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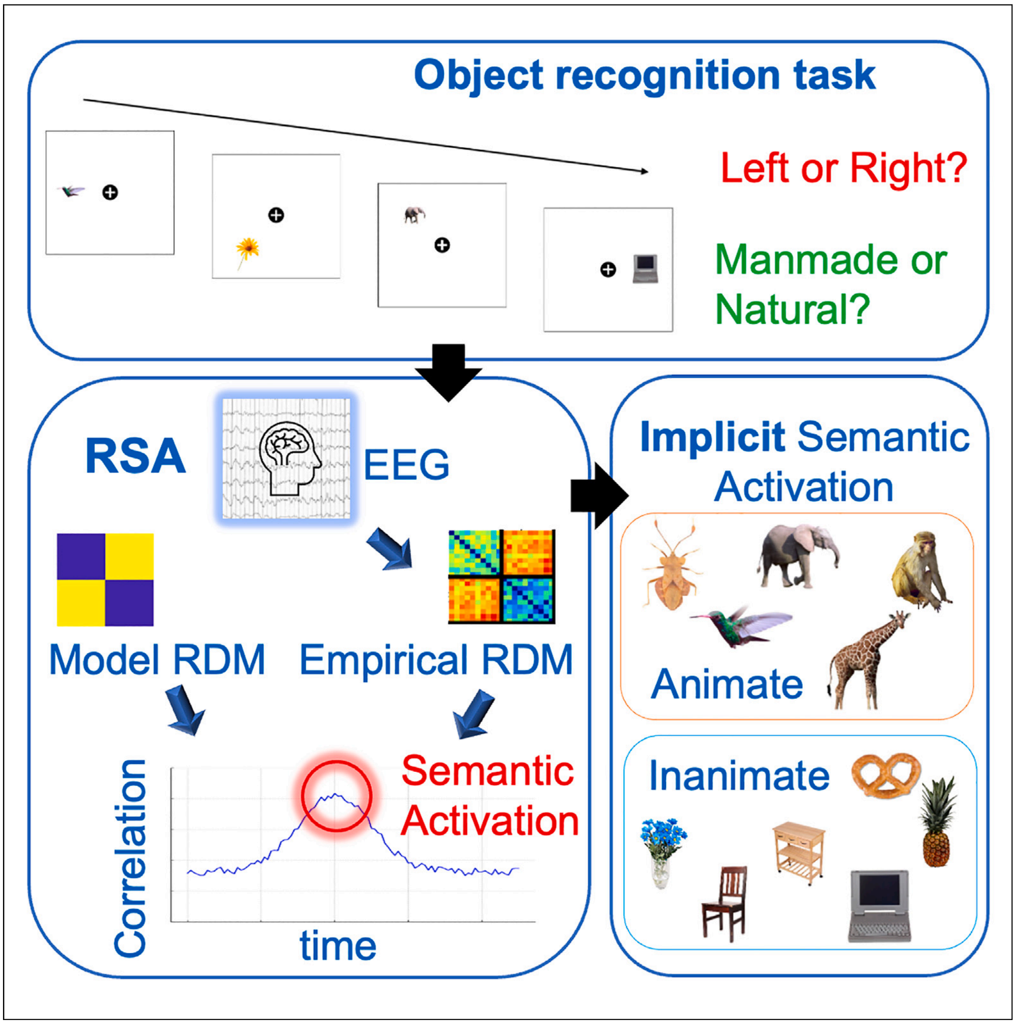

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Highlights

We explore RSA applied to EEG to assess implicit processing of semantics

Implicit processing extends to concrete and only some abstract semantic categories

Processing of the abstract category distinction animate/inanimate occurs implicitly

The abstract category distinction manmade/natural is not processed implicitly

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Correlates of implicit semantic processing as revealed by representational similarity analysis applied to EEG

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SUMMARY

Most researchers agree that some stages of object recognition can proceed implicitly. Implicit recognition occurs when an object is automatically and unintentionally encoded and represented in the brain even though the object is irrelevant to the current task. No consensus has been reached as to what level of semantic abstraction processing can go implicitly. An informative method to explore the level of abstraction and the time courses of informational content in neural representations is representational similarity analysis (RSA). Here, we apply RSA to EEG data recorded while participants processed semantics of visually presented objects. Explicit focus on semantics was given when participants classified images of objects as manmade or natural. For implicit processing of semantics, participants judged the location of images on the screen. The category animate/inanimate as well as more concrete categories (e.g., birds, fruit, musical instruments, etc.) are processed implicitly whereas the category manmade/natural is not processed implicitly.

INTRODUCTION

In our daily lives, only a small portion of the overwhelming number of visual stimuli we encounter enters our conscious minds. Different views make opposing predictions to what extent visual stimuli are analyzed implicitly.[1–4] In line with models suggesting deep implicit analyses of visual stimuli, studies on object recognition demonstrate that semantic information can be processed implicitly.[5] Others, however, stress that the depth or degree of semantic processing may be limited under implicit conditions.[6,7] In this study, we, therefore, investigate the depth, nature, and level of abstraction of neuronal representations elicited by implicit processing of visual stimuli.

We define implicit processing as the processing of information that is not relevant for the current task. Explicit processing describes the processing of information that is afforded to fulfill task instructions. If the task is to indicate an object's location, semantic information about this object is irrelevant to the task and is therefore assumed to be processed implicitly, if processed at all. Conversely, if the task focuses on an object's semantics, its location is considered to be processed implicitly. Therefore, the term "implicit" aligns closely with the concept of "preconscious" as proposed by Dehaene.[8] According to Dehaene, preconscious processes refer to neural processes that possess sufficient activation for conscious access but are temporarily stored in a nonconscious state due to a lack of top-down attentional amplification. This nonconscious processing could be due to a transient occupancy of the central workspace system with other information. In this study, implicit semantic processing of objects is studied in conditions where participants focus on the objects' location, rather than their semantic features, requiring subjects to indicate the location of depicted object on the screen.

Although there is agreement that semantic information for simple and isolated stimuli is processed implicitly,[5] the question remains open if awareness of the semantics mainly acts as an amplifier in semantic processing or if there are qualitative differences between explicit and implicit semantic processes. An early behavioral study indicated that words are implicitly processed up to semantic stages.[9] This work was followed by an extensive amount of research using priming and masking paradigms to further investigate the implicit processing of words. Neuroimaging studies revealed activation in temporal and frontal areas associated with language processes also being activated when there is no awareness of the semantics of the stimuli.[10–15] Studies using intracranial field potentials suggested that within the first 250 ms after stimulus onset implicit and explicit semantic processes evoke similar neural responses.[16] Only at later processing stages awareness of the semantics modulated the field potentials. Neural responses to unattended and unseen stimuli are often found to have smaller magnitudes, shorter durations, and later onsets than responses to attended and conscious stimuli.[17–20] Responses to unseen vs. seen stimuli thus seem to carry a

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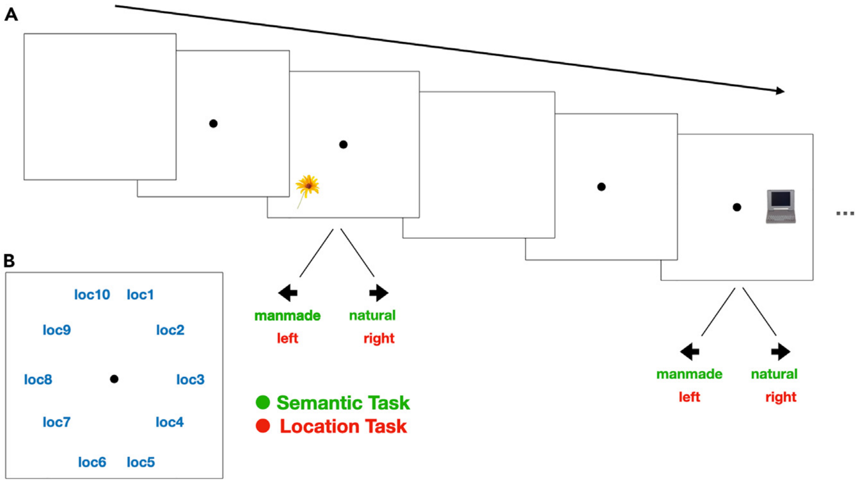

Figure 1. Experimental procedure

(A) Example sequence of stimulus presentations and tasks: There were two conditions where the participants had to press a key: in the semantic task they had to decide where the object is manmade or natural (green instructions). In the localization task, they had to decide whether the object is located on the left or right side of the screen (red instructions). In each task there were 1000 stimulus presentations; (B) Illustration of stimulus locations: Each object was displayed once at one out of 10 locations in a circle around a fixation point.

lower amount of information. However, it can be questioned if this is the case for a comparison of explicit and implicit processing, where information is presented in a way that it can enter conscious awareness but varies with respect to its task-relevance (explicit processing: task-relevant; implicit: task-irrelevant).

To study the level of semantic abstraction in implicit object recognition, we explore the level of abstraction that can be decoded from the neural signature to implicitly processed, task-irrelevant stimulus information. In explicit semantic processing, visual object recognition occurs through hierarchically organized stages advancing along the occipito-temporal pathway of object recognition. Entry-level categories dominate representations early and more abstract categories become evident later.[21–26] The time it takes to distinguish between different semantic categories depends on the abstraction level.[25]

A particularly useful method to assess the time courses and level of semantic abstraction in neuronal representations following explicit semantic processing of visual stimuli has been EEG in combination with representational similarity analyses (RSA). It is well-established that EEG data can be used to readout categorical semantic information of perceived objects.[21,27–32] It is possible to develop a visual object classifier driven by EEG data discriminating different object classes with high (>80%) accuracy.[31] EEG may thus also provide a powerful tool for estimating the level of semantic abstraction reached in implicit semantic processing. RSA is a data-analytical framework where pairwise distances between multivariate neuronal responses (e.g., voxels in fMRI or channels in EEG) to different stimuli are computed.[33] Hypothetical patterns of similarity between conditions or stimuli can then be compared to empirical similarities. The degree of representational similarity of neural responses to semantically similar stimuli can then be taken as a measure of semantic information in neuronal responses. RSA has mainly been used to investigate object recognition, especially its temporal evolution.[21,25,33,34] We use RSAs of EEG data to assess the depth of implicit semantic processing. Specifically, we compare the time course, as well as the nature and level of semantic abstraction reached under implicit (task-irrelevant) versus explicit (task-relevant) processing conditions. Our results reveal implicit semantic activation for the category animate/inanimate as well as for the specific categories. For the manmade/natural categorization we could not find any implicit semantic activation.

RESULTS

Fifteen human participants took part in the experiment. A 64-channel-EEG was recorded throughout the experiment, which consisted of two runs of 10 blocks each. In each of the ten blocks 100 images were presented in random sequences and appeared quasi-randomly in one out of 10 positions situated in a circle around the central fixation dot (Figure 1). Sequences of locations were quasi-random because there was the constraint that each image appeared in each of the 10 locations across the ten blocks in one run. Images could be subdivided into 10 categories of 10 stimuli each, with 5 categories consisting of images of manmade objects (e.g., musical instruments or furniture) and 5 categories consisting of natural objects (fruit or insects). In one of the runs, participants were instructed to judge whether an image was presented in the left part of the screen or the right (localization task). In the other run, participants were instructed to judge whether a depicted object is manmade or natural (semantic task). Order of runs was counterbalanced between participants.

Participants' behavioral performance was high suggesting high attention on task-relevant stimulus features

Participants' attention was either directed toward stimulus semantics using a manmade/natural categorization task or was directed away from stimulus semantics to location using a stimulus-localization task (left/right). Thus, semantic activation is regarded as explicit or implicit,

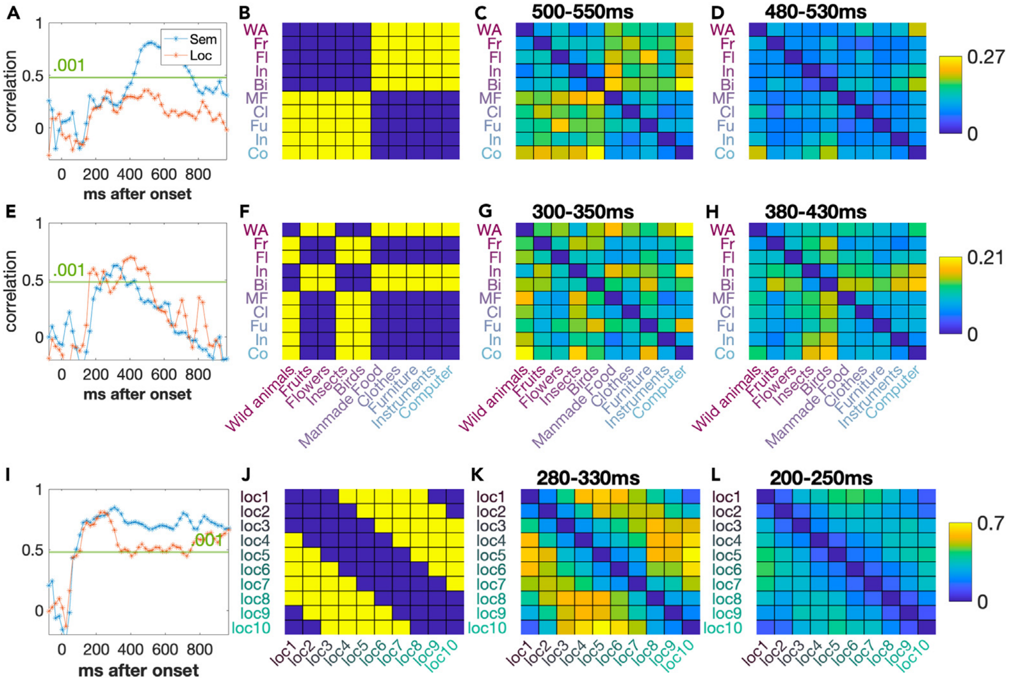

Figure 2. RSA with 10 × 10 RDMs applied to EEG data to elucidate semantic activation

(A, E, and I) correlations over time of empirical RDMs with model RDMs. The green line indicates the level of significance (*p* value) for the correlations.

(B, F, and J) model RDMs.

(C, G, and K) empirical RDM of time window where the correlation peaks in the semantic task.

(D, H, and L) Empirical RDM of time window where the correlation peaks in the localization task. (A–D) Manmade/natural. (E–H) Animate/inanimate. (I–L) Locations.

whereas activation of the locations is regarded as implicit or explicit in the semantic and the localization task, respectively. Participants' performance was near ceiling for both tasks (96.4% accuracy for the semantic task and 98.1% accuracy for the localization task) and their average response times were very short (687 ms for the semantic task and 460 ms for the localization task). Paired samples t-tests revealed that accuracy was significantly lower (t(df = 28) = 2.7, $p = 0.017$) and reactions times were significantly longer (t(df = 28) = 7.12, $p < 0.001$) for the semantic compared to the localization task. This suggests that the semantic task required more cognitive effort (longer reaction times) and was more difficult (lower accuracy) than the location task.

Standard ERPs analyses suggest different neuronal processes associated with the processing of semantics and the locations of the visual stimuli

Prior to analyzing the implicit and explicit processing of stimulus location and semantic categories, we wanted to confirm that the different stimulus categories (location: lef/right; semantic category: manmade/natural) indeed elicit distinct brain responses in the EEG. To perform this basic sanity check, we compared the ERPs between the different conditions (left vs. right; manmade vs. natural) across both tasks using cluster-based permutation tests (paired-samples t-tests, cluster formation threshold: $p < 0.05$, number of permutations = 500). The resulting sequential topographies for these contrasts (0–1000 ms after onset, 50 ms intervals) are presented as t-values in Figures S1 and S2. For the contrast manmade vs. natural, natural, we observed a significant difference in the N400 component (Figure S1), which is generally associated with semantic processing.[35] For the location contrast (left vs. right), we observed significant differences over occipital regions (Figure S2). These findings confirm that the different stimulus categories are associated with distinct patterns of electrophysiological activity that deserve further investigation using representational similarity analysis.

Stimulus location information is present in RSA on EEG traces when location is processed implicitly and explicitly

As a first step, we analyzed the implicit and explicit processing of stimulus location. The correlations of the empirical data with the location model representational dissimilarity matrices (RDMs) (Figures 2I–2L) were significant for both the semantic and the localization task starting at 85 ms (peak of correlation in semantic task at 285 ms, R = 0.89, $p < 10^{-15}$; in localization task at 265 ms, R = 0.85, $p < 10^{-14}$) and stayed significant until the end of the segment (1000 ms). These results suggest that location information is readily available in scalp EEG activity following both implicit and explicit processing of location.

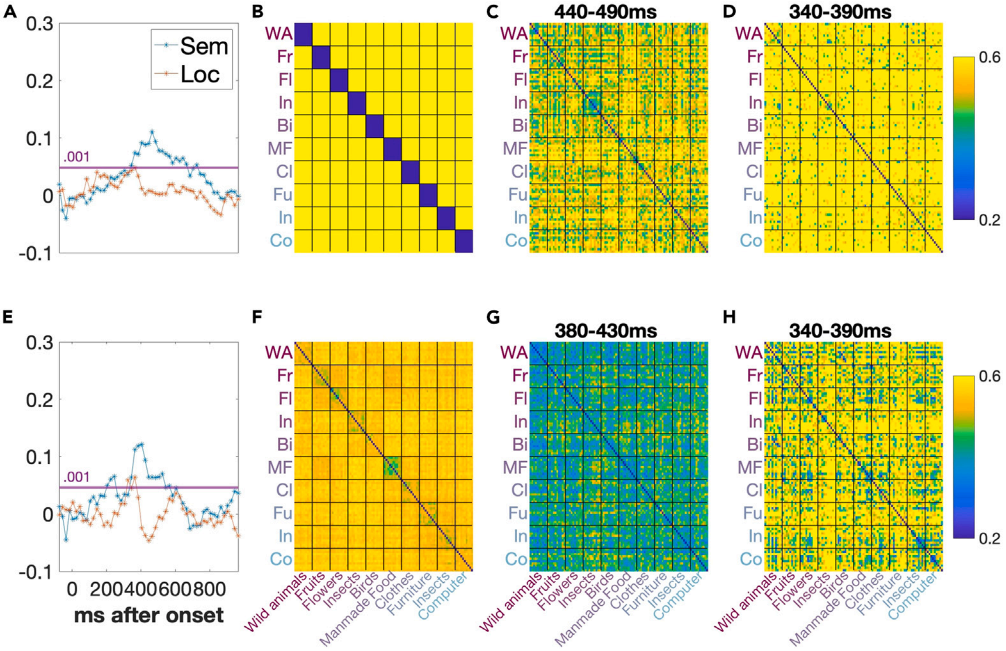

Figure 3. RSA with 100 × 100 RDMs applied to EEG data to elucidate semantic activation

(A and E) correlations over time of empirical RDMs with model RDMs. The purple line indicates the level of significance (*p* value) for the correlations.

(B and F) model RDMs.

(C and G) Empirical RDM of time window where the correlation peaks in the semantic task.

(D and H) Empirical RDM of time window where the correlation peaks in the localization task. (A–D) Analysis of 10 specific categories (E–H). Analysis of RDMs created from intracranial recordings of human single neurons also reflecting the 10 specific categories.

Semantic information of small categories and animacy but not for the manmade/natural distinction is apparent in RSA of EEG following implicit processing

Our first analysis of semantic processing focused on the processing of concrete and small categories (e.g., “wild animals”, “clothes”, “fruits”, etc.) (Figures 3A–3D). For the semantic task, the correlations of the empirical RDMs with the 10-category model RDMs (Figure 3B) were significant from 185 ms to 905 ms, peaking at 465 ms (R = 0.14, $p < 10^{-22}$), while in the localization task the correlations stayed significant from 185 ms to 365 ms, peaking at 205 ms (R = 0.062, $p < 10^{-4}$). These results suggest that categories on an intermediate level of abstraction can be readout from brain activity also following implicit processing.

Next, we analyzed the processing of the more abstract semantic category manmade/natural (Figures 2A–2D). In the semantic task the empirical RDMs showed significant correlations with the manmade/natural model RDM (Figure 2B) from 465 to 755 ms, peaking at 625 ms (R = 0.87, $p < 10^{-13}$). In the localization task, however, there were only insignificant correlations (peak of correlation R = 0.43, $p = 0.0034$). A pairwise comparison between implicit and explicit activation on single-subject correlation time-courses of empirical RDMs with model RDMs did not reach significance at any time point (Figure S3, see also in the further section). Together, these results suggest semantic activation on the level of the abstract manmade/natural category, while no evidence in favor of implicit activation could be found. To corroborate this conclusion, we further calculated Bayesian correlation tests, where Bayes Factors >3 would indicate moderate evidence for an implicit activation, and Bayes Factors <1/3 indicate evidence for an absence of implicit activation of the manmade/natural category (Figure S6). This analysis suggested that between 0 and 300 ms as well as after 600 ms after stimulus onset, data were indeed in favor of the null hypothesis (no implicit activation). Between 300 and 600 ms the data were inconclusive, meaning that we can neither confirm nor deny with confidence a (weak) implicit semantic activation in this time window. Note that we found very strong evidence (BF > 150) for the explicit processing of the manmade/natural category in the semantic task (Figure S6).

We further explored whether any other abstract semantic dimensions were processed implicitly. Theoretically, the ten specific stimulus categories could be grouped according to many different abstract, high-level semantic dimensions. We used a data driven approach to assess which other high-level semantic dimensions, if any, were processed. To this aim, we first created model RDMs for all possible combinations of the 10 specific stimulus categories into two groups ($N = 456$ possibilities, for a minimum of three categories per group). Then, we extracted the peak correlations between the empirical RDMs of the semantic task and all ($N = 456$) resulting model RDMs. Finally, we assessed whether the model RDMs showing the highest correlations with the empirical data reflected meaningful semantic dimensions. The model RDM reaching the highest peak correlation reflected a split according to the animate/inanimate dimension (Figure 4). For this model RDM, there were significant correlations not only in the semantic task (245–445 ms, peaking at 305 ms, R = 0.64, $p < 10^{-5}$), but also in the

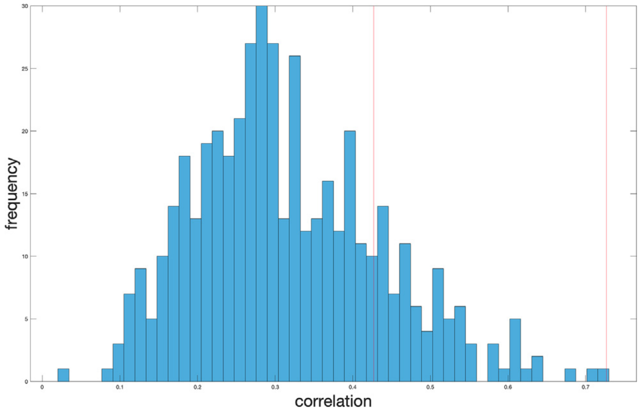

Figure 4. Rank-ordered max correlations of all possible group arrangements

(with >2 categories per group), where vertical lines indicate the correlations for the manmade/natural (R = 0.42) and the animate/inanimate (R = 0.72) distinction, respectively.

localization task (325–485 ms, peaking at 365 ms [R = 0.73, $p < 10^{-7}$]). These results hence suggest that abstract, meta-categorical representations on the level of animate/inanimate can be read out also following implicit processing of visual stimuli.

Explicit semantic activations on scalp EEG are similar to intracranial single-unit activity in the medial temporal lobe

Further, we were interested in whether there is a correspondence between neuronal representations measured at the scalp with the ones obtained from intracranial single-unit recordings in the medial temporal lobes of epilepsy patients.[36] We therefore compared our 100 × 100 RDMs to the model RDMs created out of the RDMs from the intracranial recordings of neuronal representations derived at the end of the ventral processing stream (Figures 3E–3H). The results suggest that representations similar to the ones obtained from single neuron activity in the human medial temporal lobes can be detected not only following explicit, but also following implicit processing of visual stimuli. In the semantic task the correlations stayed significant from 225 ms–625 ms, peaking at 505 ms (R = 0.15, $p < 10^{-25}$) and in the localization task the correlations stayed significant from 185 ms–205 ms and from 245 ms to 365 ms, peaking at 285 ms (R = 0.10, $p < 10^{-11}$). This result hence supports the conclusion that representations similar to the ones at the higher-order stages of object recognition and semantic analyses can be readout from EEG following implicit processing of semantics.

Semantic information peaks earlier for concrete vs. abstract, and implicit vs. explicit information

Next, we were interested in the temporal evolution of the previous effects. To be able to compute inference statistics on peak-latencies, we correlated the subject-level RDMs with the model RDM to obtain time courses on a subject level. As an initial sanity check, we grand-averaged these time courses of correlations (Figure S3). These analyses lead to the same conclusions as from the analyses correlating group-level RDMs with the model RDM (Figures 2 and 3). We assessed the significance of the averaged subject-level correlation time courses, by calculating a cluster-based permutation test[37] with 1000 permutations (Figure S3). We used a cluster-alpha threshold of 0.005, an alpha threshold of 0.05 and a minimum cluster-size of 5. To evaluate differences in peak latencies, we determined the peak latencies of subject-level time courses and then conducted a paired t-test between conditions. The mean peak latencies reported in this section are the mean peaks across subjects. They thus differ slightly from the peak latencies of the correlations of group-level RDMs with model RDM (Figures 3 and 4, reported earlier) as well as from the peaks of the averaged subject-level correlation time courses (Figure S3).

We compared implicit and explicit semantic processing as well as the processing of categories with different levels of abstractness. Note that it is not possible to compare peak latencies for the implicit and explicit semantic processing of the manmade/natural category because there was no significant peak for the implicit processing of this category in the localization task. Furthermore, it is not possible to compare peak latencies for the implicit and explicit processing of the animate/inanimate category because there was no instruction at all to explicitly process this category. We therefore decided to contrast the temporal evolution of implicit and explicit semantic processing by comparing the peak latencies of the manmade/natural category in the semantic task (explicit processing) with those from the animate/inanimate category in the localization task (implicit processing).

Explicit semantic processing of the manmade/natural category in the semantic task peaked significantly later than implicit processing of the animate/inanimate condition in the location task (549 ms vs., 349 ms, t(df = 14) = 3.14, $p = 0.007$). Furthermore, we compared peak latencies for the explicit vs. implicit processing of the specific categories by contrasting the activation of these categories in the semantic vs. the localization task. The specific categories peaked at 510 ms under explicit semantic processing (semantic task), which was significantly later (t(df = 14) = 2.20, $p = 0.045$) than the peak at 336 ms under implicit semantic processing (location task). To investigate the temporal evolution of explicit semantic processing of categories with different levels of abstractness, we compared the peak latency of the manmade/natural category with the peak latency of specific categories in the semantic task. The peak for the explicit semantic processing of the manmade/natural category at 549 ms in the semantic task was not significantly later (t(df = 14) = 0.48, $p = 0.64$) than the peak of the specific categories at 510 ms.

DISCUSSION

In this study, we applied RSAs to EEG data to investigate implicit processing of semantic information. We assessed how semantic information, ranging from specific categories (such as fruits, flowers, furniture, etc.) to more abstract categories (such as manmade vs. natural, animate vs. inanimate), is processed implicitly in a stimulus-localization task where semantic categories are irrelevant. Additionally, we explored the implicit processing of perceptual information, specifically stimulus location, in a semantic categorization task, where stimulus location is irrelevant. Importantly, our analysis included comparisons of both the degree and the timing of implicit processing for perceptual information and semantic content across different levels of abstraction. Our results revealed significant implicit semantic processing of the abstract categories animate/inanimate and of the more concrete categories, as well as implicit perceptual processing of the location of an object. Finally, we found that the EEG-derived implicit semantic representations of concrete categories were highly similar to the implicit representations derived from intracranial EEG data that was recorded in the medial temporal lobes of epilepsy patients.[36]

As proof of principle, our method reliably detected semantic and perceptual information in neural representations when task instructions put an explicit focus on semantic and perceptual information, respectively. Furthermore, in the semantic task, where the participants had to decide whether the object is manmade/natural, there was an implicit activation of location information (Figure 2I). This result further speaks to the validity of our method and confirms previous reports of implicit processing of task-irrelevant perceptual information early after stimulus onset.[38,39] Importantly, the correlations we observed between empirical RDMs and model RDMs are similar in magnitude to the correlations found in other studies using RSAs, which generally report correlations ranging between 0.1 and 0.15.[22,40,41] Since our model RDMs represent ideal brain states, rather low correlations are expected, especially given the spatially rather coarse measure of neural activity we use (i.e., EEG).

Our results are in line with current research on explicit semantic processing stating that specific categories are semantically represented earlier than more abstract categories.[21–26] We assumed the peak of the significant correlations over time (and not the first time point of a significant correlation) to be the optimal estimate of when semantic processing of a particular category most likely happens. Under this assumption, processing of specific categories was identified earlier (peak at 465 ms, Figure 3A) than processing of the more abstract category manmade/natural (peak at 625 ms, Figure 2A), both under explicit and implicit semantic processing conditions, i.e., in the semantic and the localization task. Note that when analyzed at the subject-level, the processing of the abstract category manmade/natural in the semantic task, too, followed the earlier processing of the specific category in the explicit semantic condition. However, the difference between the peak latencies of the manmade/natural category in the semantic task and the concrete categories in the semantic task on subject-level did not reach significance. Nonetheless, the time course of correlations of the specific categories in the semantic task (Figure S3D) revealed a significant early local peak. This peak indicates successful processing of the specific categories.

Our results suggest that implicit semantic processing at a high level of abstraction precedes explicit processing at the same level of abstraction (Figures 2A, 3A, and 3E). This pattern was additionally confirmed using a subject-level analysis of the peak latency differences (Figures S3A and S3B). In sum, we observed qualitative differences in the time course of semantic processing under explicit and implicit conditions. While an early peak of semantic processing was present in both conditions, a late, strong, and long-lasting second peak only occurred under explicit conditions. We observed this for the processing of abstract as well as concrete semantic information. We speculate that the first peak may reflect the initial feedforward sweep of activity along the ventral stream followed by re-entrant top-down activity at later points in time.[42]

Our results draw parallels with those from studies on the processing of conscious and unconscious stimuli. In fact, several studies reported that the neuronal responses to unattended (unconscious) stimuli were smaller in magnitude and shorter in duration than neuronal responses to attended (conscious) stimuli.[17–20,43] Similarly, in our study, the peak of the neural activation of the manmade/natural category in the semantic task was higher than the peak activations of any other semantic category in both the semantic task and the localization task. This suggests that the quality of semantic processing is better under explicit compared to implicit processing conditions. Nevertheless, it is possible that the high correlations arose because the category manmade/natural is part of the semantic task. Thus, it is not entirely certain that they signify an increase in signal quality due to explicit processing in general. However, the correlations for animate/inanimate are also substantially higher than the correlations of the concrete categories, although the category animate/inanimate is not part of the task. Thus, the differences in correlations between the manmade/natural category and the concrete categories cannot be entirely reduced to the fact, that the category manmade/natural is part of the semantic task whereas the concrete categories are not.

A key finding of our study is that implicit semantic processing of abstract, high-level information was most prominent for the animacy dimension. Hence, humans automatically carry out a categorization of animate/inanimate whenever they encounter an object. An explanation of why this specific categorization is performed automatically and implicitly could lie in the vital evolutionary importance of a rapid and reliable animacy categorization.[1] Living organisms may call for a different set of actions than non-living objects. Hence, a rapid, automatic detection of an object's animacy may allow for a faster recruitment of relevant behavioral repertoires. This may carry evolutionary benefits. This argument is in line with research showing evidence that newborns (4–10 months) develop the categorization of animate/inanimate as one of the first semantic divisions.[44,45] Studies investigating patients with deficits in producing and understanding the names of animate objects indicate distinct neural mechanisms for the processing of animate/inanimate objects[46]; Animate objects elicit higher neuronal responses in the lateral ventral temporal cortex (VTC)[33] and inanimate objects in the medial VTC.[47,48] The observed preferential processing of the animate/inanimate category under implicit conditions further supports the claim that only evolutionary important or intensely studied categories can be processed implicitly[1] and is in line with the finding that task-irrelevant but salient abstract-level can be processed implicitly to guide attention.[49]

A long debate has been going on whether the distinct patterns of neural activation induced by animate and inanimate objects genuinely reflect the neural representation of the animacy category in the brain, or whether these patterns merely mirror distinct perceptual properties such as color or shape, that are associated with the specific categories.[46,50,51] Using our method on an extended stimulus set that controls for perceptual differences between semantic categories could help resolve this debate.

We observed that the neural representations of semantic categories as derived from our EEG data were highly similar to the representations obtained from intracranial EEG that was recorded from within the medial temporal lobe. Specifically, the time course of correlations of the empirical RDM's compared to the model RDM (Figure 3A) are similar to the time course of correlations of the empirical RDM's compared to the intracranial model RDM (Figure 3E). Both comparisons represent the same categories (the specific categories "fruits", "instruments" etc.) where the model RDM is a purely hypothetical assumption about the semantic activation of these categories and the intracranial model RDM is to be understood as an empirically based or data-based representation of the categories in anatomical regions receiving their input from the final stages of the ventral visual pathway involved in object recognition. Representations similar to those observed in the medial temporal lobe can also be activated implicitly. It seems also noteworthy that the peak latency of the correlations coincides with response latencies of single neurons in these MTL regions.[20,52] These neurons are known to respond invariantly to a diverse set of stimuli (written, spoken, pictorial) all conveying the same semantic concept.[53] These findings hence inform the debate on whether the medial temporal lobe is recruited exclusively for explicit processes.[54–57]

This study opens several avenues for further investigation that promise to advance our understanding of implicit semantic processing. As in most studies on implicit processing, we presented objects in isolation instead of in a natural scene. Future work should investigate whether objects are implicitly processed in a similar way when presented in a natural context.[58] Future studies could further extend the stimulus set in order to analyze the implicit semantic processing of the category human/nonhuman and compare it to our results of the animate/inanimate category. The human-nonhuman distinction seems to be an essential category as well.[34,59] Finally, future work could use our method to investigate subliminal unconscious processing of semantics, where one is unaware of the mere presence of the stimulus.

Our findings generally are in line with the global neuronal workspace (GNW) theory of consciousness,[1,60,61] which states that implicit processing of semantic information is possible only for highly relevant content or following intense learning and automatization. The implicit distinction of the animate/inanimate category is in line with GNW, since it is an evolutionarily important category and therefore could very well occur on a separate functional path.[1] The early activation of the animacy category compared to e.g., the later explicit semantic activation of the manmade/natural category lends further support to this assumption. The manmade/natural categorization is rather unusual and artificial and likely has not been performed numerous times already by our participants. It hence required the flexibility of adjusting cognition to this novel task and therefore also consciousness according to GNW. The implicit activation of the specific categories seems also in line with GNW, as these roughly correspond to entry-level semantic categories and can be seen as the result of general-purpose object recognition, which is highly automated and learnt during development and can hence also operate implicitly.

Our findings are less in line with recurrent processing theories RPT [2,3] ; which assume that processing of information reaches conscious awareness as soon as a system engages in top-down recurrent interactions. RPTs would assume all semantic processing we investigated here to be feasible also implicitly. The absence of implicit semantic activation for the manmade/natural category hence conflicts with RPT. The relative temporal evolution of the activation for specific categories is in line with RPT since it shows an early peak of implicit semantic activation corresponding likely to an initial feedforward component. Depending on the task, a later explicit semantic activation of the categories then likely corresponds to reverberating recurrent interactions.

Concluding, in our study, we extended the application of RSA to be used as an effective tool for investigating implicit semantic processing. This allowed us to draw parallels to predictions of current models of consciousness on a neuronal basis. We found that semantic information is implicitly processed up to concrete entry-level categories. While processing of the manmade/natural category only occurred explicitly, we found that the animate/inanimate category was processed implicitly.

Limitations of the study

One limitation of our study is that our experimental design cannot reliably determine whether task-irrelevant information was processed consistently at an implicit level, or whether it was sometimes processed explicitly. Studies investigating implicit or unconscious processing typically use specific stimulation techniques to prevent awareness of the stimulus material and further administer behavioral tasks and questionnaires to demonstrate a lack of awareness.[5] In our study, we had participants willfully attend clearly visible stimuli. Furthermore, we did not probe participants' level of awareness for task-irrelevant information. Hence, our study design provides a less rigorous, but arguably more ecologically valid assessment of implicit or incidental processing.[58] Importantly, our pattern of results indicates that task-irrelevant semantic categories were indeed not processed explicitly in the localization task (at least for the categories relevant in this study): In the semantic task, where participants were instructed to decide whether objects were manmade or natural, we observed neural processing of the manmade/natural category. In the localization task, we did not find neural processing of this category. This finding suggests that explicit processing of semantics of the manmade/natural category was absent when it was not task-relevant. Furthermore, we observed processing of the animate/inanimate category, even though participants were never instructed to categorize stimuli on this dimension. This pattern of results indicates that the animate/inanimate category was indeed processed implicitly, especially in the localization task, where no semantic categorization

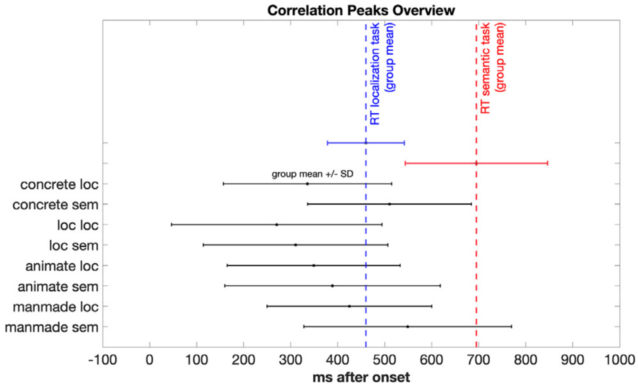

Figure 5. Overview of correlation peaks

Dots represented the Mean, error bars the standard deviations (SD) of peak latencies from all participants for each stimulus category (concrete, loc = location; animate = animacy; manmade = manmade/natural) and each task (sem = semantic task; loc = location task). Stimulus category and task are indicated on the y axis.

was required. Note that participants performed almost at ceiling for both the semantic and the localization task and further responded very rapidly. This suggests that participants easily and consistently performed only the specific, instructed task, instead of both tasks at once. Finally, the time course of the neural activation of the animate/inanimate category in the localization task suggested implicit rather than explicit semantic processing of this category in this task. In fact, the peak activation for the animate/inanimate category coincided with the peak activation of stimulus location as well as with the motor response in the localization task, where stimulus location was processed explicitly (Figure 5 or Figure S3). Assuming that explicit processes compete for the same attentional resources and thus tend to occur serially rather than in parallel, it is highly unlikely that both, the categorization of the stimulus location, and the categorization on the animate/inanimate distinction, were performed explicitly.

We did not analyze how age or gender affects the reported effects as our primary aim is to understand general principles of neuronal processing in humans. Furthermore, our sample size is too small to have sufficient statistical power to detect such effects reliably.

In EEG studies employing RSAs, a notable limitation often arises from the potential contamination of results by eye movements. However, we are confident that our findings were not biased by eye movement-related artifacts. First of all, stimulus location and stimulus identity were fully orthogonal because each stimulus was presented at each of the ten locations. Hence, it is technically impossible to read out category information from stimulus location or eye movements. Furthermore, the qualitative pattern of results did not change when eye movement-related activity was left in the data (Figures S4 and S5) vs. when it was removed from the EEG by means of independent component analyses (as reported in the main results). The temporal evolution of the correlations between empirical RDMs and model RDMs were highly similar when compared between empirical data where eye movement-related activity was present vs. removed (Figures S4 and S5 vs; Figures 3 and 4). Only for the processing of stimulus location in the localization task, correlations between empirical and model RDMs were significantly decreased (Figure 3), falling below the significance threshold, when eye-movements were removed. This could suggest that the participants did not fully adhere to the instruction to fixate their gaze centrally on the fixation point. However, eye movements did not change the patterns of correlation for the manmade/natural category or for the animate/inanimate category. Hence, our main results and conclusions are not influenced by eye movement-related artifacts.

Though we are confident that eye movements did not influence our results, we cannot fully exclude the possibility that a refixation of gaze might be confounding our differences in the location and semantic task for the manmade/natural category. More specifically, it is possible, that the strong late activation of the manmade/natural category (Figure 2A) might be partly due to a refixation of gaze. Removing the eye components only addresses eyeball-related movements but not visual activation following re-fixation.

A further potential limitation of RSA-based studies lies in the risk of specific motor responses being associated with a given task or condition. This can lead to the false conclusion that representational dissimilarities between categories or conditions of interest mirror differences in cognitive processes, even though these dissimilarities are fully accounted for by distinct motor responses. We are confident that in our study, the observed differences in EEG patterns were not confounded by our response mapping. First of all, conventional EEG, with its low spatial resolution only allows for a distinction of gross movements (e.g., left vs. right hand grasp). Decoding of precise movements (like finger movements) can only be achieved with invasive recordings such as e.g., high-density electrocorticography grids or using spectral features from high-density scalp EEG.[62] Second, the location of the objects and their semantic category are independent because all objects were presented in all locations. Motor response and conditions of interest were fully orthogonal for these contrasts. For these reasons, we conclude that finger movement did not influence our results.

RESOURCE AVAILABILITY

Lead contact

Information and requests will be fulfilled by the lead contact, Thomas P. Reber (thomas.reber@fernuni.ch).

Materials availability

This study did not generate new unique reagents.

Data and code availability

- Data are available on zenodo (see key resources table for the link).
- Code is available on the open science framework (see key resources table for the link).
- Further information will be provided by the lead contact on request.

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AUTHOR CONTRIBUTIONS

V.W.: conceptualization, data curation, formal analysis, methodology, validation, visualization data, writing—original draft, writing—review and editing, S.R.: methodology, validation, writing—review and editing, supervision, N.H.S.: investigation, N.R.: conceptualization, writing—review and editing, T.P.R.: conceptualization, project administration, supervision, resources, validation, writing—original draft, writing—review and editing, funding acquisition.

DECLARATION OF INTERESTS

The authors declare no competing interests.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Raw EEG Data	This paper	https://zenodo.org/records/10776597
Software and algorithms		
Analysis Scripts	This paper	https://osf.io/ca7qn

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

Participants

Nineteen participants were recruited for the experiment. Data of 15 participants are reported (19–58 years, 7 females, all right-handed). Participants reported to have normal or corrected-to-normal (≥20/25) vision. A (corrected) visual acuity of 20/25 means that a person can see at a 0.8m distance what a person with normal vision can see at 1m distance in a standardized test.[63] Four participants were excluded either due to excessive movement artifacts ($N = 3$) or due to premature termination of the experimental procedures by one of the participants. Participants were students of the UniDistance Suisse and earned CHF 75 or academic credits for 3 h. The study was approved by the Ethics Committee of the UniDistance Suisse (ref. 2019-11-02). Written informed consent was obtained from each participant.

METHOD DETAILS

Task and stimuli

The stimulus set consisted of one hundred color images of objects that can be grouped in ten semantic categories of ten exemplars each.[36] The ten categories can be grouped in two meta-categories, namely natural objects (wild animals, fruit, flowers, insects, and birds), and manmade objects (manmade food, clothes, furniture, instruments, and computers). Each image was presented in one out of ten positions in a circle around a fixation point (Figure 1B). The distance between screen and participants was 60cm. The size of the objects was $2.167^\circ \times 2.06^\circ$ in visual angle (corresponds to an object size of 2.27 cm × 2.16 cm on the screen). A trial consisted of the presentation of a fixation spot for 300ms, followed by the image that stayed on the screen together with the central fixation spot until participants responded (Figure 1A). Participants were instructed to keep their gaze fixated on the central dot and avoid eye movements toward images of the objects. Participants performed two tasks in two consecutive runs of the experiment. In the semantic task subjects were required to explicitly focus on semantic features of stimuli by judging for each presented object whether it is a manmade or natural object. This task is thus referred to as the "explicit semantic condition". In the localization task, participants' attention was directed away from the semantics in that they only had to indicate by button press whether the image was presented on the left or right side of the screen. We therefore consider any semantic information we read out from neural responses under this instruction a consequence of implicit semantic processing and thus refer to this task as the "implicit semantic condition".

In this within-subject experimental design, all participants underwent all experimental conditions. Each participant underwent a run of 1000 trials with the semantic task and a run of another 1000 trials with the localization task. The sequence of instructions was counterbalanced between participants. The sequences of stimuli and locations were randomized within participant. The participants responded by pressing the left and right arrow keys on a standard USB keyboard using the index and middle finger of their dominant hand. The left arrow key corresponded to the manmade category or left location and the right arrow key to the natural category or the right location. To orthogonalize stimulus location and identity, randomization was done with the constraint that the 10 presentations of a stimulus each were assigned one of the ten locations. A standard Desktop Computer running Linux (Debian 9) and GNU Octave V5.1.0 [64] with Psychtoolbox-3[65–67] was used.

Electrophysiological (EEG) recording and analysis

EEG data were recorded using a BrainVision System with 64 acticap slim electrodes (©Brain Products GmbH, Munich, Germany; ground: FPz, reference: Cz) which were fixed with Standard 64Ch actiCAP snap caps. Data were sampled at 1 kHz and electrode impedances were kept below 5 kOhm. The data were resampled to 250 Hz and bandpass filtered from 0.1 to 36 Hz. Scalp channels were Fp1, Fp2, AF3, AF4, AF8, AFz, F1, F2, F3, F4, F5, F6, F7, F8, Fz, FT7, FT8, FT9, FT10, FC1, FC2, FC3, FC4, FC5, FC6, FCz, T7, T8, C1, C2, C3, C4, C5, C6, TP7, TP8, TP9, TP10, CP1, CP2, CP3, CP4, CP5, CP6, CPz, P1, P2, P3, P4, P5, P6, P7, P8, Pz, PO3, PO4, PO7, PO8, POz, O1, O2,Oz, Cz re-referenced to common average. During preprocessing, for seven subjects the data from one channel was rejected, for three subjects data from two, three, and seven channels was rejected. Data were epoched from −200ms before stimulus onset to 1000ms after stimulus onset. The entire pre-stimulus window was used for baseline correction. Epochs in which the absolute amplitude exceeded [-60μV 60μV] or [-120μV 120μV] (specified for each participant, see code on the accompanying osf repository) were rejected from analysis. No further artifact rejection was performed. Independent component analyses were used to identify and remove eye movement-related activity. Eye components were identified with the EEGLAB extension "iclabel"[68] and removed. The BrainVision Recorder software (2017) ran on a standard Microsoft Windows 10 Home LENOVO laptop (x64-based PC system, 8 GB RAM). Data preprocessing was performed with EEGLAB[69] and the ERPLAB Toolbox[70] in MATLAB (2020).

QUANTIFICATION & STATISTICAL ANALYSES

Representational similarity analysis (RSA)

We performed time-resolved RSAs using custom MATLAB scripts. In brief, this involved (1) computing the relevant representational dissimilarity matrices (RDMs) for each participant at every time-point of interest, (2) averaging these first-level RDMs across participants, (3) and then assessing how well these group-level RDMs fit the corresponding model RDMs.

First, we calculated ERPs for every task and condition of interest (i.e., for all possible combinations of category-levels, object locations, and task conditions) and for each participant. This was done by averaging the EEG data of the relevant trials separately for each electrode, time point, and participant. ERPs were extracted for a time window from −200 ms before to 1000 ms after stimulus onset.

Next, we computed RDMs for each participant and for every time point of interest. This involved calculating Pearson correlations between the voltage distributions across channels of all n ERPs that were relevant for a given RSA. RDMs were calculated for EEG data segments of 50 ms duration at intervals of 20 ms from −100 ms before stimulus onset until 1000 ms post stimulus onset. Voltages were averaged across samples within each 50 ms segment before calculating correlations. Only the lower triangular (without the entries in the diagonal) of the symmetric n*n correlation matrix was used. The x,y-coordinates of the RDM correspond to either the 10 categories (e.g., furniture, instruments, wild animal, etc.), the 10 locations or the 100 stimuli (table, saxophone, elephant, etc.). Thus, we created 10 × 10 or 100 × 100 RDMs. For every RDM-type the ERP per electrode over a defined time window t was taken and the Pearson correlations r between the vector $V_{x,t}$ with the values of all 64 electrodes for an x-coordinate (e.g., Elephant) and the vector $V_{y,t}$ of all 64 electrodes for an y-coordinate (e.g., Saxophone) was calculated.

This Correlation $R_{xy,t}$ was performed for all x,y-coordinate pairs resulting in an RDM_t for a defined time window t. To adhere to the convention of using measures of distance in these types of analyses, we stored 1-$R_{xy,t}$ in the RDMs. So every entry of an RDM_t is calculated by the following formula:

$$Dist\left(V_{x,t}, V_{y,t} \ = \ 1 \ - \ R_{xy,t}\right)$$

E.g., Dist($V_{\text{Elephant,100–150ms}}$, $V_{\text{Saxophone, 100–150ms}}$) = 1- $R_{\text{Elephant, Saxophone,100–150ms}}$ results in one RDM_t entry for a specific time window t, where RDM_t has a dimension of 100 × 100. In that way, we created empirical RDMs for overlapping time windows t.

We then averaged the first-level RDMs across participants within each task and condition of interest and then assessed how well each resulting group-level RDM fit their corresponding model RDMs.

Model RDMs represent perfectly separable locations or semantic categories and refer to an ideal state of brain activity. They consist only of ones and zeros (e.g., a 100 × 100 model RDM_{mod} representing the manmade/natural category would have the entry elephant-flower set to 0 and the entry elephant-hammer set to 1, etc.). Correlating the model RDMs with the empirical RDMs for all time windows results in a Vector R_t:

$$R_t \ = \ Corr(RDM_{mod,t}, RDM_t)$$

R_t describes the similarity of the actual brain activity with the ideal brain activity for all time windows,[33] which is plotted in e.g., Figure 2A. Because we calculated 53 correlations (one for each time point), we controlled for multiple testing by applying Bonferroni corrections $\alpha \ = \ 0.05$. The corrected significance level for each correlation was approximately 0.001 as calculated by the following formula:

$$p^* < \frac{\alpha}{n} = \frac{0.05}{53} \approx .001$$

If the correlations of the RDMs with the model RDM reached a significance level of less than 0.001, we assume that the features captured in the model RDM are present in brain activity as measured with EEG.

For analyses or results where the absence of a significant correlation seemed relevant, we further calculated Bayes Factors for the correlations to assess the amount of evidence in favor of the null hypothesis (no neural representation of the category of interest). These Bayesian Correlation tests were performed using the bayesFactor toolbox v.1.0.0 for Matlab.[71]

Construction of model RDMs

To assess the neuronal activation for the spatial location we created model RDMs (Figures 2B, 2F, 2J, 3B and 3F) assuming equal neuronal representation for neighboring stimuli (for example when we focus on loc5, we assume that loc3 and loc4, as well as loc6 and loc7 have an equally distant neuronal representation to loc5). For the semantic categories, we started on the most concrete level of abstraction and tested for the ten specific categories (fruits, instruments etc.). Since the ten categories were split into manmade/natural objects for the semantic task, we analyzed the semantic activation for these categories. We further constructed model RDMs for all possible splits of the ten categories into two groups with a minimum of three categories per group. This results in 456 possible splits which also corresponds to the number of model RDMs representing the groups. We observed the highest correlation (for all possible time windows from 200 to

800 ms after stimulus onset) between empirical RDMs and these model RDMs (and thus the highest implicit semantic activation) for the model RDM reflecting the meta-category animate/inanimate. Therefore, we included this level of categorization in our analyses of the depth of implicit semantic processing. The three entry-level categories "wild animals", "insects" and "birds" belong to the category animate and the remaining seven entry-level categories belong to the category inanimate.

Additionally, we used RDMs from a study conducted by Reber et al.,[36] who used intracranial single neuron recordings in the medial temporal lobe (MTL) and similar experimental procedures as we did. We can therefore use the RDMs from Reber et al.[36] as model RDMs for MTL representations. They computed the RDMs from intracranial recordings of human single neurons in the first 1000ms after stimulus onset (normalized using the distribution of the baseline firing rates in the first 500 ms prior to stimulus onset) in the amygdala (AM), hippocampus (HC), entorhinal cortex (EC) and parahippocampal cortex (PHC) where high levels of semantic abstraction are most likely represented. Since for the AM, HC and EC abstract representations were found, we averaged the RDMs across these regions and used the resulting RDMs as model RDMs. We refrained from trying to localize the specific brain regions that were involved in the processing of semantic categories or stimulus locations based on our EEG data, because of the poor spatial resolution of EEG.

Definition of the level of semantic abstractness

We define the abstractness level of a category based on the count of identifiable subcategories within our stimulus material (the categories animate/inanimate and manmade/natural contain 50 stimuli each and are thus more abstract than e.g., the specific category "furniture", which only contains 10 stimuli). For this reason, we regard two levels of abstractness: specific categories, which contain 10 stimuli each, and abstract categories (animacy, naturalness), which contain 50 stimuli each. This definition of abstractness aligns with the use of the term in the literature.[21,22,72]

Subject-level analysis and peak latency differences

All reported results build on the correlation between model RDMs and the average RDMs that were obtained by averaging all individual empirical RDMs across all participants. In theory, this could yield positive correlations between empirical and model RDMs even if only a subset of participants showed the expected pattern of neural activation. To validate our analytic approach and the obtained results, and to further compare the latencies of different semantic activations, we additionally correlated the subject-level RDMs instead of the group-averaged RDMs with the model RDMs and then averaged these correlation time courses across subjects. To assess differences in peak latencies for the implicit vs. explicit semantic condition and for different levels of abstraction, we identified the peaks at the subject-level, extracted the peak latencies, and then compared these latencies between conditions using paired t-tests. We only attended to time windows between 100 ms and 1000 ms after stimulus onset. We assumed that the latency of the correlation peak refers to the point in time where semantic activation of a category most likely occurs. We further calculated a cluster-based permutation test on subject-level to compare different conditions against each other (semantic categorization task vs. localization task of different categories) and against zero (no correlation).[37]

Reliability analysis

We aimed to analyze the reliability of the parameters and coefficients that we used to estimate semantic activation and semantic representations. The reliability coefficients were computed with a split-half method in combination with random resampling with replacement (i.e., bootstrapping) of the split-halves. For the split-halves method, the number of repeated measurements is divided into two parts and subsequently, the pattern of results is correlated. To infer from this correlation coefficient derived from fewer trials than the full experiment the reliability of the complete experiment, the Spearman-Brown formula is used. Trials for every participant were divided into two random groups and for both groups of trials, one RDM was computed for certain time frames (200-400ms, 300-500ms and 500-700ms). Then the RDMs were averaged across participants resulting in two RDMs for every time frame. The RDMs then were correlated with each other, and the correlation coefficient was adjusted with the spearman-brown formula. This procedure was repeated 300 times with different random splits of the data for the semantic RDM and for the location RDM and then averaged over iterations resulting in one reliability coefficient for each window and for each RDM-type. For the semantic RDM the Reliabilities are $r = 0.46$ (for 200-400 ms), $r = 0.55$ (for 300-500 ms) and $r = 0.55$ (for 500-700 ms) and for the localization task $r = 0.98$, $r = 0.98$ and $r = 0.97$ (following the same order of time windows). The results suggest satisfying split-half reliabilities for both RDM types. The reliabilities for the semantic task in the first time window were poor (<0.5), possibly due to a lack of processing of semantics at that early stage. For later time windows, the reliabilities for the semantic task are moderate (0.5 - 0.7). For the localization task the reliabilities are excellent for all time windows (>0.9).[73]