

Event-related potentials uncover the neurocognitive encoding and retrieval mechanisms of animacy effects in episodic memory

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ARTICLE INFO

Keywords:

Subsequent memory effect
Old/new effect
Event-related potential
Animacy
Episodic memory

ABSTRACT

Episodic memory performance is consistently higher for animate stimuli like humans or animals than for inanimate objects. To examine the mechanisms underlying this “animacy effect”, we recorded event-related potentials (ERPs) while healthy, young adults encoded and subsequently freely recalled (Experiment 1) or recognized (Experiment 2) words referring to animate and inanimate objects. In both experiments, we replicated the animacy effect. Further, in both experiments, animates elicited smaller N400-amplitudes than inanimates during encoding, suggesting that semantic access is facilitated for animate stimuli. No differences were found between stimulus types in any ERP markers thought to index elaborative encoding. In Experiment 2, the word types did not differ in the early mid-frontal and the left parietal old/new effects during recognition, indexing familiarity and bottom-up recollection, respectively. However, the late posterior negativity, presumably indexing controlled, effortful reconstruction of the study episode, was prominent for animates but absent for inanimates. Taken together, these results support a difference in the semantic representation between animates and inanimates, and more effortful recollection of a more complex episodic memory trace of animates during retrieval. Notably, these ERP patterns differ qualitatively from recent results on the survival processing effect, supporting a dissociation of the mechanisms behind the two effects.

1. Introduction

The “adaptive memory” view proposes that episodic memory has been shaped during evolution to optimize our chances of survival and reproduction (e.g. Erdfelder & Kroneisen, 2014; Nairne, 2005; Nairne, 2010). One example is that animate objects, referring to humans or animals, are typically better remembered than inanimate objects (Bonin et al., 2014; Nairne et al., 2013; for a review, see Altarriba and Kazanas, 2019). This “animacy effect” in episodic memory is quite robust and is even observed for non-words that are associated with animate features (VanArsdall et al., 2013), for foreign vocabulary with animate meaning (VanArsdall et al., 2015) or in prospective memory (Félix et al., 2024). Animate objects may thus be prioritized by our memory system because they are more relevant to our survival and reproduction as they are potential mates, social allies or sources of nutrition (Nairne, 2015). However, although plausible, this “ultimate” explanation of the animacy effect leaves open the proximate neurocognitive mechanisms that mediate the memory advantage of animates (Scott-Phillips et al., 2011)

and is thus incomplete. Our current research aims at evidence that helps to close this gap.

The starting point of the present study was the “richness of encoding hypothesis”, which suggests that when animate objects are encountered, they stimulate deep processing which enriches the memory trace with various links to other information in memory (e.g. Meinhardt et al., 2020). This view thus relates the animacy effect to the “survival processing effect”, referring to a memory advantage when information is processed in the context of a survival scenario (Kroneisen & Erdfelder, 2011; Erdfelder & Kroneisen, 2014). Initial evidence supported the richness-of-encoding hypothesis of the animacy effect. For example, participants spontaneously report more ideas that come to mind when presented with animate, compared to inanimate objects (Meinhardt et al., 2020; Bonin et al. 2022). However, a recent series of experiments that explicitly manipulated richness of encoding has cast doubt on the hypothesis (see Komar et al., 2024): When idea generation was experimentally restricted (Experiments 1 and 2), when elaboration was prevented by a dual-task condition (Experiment 3), or when thoughts of

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<https://doi.org/10.1016/j.nlm.2025.108112>

Received 7 July 2025; Received in revised form 17 September 2025; Accepted 24 October 2025

Available online 25 October 2025

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survival relevance were stimulated to enhance elaboration (Experiment 4), the animacy effect was unaffected.

Other initially promising ideas regarding the proximate mechanisms of the animacy effect have also received only limited or at best mixed empirical support. For example, VanArsdall et al. (2017) experimentally manipulated categorization processes during encoding and retrieval, while Serra (2021) analyzed the retrieval dynamics of animates and inanimates in free recall. Both studies suggest that organizational processes play a minor role in the animacy effect and rather suggest a role of item-specific processes. However, since the animacy effect remains stable after controlling the stimulus material for emotional arousal (Meinhardt et al., 2018; Popp & Serra, 2018), emotional item processing also does not appear to play a major role. Further, a sequence of experiments in which mental imagery was manipulated or queried yielded mostly negative evidence regarding its role in the animacy effect (Gelin et al., 2019).

If animate objects are preferentially processed, the effect should depend on the allocation of attentional resources. In support of this idea, in a modified Stroop-task, Bugajska et al. (2019) reported longer response times to the font color for animate versus inanimate objects. However, Bonin et al. (2015) as well as Rawlinson and Kelley (2021) reported that dual-task manipulations did not affect the animacy effect, speaking against a role of attention in the effect.

Interestingly, Rawlinson and Kelley (2021) also reported that animates on average have a higher number of semantic features than inanimates, and that the number of features partially mediates the effect of animacy on free recall. Their interpretation was that a richer representation of animates in semantic memory leads to a more distinct (i.e., containing more features) item-representation in episodic memory, thus facilitating subsequent retrieval of animates.

Taken together, research on the proximate mechanisms of the animacy effect has been largely inconclusive so far. One difficulty with inferring memory mechanisms from behavior is that behavioral performance is the product of a myriad of subprocesses that occur during encoding, consolidation and retrieval. Unique insights into subprocesses engaged at encoding and retrieval can be gained by recording event-related potentials (ERP) during a memory task (Kwon et al., 2023; Mecklinger & Kamp, 2023; Rugg & Coles, 1995). This was the main goal of the present research, with Experiment 1 examining ERPs at encoding and Experiment 2 at retrieval.

2. Experiment 1

Experiment 1 examined ERPs during the encoding phase of a memory task with animate and inanimate words. In a within-subject design, we analysed differences in ERP component amplitudes between animates and inanimates, as well as subsequent memory effects (SME): Differences in ERP activity depending on subsequent recall, which indicates whether the activity is, on an individual trial level, relevant for subsequent memory (Mecklinger & Kamp, 2023). Three kinds of ERP components/ERP SME were examined at encoding, which are briefly introduced here.

2.1. Early (frontal) SME/N400

The N400 was originally reported for semantically unexpected words and has since been shown to be sensitive to a number of manipulations affecting semantic processing (for a review, see Kutas & Federmeier, 2011). When individual words are processed, an attenuated N400 amplitude indexes the ease of semantic access (Kutas & Federmeier, 2011). One example is that high frequency words elicit an attenuated N400, compared to low frequency words (e.g. Bridger et al., 2014).

Weckerly and Kutas (1999) reported an attenuated N400 amplitude for animates versus inanimates in a sentence position where the (grammatical) subject was expected. While it is possible that the N400 is more sensitive to whether an animate or inanimate object is expected rather

than animacy *per se* (Szewczyk and Schriefers, 2018), other research has shown that animates elicit attenuated N400 amplitudes even if an inanimate object was expected (e.g. Bugajska et al., 2019).

In the N400 time window, a SME is commonly observed in tasks that emphasize the processing of semantic stimulus features, which is hence thought to reflect a contribution of semantic processing to encoding (Mecklinger & Kamp, 2023). The distribution of the SME is typically more frontal than is typical for the N400. This SME has often been reported in tasks where stimuli had to be judged regarding their animacy, but not in perceptual tasks (e.g., alphabetic judgments, Otten & Rugg, 2001). To our knowledge, no studies have examined the N400 and the early SME in a single-word memory task with a controlled animacy manipulation of the stimulus content.

2.2. Early parietal SME/P300

The P300 is elicited by deviant, distinctive or meaningful events, including emotional stimuli, and co-varies with attentional allocation to a stimulus (e.g. Kamp & Donchin, 2015; Kamp, 2020). Similarly, when such item-specific stimulus features are relevant to subsequent memory, an SME that co-occurs with the P300 is commonly observed (Kamp et al., 2013; Kamp et al., 2015). This SME has been interpreted to index item-specific encoding processes of familiar and semantically meaningful stimuli, which are not elaborative or associative in nature (Mecklinger & Kamp, 2023). Notably, this SME often temporally overlaps with the early frontal SME but typically extends to over 500 ms after stimulus onset.

2.3. Slow wave/slow wave SME

ERP activity extending well beyond 1000 ms after stimulus onset is referred to as slow wave activity, varies with working memory load, and may index enhanced elaboration in episodic memory tasks (Mecklinger & Kamp, 2023). A SME in this time window is typically observed in deep encoding tasks (e.g. Otten & Rugg, 2001) and when associations are encoded and subsequently retrieved (e.g. Kamp & Zimmer, 2015).

2.4. Hypotheses

In two previous studies (Forester et al., 2020a; 2020b), we found that when words were rated in the context of a survival scenario, the P300 SME was absent (whereas it was prominent in the control scenario), while the frontal slow wave was overall increased. This pattern thus supports the richness-of-encoding hypothesis of the survival processing effect. Hence, we hypothesized in the present study, that if effortful, elaborative encoding is more relevant for subsequent retrieval of animates than inanimates, an enhanced slow wave and/or a slow wave SME, as well as a reduced early parietal SME should be observed for animates.

Alternatively, differences in the semantic representations of animate and inanimate words should be reflected in differences in N400 amplitude. If semantic processing differentially contributes to subsequent memory, this should be reflected in a differential SME in this time window depending on word type. If attentional or emotional processes play a role in the animacy effect, amplitude differences and/or differences in the SME in the time window of the P300 would be expected, with a more pronounced P300 for animates.

2.5. Methods

All procedures of Experiments 1 and 2 were reviewed and approved by the local ethics committee at Trier University. Data sheets and stimulus materials are openly available at https://osf.io/k7ap6/overview?view_only=3963fbfc26cb442f86af451dacaab706 = 442b9ef7554c47ef83ba520c795daf67.

2.5.1. Participants

To detect a medium-sized effect ($d_z = 0.50$) of word type (animate vs. inanimate) with a power of $1 - \beta = 0.80$ in a two-sided matched-pairs t test based on $\alpha = 0.05$, $N = 34$ participants were needed (Faul et al., 2007). Since this was the main effect of interest, we collected data until $N = 34$ suitable data sets were available for both the behavioral and the ERP SME analysis.

A total of $N = 45$ university students took part either in exchange for partial course credit or 10 €/hour. Recall data were obtained from all 45 participants. For one participant, no EEG was recorded due to a technical error. Data from another 10 participants were unsuitable for the ERP SME analysis due to low recall performance leading to less than 6 artifact-free trials in either the inanimate-subsequently recalled category (5 participants) or in both the animate-subsequently recalled and the inanimate-subsequently recalled categories (5 participants), leaving $N = 34$ for the ERP SME analysis.¹ The full sample consisted of 33 female, 11 male and 1 non-binary participants with an age range of 20–33 years ($M = 23.40$, $SD = 2.86$). The ERP sub-sample contained 25 female, 8 male and 1 non-binary participants with an age of $M = 23.76$ ($SD = 2.53$).

2.5.2. Stimuli

To construct the critical word list, a total of 100 nouns, including 50 animates (referring to humans or animals) and 50 inanimates (referring to inanimate objects), were selected from the BAWL-R database (Vö et al., 2009). All words were 4–6 letters long. The lists of animates and inanimates were matched for valence ($M_{animate} = 0.57$; $M_{inanimate} = 0.58$), arousal ($M_{animate} = 2.41$; $M_{inanimate} = 2.44$) and imageability ($M_{animate} = 5.60$; $M_{inanimate} = 5.61$) (all p -values > 0.81). Word frequency also did not differ between the word types ($M_{animate} = 18.66$; $M_{inanimate} = 23.92$) (all $p = 0.53$). However, on average, inanimates had slightly more letters than animates ($M_{animate} = 5.02$, $M_{inanimate} = 5.22$, $p = 0.01$).

2.5.3. Procedure and task

After the preparations for the EEG recording, which took a maximum of 45 min, participants were instructed to memorize a word list, presented one at a time on a computer screen. This list contained 100 critical words (50 animates, 50 inanimates), as well as 3 additional words at the beginning and the end of the list, respectively, to absorb primacy and recency effects. The critical words were presented in a random order, which was different for each participant. Participants were not informed about the two word types or about the nature of the memory test that would follow.

Each word was presented for 3000 ms in white, bold Courier New font, size 40, on a gray background. In between two words, a fixation cross was shown for 700 ms.

After the last word was presented, there was a 2-minute pause, after which participants were prompted to enter all words that they could retrieve from the list using a standard computer keyboard. There was no time limit for recall.

2.5.4. Behavioral analysis

A word was coded as recalled if the word was correctly entered during recall or if it contained only minor typos that left the word clearly recognizable. Responses that did not correspond to a word from the encoding phase were counted as intrusions. Words referring to humans or animals were counted as animate intrusions, while words referring to inanimate objects were counted as inanimate intrusions. Letter strings that were not clearly recognizable as words were disregarded.

2.5.5. EEG recording and ERP analysis

The EEG was recorded using a NeurOne Tesla amplifier (Bittium

¹ A caveat of this procedure is that the present ERP results may not generalize to very low performers.

Corporation, Finland) with 32 Ag/AgCl electrode channels embedded according to the 10/20 system in an elastic cap. The ground electrode was placed at position AFz and the on-line reference was electrode FCz. Using Brain Vision Analyzer 2.2 (Brain Products, GmbH), the data were re-referenced to average mastoids (TP9, TP10) and 20 Hz-low-pass filtered with a Zero phase shift Butterworth IIR filters (order 4). Segments were then extracted, including 400 ms before to 2000 ms after the critical word presentation. A semi-automatic ICA artifact detection using the Infomax-algorithm was used to remove eye blinks and horizontal saccades. Segments were rejected from further analysis if there was an amplitude difference of more than 100 μ V in a 1000 ms window at any electrode. Next, participant-specific ERP averages were built for animates that were subsequently correctly recalled (animate/recalled), animates that were subsequently not recalled (animate/not recalled), with the same logic for inanimates. Finally, the averages were baseline corrected.

ERP data of any participant were excluded if less than 6 trials were available for any of the four ERP averages (following prior subsequent memory studies, Kamp & Zimmer, 2015). Mean trial numbers within the final subsample of $N = 34$ were: Animate/recalled: $M = 15.71$, $SD = 7.11$ (range: 6–30, $SE = 1.22$, median = 15), animate/not recalled: $M = 29.41$, $SD = 7.54$ (range: 12–44, $SE = 1.29$, median = 30.5), inanimate/recalled: $M = 13.06$, $SD = 6.56$ (range: 6–25, $SE = 1.12$, median = 10), inanimate/not recalled: $M = 32.94$, $SD = 6.88$ (range: 21–44, $SE = 1.18$, median = 33.5).

Mean ERP amplitudes were extracted for time windows corresponding to the three ERP components/SME of interest: an early (300–500 ms), a middle (500–700 ms) and a late (1000–2000 ms) time window. As variable scalp distributions for each ERP SME have been reported in the literature, we analyzed ERPs in a 3x3 electrode grid (electrodes F3, Fz, F4, C3, Cz, C4, P3, Pz, P4).

2.5.6. Statistical analysis

For inferential statistics, we used IBM SPSS 21.0.0.0. The number of recalled words and intrusions were compared between animates and inanimates with matched-pairs t -tests.

To statistically analyze ERPs at the 3x3 electrode grid, we conducted repeated measures ANOVAs with the factors animacy (animate/inanimate) and subsequent recall (subsequently recalled/not recalled), as well as the electrode factors anteriority (frontal/F, central/C, parietal/P) and laterality (left/3, middle/z, right/4). Main or interaction effects which only included the electrode factors are not of theoretical interest, but are reported for the purpose of completeness. Interaction effects involving electrode factors and either animacy or subsequent recall, or both, have to be regarded with caution if the respective main effects including animacy and/or subsequent recall are not significant.

Of special interest to the present research question were interactions between animacy and subsequent recall. Where no significant main or interaction effects of animacy and subsequent recall were found, we calculated a Bayes Factor for the ERPs averaged across all 9 electrodes analyzed, to assess the strength of the evidence for the null hypothesis of no interaction using JASP 0.19.0.0 (JASP Team, 2025). We report BF_{10} for matched models, where $BF_{10} < 1$ indicates that there is stronger evidence for the absence of the effect, whereas $BF_{10} > 1$ indicates that there is more evidence in favor of the presence of the respective effect.

Figures were generated using JASP and several R packages (Auguie, 2022; Urbanek, 2022; Wickham, 2016; Wickham & Bryan, 2025; Wickham et al., 2019; Wickham et al., 2023; Yu, 2025).

2.6. Results

2.6.1. Recall rates

In the full sample, participants recalled more animate than inanimate words ($M_{animate} = 15.27$, $SD = 8.00$; $M_{inanimate} = 11.40$, $SD = 7.80$), $t(44) = 5.25$, $p < 0.001$, $\hat{d}_z = 0.78$ (Fig. 1a). The number of intrusions

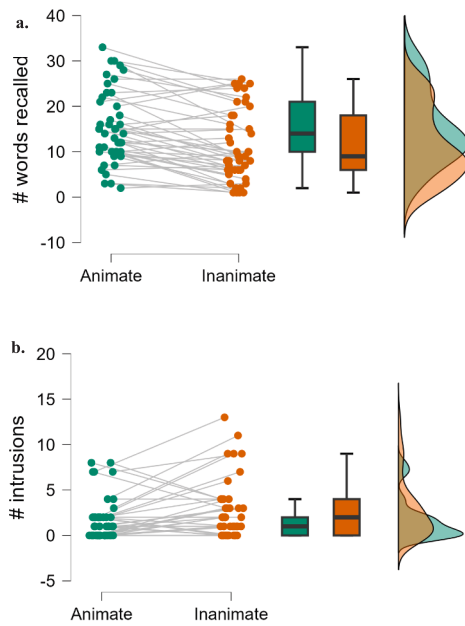


Fig. 1. Raincloud plots, boxplots, and violin plots for the number of words recalled (a) and number of intrusions (b) by word type (total number of words for each word type = 50) for the full sample ($N = 45$) of Experiment 1.

referring to animate objects ($M = 1.68$, $SD = 2.32$) was lower than to inanimate objects ($M = 2.67$, $SD = 3.23$), $t(44) = 2.58$, $p = 0.01$, $\widehat{d}_z = 0.38$ (Fig. 1b).

Within the sub-sample of participants that entered the ERP analysis, the same result pattern was obtained [recall: $M_{animate} = 17.32$, $SD = 7.55$, $M_{inanimate} = 14.15$, $SD = 6.89$, $t(33) = 3.74$, $p < 0.001$, $\widehat{d}_z = 0.64$; intrusions: $M_{animate} = 1.32$, $SD = 2.08$, $M_{inanimate} = 2.21$, $SD = 3.06$, $t(33) = 2.37$, $p = 0.024$, $\widehat{d}_z = 0.41$].

2.6.2. ERPs: Early time window (300–500 ms)

In the early time window, the ANOVA revealed a main effect of animacy, $F(1, 33) = 4.64$, $p = 0.039$, $\widehat{\eta}_p^2 = 0.12$: Animate words elicited an attenuated negativity, relative to inanimates (Fig. 2a). There was a main effect of subsequent recall, $F(1, 33) = 6.83$, $p = 0.013$, $\widehat{\eta}_p^2 = 0.17$, indicating that subsequently recalled words elicited an attenuated negativity, compared to subsequently not recalled words (Fig. 2a). There was no interaction of animacy and subsequent recall, $F(1, 33) = 0.21$, $p = 0.65$, $BF_{10} = 0.338$, and no other main or interaction effects that included the factors animacy and/or subsequent recall (all p -values > 0.073). Main effects of anteriority and laterality, as well as the interaction of these two factors, were significant (all p -values < 0.007), but were not of theoretical interest as they did not involve the factors subsequent recall or animacy.

Fig. S1 shows Supplementary Figures of each ERP waveform and difference waveform (subsequently recalled-not recalled; animate-inanimate), including the standard error of the mean as a measure of variability.

2.6.3. ERPs: Middle time window (500–700 ms)

In the middle time window, subsequently recalled words tended to elicit more positive-going ERP amplitudes than not recalled words albeit not significantly, $F(1, 33) = 3.28$, $p = 0.079$, $\widehat{\eta}_p^2 = 0.09$, $BF_{10} = 0.564$. The effect of animacy, $F(1, 33) = 0.54$, $p = 0.47$, $BF_{10} = 0.302$, and the animacy \times subsequent recall interaction, $F(1, 33) = 0.18$, $p = 0.67$, $BF_{10} = 0.289$, as well as all other interactions involving the factors

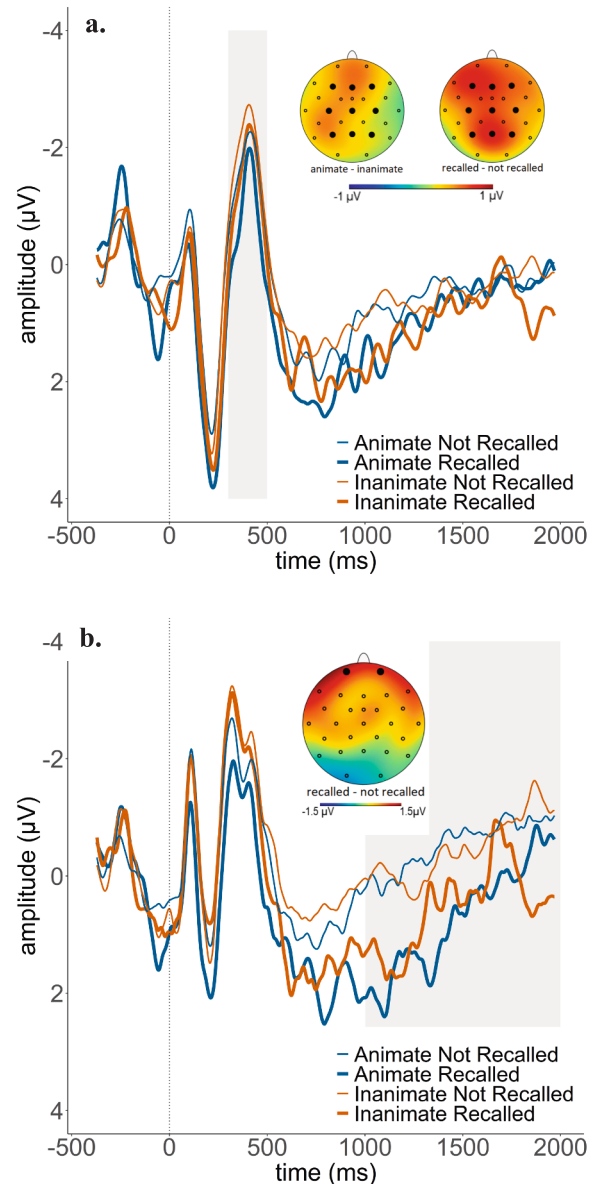


Fig. 2. Illustration of the ERP results from Experiment 1. Fig. 2a: ERP average across the 9 analyzed electrodes (F3, Fz, F4, C3, Cz, C4, P3, Pz, P4; highlighted by large dots in the scalp maps). The grey box highlights the time window in which significant main effects of animacy and subsequent recall were found, i. e., 300–500 ms. The scalp distributions of both effects (i. e., amplitude differences between animates and inanimates, and between subsequently recalled and not recalled trials) in this time window are shown in the scalp maps. Fig. 2b: ERP averages at the fronto-polar electrodes (Fp1, Fp2; highlighted in the scalp maps) and scalp distribution of the slow wave SME (1000–2000 ms).

subsequent recall and/or animacy (all p -values > 0.2) were not significant, except for a laterality \times animacy \times subsequent recall interaction, $F(2, 66) = 3.64$, $p = 0.032$, $\widehat{\eta}_p^2 = 0.10$. We did not interpret this interaction further due to the superseding animacy \times subsequent recall interaction being non-significant. There was also a main effect of anteriority, $F(2, 66) = 12.99$, $p < 0.001$, $\widehat{\eta}_p^2 = 0.28$.

2.6.4. ERPs: Slow wave (1000–2000 ms)

In the slow wave time window, there were no main effects of subsequent recall, $F(1, 33) = 1.63$, $p = 0.21$, $BF_{10} = 0.352$, or animacy, $F(1, 33) = 0.06$, $p = 0.80$, $BF_{10} = 0.237$, no interaction of both factors, $F(1,$

33) = 0.08, $p = 0.78$, $BF_{10} = 0.219$, and no other significant interactions involving the factors animacy and/or subsequent recall (all p -values > 0.07). There was a main effect of anteriority as well as an anteriority \times laterality interaction (both p -values < 0.015).

Since it appeared (Fig. 2b, Supplementary Fig. 1b) that a SME was in fact evident in the slow wave time window, but with a more frontal distribution than covered by the analyzed 3x3 electrode grid, we conducted an exploratory analysis on the two fronto-polar electrodes with a 2 (electrode: Fp1, Fp2) \times 2 (animacy) \times 2 (subsequent recall) ANOVA. Indeed, there was a main effect of subsequent recall, $F(1, 33) = 4.98$, $p = 0.03$, $\eta_p^2 = 0.13$. However, there was no main effect of animacy, $F(1, 33) = 0.01$, $p = 0.94$, $BF_{10} = 0.359$, no subsequent recall \times animacy interaction, $F(1, 33) = 0.13$, $p = 0.72$, $BF_{10} = 0.241$, and no other interactions involving the factors subsequent recall and/or animacy (all p -values > 0.36).

2.7. Discussion

In the study phase of a memory task, in the P300 and the slow wave time window, neither main effects of animacy nor animacy \times subsequent recall interactions were observed. Further, although a SME with a fronto-polar distribution was present in the slow wave time window, which took the typical form of more positive-going amplitudes for subsequently recalled than not recalled words, no main or interaction effects of animacy were present. Hence, these results differ from those of our previous studies on the survival processing effect (Forester et al., 2020a; 2020b) and are inconsistent with our predictions derived from the richness of encoding hypothesis of the animacy effect. Furthermore, these results are also inconsistent with a role of attentional processes or of emotional arousal in the animacy effect, as these processes would both be reflected in main or interaction effects of animacy in the middle time window/P300.

Importantly, animate words elicited an attenuated negativity in the N400 time window. This suggests that semantic access is facilitated for animates and is consistent with the idea that animates and inanimates differ in the richness of their semantic representation (Rawlinson & Kelley, 2021) – not to be confused with richness of encoding, which refers to an effortful, controlled cognitive activity during encoding rather than to an automatic process of accessing semantic object features as indexed by the attenuated negativity in the N400 time window. Further, an attenuated negativity for subsequently recalled compared to not recalled words was observed in the same time window. This SME indicates that semantic processing generally plays a role in successful encoding in the present paradigm. The lack of an interaction between both factors suggests that trial-by-trial variability in the engagement of early semantic processes was similarly relevant for successful subsequent recall for both word types.

3. Experiment 2

Experiment 2 examined retrieval-related ERPs during the recognition phase including animate and inanimate words. We analyzed old/new effects, which represent the difference in ERPs elicited by previously studied versus unstudied stimuli in a recognition test (for a review, see Rugg & Curran, 2007). Three types of old/new effects were of interest, which are briefly introduced here.

3.1. Early mid-frontal old/new effect

The early mid-frontal old/new effect is an attenuated negativity elicited by previously studied stimuli and occurs in the N400 time window, but shows a more frontal distribution than the typical N400 (Bridger et al., 2014). While the N400 is sensitive to the familiarity of a stimulus based on all prior experiences with it (“absolute familiarity”), the mid-frontal old/new effect indexes the enhanced familiarity signal

elicited when a stimulus has been recently encountered (“relative familiarity”; for a review, see Mecklinger & Bader, 2020).

3.2. Left parietal old/new effect

The left parietal old/new effect occurs subsequently to the early mid-frontal old/new effect and is observed when retrieval is based on recollection. It takes the form of an enhanced P300-like positivity for previously studied stimuli that are retrieved based on recollection (for a review, see Rugg & Curran, 2007).

3.3. Late posterior negativity (LPN)

While both the mid-frontal and the left parietal old/new effect have been extensively studied and their interpretation as correlates of familiarity and recollection, respectively, is relatively uncontroversial, there is somewhat less research regarding a subsequent, polarity-reversed old/new effect, the LPN. The LPN presents as a slow wave-like activity, which is typically more negative-going for previously studied than new stimuli (Mecklinger et al., 2016). It is typically prominent in tasks that require or stimulate the controlled retrieval of specific details from the study episode, such as source memory tasks (e.g., Mecklinger et al., 2007) or recognition tasks with complex, feature-rich stimuli (e.g., Endemann & Kamp, 2024). The LPN is morphologically and functionally dissociable from another negative-going ERP effect, the “broad central negativity”, which reflects familiarity with the source of a relatively weak item memory trace (Addante et al., 2024). The prevailing model of the LPN suggests that it indexes an effortful, controlled search process reflecting the attempt to reconstruct details of the study episode. It is particularly pronounced when this reconstruction is difficult due to a large number of features to be reconstructed, or due to a large feature overlap between study episodes (for a review, see Mecklinger et al., 2016). According to this model, the left parietal old/new effect thus reflects a relatively effortless “bottom-up”-recollection process elicited by readily presented features of the stimulus display, while the LPN represents effortful, slow, “top-down” reconstruction of study details.

3.4. Hypotheses

In a previous study on the survival processing effect, we reported that both an enhanced early mid-frontal, as well as an enhanced left parietal old/new effect were elicited in the survival condition (Forester et al., 2019), suggesting that both familiarity and (“bottom-up”) recollection were enhanced in this condition. Behavioral (receiver operating characteristics, ROC; Yonelinas & Parks, 2007) analyses suggested that although both retrieval signals were enhanced, participants’ recognition judgments relied primarily on recollection. In line with this pattern and with prior research, which suggests that the animacy effect is mainly due to enhanced recollection, but not familiarity (Komar et al., 2023), we hypothesized that the left parietal old/new effect (and potentially also the LPN) should be enhanced for animates, compared to inanimates.

In Experiment 2, we additionally examined ERP activity during encoding in order to replicate the main effect of animacy in the early (N400) time window during encoding observed in Experiment 1. A SME analysis, however, was not possible in Experiment 2, because fewer trials were available during encoding, resulting in low trial numbers after the division into subsequently recognized versus unrecognized trials.

3.5. Methods

3.5.1. Participants

The sample size primarily targeted a within-subject animacy main effect of at least medium size (i.e., $d_z = 0.50$). Thus, analogously to Experiment 1, we planned to collect data from $N = 34$ participants. For

one participant, EEG data was recorded only during recognition. The encoding ERP analysis is hence based on only $N = 33$ participants, while the behavioral and recognition ERP analyses are based on the full sample of $N = 34$ participants. The sample included 20 female and 14 male participants, with an age range of 19–34 years ($M = 25.28$, $SD = 3.97$).

3.5.2. Procedure and task

After preparation of the EEG recording, participants were instructed to memorize a word list for a later memory test without any mention of the test format. Next, 30 animates and 30 inanimates were presented in a random order, preceded by 3 buffer words at the beginning of the study list. During encoding, the individual words were each presented for 3000 ms with the same visual characteristics as for Experiment 1, with a fixation cross of 1000 ms in between trials.

The encoding phase was followed by a 10-minute break that included an experimenter-led digit span task (Wechsler, 2008) and some questionnaires. These measures served to allow for a comparison of participant characteristics with a sample of older adults collected for a separate study and are hence not reported in the present manuscript.

The subsequent recognition test again started with the presentation of 3 buffer words, followed by 60 animate and 60 inanimate words, of which 30 each had been previously studied and 30 were new/unstudied. The order of presentation was random and different for each participant, as was the assignment of stimuli to the encoding phase (old items) or only the recognition phase (new items). A recognition trial started with the presentation of a fixation cross for 1000 ms, followed by a word for 1500 ms. Next, a rating scale of 1= “definitely old”, 2= “probably old”, 3= “maybe old”, 4= “maybe new”, 5= “probably new”, 6= “definitely new”, was shown while the word remained on the screen. Participants had unlimited time to provide their rating, and their response automatically started the next recognition trial.

3.5.3. Stimuli

A new stimulus set was created based on the BAWL-R database. We selected 60 animates (referring to humans and animals) and 60 inanimates that were 4–8 letters long such that the word groups were matched for valence ($M_{animate} = 0.12$; $M_{inanimate} = 0.14$), arousal ($M_{animate} = 2.41$; $M_{inanimate} = 2.43$) and imageability ($M_{animate} = 5.15$; $M_{inanimate} = 5.17$) (all p -values > 0.59). The word types did not differ in the number of letters, phonemes, or syllables (all p -values > 0.21) or in word frequency ($p = 0.95$).

3.5.4. Behavioral analysis

A simple corrected recognition score was calculated for each word type by subtracting false alarm rates from hit rates (both measures collapsed across all confidence levels).

To assess contributions of recollection and familiarity to overall recognition, we followed Forester et al. (2019) and performed an additional analysis of the rating-based receiver operating characteristic (ROC) curve of the recognition data. Using the Excel solver function, we fitted a Dual-Process Signal-Detection model to our data, assuming equal variances of the signal for studied and unstudied items (Yonelinas & Parks, 2007). We thus derived estimates for familiarity (d') and recollection (Ro) (as well as for the criteria corresponding to each confidence judgment) for each subject and word type. Each parameter was restricted to be above zero. We also report the area under the curve (AUC), as well as the sum of squared deviations between the estimated and the actual hit and false alarm rates at each confidence level to evaluate the model fit.

3.5.5. EEG recording and ERP analysis

The EEG recording setup and all steps of the EEG data analysis were the same as in Experiment 1, with the exception of the segmentation step. For the encoding phase, we extracted segments for animates and inanimates, but performed no SME analysis. The analyzed time windows

were the same as in Experiment 1. For the recognition phase, trial-specific ERPs were separated depending on whether they were previously studied (old) or unstudied (new), separately for animates and inanimates. The descriptive statistics of the ERP trial were: animates at encoding: $M = 28.09$, $SD = 5.02$ (range: 6–30, $SE = 0.87$, median = 30), inanimates at encoding: $M = 27.85$, $SD = 4.94$ (range: 9–30, $SE = 0.87$, median = 30), animate-old: $M = 29.03$, $SD = 1.62$ (range: 22–30, $SE = 0.39$, median = 30), animate-new: $M = 28.67$, $SD = 2.26$ (range: 20–30, $SE = 0.39$, median = 30), inanimate-old: $M = 28.62$, $SD = 2.31$ (range: 19–30, $SE = 0.40$, median = 29.5), inanimate-new: $M = 29.06$, $SD = 1.75$ (range: 21–30, $SE = 0.30$, median = 30).

Each old/new effect was analyzed at a specific time window derived from prior studies (e.g., Forester et al., 2019): 300–500 ms for the early mid-frontal, 500–700 ms for the left parietal, 1000–1500 ms for the LPN.

3.5.6. Statistical analysis

Corrected recognition scores as well as recollection and familiarity measures were compared between word types with matched-pairs t -tests. Encoding ERPs were analyzed with animacy (2) \times anteriority (3: F, C, P) \times laterality (3: 3, z, 4) repeated measures ANOVAs while old/new effects were analyzed with animacy (2) \times old/new (2) \times anteriority (3: F, C, P) \times laterality (3: 3, z, 4) ANOVAs for each time window. For non-significant main effects of animacy or old/new, or their interaction, we calculated BF_{10} as described in Experiment 1.

3.6. Results

3.6.1. Recognition performance

Corrected recognition scores (hit rate-false alarm rate) were higher for animates ($M = 0.54$, $SD = 0.23$) than for inanimates ($M = 0.49$, $SD = 0.23$), $t(33) = 2.17$, $p = 0.037$, $\widehat{d}_z = 0.37$ (Fig. 3). This difference was driven by a higher false alarm rate for the inanimates ($M_{animate} = 0.24$, $SD = 0.17$; $M_{inanimate} = 0.29$, $SD = 0.20$), $t(33) = 2.62$, $p = 0.013$, $\widehat{d}_z = 0.45$, while the hit rates did not differ between word types ($M_{animate} = 0.78$, $SD = 0.12$, $M_{inanimate} = 0.78$, $SD = 0.12$), $t(33) = 0.09$, $p = 0.93$.

Regarding the ROC analysis, the sum of squared deviations between the estimated and the actual hit and false alarm rates at each confidence level was generally low ($M = 0.0036$, $SD = 0.0037$, max = 0.020), suggesting a good fit of the dual process model. The area under the curve (AUC) tended to be larger for animates ($M = 0.840$, $SD = 0.100$) than for inanimates ($M = 0.819$, $SD = 0.108$), $t(33) = 1.77$, $p = 0.085$, $\widehat{d}_z = 0.304$, albeit not significantly in a two-sided test (which can, however, be considered conservative, given the clear directed hypothesis).

Neither the estimate of familiarity (d' ; $M_{animate} = 1.26$, $SD = 0.93$; $M_{inanimate} = 1.08$, $SD = 0.81$), $t(33) = 1.51$, $p = 0.14$, $BF_{10} = 0.515$, nor of recollection (Ro ; $M_{animate} = 0.37$, $SD = 0.24$; $M_{inanimate} = 0.36$, $SD = 0.22$), $t(33) = 0.18$, $p = 0.86$, $BF_{10} = 0.188$, differed significantly between word types.

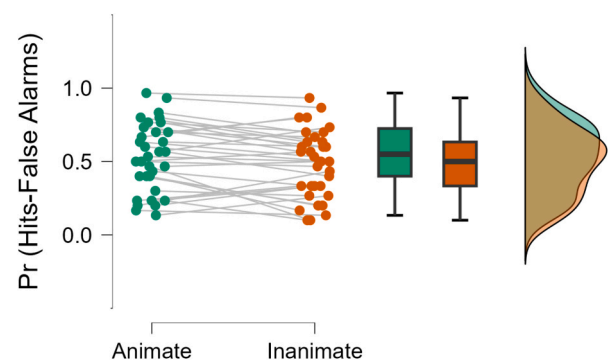


Fig. 3. Recognition performance (hit rate-false alarm rate) for animates and inanimates in Experiment 2.

3.6.2. Encoding ERPs

In the early time window (300–500 ms), the 2 (animacy) \times 3 (anteriority: F, C, P) \times 3 (laterality: 3, z, 4) ANOVA revealed a main effect of animacy, $F(1, 32) = 7.83, p = 0.009, \eta_p^2 = 0.20$, with animates eliciting an attenuated negativity (Fig. 4, Supplementary Fig. 2). Animacy did not interact with any electrode factor (all p -values > 0.29). There were significant main effects of anteriority and laterality (both p -values < 0.001).

Similarly, in the middle time window (500–700 ms), there was a main effect of animacy, $F(1, 32) = 6.06, p = 0.019, \eta_p^2 = 0.16$, but no interactions involving the factor animacy (all p -values > 0.22). There was a main effect of anteriority as well as an anteriority \times laterality interaction (both p -values < 0.022).

In the slow wave time window (1000–2000 ms), there was no main effect of animacy, $F(1, 32) = 1.02, p = 0.32, BF_{10} = 0.297$, and no interaction effects of animacy with any combination of electrode factors (all p -values > 0.40).

3.6.3. Recognition ERPs: Mid-frontal old/new effect (300–500 ms, electrode Fz)

A 2 (animacy) \times 2 (old/new) \times 3 (anteriority: F, C, P) \times 3 (laterality: 3, z, 4) ANOVA revealed a main effect of old/new, $F(1, 33) = 7.02, p = 0.012, \eta_p^2 = 0.18$, and a main effect of animacy, $F(1, 33) = 5.11, p = 0.031, \eta_p^2 = 0.13$, qualified by a laterality \times animacy interaction, $F(1, 33) = 5.34, p = 0.007, \eta_p^2 = 0.14$. Furthermore, all main and interaction effects including only electrode factors were significant (all p -values < 0.005). Importantly, there was no animacy \times old/new interaction, $F(1, 33) = 0.27, p = 0.61, BF_{10} = 0.370$ (interactions involving animacy, old/new and any combination of electrode factors: all p -values > 0.2). Hence, these results do not support the idea that the mid-frontal old/new effect differs between animates and inanimates (Fig. 5A, Supplementary Fig. 3A).

3.6.4. Recognition ERPs: Left parietal old/new effect (500–700 ms, electrode P3)

A 2 (animacy) \times 2 (old/new) \times 3 (anteriority: F, C, P) \times 3 (laterality: 3, z, 4) ANOVA revealed a main effect of old/new, $F(1, 33) = 7.46, p = 0.01, \eta_p^2 = 0.18$, and a main effect of animacy, $F(1, 33) = 7.09, p = 0.012, \eta_p^2 = 0.18$. Old/new interacted with anteriority, $F(2, 66) = 4.89, p = 0.010, \eta_p^2 = 0.13$. All main and interaction effects including only electrode factors were significant (all p -values < 0.02). Again, there was no interaction of animacy and old/new, $F(1, 33) = 1.65, p = 0.21, BF_{10} = 0.580$ (interactions involving animacy, old/new and any combination of electrode factors: all p -values > 0.37) (Fig. 5B, Supplementary Fig. 3B).

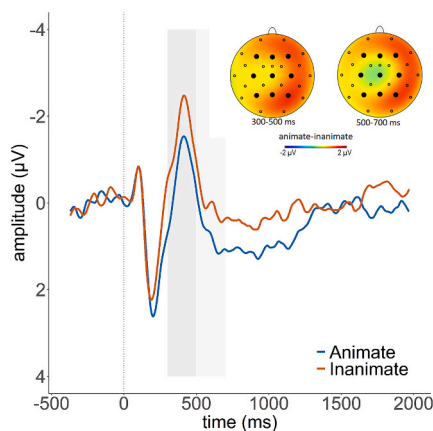


Fig. 4. Grand average ERPs from the encoding phase of Experiment 2 across the 9 analyzed electrodes (F3, Fz, F4, C3, Cz, C4, P3, Pz, P4). In the shaded time windows, main effects of animacy were observed. The scalp distribution of animate-inanimate amplitude differences is illustrated in the scalp maps.

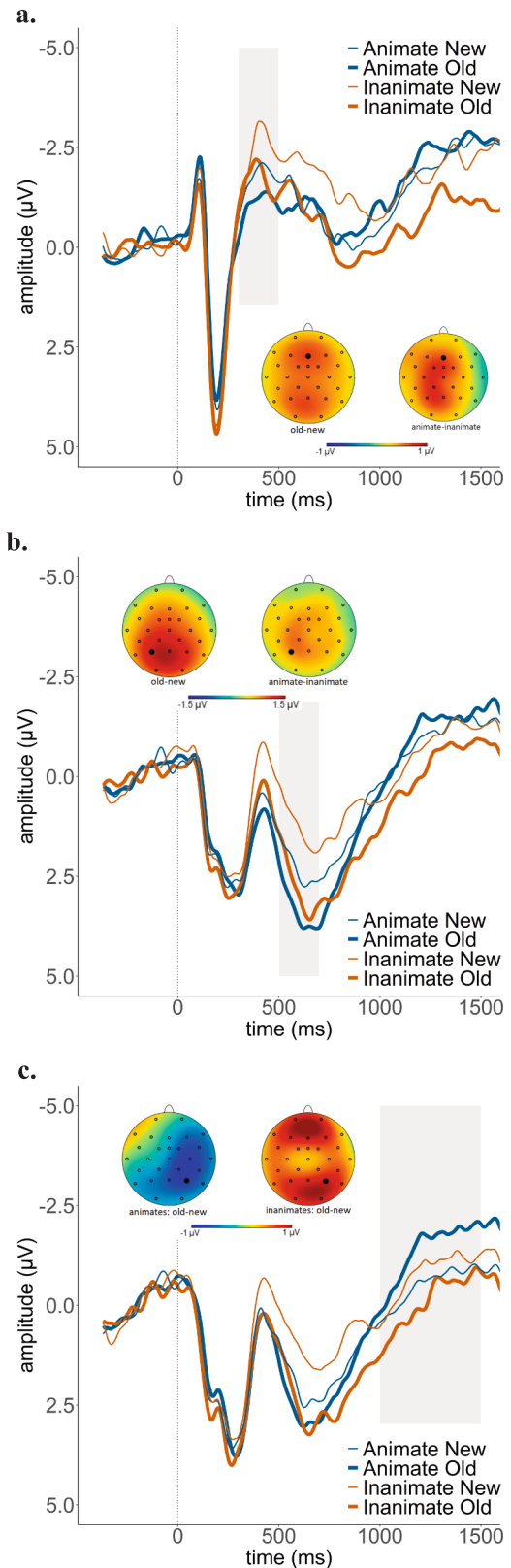


Fig. 5. Grand average ERPs and scalp distributions from the recognition phase of Experiment 2 at representative electrodes. Fig. 5a: Mid-frontal electrode Fz, showing the mid-frontal old/new effect and a main effect of word type (300–500 ms). Fig. 5b: left parietal electrode P3, showing the left parietal old/new effect and a main effect of word type (500–700 ms). Fig. 5c: right parietal electrode P4, showing the LPN (1000–1500 ms), which is observed only for the animates.

3.6.5. Recognition ERPs: LPN (1000–1500 ms, electrode P4)

A 2 (animacy) \times 2 (old/new) \times 3 (anteriority: F, C, P) \times 3 (laterality: 3, z, 4) ANOVA revealed a main effect of animacy, $F(1, 33) = 4.66$, $p = 0.038$, $\eta_p^2 = 0.12$, but no effect of old/new, $F(1, 33) = 0.13$, $p = 0.72$. However, there was an animacy \times old/new interaction, $F(1, 33) = 5.62$, $p = 0.024$, $\eta_p^2 = 0.15$. A main effect of laterality was also observed, $F(2, 66) = 15.94$, $p < 0.001$, $\eta_p^2 = 0.33$. The animacy \times old/new interaction was followed up by matched-pairs t -tests at electrode P4. These revealed a significant old-new effect for animates, $t(33) = 2.46$, $p = 0.019$, $\widehat{d}_z = 0.42$ (two-sided, uncorrected), such that animate-old words were associated with a larger negativity than animate-new words. There was no difference between old and new trials for inanimates, $t(33) = 1.59$, $p = 0.12$, $BF_{10} = 0.577$. Indeed, for inanimates, the descriptive trend was in the other direction as for animates (i.e., more positive-going ERPs for old than for new trials; Fig. 5c, Supplementary Fig. 3c).

3.7. Discussion

The encoding ERPs replicate those of Experiment 1, such that an attenuated negativity in an N400 time window (300–500 ms) was elicited by animates, compared to inanimates, supporting the idea that the two word types differ in ease of semantic access during encoding. In Experiment 2, the effect size of this difference during encoding was even somewhat larger than in Experiment 1, and it extended into the subsequent time window (Fig. 4). Hence, the differences between animates and inanimates in Experiment 1 are not due to the slight differences in average word length between the word types. Notably, the extension of the effect into the subsequent time window (500–700 ms) could index that there were some differences in attentional or emotional processes between animates and inanimates. However, since the scalp distributions were similar in both time windows (Fig. 4), and the differences became somewhat smaller in magnitude from 300–500 ms to 500–700 ms, it is likely that this is just a continuation of the preceding effect. Nevertheless, a role of attentional or emotional differences between word types cannot be completely ruled out based on the ERP results in Experiment 2 (unlike Experiment 1).

The analysis of ERPs during the recognition test revealed both an early mid-frontal old/new effect and a left parietal old/new effect, but no evidence for any differences between animates and inanimates in these old/new effects. Indeed, any descriptive differences were in the opposite direction than would be expected if animates elicited stronger familiarity or recollection processes (Figs. 5a and b). Familiarity and recollection, as reflected in these old/new effects, hence do not appear to differ between animates and inanimates. These findings were in line with our ROC analysis, in which we found no significant differences between animates and inanimates in familiarity or recollection parameters.

A clear difference in neural correlates of retrieval processes between the word types, however, became apparent within the LPN: More negative-going amplitudes for old than for new items were elicited by animates, but not by inanimates. The LPN is prominent in tasks that require the recollection of specific details of the study episode, such as source memory tasks (Mecklinger et al., 2007). It is thus thought to index effortful reconstruction of the study episode, a process that is stimulated by difficult to distinguish memory episodes with many attributes (Mecklinger et al., 2016). In a recent study, Endemann and Kamp (2024) found that the LPN was more pronounced for visually more complex, feature-rich pictures of objects (which were semantically meaningful), compared to less complex images of the same objects. The complex stimuli were richer in detail and closer to real-world perceptions and were also associated with higher recognition performance. We interpreted this pattern such that participants engaged more strongly in reconstructing the details of study episodes of visually complex images during retrieval. In the present study, there is no reason to assume that animate and inanimate words differ in visual complexity. However,

upon encounter with an animate word, participants may engage more strongly in the attempt to reconstruct the semantic stimulus features themselves, or self-generated images or associations that they experienced or actively generated during encoding. Notably, Komar et al. (2023) and Félix and Pandeirada (2024) recently reported converging evidence that animate objects elicited enhanced top-down recollection, but not familiarity. Similarly, Gelin et al. (2018) observed enhanced source memory for animates. Hence, animacy appears to affect top-down and bottom-up retrieval processes differently: While top-down, controlled reconstruction processes seem to be more pronounced for animates relative to inanimates, bottom-up recollection as reflected in the left-parietal old/new effect during (item) recognition does not.

In general, the animacy effect has been more robustly observed in free recall than in recognition tasks in the prior literature. Also, the type of learning appears to moderate the animacy effect in recognition memory, with incidental learning producing an animacy effect while intentional learning diminishes the animacy effect in recognition accuracy (for a review and additional experimental evidence, see Félix & Pandeirada, 2024). The present results extend these prior findings to suggest that recollective processing for animates occurs through effortful reconstruction of details from the study episode at retrieval. This is consistent with the notion of a richer network of semantic features for animates (Rawlinson & Kelley, 2021), which in turn may lead to an episodic memory trace containing more attributes and perhaps more distinctive features.

4. General Discussion

In the present study, we replicated the behavioral animacy effect in free recall (Experiment 1) and recognition (Experiment 2). In recognition memory, the effect was somewhat less pronounced and driven by reduced false alarm rates in animates, with no differences in hit rates. In the prior literature, the animacy effect has been more consistently observed in free recall, with mixed evidence in recognition (Félix & Pandeirada, 2024), which is consistent with the pattern we observed.

The starting point of the present study was the richness of encoding hypothesis, which was previously well-supported for the survival processing effect (Bell et al., 2015; Erdfelder & Kroneisen, 2014, Kroneisen & Erdfelder, 2011; Kroneisen et al., 2013, 2021; Röer et al., 2013), including strong support by ERP evidence. Specifically, an enhanced frontal slow wave amplitude during encoding along with a reduced SME in the P300 time window (Forester et al., 2020a, 2020b), as well as an enhanced left parietal old/new effect (Forester et al., 2019), suggested that a shift towards effortful working-memory based elaborative processes and away from more basic attentional processing during encoding, and more recollective processing during retrieval, were responsible for the enhanced memory performance in the survival processing condition.

In the present study, the ERP patterns regarding the animacy effect were clearly different. That is, there was no evidence for differences between the word types in the frontal slow wave or P300, neither in main effects of word type, nor in the SME. Furthermore, there was no evidence for a difference between the word types in the early mid-frontal or the left parietal old/new effect. Taken together, the neural mechanisms, measured by ERPs, differ between the survival processing and the animacy paradigm. While the ERP patterns observed in the survival processing paradigm in previous studies were consistent with predictions derived from the richness-of-encoding hypothesis, the findings of the present study were inconsistent with these predictions for the animacy effect. In this regard, the present results fully align with Komar et al. (2024)'s results showing that richness of encoding manipulations that affect the survival processing effect (Kroneisen & Erdfelder, 2011) do not affect the animacy effect in the same manner. However, since other recent results have supported the richness-of-encoding hypothesis (Meinhardt et al., 2020), future research should further test this hypothesis before it is completely rejected.

The question regarding the proximate mechanisms underlying the animacy effect thus remains to be answered. If emotional item processing plays a role, one would expect an enlarged P300 and a P300 SME for the animates (e.g., Kamp et al., 2015). The same prediction would also be derived from the idea that animates attract more attentional resources (e.g. Kamp & Donchin, 2015). In Experiment 1 there was no evidence in this direction, and in Experiment 2, although there was a main effect of animacy in the P300 time window during encoding, this appeared to be explainable by a continuation of the preceding N400 effect. From the theoretical perspective that imagery processes may differ between the word types, by contrast, one would expect that slow wave amplitudes or the slow wave SME differ between animates and inanimates (e.g. Kamp & Zimmer, 2015), but we did not observe this.

So where does all this leave us? The reduced N400 amplitude we observed in the encoding phase of both experiments, reflecting easier semantic access for the animates, is consistent with the view that the semantic representation of animates differs from that of inanimates, and more specifically with the view that encoding of animates is characterized by automatic access to a richer network of features in semantic memory (Rawlinson & Kelley, 2021). This view would also explain why working memory load due to secondary tasks in the encoding phase, which has been shown to diminish the elaboration-based survival processing effect significantly (Kroneisen et al., 2014, 2016, Kroneisen et al. (2024)), leaves the animacy effect virtually unaffected (e.g. Bonin et al., 2015, Komar et al., 2024, Rawlinson & Kelley, 2021): If the latter effect is based on automatic access to semantic features, it should largely be immune against attention-demanding secondary tasks at encoding.

By contrast, the pronounced LPN for animates in the recognition phase, which was absent for inanimates, is in turn consistent with the view that participants engage more effort at retrieval in a detailed reconstruction of the study episode, potentially due to more distinctive features or a more complex memory representation of the episodic memory trace of animates. Further exploring this view is hence a fruitful route for further research.

In conclusion, the present study does not support the view that the animacy effect in episodic memory is due to enhanced elaborative encoding for animate stimuli (richness of encoding hypothesis). Hence, the proximate mechanisms of the animacy effect seem to differ from those of the survival processing effect. Further research is needed to precisely pinpoint the proximate mechanisms underlying the animacy effect. Given our results, one promising view is that a difference in the semantic representations, implying automatic access to more distinctive features for animates than for inanimates at encoding, necessitates or stimulates the controlled reconstruction of more complex details from the study episode during retrieval of animates.

CRedit authorship contribution statement

Siri-Maria Kamp: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Luisa Knopf:** Writing – review & editing, Validation, Software, Project administration, Investigation, Data curation. **Meike Kroneisen:** Writing – review & editing, Funding acquisition, Conceptualization. **Edgar Erdfelder:** Writing – review & editing, Funding acquisition, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This work was supported by the German Research Foundation: GZ: KA 4867/1-2, KR 4545/1-2, and ER 224/3-2.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.nlm.2025.108112>.

Data availability

The link to the data is included in the manuscript.

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