The engagement of occipital and fusiform regions during the processing of animals and body parts using  
21   image-based stimuli corroborates findings from Martin(150) and Cortinovis *et al.*(151), who argued for  
22   the critical role of visual association areas in object categorization. Interestingly, the overlap in visual  
23   pathways between animals and body parts supports the idea that these categories may share  
24   perceptual features (e.g., biological form, movement cues) despite their conceptual differences, a  
25   nuance that has also been noted in multivariate pattern analyses.

26   The robust activation of the inferior parietal lobule, premotor cortex, and inferior temporal gyrus during  
27   tool perception underscores the deep integration of sensorimotor schemas in tool-related knowledge.  
28   These findings echo theories of grounded cognition and are consistent with reports that suggest tool use  
29   concepts are deeply rooted in the brain's praxis network(113, 116, 131). This result is particularly  
30   significant given that these regions were consistently active across both image and word-based stimuli,  
31   reinforcing the idea that the neural encoding of tool semantics transcends input modality.

1 The food category presented a markedly different activation profile, involving the amygdala, putamen,  
2 and parahippocampal gyrus. These structures are known for their role in reward processing, emotional  
3 evaluation, and memory contextualization, respectively(135-137). While prior studies have emphasized  
4 the affective salience of food stimuli, our meta-analytic results provide a modality-controlled  
5 confirmation of these patterns, offering stronger support for the hypothesis that food-related concepts  
6 are preferentially processed through motivational and emotional neural pathways.

7 In the case of music, we observed reliable activation in the bilateral superior temporal gyrus, the insula,  
8 and the precentral gyrus, areas well established in pitch perception, rhythmic processing, and affective  
9 responses to sound. This finding mirrors the conceptual model proposed in(113, 141, 142), which posits  
10 that music semantics are co-constructed from auditory, emotional, and motor representations, further  
11 supported by insular involvement.

12 Pain stimuli elicited activity in canonical pain-related regions, including the anterior cingulate cortex  
13 (ACC), insula, thalamus, and somatosensory cortex. These regions form the well-known pain matrix and  
14 their consistent activation aligns with earlier researches(116, 145) that describe both the sensory-  
15 discriminative and affective-motivational dimensions of pain perception.

16 Across all categories, our findings advance a hybrid model of semantic representation that integrates  
17 distributed processing with domain-specific specialization. Unlike prior reviews that primarily described  
18 activation loci, this work quantitatively demonstrates how modality control and overlap mapping clarify  
19 the functional boundaries between conceptual domains. This evidence supports the view that semantic  
20 knowledge arises from cooperative interactions among sensory-specific regions and higher-order  
21 associative hubs, providing a data-driven framework for assessing conceptual separability in the human  
22 brain.

23 By systematically charting concept-dependent activations, our meta-analysis offers a conceptually  
24 integrated account of how perceptual, motor, affective, and associative systems jointly construct  
25 meaning. These results refine existing theories of semantic cognition and suggest that meaning  
26 representation is a dynamic, multi-level process rather than a fixed localization pattern. Beyond  
27 theoretical significance, this framework also informs applied directions, such as optimizing neural  
28 decoding models and guiding BCI designs that rely on semantic differentiation. Together, these  
29 contributions move the field from descriptive classification toward a mechanistic and predictive  
30 understanding of how the brain organizes conceptual knowledge.

31

## 7.2. Overlap and Discriminability of Semantic Representations

By examining overlap in neural activation across different concepts processed within the same stimulus modality, we identified a graded architecture of shared versus distinct neural representations. Concepts such as animals and tools showed overlapping activity in the lateral occipital cortex, indicating that partially common visual processing streams support object-based recognition across these domains. In contrast, food-related stimuli demonstrated minimal overlap with other categories, pointing to a highly specialized, domain-specific representation that engages motivational and affective circuits rather than perceptual ones. Within the auditory domain, music and animal sounds exhibited partial convergence in the superior temporal gyrus and insula, reflecting shared spectrotemporal analysis pathways, yet retained distinct subregional activations consistent with category-level discrimination.

These results collectively highlight that stimulus modality acts as a key organizing dimension for conceptual representation in the brain. While some networks are tuned to domain-specific knowledge, others reveal graded convergence driven by shared perceptual or cognitive demands. This dual structure of specialization embedded within partial overlap illustrates that semantic encoding is both differentiated and hierarchically integrated, challenging simplified categorical boundaries.

Crucially, our study extends prior work by providing a systematic, quantitative assessment of inter-category similarity using the Jaccard index applied to ALE-derived activation maps. This method enabled controlled, modality-specific comparisons across multiple conceptual domains, something rarely achieved in earlier meta-analyses. Through this quantitative lens, we identified subtle but reliable distinctions in representational proximity, such as the consistent separability of food from all other categories, and the modest auditory overlap between music and animals. These findings empirically ground the notion of graded conceptual distance, offering measurable evidence of how neural representations cluster or diverge across semantic domains.

Beyond its theoretical contribution, this mapping has clear methodological and applied implications. The quantitative overlap matrix provides a principled framework for evaluating semantic distinctiveness and for selecting functionally separable categories in neural decoding and BCI applications. By linking representational geometry to decoding feasibility, our findings bridge the gap between cognitive neuroscience of meaning and practical neural engineering, advancing both domains toward a mechanistic understanding of conceptual representation in the human brain.

### 1      7.3.      Limitations and Future Directions

2      Despite the strength and consistency of our meta-analytic findings, several limitations warrant  
3      consideration. A primary concern in coordinate-based meta-analysis lies in the heterogeneity of the  
4      included studies, particularly with respect to task design, stimulus type, and participant demographics.  
5      While such variability is often viewed as a confounding factor, our results demonstrate that meaningful  
6      and consistent activation patterns can still emerge. This suggests that meta-analytic approaches like  
7      ours can offer robust insights even across diverse experimental protocols, thus providing a solid  
8      foundation for hypothesis generation in future research.

9      That said, there are dimensions we could not directly control. While we accounted for stimulus modality  
10     in our analysis, other factors such as task demands, attentional load, and inter-individual differences in  
11     semantic processing likely introduced additional variance. Future studies may benefit from designs that  
12     systematically manipulate these variables to examine their specific contributions to conceptual  
13     representation.

14     Additionally, the current study focused on six conceptually grounded categories. Although these offer  
15     valuable insights into domain-level semantic organization, they do not encompass the full spectrum of  
16     human concepts, particularly abstract or relational constructs. Future meta-analyses or empirical studies  
17     should consider incorporating a wider conceptual range, including emotional and cultural categories.

18     Finally, while our analysis provides spatially precise insights into conceptual organization, it is limited in  
19     its ability to capture temporal dynamics. Integrating fMRI meta-analytic findings with high-temporal-  
20     resolution modalities such as EEG or MEG may provide a more complete picture of how semantic  
21     representations unfold over time and across cortical hierarchies.

22     In the context of semantic BCI development, several engineering factors, such as real-time decodability,  
23     signal-to-noise ratio (SNR) constraints, individual variability in neural representations, and the choice of  
24     computational models, play essential roles in shaping system-level performance. While such aspects  
25     cannot be directly evaluated within a coordinate-based meta-analytic framework, the present study  
26     provides the conceptual foundation upon which these later engineering stages depend. By identifying  
27     concept domains that exhibit high separability, low cross-category interference, and consistent modality-  
28     dependent structure, our findings help define an optimized semantic vocabulary for future decoding  
29     pipelines. Establishing this structured representational space is a prerequisite for designing high-SNR  
30     decoding tasks, selecting discriminable feature sets for classifier training, and mitigating subject-specific

1 variability through the use of inherently robust conceptual categories. Thus, this work constitutes a  
2 foundational stage that enables and constrains subsequent phases of semantic BCI development,  
3 including participant-level recordings, model training, and real-time implementation.

#### 4 7.4. Conclusion

5 This meta-analysis provides a comprehensive and quantitatively grounded framework for understanding  
6 how semantic concepts are organized in the human brain. By integrating domain-specific and cross-  
7 category comparisons under tightly controlled modality-based constraints, our findings reveal that the  
8 semantic system is not merely distributed but systematically structured along both conceptual and  
9 sensory dimensions. This structural differentiation clarifies how meaning emerges from the coordinated  
10 activity of modality-sensitive perceptual systems and higher-order associative networks.

11 Through separate analyses of six conceptual domains and across multiple stimulus modalities, we  
12 identified both the core neural substrates of each domain and the degree of representational overlap  
13 among them. Using spatial meta-analysis combined with Jaccard-based overlap metrics, we  
14 quantitatively captured the continuum between neural similarity and distinctiveness that defines  
15 semantic space. This level of precision goes beyond previous descriptive accounts of distributed  
16 semantics and establishes a measurable basis for conceptual differentiation in the brain.

17 The most critical insight of this work is that semantic representational structure is governed jointly by  
18 conceptual content and sensory format. For instance, the consistent separation of food-related  
19 activations underscores a functionally segregated motivational-affective pathway, while the partial  
20 overlap between tools and animals points to shared visuomotor processing streams. These findings  
21 demonstrate that the semantic architecture of the brain is both content-sensitive and modality-  
22 dependent, reflecting an adaptive integration of perceptual, affective, and motor systems in meaning  
23 construction.

24 Beyond theoretical implications, our results offer a methodological and translational contribution. The  
25 overlap-based analytical framework introduced here provides a principled approach for quantifying  
26 conceptual separability in neural space. This is particularly valuable for applied domains such as  
27 semantic neural decoding and BCIs, where identifying concept pairs with minimal neural overlap can  
28 enhance classification accuracy and reduce cross-category interference. Accordingly, this study bridges  
29 the gap between cognitive theory and neuro-engineering practice, advancing the field toward a  
30 mechanistic and application-ready understanding of semantic organization in the human brain.

## 1 Acknowledgements

2 This research was supported by funding from the Leverhulme Trust [Grant Number: 109535]. The  
3 authors would like to thank the members of the Brain-Computer Interfaces and Neural Engineering  
4 Laboratory at the University of Essex for their valuable feedback and support during this work.

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