Electrophysiological Correlates of Competitor Activation Predict Retrieval-Induced Forgetting

Robin Hellerstedt and Mikael Johansson
Department of Psychology, Lund University, Lund, Sweden

Address correspondence to M. Johansson, Department of Psychology, Lund University, PO Box 213, SE-221 00 Lund, Sweden. Email: mikael.johansson@psy.lu.se

The very act of retrieval modifies the accessibility of memory for knowledge and past events and can also cause forgetting. A prominent theory of such retrieval-induced forgetting (RIF) holds that retrieval recruits inhibition to overcome interference from competing memories, rendering these memories inaccessible. The present study tested a fundamental tenet of the inhibitory-control account: The competition-dependence assumption. Event-related potentials (ERPs) were recorded while participants engaged in a competitive retrieval task. Competition levels were manipulated within the retrieval task by varying the cue–item associative strength of competing items. In order to temporally separate ERP correlates of competitor activation and target retrieval, memory was probed with the sequential presentation of 2 cues: A category cue, to reactivate competitors, and a target cue. As predicted by the inhibitory-control account, competitors with strong compared with weak cue–competitor association were more susceptible to forgetting. Furthermore, competition-sensitive ERP modulations, elicited by the category cue, were observed over anterior regions and reflected individual differences in ensuing forgetting. The present study demonstrates ERP correlates of the reactivation of tightly bound associated memories (the competitors) and provides support for the inhibitory-control account of RIF.

Keywords: cognitive control, ERP inhibition, long-term memory, retrieval competition

Introduction
The question of why we forget is a long-standing and fundamental issue in the memory literature. Accumulating evidence from the last 2 decades of memory research implies that forgetting in some instances can be a subsidiary effect of remembering (for review see Anderson 2003). This phenomenon is referred to as retrieval-induced forgetting (RIF; Anderson et al. 1994). There is currently an ongoing debate about whether this forgetting phenomenon is caused by the inhibition of competing memories, or interference from retrieved memories. The present study employed electrophysiological recordings of brain activity to elucidate the neural mechanisms underlying RIF and to test key predictions from the inhibitory-control account.

RIF is studied experimentally with the retrieval-practice paradigm (Anderson et al. 1994). In the classic version of this paradigm, participants encode category–exemplar pairs (e.g. FRUIT—Apple, FRUIT—Mango) before they engage in category-plus-word-stem-cued retrieval practice (FRUIT—Ma—__) of half of the exemplars from half of the categories. Finally, after having engaged in a distractor task, participants are given a category-cued recall test (FRUIT—__) of all exemplars from the initial encoding phase. RIF is evident in reduced performance, in the final recall test, for nonpracticed exemplars associated with practiced categories compared with exemplars associated with nonpracticed categories (for reviews see Anderson 2003; Storm and Levy 2012).

Interference theory has been one of the most prominent theories of forgetting since it was introduced in the beginning of the 20th century (for review see Anderson and Neely 1996). Hypotheses regarding the cognitive mechanisms causing RIF can be postulated from this theory via the concepts of competitive retrieval and blocking. According to interference theory, memory representations sharing a common cue compete for retrieval when the cue is presented (e.g. McGeoch 1932), a condition referred to as competitive retrieval. The associative strength between the cue and the memory trace varies among memories. Newly acquired memories have, for instance, a stronger cue–item association relative to older memories. The interference theory suggests that items with strong cue–item association have the potential to interfere with and block retrieval of memories with weaker associative strength during competitive retrieval (associative blocking). In the context of the retrieval-practice paradigm, based on interference theory, the associative-blocking account proposes that retrieval practice increases the associative strength between the practiced items (i.e. the target) and the cue (e.g. Anderson and Spellman 1995; Camp et al. 2007). In the final recall test, the practiced items are thus readily activated when the cue is presented and block retrieval of the nonpracticed items (i.e. the competitors) due to their relatively stronger association with the cue. The blocked retrieval of competitors leads to reduced memory performance for these items compared with items from nonpracticed categories, viz. to RIF.

Another explanation of this forgetting phenomenon is provided by the highly influential inhibitory-control account (Anderson et al. 1994). This account is based on interference theory as it also assumes that memories associated with a common cue compete for retrieval when the cue is presented, but differs from the associative-blocking account in that it involves an active inhibition mechanism (Anderson and Spellman 1995; Levy and Anderson 2002; Anderson 2003). The inhibition mechanism is assumed to resolve interference by reducing the activation of competing memory representations and thereby facilitating the retrieval of the sought-after target memory. A consequence is weakened memory strength of competitors that may be inaccessible if they later on become relevant; hence, they may suffer from RIF. According to the inhibitory-control account, RIF is caused by the inhibition of nonpracticed items (i.e. competitors) during competitive retrieval in the intermediate retrieval practice phase rather than by the strengthening of the practiced items (i.e. the targets) as proposed by the associative-blocking account.

Although a large body of evidence supports the inhibitory-control account (for review see Storm and Levy 2012), one of
the most fundamental tenets of this theory, the competition-dependence assumption, remains controversial. The inhibitory-control account holds that inhibition is recruited to suppress competing memories during selective retrieval. Thus, only items that compete for retrieval will be inhibited and suffer from RIF. This supposition is referred to as the competition-dependence assumption (Anderson 2003; Storm and Levy 2012). Competition levels can be varied via manipulations of cue–item associative strength, and the 2 accounts of RIF differ in terms of the predictions they make about how such manipulations affect RIF. According to the inhibitory-control account, strong association between the cue and the competitors (nonpracticed items from practiced categories) increases the probability that competitors compete for retrieval when the cue is presented during retrieval practice, which in turn enhances the need for inhibition and the likelihood of ensuing forgetting. The associative-blocking account, on the contrary, holds that RIF depends on the association between the cue and the targets (practiced items) and predicts higher levels of RIF following a relative increment in associative strength for practiced targets compared with the nonpracticed competitors.

Previous research designed to test the competition-dependence assumption has provided mixed results. Consistent with predictions from the inhibitory-control account, Anderson et al. (1994) showed that RIF was not only related to the cue–competitor associative strength, but also unrelated to the associative strength of targets. Subsequent studies have reported additional evidence for the competition dependence of RIF (Bäuml 1998; Anderson, Green, McCulloch 2000; Shivde and Anderson 2001; Levy et al. 2007; Storm et al. 2007; Bäuml and Samenieh 2010; Hanslmayr et al. 2010). However, predictions based on the competition-dependence assumption have not always been met, and there is currently an ongoing debate about the validity of this assumption and consequently on the need for an inhibitory control mechanism to account for RIF (Williams and Zacks 2001; Jakab and Raaijmakers 2009; Jonker and MacLeod 2012; Raaijmakers and Jakab 2012). As noted by Storm and Levy (2012), many of the studies that have failed to find evidence for competition dependence did not control for output interference in the final recall test, and the results may therefore be difficult to interpret. However, Jonker and MacLeod (2012) recently showed that RIF can occur in a noncompetitive category retrieval task even when output interference is controlled for, which suggests that factors other than output interference contribute to the inconsistencies observed across studies.

**The Present Study**

The aim of the present study was to test the competition-dependence assumption by directly examining the neural mechanisms underlying competitor activation when this is hypothesized to occur in the retrieval-practice paradigm. Investigation of the neural correlates of competitor activation requires differentiation of competitor activation from target retrieval. Recent studies have tried to disentangle competitor activation from target retrieval spatially (Kuhl et al. 2011, 2012; Jost et al. 2012; Waldhauser et al. 2012). In the present study, a new complementary approach was adopted; namely to temporally separate competitor activation from target retrieval. Memory was probed by the sequential presentation of 2 cues: One category cue to reactivate recently studied competitors and another target cue in the form of a word stem to constrain the search to a particular exemplar. The excellent temporal resolution of electrophysiological brain imaging techniques makes event-related potentials (ERPs) well suited to reveal the relative time course of cognitive processes engaged during competitive retrieval. In order to reduce the probability that the category cue also activated the target, we employed a semantic generation task known to cause RIF (cf. Bäuml 2002). In this task, participants are provided with a category-plus-word-stem cue (e.g. FRUIT—Ma___?) and are instructed to generate an exemplar that matches the cue. The target exemplar (in this case Mango) has not been presented during the preceding study phase of the experiment, but is associated with the same category cue as the studied exemplars. This semantic generation version of the retrieval-practice paradigm was employed in the present study since it made it possible to probe competitors and targets separately by the sequential presentation of the competitor-related category cue and the target-unique word-stem cue. The preceding study phase served to bias the spread of activation elicited by the category cue toward the competitors (i.e. the studied exemplars). The manipulation of competition, on the other hand, was based on pre-experimental category–exemplar associative strength. That is, competitors in the high—relative to low—competition condition were more likely to be primed by the category cue, due to their relatively stronger pre-experimental cue–item associative strength (e.g. strong: FRUIT—Apple vs. weak: FRUIT—Mango).

The neural underpinnings of RIF have recently been investigated with functional magnetic resonance imaging (Kuhl et al. 2007; Wimber et al. 2008, 2009, 2011) and electrophysiological methods (Johansson et al. 2007; Spitzer et al. 2009; Hanslmayr et al. 2010; Staudigl et al. 2010). Previous electrophysiological studies of RIF have contrasted brain activity recorded during competitive retrieval with brain activity observed during representation of previously studied items (Johansson et al. 2007; Staudigl et al. 2010) or during exemplar-cued category retrieval (Hanslmayr et al. 2010). In the present study, however, we contrasted 2 conditions within the same retrieval task that differed only in terms of their level of competition. The within-task comparison in the present study made it possible to exclude theoretically irrelevant between-task differences that may complicate interpretation of the results in previous studies. For example, a contrast between a retrieval task and a nonretrieval task captures multiple processes, not only those related to retrieval competition and inhibitory control. Competition levels were manipulated by varying the cue–item associative strength in an otherwise identical semantic generation task. In the high-competition condition, participants studied items with strong cue–item associative strength and generated items with weak associative strength. The opposite arrangement was used in the low-competition condition. Importantly, opposite predictions the inhibitory-control account and the associative-blocking account provide opposite predictions regarding these 2 conditions' proneness to RIF.

The semantic nature of the association between the competitors (exemplars of a semantic category) and the category cue suggests that automatic retrieval of competitors will occur in a time window when the semantic properties of the category cue are processed. A vast literature indicates that the processing of the semantic aspects of a stimulus is linked to the
modulation of a negative-going shift 300–500 ms poststimulus presentation (the so-called N400 component; for reviews see Kutas and Federmeier 2000, 2011). A more anterior ERP modulation in the same time window, the FN400, has been related to the facilitated automatic retrieval of semantic information resulting from item repetition, referred to as conceptual priming (Paller et al. 2007). Interestingly, previous research has demonstrated a relationship between the FN400 elicited by a recognition memory test probe and the reactivation of semantic associates previously encoded together with the test probe (Opitz and Cornell 2006). The FN400 effect was found sensitive to the number of remembered semantic associates and showed a more positive-going modulation when many as compared with few associates were retrieved. An analogous modulation of the FN400 may be considered a putative ERP correlate of competitor activation in the present study. The category cue should more readily reactivate previously studied exemplars with strong when compared with weak category–exemplar associative strength. Consequently, we predicted more positive-going, anterior ERPs elicited by the presentation of the category cue in the high- than in the low-competition condition.

Unlike competitor activation, target retrieval from semantic memory is consciously controlled and more effortful. The timing of successful target retrieval in the semantic generation task is therefore likely to vary across trials and participants. Since previous ERP studies of cued recall suggest that memory retrieval may be revealed approximately 300 ms post cue presentation (Allan et al. 1996; Friedman and Johnson 2000), ERP correlates of target retrieval were predicted to commence no earlier than 300 ms after presentation of the target word-stem cue.

Differing predictions can be derived from the 2 conflicting theories of RIF. The inhibitory-control account predicts (1) more RIF in the high- versus low-competition condition, (2) larger ERP correlate of competitor activation in the high-versus low-competition condition (elicited by the competitor cue), and (3) that this ERP correlate of competitor activation is related to ensuing RIF. In contrast, the associative-blocking account predicts (1) more RIF in the low- versus high-competition condition, and (2) that ERP correlates of target retrieval success (elicited by the target word-stem cue) will be related to RIF.

In summary, the present study aimed at testing a fundamental tenet of the inhibitory-control account of RIF: The principle of competition dependence. To this end, we manipulated the cue–item associative strength and examined the neural mechanisms underlying varying levels of retrieval competition. Our paradigm was designed to disentangle competitor activation from target retrieval. The finding of a competition- and forgetting-sensitive ERP effect elicited by the competitor-related category cue would provide evidence for the reactivation of tightly bound associative memories during competitive retrieval and lend support to the inhibitory-control account of RIF.

### Materials and Methods

#### Participants

Twenty-eight students (13 females, mean age = 24 years, range = 18–28) gave written consent before participating in exchange for a cinema ticket. All participants were right-handed, native Swedish speakers with normal or corrected-to-normal vision. The study was approved by the regional ethics committee at Lund University.

#### Materials

Twenty-four categories were selected from the Hellerstedt et al. (2012) Swedish category norms. The categories were divided into 4 lists. These lists were matched regarding taxonomic frequency and word length. Each category contained 6 exemplars of high-taxonomic frequency (mean rank 10.5 across category lists) and 6 exemplars of low-taxonomic frequency (mean rank 38.3 across category lists). All exemplars had a unique initial letter within each category.

#### Design

The experiment consisted of 3 blocks. Each block included an encoding phase, a competitive retrieval phase, a 5-min nonverbal distractor phase (Digit Stroop), and a test phase. In the high-competition condition, participants studied exemplars of high-taxonomic frequency and generated related exemplars of low-taxonomic frequency from semantic long-term memory. The opposite pattern characterized the low-competition condition. To investigate the consequences of competitive retrieval, 2 baseline conditions (excluded from the intermediate competitive retrieval phase) were added to the design. In these 2 conditions, participants studied and were tested on exemplars of high-taxonomic frequency (baseline condition for high competition) or low-taxonomic frequency (baseline condition for low competition). All 4 conditions were included in each of the 3 experimental blocks (2 categories per condition in each block). The 4 stimulus lists described above were assigned to the 4 conditions, and this assignment was counterbalanced across participants. Although it would have been interesting to also include conditions in which participants studied and generated items of equal levels of taxonomic frequency (e.g., study of exemplars of high-taxonomic frequency and generation of exemplars of high-taxonomic frequency), this was not feasible due to time and stimulus material constraints. The 2 conditions used in the present study were selected because they give rise to the maximum (high-competition condition) and minimum level of competition (low-competition condition) among the combinations, due to the relative difference in cue-associative strength between the targets and the competitors (competitors are more likely to intrude during retrieval if the cue–competitor associative strength is relatively stronger than the cue–target associative strength), and the 2 accounts of RIF clearly have opposite predictions about their relationship to the forgetting effect.

#### Procedure

Within each block, participants studied 48 exemplars from 8 semantic categories. The items were presented successively for 2000 ms on a 17-in. computer screen (e.g., FRUIT—Apple). Prior to each presentation of the category–exemplar word pairs, a fixation cross was shown for 500 ms followed by a blank screen (with a duration of 500 ms). After the encoding phase, participants engaged in cued semantic generation of unstudied exemplars from half of the studied categories. In this competitive retrieval phase (Fig. 1), a category cue (e.g., FRUIT) was presented for 500 ms, followed by a blank screen for 100 ms, and the presentation of a 2-letter target word-stem cue (e.g., Ma___) for 2000 ms. Participants were instructed to generate an exemplar from the given category that completed the word stem and to respond orally within a 2000-ms response window indexed by a question mark. In each block, 24 exemplars associated with 4 studied categories were included in the competitive retrieval phase. High- and low-competition trials were intermixed within each block (i.e. the design was event related), which served to eliminate any systematic difference in preparatory activity between conditions. Participants engaged in a nonverbal distractor task (Digit Stroop) for 5 min between the competitive retrieval and the final memory test. In this test, the 48 studied exemplars were tested in random order. Each trial started with a sequential presentation of a fixation cross and a blank screen (each shown for 500 ms). Next, a category-plus-first-letter cue (e.g., FRUIT—A___) was shown for 2500 ms, and the participants responded orally within a subsequent 2000-ms response
window. To avoid muscle artifacts in the electrophysiological recordings, the participants were instructed to withhold their response during the presentation of the category-plus-first-letter cue.

**Electroencephalogram Recording and Preprocessing**

The electroencephalogram (EEG) was recorded continuously from 32 silver/silver chloride scalp electrodes mounted in an elastic cap and positioned according to the extended 10–20 system (Jasper 1958). Additional electrodes were placed over and below the left eye and at the left and right outer canthi to measure the vertical and the horizontal electrooculogram. All channels were digitized with 32 bit resolution at a sample rate of 500 Hz. Electrode-scalp impedances were kept below 5 kΩ. A digital band-pass filter of the continuous EEG (0.1–15 Hz) was applied off-line to increase the signal-to-noise ratio. The continuous EEG was segmented into epochs beginning 200 ms prior to stimulus presentation and ending 1500 ms post stimulus presentation. The ERPs were baseline corrected using the prestimulus interval. Ocular artifacts were corrected using a linear regression approach implemented in Neurocan Edit 4.4 (Compumedics, El Paso, TX, USA). Trials containing recording-related artifacts were rejected prior to averaging (with a minimum of 16 accepted trials per condition and participant).

**ERP Data Analysis**

To quantify the ERP waveforms in both the high- and low-competition conditions, mean amplitudes in a category cue time window (300–600 ms) and 3 consecutive target cue time windows (600–900, 900–1200, and 1200–1500 ms) were measured (the mean number of trials was 28 and 27 in the high- and low-competition conditions, respectively). A Competition (high vs. low) × Region (frontal: F3, FZ, F4; frontocentral: FC3, FCZ, FC4; central: C3, CZ, C4, centro-parietal: CP3, CPZ, CP3; parietal P3, PZ, P4; and occipital: O1, OZ, O2) × Hemisphere (left, midline, and right) repeated-measures analysis of variance (ANOVA) was performed separately for each of the 4 time windows. To test if potential effects showed different scalp distributions across time windows, a Time window × Competition × Region × Hemisphere repeated-measures ANOVA was conducted. Greenhouse-Geisser adjustment was used when data violated the assumption of sphericity. Only significant results involving the factor competition are reported.

**Results**

**Behavioral Results**

**Competitive Retrieval Phase**

Participants' semantic generation performance was significantly higher in the low- than in the high-competition condition (62.6%, standard deviation [SD] = 9.8% vs. 47.7%, SD = 12.1) ($F_{1,27} = 74.580, P < 0.001, \eta^2_p = 0.734$).

**Test Phase**

Average memory performance in each condition was: High competition, 39.8%, SD = 11.4; high-competition control, 50.6%, SD = 11.9; low competition, 35%, SD = 10.0; low-competition control, 40%, SD = 12.3. A Competition (high vs. low) × Task (competitive retrieval vs. baseline) repeated-measures ANOVA was performed to test whether competitive retrieval caused reliable levels of RIF and whether such forgetting was larger in the high- than in the low-competition condition. Memory performance was higher in general for items in the high- than in the low-competition conditions, indicating that the manipulation of associative strength was successful ($F_{1,27} = 29.6, P < 0.001, \eta^2_p = 0.476$). Replicating previous studies, competitive retrieval significantly induced forgetting of related items compared with control items ($F_{1,27} = 24.5, P < 0.001, \eta^2_p = 0.523$). Importantly, a significant Competition × Task interaction was revealed ($F_{1,27} = 4.5, P = 0.043, \eta^2_p = 0.143$). Planned pairwise comparisons confirmed reliable RIF effects in both conditions (high competition: $F_{1,27} = 20.5, P < 0.001, \eta^2_p = 0.432$; low competition: $F_{1,27} = 5.6, P = 0.025, \eta^2_p = 0.173$), and in accordance with the competition-dependence assumption, the forgetting effect was larger in the high- than in the low-competition condition (10.8%, SD = 12.6 vs. 4.5%, SD = 10.0).

Finally, we investigated the relationship between target retrieval in the intermediate competitive-retrieval phase and the amount of the RIF of related studied items in the final recall test. Inconsistent with predictions from the associative-blocking account, we observed no significant correlations between retrieval success and RIF in the high-competition condition ($r = -0.314$, $P = 0.104$, not significant [NS]), in the low-competition condition ($r = -0.253$, $P = 0.193$, NS), or collapsed across competition conditions ($r = -0.263$, $P = 0.117$, NS). Although we are reluctant to interpret these nonsignificant correlations, we note that the negative direction is opposite to what would have been predicted by the associative-blocking account.

**ERP Results**

**Competition-Sensitive ERP Modulations**

Grand averages of ERPs recorded during the competitive-retrieval phase of the experiment are depicted in Figure 2A. The most prominent difference between conditions is a sustained positive-going shift over anterior electrodes in the high- compared with the low-competition condition. Crucially, this effect onsets approximately 300 ms before presentation of the target cue (300 ms into the recording epoch) and lasts until about 300 ms post target cue presentation (900 ms into the recording epoch).

The significant main effects of Competition were evident in the category cue time window (300–600 ms; $F_{1,27} = 4.231, P = 0.049, \eta^2_p = 0.135$) and the first target cue time window (600–900 ms; $F_{1,27} = 5.657, P = 0.025, \eta^2_p = 0.173$), indicating that the high-competition condition elicited more positive amplitude in general compared with the low-competition condition in these time windows. A reliable interaction between Competition and Region was found in the category cue time window (300–600 ms; $F_{5,135} = 5.989, P = 0.007, \eta^2_p = 0.182$).
and in the first target cue time window (600–900 ms; $F_{5,135} = 3.677$, $P = 0.036$, $\eta_p^2 = 0.120$). As can be seen in Figure 2B, follow-up analyses showed that the effect was restricted to frontal ($F_{1,27} = 11.063$, $P = 0.003$, $\eta_p^2 = 0.291$), frontocentral ($F_{1,27} = 11.334$, $P = 0.002$, $\eta_p^2 = 0.296$), and central ($F_{1,27} = 5.621$, $P = 0.025$, $\eta_p^2 = 0.172$) regions in the category cue time window. The same kind of subsidiary analysis of the first target cue time window (600–900 ms) indicated that the effect was significant over frontal ($F_{1,27} = 6.544$, $P = 0.016$, $\eta_p^2 = 0.195$), frontocentral ($F_{1,27} = 8.147$, $P = 0.008$, $\eta_p^2 = 0.232$), central ($F_{1,27} = 6.690$, $P = 0.015$, $\eta_p^2 = 0.199$), and centroparietal ($F_{1,27} = 5.312$, $P = 0.029$, $\eta_p^2 = 0.164$) regions.

Significant interactions involving the factor Competition were found in the category cue time window (300–600 ms) and the first target cue time window (600–900 ms). An ANOVA was performed to test whether the scalp distribution of the competition-sensitive effect differed as a function of time window (Fig. 2B), but did not reveal any significant interactions involving the factors Time window and Competition ($F_s \leq 1.413$, NS).

**Relationship Between the Competition-Sensitive ERP Modulation and Retrieval-Induced Forgetting**

A forgetting index was calculated in order to examine the relationship between the ERP effects and individual differences in RIF. This index was computed by subtracting average recall performance in the generation conditions from average recall performance in the control conditions. To control for baseline performance, this difference measure was divided by average recall performance in the control conditions (cf. Kuhl et al. 2007). Two groups of participants were formed based on a median split on the index: A high-forgetting group (RIF, 24.7%, SD = 7.1; mean recall; competition, 36.8%, SD = 6.3; and control, 50.8%, SD = 6.5) and a low-forgetting group (RIF, 1.0%, SD = 13.9; competition, 38.1%, SD = 11.8; and control, 39.4%, SD = 11). To investigate whether the identified ERP effects were related to individual differences in RIF, a Competition × Region × Hemisphere × Forgetting group (high vs. low) mixed ANOVA was conducted on data from the 2 time windows in which the Competition × Region interaction was significant (300–600 and 600–900 ms). Importantly, in accordance with predictions by the inhibitory-control account, a significant Competition × Region × Forgetting group interaction was evident in the category cue time window ($F_{5,130} = 5.694$, $P = 0.001$, $\eta_p^2 = 0.180$). No interaction involving the factor Forgetting group was evident in the target cue time window ($F_{5,130} = 1.979$, NS). As demonstrated in Figure 3, follow-up analyses revealed significant differences between conditions in the high-forgetting group over frontal ($F_{1,13} = 17.716$, $P = 0.001$, $\eta_p^2 = 0.577$) and frontocentral ($F_{1,13} = 14.719$, $P = 0.002$, $\eta_p^2 = 0.531$) regions in the category cue time window.
Comparable analyses did not result in any reliable differences between conditions in the low-forgetting group (Fs ≤ 2.011, NS).

ERP Correlates of Target Retrieval in the Competitive Retrieval Phase

A second set of ERP analyses was conducted to investigate the ERP correlates of target retrieval. In these analyses, ERPs from successful and unsuccessful retrieval attempts were contrasted (collapsed over high- and low-competition conditions). As depicted in Figure 4, target retrieval was associated with a late onsetting, widespread positive-going slow wave showing a successful > unsuccessful pattern. A Retrieval success (successful vs. unsuccessful) × Region × Hemisphere ANOVA was conducted for each of the 4 time windows. Importantly, there was no significant main effect or interaction involving the factor Retrieval success in the category cue time window (Fs ≤ 1.619, NS). This is consistent with the interpretation that the early competition-sensitive ERP effect reflects the activation of competitors rather than the retrieval of targets. Furthermore, ERP correlates of retrieval success were observed after the presentation of the target cue as predicted. More specifically, in the final target cue time window (1200–1500 ms), where there was a main effect of Retrieval success (F1,27 = 20.444, P < 0.001, ηp² = 0.431), a Retrieval success × Region interaction (F5,135 = 3.932, P = 0.037, ηp² = 0.127), and a Retrieval success × Region × Hemisphere interaction (F10,270 = 2.254, P = 0.037, ηp² = 0.077). Follow-up analysis revealed that while the target retrieval effect was reliable over all regions (minimum: F1,27 = 7.295, P = 0.012, ηp² = 0.213, maximum: F1,27 = 24.255, P < 0.001, ηp² = 0.473), it showed a bilateral posterior maximum and tended to be more pronounced over right than left anterior recording sites.

A final ANOVA with the factors Retrieval success × Region × Hemisphere × Forgetting group was performed to assess whether this ERP correlate of target retrieval was related to...
ensuing RIF. In contrast to predictions from the associative-blocking account, there was no significant interaction between Retrieval success and Forgetting group (Fs ≤ 2.919, NS).

Discussion

The phenomenon that retrieval can cause forgetting of related memories has puzzled memory researchers for nearly 2 decades and has given rise to a vast amount of research aimed at elucidating the underlying mechanisms. Although the prominent inhibitory-control account has received compelling support from these studies of RIF in general, the fundamental tenet of competition dependence remains controversial. The competition-dependence assumption is crucial for the inhibitory-control account, since inhibition is thought to be recruited to solve interference among competing memory representations (Anderson 2003). Without competition, there is simply no need for inhibition. Consequently, the goal of the present study was to test the inhibitory-control account via an investigation of the competition-dependence assumption.

The competition-dependence assumption was examined behaviorally by manipulation of the cue–item associative strength of the competitors. As predicted by the inhibitory-control account, competitors with strong cue–item associative strength were more prone to RIF compared with competitors with weak associative strength. These behavioral results replicate the original findings of Anderson et al. (1994) and add weight to the proposition that RIF is competition dependent.

To further test the competition-dependence assumption of the inhibitory-control account, ERPs were recorded during the competitive retrieval phase of the experiment with an aim to investigate the neural correlates of retrieval competition. Two alterations to the design were introduced in the present study that enabled an examination of the neural correlates of competitor activation. First, a within-task comparison was used to exclude competition-unrelated between-task differences from the contrast. By contrasting 2 conditions characterized by different levels of competition within the same memory retrieval task, we excluded theoretically irrelevant processes that may be captured in between task comparisons (e.g., generic retrieval-related processes in a retrieval vs. re-presentation contrast) and isolated the process of interest: Retrieval competition. Secondly, the sequential presentation of distinct cues for competitors and targets during the competitive retrieval phase made it possible to distinguish ERP correlates of competitor activation from target retrieval.

In accordance with predictions from the inhibitory-control account, we observed a competition-sensitive ERP modulation in the category cue time window that was sensitive to ensuing RIF. The onset time, the anterior distribution, and the polarity of the effect (more positive going for the high- when compared with the low-competition condition) together mimic the FN400 effect observed in previous ERP studies of conceptual priming and are consistent with the idea that the competition-sensitive effect observed in the present study reflects automatic retrieval of semantic associates (i.e. the competitors).

The FN400 component has also been linked to familiarity in dual-process models of recognition memory (Rugg and Curran 2007), and there is currently a discussion on how to best describe the functional significance of the FN400 effect; in terms of conceptual priming or familiarity (e.g. Stenberg et al. 2009; Voss et al. 2010). From a familiarity perspective, the FN400 effect in the present study may reflect an increased familiarity signal for category cues in the high- compared with the low-competition condition. Importantly, however, the category cues were presented equally often in the 2 conditions (equal strengthening), and the assignment of the category cue to condition was counterbalanced across participants (excluding item-specific effects), rendering the associative strength between the category cues and the studied competitors the only difference between conditions. Hence, if the FN400 in the present study reflects increased familiarity for the category cue, the increment in this familiarity signal is likely to be based on the reactivation of previously encoded semantic associates (i.e. the level of competitor activation). This interpretation of the FN400, as an indicator of competitor reactivation, may be considered congruent with both the conceptual priming and the familiarity view.

Further support for our interpretation comes from the ERP memory study reported by Opitz and Cornell (2006). In their study phase, participants encoded word quartets in either an associative condition in which 3 of the words were semantically associated, and the task was to point out the word that did not fit the context, or a relational condition in which the 4 words were semantically unrelated and the task was to decide which word referred to the smallest object. A robust FN400 old/new effect was observed in the subsequent recognition memory task, but only for words encoded in the associative condition. Moreover, this midfrontal positivity was larger in amplitude for recognized items for which participants remembered all 3 of the previously encoded associates when compared with only one. Analogous to the findings of the present study, the FN400 effect was sensitive to the pre-experimental semantic association strength between the test probe and the previously coencoded words. Furthermore, the effect was sensitive to the memory performance for the words encoded together with the test probe, a finding that is consistent with the interpretation of the FN400 effect in the present study as an ERP correlate of competitor reactivation.

It is conceivable that the FN400 reflects the accessibility of memory representations associated with the test probe. The binding between a test probe and related memories will be affected by multiple factors. In the current study, the association between the category cue and the competitors will vary according to both pre-experimental association strength and the strengthening (or biasing) that follows from the exposure in the experimental encoding task. Presumably, the greater positivity in the high-competition condition reflects the facilitated access of the category cue representation bound to the coencoded typical category members when compared with the atypical category members (cf. Opitz and Cornell 2006).

Recent research suggests that familiarity can mediate associative recognition when encoding conditions encourage the unitization of between-item or item-context associations (e.g. Quamme et al. 2007; Montaldi and Mayes 2010; Mollison and Curran 2012). It is likely that the intentional encoding of category–word associations and the category-plus-first-letter cued recall task used in the present study may have motivated the use of such a unitized encoding strategy. Although
speculatively, it is conceivable that the typical associates were easier to unitize with the category cue at encoding than the atypical associates, resulting in a greater familiarity signal and FN400 positivity in the high- when compared with the low-competition condition.

We have argued for the observed FN400 effect as an ERP correlate of competitor reactivation. An alternative is that the effect is sensitive to preparatory retrieval processes that might differ between conditions. It could be argued that participants gained knowledge about the generation requirement associated with each category (i.e. either typical or atypical), which allowed them to prepare for generating either a typical or atypical exemplar. The FN400 effect might thus reflect a restriction of search in semantic memory. However, competition levels were manipulated on a trial-by-trial basis, so participants would have needed to recall this information on cue presentation and then engage in restricted search in semantic memory within the 600-ms time window that preceded the presentation of the target cue. We consider this scenario as unlikely.

Another related interpretation of the FN400 in the present study is that it reflects processing related to successful target retrieval, given that the high- and low-competition conditions not only differed in the levels of competition, but also in the levels of retrieval success. To test such a retrieval-success interpretation, which would have been more in line with a blocking account, ERPs elicited by successful and unsuccessful retrieval trials were contrasted. Inconsistent with this interpretation, there was no effect of target retrieval in the category cue time window.

No previous study has, to our knowledge, investigated the ERP correlates of retrieval success in a semantic word-stem cued recall task, but successful semantic cued recall has been used as a baseline condition in several ERP studies of episodic cued recall (e.g. Allan et al. 1996; Allan and Rugg 1997; Johnson et al. 1998). These studies have shown that while the morphology of the ERPs is similar in the 2 retrieval modes (Johnson et al. 1998), the episodic compared with semantic cued recall tend to elicit sustained, more positive-going ERP modulation (e.g. Allan et al. 1998; Osorio et al. 2009; Angel et al. 2010). This effect has been interpreted as an ERP correlate of successful episodic cued recall. The present results suggest that successful cued recall in the semantic retrieval mode manifests in a positive-going ERP modulation with comparable spatiotemporal characteristics.

The current finding that competitors with strong cue–item associative strength were more susceptible to RIF and the evidence of neural correlates of competitor activation during competitive retrieval are both consistent with the competition-dependence assumption and strongly support the inhibitory-control account. Although the present study was not primarily designed to test the associative-blocking account of RIF, it is important to note that the results in the present study not only support the inhibitory-control account, but are also inconsistent with the associative-blocking account.

Starting with the behavioral results, this account predicts larger RIF in the low-competition condition, due to higher target retrieval success rates in the competitive retrieval phase in this condition. The behavioral results confirmed that the participants indeed were more successful in retrieving targets in the low-competition condition, but contrary to predictions by the associative-blocking account, the RIF effect was larger in the high-competition condition. A factor that may complicate predictions from the associative-blocking account is that weak associations tend to be strengthened more by retrieval practice (e.g. Mandler 1980). That is, although the targets in the high-competition condition are retrieved less often, these items are likely to be strengthened to a greater extent when they are retrieved. Accordingly, the associative-blocking account may also predict larger RIF in the high-competition condition. Even if the associative-blocking account may not have clear predictions regarding the relationship between levels of competition and RIF, this theory still predicts that retrieval success should correlate with RIF within the 2 competition conditions. However, no such correlation was evident within neither of the 2 conditions.

Turning to the ERP results, the associative-blocking account predicts that a retrieval-success-related ERP modulation in the target cue time window would be related to RIF. A retrieval-success-sensitive ERP modulation was found in the late target time window (1200–1500 ms), but contrary to predictions from the associative-blocking account this ERP effect did not interact with forgetting.

The presentation of the category cue in the competitive retrieval phase of the present experiment was expected to lead to automatic retrieval of the competitors, since these items had been presented together with the category cue in the encoding phase. Given that the targets in the competitive retrieval phase had not been presented in the encoding phase, they were less likely to be activated when the category cue was presented. Although this makes sense, it cannot be completely ruled out that the targets also may have been activated, as the targets were semantically associated with the category. However, given that there was no retrieval-success sensitive ERP effect in the category cue time window, we believe that it is justifiable to consider the competition-sensitive ERP modulation in this early time window as a reflection of primarily competitor activation.

Inhibition is theorized to be an adaptive process recruited to reduce the costs of competition (e.g. prolonged retrieval times and reduced target retrieval success; for review see Levy and Anderson 2002). Although the ERP correlate of competitor activation was related to ensuing negative consequences of competition (RIF of competitors), there was no relation to immediate costs of competition in the present study, since there was no relationship between target retrieval success rates and the FN400 effect. RIF has previously been shown to be unrelated to target retrieval success (i.e. Storm et al. 2006; Storm and Nestojko 2010), but related to prolonged target retrieval times (e.g. Kuhl et al. 2007), so response times may be a more sensitive behavioral measure of the costs of competition. Although it would have been interesting to investigate the relationship between the FN400 and the time it takes to generate the target exemplar, this was not feasible in the present experiment. Our experimental design was optimized to examine the ERP correlates of competitor activation, and it was therefore necessary to instruct the participants to withhold their oral response to avoid excessive muscle artifacts in the critical time window. Future EEG studies investigating the relationship between the FN400 and response latencies may consider using a combination of a speeded nonverbal response and a postponed verbal response that assesses generation success.
Competitor activation is by definition a prerequisite for inhibition according to the inhibitory-control account, but the exact temporal relationship between competition and inhibition is still unknown. Inhibition may operate immediately when competition builds up, or be recruited after the target has been specified to facilitate retrieval. The competition-sensitive ERP modulation in the present study could either reflect competitor activation only, or competitor activation plus inhibition of these interfering memory representations. Although the target was unspecified in the category cue time window, the participants knew that the previously studied items (the competitors) were irrelevant for the semantic generation task, so inhibition may have been recruited prior to target specification in the present experiment. A challenge for upcoming research will be to disentangle competition from inhibition and to investigate the temporal relationship between these 2 processes.

Competitor activation during competitive retrieval and its effect on memory have so far mainly been studied with indirect behavioral measures of interference such as forgetting and prolonged response times (e.g., Underwood 1957). Despite the crucial role of competition in long-term memory retrieval and forgetting, few studies have directly investigated the neural mechanisms underlying activation of competing memory representations. Recent neuroimaging studies have studied the neural correlates of competitor activation in the visual domain (Kuhl et al. 2011, 2012; Jost et al. 2012; Waldhauser et al. 2012), but few studies have studied the activation of competing semantic associates (Öztekin and Badre 2011; Bergström et al. 2012). The interpretation of the suggested neural correlates of competitor activation in these studies is complicated by concurrent target retrieval, since competitor activation was not differentiated from target retrieval. The present study bridges a gap between the classic behavioral literature on interference in long-term memory and recent neuroimaging studies of the neural processes underlying retrieval competition by temporally isolating competitor activation from target retrieval and by relating neural correlates of competitor activation to behavioral measures of memory impairment for the competitors.

RIF has previously been shown to be absent or diminished in several clinical populations, for example, attention deficit-hyperactivity disorder (Storm and White 2010), post-traumatic stress disorder (Amir et al. 2009), clinical depression (Groom and Sterkaj 2010), and schizophrenia (Soriano et al. 2009). Accordingly, investigation of the neurocognitive mechanisms underlying the RIF phenomenon has the potential to increase our understanding of the memory deficits that are related to these psychiatric disorders. Speculatively, given that the competition-sensitive ERP effect primarily reflects competitor reactivation, it can potentially be used in future studies to investigate whether the absence of RIF in the mentioned clinical populations is caused either by an absence of competitor activation or by an inhibitory deficit.

The inhibitory-control account has held up well since it was introduced. Studies examining RIF have revealed several properties of this forgetting phenomenon that are consistent with the inhibitory-control account and difficult to reconcile with the associative-blocking account (for review see Storm and Levy 2012). Numerous studies have provided evidence that RIF is cue independent by showing reliable levels of RIF in tests with novel test probes (e.g. Anderson and Spellman 1995; Anderson, Green, McCulloch 2000; Anderson and Bell 2001; but see, e.g. Williams and Zacks 2001 for conflicting results) and in tests of item recognition memory rather than cued recall (e.g. Hicks and Starns 2004; Starns and Hicks 2004; Verde 2004; Spitzer and Bäuml 2007). RIF has also been demonstrated to be retrieval specific, that is, a mere re-presentation of targets is not sufficient to induce forgetting of competitors (e.g. Ciranni and Shimamura 1999; Anderson, Bjork, Bjork 2000; Bäuml 2002). In fact, RIF appears unrelated to the level of strengthening of the practiced targets and is even observed following retrieval practice with cues that are impossible to complete (i.e., no target is strengthened; Storm et al. 2006; Storm and Nestojko 2010), a finding that clearly speaks against blocking and in favor of the inhibitory-control account. However, mixed results have been reported concerning the supposition that competitor interference during target retrieval is a prerequisite for inhibition and resulting RIF. The present study tested this hypothesis by manipulating the cue–competitor association strength during target retrieval. By showing that competitors with strong compared with weak cue–competitor association were more susceptible to forgetting and by revealing neural correlates of competitor reactivation, the present study provides strong support for the inhibitory-control account.

Conclusions

The present study tested the competition-dependence assumption of the inhibitory-control account via examination of the neural correlates of competitor activation during competitive retrieval. A novel method for the temporal separation of competitor activation from target retrieval allowed an investigation of the neural mechanisms underlying retrieval competition. The ERP results suggest that tightly bound memory representations are reactivated upon cue presentation. Furthermore, the ERP correlae of such competitor activation was related to ensuing forgetting of the reactivated memory representations. Since retrieval competition is considered a prerequisite for inhibition, the presented neural correlates of retrieval competition provide new evidence of the need for inhibition during selective memory retrieval and consequently add further support to the inhibitory-control account of RIF. Beyond and above the relevance to the understanding of forgetting, the present findings more generally inform theories of associative memory by revealing mechanisms affecting the accessibility of long-term memory representations, and by suggesting ERP correlates of the reactivation of associated memories.

Funding

This work was supported by the Swedish Research Council (VR 60229601 to M.J.).

Notes

The authors are grateful to Sofie Nilsson for assistance with data collection and to 3 anonymous reviewers for their helpful comments on an earlier version of the manuscript. Conflict of Interest: None declared.
References


Öztekin I, Badre D. 2011. Distributed patterns of brain activity that lead to forgetting. Front Hum Neurosci. 5:86.


