Neural Bases of Automaticity

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Automaticity allows us to perform tasks in a fast, efficient, and effortless manner after sufficient practice. Theories of automaticity propose that across practice processing transitions from being controlled by working memory to being controlled by long-term memory retrieval. Recent event-related potential (ERP) studies have sought to test this prediction, however, these experiments did not use the canonical paradigms used to study automaticity. Specifically, automaticity is typically studied using practice regimes with consistent mapping between targets and distractors and spaced practice with individual targets, features that these previous studies lacked. The aim of the present work was to examine whether the practice-induced shift from working memory to long-term memory inferred from subjects' ERPs is observed under the conditions in which automaticity is traditionally studied. We found that to be the case in 3 experiments, firmly supporting the predictions of theories. In addition, we found that the temporal distribution of practice (massed vs. spaced) modulates the shape of learning curves. The ERP data revealed that the switch to long-term memory is slower for spaced than massed practice, suggesting that memory systems are used in a strategic manner. This finding provides new constraints for theories of learning and automaticity.

Keywords: automaticity, learning, working memory, long-term memory, event-related potentials

Imagine yourself listening to a professional violinist playing Bach's sonatas in a concert hall. The performance is so smooth that it seems to be effortless. The day after, you accompany your daughter to her very first violin lesson at the music academy. The sound is grinding, and you suddenly realize the difficulty of planning the fingering while controlling the pressure and speed of the bow. The hypothesis that human performance is driven by two modes of information processing, controlled versus automatic, has motivated a large amount of research since the dawn of cognitive psychology (Anderson, 1982; James, 1890; Logan, 1978, 1988, 1990, 1992, 2002; Palmeri, 1997, 1999; Rickard, 1997; Schneider & Chein, 2003; Schneider & Shiffrin, 1977; Shiffrin & Schneider, 1977; Siegler, 1987; Stroop, 1935; Ulrich, Schroter, Leuthold, & Birngruber, 2015; Wundt, 1903). Controlled processing is generally conceived as a serial process that demands attention and engages working memory mechanisms (Atkinson & Shiffrin, 1968; Logan, 1980; Shiffrin & Schneider, 1977). By contrast, automatic processing is fast and parallel, effortless, and robust to dual task interference (Bargh, 1992; LaBerge, 1981; Logan, 1978; Moors & De Houwer, 2006; Schneider & Chein, 2003; Shiffrin & Schneider, 1977). Automatization is thought to develop with consistent mapping of stimuli onto responses, resulting in a transition from performance that is controlled by working memory to performance that is controlled by long-term memory retrieval (Anderson,

2000; Logan, 1988, 2002; Palmeri, 1997; Rickard, 1997; Shiffrin & Schneider, 1977; Siegler, 1987). The aim of the present work was to test hypotheses about the transition of control from working memory to long-term memory by measuring event-related potentials (ERPs) derived from electroencephalographic (EEG) recordings that reflect the involvement of the two memory systems.

Controlled and Automatic processing: Behavior and Theories

Visual and memory search paradigms have traditionally been used to study controlled and automatic processes. In each trial, subjects are presented with a memory set of m items. After some delay, they have to search for the presence of the memorized items among a display set of d probe items.[1] The product $m \times d$, termed load, determines the difficulty of the task. A probe that matches any of the memorized items is called a target. A probe that doesn't match any of the memorized items is called a distractor. Subjects are instructed to give a positive response to target-present trials, and a negative response to target-absent trials. Response times (RTs) and accuracy are the dependent measures.

Memory and distractor sets are usually sampled from larger groups of items, called memory and distractor ensembles. If memory and distractor ensembles do not overlap, a so-called *consistent mapping* procedure is used. Alternatively, a *varied mapping* procedure is used if the two ensembles overlap. Results from varied mapping procedures generally show a linear increase in mean RT as a function of memory load for both positive and negative responses, suggestive of a serial memory comparison process (e.g., Hockley, 1984; Sternberg, 1966). By contrast, memory load has little effect on mean RT and accuracy when the mapping is

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[1] If $m > 1$ and $d = 1$, the task is called a memory search. If $d > 1$, the task is called a visual search.

consistent (Schneider & Shiffrin, 1977, Experiments 1 and 2), presumably due to automatization of the search and parallel memory comparisons.

Quantitative theories such as the instance theory of automatization (Logan, 1988, 1990, 1992) predict that RTs decrease as a power function of practice:

$$RT = a + bN^{-c}$$

where N is the number of practice trials, a is the asymptotic RT, b is the difference between initial and final performance. The exponent c specifies the shape of the function. The power function speed-up of RT with practice has been so consistently observed that it has been proposed to be a psychological law (Newell & Rosenbloom, 1981; but see Heathcote, Brown, & Mewhort, 2000).

The instance theory of automaticity provides a mapping of power function parameters onto specific cognitive processes involved during learning. According to the theory, long-term memory traces (i.e., *instances*) accumulate as a function of stimulus repetition. Retrieval from long-term memory is modeled as a race between instances, and finishing times for the race follow a power function. In addition, subjects can decide to rely on the instance retrieved from long-term memory versus working memory. The decision process is modeled as a race between the two memory systems, and modulates the exponent (c) of the power function (Logan, 1988, 1992). Over practice, long-term memory will dominate the race. Automaticity occurs when performance is only determined by long-term memory, and this is reflected by the asymptotic RT of the power function (parameter a). Consequently, the power function can be fit to data to infer working memory and long-term memory contributions (e.g., Logan & Klapp, 1991).

Neural Bases of Automaticity

Early neurophysiological investigations focused on the locus of automatic versus controlled processing (e.g., Chein & Schneider, 2005; Schneider & Chein, 2003), or the modulation of perceptual-cognitive demands as a function of practice (e.g., Kramer, Strayer, & Buckley, 1991). Carlisle, Arita, Pardo, and Woodman (2011, Experiment 3) used ERP measures to examine the transition between working memory and long-term memory as a function of learning. Subjects performed a visual search task with a memory set $m = 1$ and a display set $d = 12$. Stimuli were Landolt Cs of 8 possible orientations. Subjects were instructed to give a positive response if the display set contained a target and a negative response otherwise. Critically, the very same memory set was repeated during 3, 5, or 7 trials, so mapping was *locally consistent* within a set of trials but *globally inconsistent* across the experiment. Carlisle et al. examined the effects of practice on working memory and long-term memory ERPs. Working memory was evaluated through an analysis of the contralateral delay activity (CDA). The CDA is a sustained negativity that indexes mechanisms that maintain visual representations in working memory (Berggren & Eimer, 2016; Luria, Balaban, Awh, & Vogel, 2016; Reinhart et al., 2012; Vogel & Machizawa, 2004; Vogel, McCollough, & Machizawa, 2005). It is maximal over posterior brain regions contralateral to the memorized hemifield. Results showed a power-function decrease of CDA amplitude as a function of memory set repetition, mirroring the power function speed-up of RT. Long-term memory was evaluated through an analysis of the

frontal P170. The decrease in CDA amplitude was accompanied by a power-function increase in the amplitude of frontal P170 potentials (Woodman, Carlisle, & Reinhart, 2013). The amplitude of the frontal P170 is proportional to repetition priming magnitude, a form of long-term memory (Voss, Schendan, & Paller, 2010). Logan (1990) showed that automaticity and repetition priming exhibit similar properties, and proposed that they result from a common mechanism. In particular, repetition priming is associated with a power-function speed-up of RT, and is highly item-specific, with little transfer to new items (see also Scarborough, Gerard, & Cortese, 1979). Repetition priming (and associated P170 potentials) might thus reflect the progressive reliance on long-term memory traces assumed by theories of automaticity. The tradeoff between CDA and P170 amplitude as a function of memory set repetition has been replicated several times, using similar experimental designs (e.g., Reinhart, McClenahan, & Woodman, 2016; Reinhart & Woodman, 2014, 2015).

The work of Logan, Woodman and colleagues offers a bridge between behavior, theory, and neural data, providing a framework for understanding learning mechanisms and the development of automaticity. The bridge, however, is weakened by methodological discrepancies between behavioral and ERP studies. First, the ERP studies conducted thus far have used a global varied mapping procedure with local consistent mapping sequences: although a given memory set was repeated over a learning run (local consistent mapping), it could become a distractor in another learning run (global varied mapping). Behavioral studies have shown that automaticity does not develop under varied mapping conditions (Fisk & Schneider, 1982, 1983; Hockley, 1984; Logan, 1978; Schneider & Shiffrin, 1977; Shiffrin & Schneider, 1977; Sternberg, 1966; reviewed by Shiffrin, 1988), questioning the nature of the mechanism underlying the speed-up of RT observed in previous ERP studies.

Second, long-term memory traces in the previous ERP studies are inferred from the speed-up of RT with practice and corresponding modulations of frontal P170 potentials. Since Ebbinghaus (1885), behavioral studies have used retention or transfer tests to assess learning and evaluate the strength of long-term memory traces (e.g., Bahrick, Bahrick, Bahrick, & Bahrick, 1993; Cepeda et al., 2009; Logan, 1990; McAllister & Ley, 1972; Scarborough et al., 1979). Retention or transfer tests are necessary to confirm whether the speed-up of RT (and corresponding modulations of frontal P170 potentials) reflect the formation of long-term memory traces.

Finally, the previous ERP studies have focused on a particular type of learning that involves consecutive presentations of the same memory set (i.e., *massed* practice). Skill acquisition (e.g., learning to play the violin, learning to read), however, generally involves *spaced* practice episodes. The temporal distribution of practice has been the subject of intense investigations (e.g., Bloom & Shuell, 1981; Brown & Huda, 1961; Childers & Tomasello, 2002; Hintzman, 1976; Pashler, Zarow, & Triplett, 2003; Ruch, 1928; Toppino & Schneider, 1999; Underwood, 1961). A recent meta-analysis concludes that spaced practice leads to stronger long-term memory traces and better recall performance (whatever the retention interval) than massed practice when total study time of each item is equated between conditions (Cepeda, Pashler, Vul, Wixted, & Rohrer, 2006; see also Donovan & Radosevich, 1999; Janiszewski, Noel, & Sawyer, 2003).

The aim of the present work was to examine whether the shift from working memory to long-term memory inferred from sub-

jects' ERPs is observed under the conditions in which automaticity is traditionally studied. Experiment 1 used a true consistent mapping procedure, massed practice, and incorporated a retention test to probe long-term memory traces and assess learning. Memory and distractor sets were drawn from a set of 2400 pictures representing real-world unique objects (Brady, Konkle, Alvarez, & Oliva, 2008). For simplicity, we used a search task with a memory set $m = 1$ and a display set $d = 1$. Experiment 2 extended this design to spaced practice. Finally, Experiment 3 sought to replicate empirical findings from Experiments 1 and 2 by treating massed versus spaced practice as a within-subject factor.

Experiment 1

The goal of Experiment 1 was to test predictions of theories of automaticity (e.g., Logan, 1988) by measuring ERP indices of working memory and long-term memory to track the memory representations that subjects were using to perform their task. As shown in Figure 1, the participant's task was to determine whether the memory set picture matched the display picture shown next. Thus, they were shown their target on each trial. A consistent mapping of stimuli onto responses was used, similar to automaticity studies. Based on current theories, we predicted that we should initially observe people relying on representations in visual working memory to guide processing of the display set. This should be expressed as a large CDA measured on the first presentation of a given memory set. With practice, long-term memory representations should be stored, and these long-term memory representations should become sufficient to perform the target discrimination task. This storage in long-term memory should be measured as the systematic change in long-term memory ERP components. Thus, we should observe the CDA decrease in amplitude as the long-term memory potentials increase.

Carlisle et al. (2011) used a set of 8 abstract shapes as stimuli (Landolt Cs). The present study used real-world pictures for two reasons. First, pictures allowed us to address the main issue with the design of ERP studies, in which mapping was locally consistent but globally inconsistent. Pictures allowed us to fully separate memory and distractor ensembles, and have mapping consistent both locally and globally. Second, a large corpus of research has

shown excellent long-term memory for pictures (e.g., Brady et al., 2008; Shepard, 1967; Standing, 1973). The use of pictures as stimuli in the present study should promote the development of long-term memory traces.

It has been demonstrated that the repetition of meaningful stimuli modulates a negative-going wave that develops between 200 and 600 ms after stimulus onset (N400), largest over centro-parietal scalp locations (Kutas & Donchin, 1980). Although the functional significance of the N400 is still under debate, a large corpus of research suggests that it reflects stimulus-induced semantic activity in long-term memory (Kutas & Federmeier, 2011). Specifically, the amplitude of the N400 becomes more positive as activity in long-term memory increases (Bentin, McCarthy, & Wood, 1985; Kutas & Federmeier, 2000; Kutas & Van Petten, 1988). N400 repetition effects vanish for meaningless stimuli (e.g., Danker et al., 2008; Voss, Lucas, & Paller, 2010; Voss & Paller, 2007; Voss, Schendan, & Paller, 2010), explaining why such modulations have not been observed in previous automaticity ERP experiments that used abstract shapes. However, the meaningful pictures used in the present work should elicit robust N400 potentials. Voss, Schendan, and Paller (2010) argued that the P170 indexes perceptual priming and the N400 reflects semantic priming. For our purposes, we only retain the link between these potentials and long-term memory. We expected modulations in P170 and N400 amplitude as a function of practice, and these modulations should be tightly related to the behavioral indices of learning.

Alternatively, it is possible that the previous experiments that used a global varied mapping procedure with local consistent mapping sequences observed a pattern of ERPs that do not generalize to the paradigms typically used to study automaticity, and the learning that results in this state of information processing. If the latter is the case, then we should find that the modulations of CDA and long-term memory potentials are unrelated to the behavioral indices of learning.

Materials and Method

Participants. Sixteen right-handed volunteers (21–35 years of age) participated in the experiment in exchange for monetary compensation. Eight were male, and all had normal or corrected-
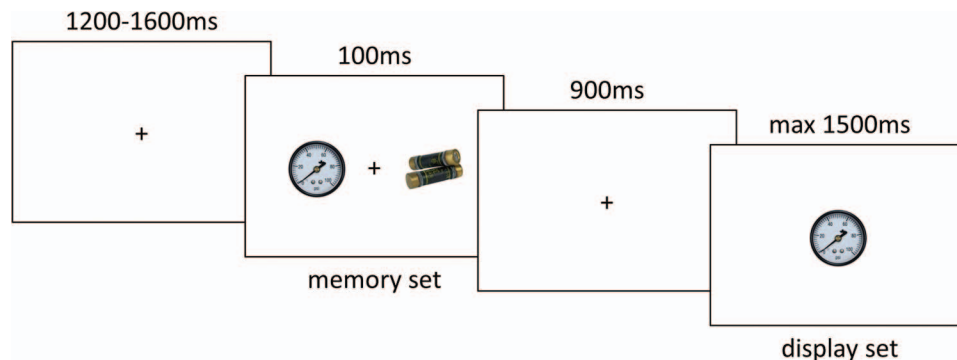

Figure 1. Diagram of the experimental design. In each trial, a lateralized memory set was presented during 100 ms. The display set appeared at the center of the screen 900 ms after the extinction of the memory set, and remained on-screen until response (with a deadline set at 1,500 ms). The participant's task was to determine whether the memory set picture matched the display picture shown next. Thus, they were shown their target on each trial.

to-normal vision and no history of neurological problems. One subject was excluded due to an excessive number of ocular artifacts in the EEG. Informed consent was obtained prior to the beginning of the experiment. All procedures were approved by the Vanderbilt Institutional Review Board.

Stimuli. The experiment was run using Matlab and the Psychophysics toolbox (Brainard, 1997). Stimuli were drawn from a collection of 2400 pictures representing real-world unique objects (Brady et al., 2008). They were presented on a white visual field (48.6 cd/m^2) at a viewing distance of 120 cm. For each subject, we constructed memory (μ) and distractor (δ) ensembles by randomly sampling (without replacement) $\mu = 100$ and $\delta = 400$ pictures respectively. Memory and distractor ensembles did not overlap (i.e., consistent mapping). For each trial, a central black fixation cross (0.22° × 0.22°, 0.25 cd/m^2) remained on screen until the presentation of the display set. The display set (d) consisted of 1 centrally presented picture (1.96° × 1.96°) drawn from either the memory or the distractor ensemble. The memory set (m) consisted of 1 picture (1.96° × 1.96°) drawn from the memory ensemble, and was presented 1.42° to the left or to the right of the central fixation cross.

Procedure. The experiment took place in a sound and electrically shielded booth (i.e., a Faraday cage). Each trial was initiated by the onset of the central fixation cross for 1,200–1,600 ms (randomly jittered using a uniform distribution) before the onset of the memory set (see Figure 1). The memory set was presented for 100 ms, to the left of fixation for half of the trials, and to the right for the other half (order balanced across subjects). The memory set was always accompanied by a control picture presented symmetrically on the opposite side to rule out physical explanations for the lateralized ERP effects (Woodman, 2010). The control picture was randomly sampled (without replacement) from an ensemble of 800 pictures that did not overlap with memory and distractor ensembles. The display set was presented at the center of the screen 900 ms after the extinction of the memory set, and was removed as soon as the subject responded or after 1,500 ms if the subject had not responded by then. Participant's task was to press one button if the picture cued in the memory set was in the display set, and the other button if the display set did not match the memory set picture. Thus they were shown their target on each trial. The extinction of the display set marked the beginning of the intertrial interval (1,200–1,600 ms, randomly jittered using a uniform distribution), during which participants were allowed to blink.

Memory sets were randomly selected (without replacement) from the memory ensemble. Each memory set was presented during 8 consecutive trials to examine the effects of massed practice on working memory and long-term memory ERP components. Participants thus completed 800 trials (100 memory sets × 8 repetitions), divided into 2 sets of 400 trials. Within each set of 400 trials, participants were given a short break every 80 trials to allow them to rest. The content of the display set (target vs. distractor) was determined randomly, but with equal probability between the two alternatives. Distractors were randomly sampled (without replacement) from the distractor ensemble. Participants were instructed to respond as fast and as accurately as possible to the display set by pressing a left or a right button on a handheld gameplay (Logitech Precision). The stimulus-response mapping (e.g., left response to a target, right response to a distractor) was reversed between the two sets of trials. The stimulus-response mapping and the side of the memory set were fully counterbalanced across sets of trials and participants.

After completion of the 800 trials (referred to as *learning phase*), participants performed a retention test with a similar trial structure and similar task instructions. The memory ensemble (μ') for the retention test contained the 100 previously learned old pictures (ensemble μ) plus 100 new pictures that never appeared during the learning phase. Ensembles for distractors and control items also contained new pictures. Memory sets were randomly sampled (without replacement) from the memory ensemble μ', and were not repeated. Participants thus completed 200 trials, divided into two sets of 100 trials. The stimulus-response mapping and the side of the memory set across the two sets of trials were identical to the learning phase.

Participants completed 16 practice trials at the beginning of each set of trials of the learning phase to ensure they understood the task, the stimulus-response mapping, and could maintain fixation. Participants also completed 8 practice trials at the beginning of each set of trials of the retention test.

ERP recording and analysis. The subjects' EEG was recorded continuously from tin electrodes held on the scalp with an elastic cap, using a subset of the International 10/20 System sites (Fz, Cz, Pz, F3, F4, C3, C4, P3, P4, PO3, PO4, T3, T4, T5, T6, O1, and O2) and the nonstandard sites OL (halfway between O1 and T5) and OR (halfway between O2 and T6). The sampling rate was 250 Hz (0.01–100 Hz bandpass filter). Voltage was referenced to a right mastoid electrode and rereferenced offline to the average of the left and right mastoids. Electrode impedance was kept below 5 kΩ. The electrooculogram (EOG) was recorded by placing electrodes on each outer canthus to measure horizontal eye movements (bipolar derivation), and below the left eye (referenced to the right mastoid) to measure blinks.

Incorrect trials and trials containing artifacts (ocular or facial muscle artifacts, electrical shifts, signal losses) were excluded from analyses. Ocular artifact rejection was performed using a two-step procedure described in previous work (Woodman & Luck, 2003). One subject was excluded from all analyses due to excessive eye movements (>35%). On average, the proportion of rejected trials was 9.5%, (max = 26.2%) in the learning phase and 9.4% (max = 26.3%) in the retention test.

All ERP components were baseline-corrected to a 200 ms prestimulus window. The CDA was measured as the difference in mean amplitude between contralateral and ipsilateral posterior parietal, temporal and occipital sites (PO3/4, T5/6, O1/2 and OL/R) in a 300- to 1,000-ms window after memory set onset, similar to previous CDA experiments (Reinhart & Woodman, 2014; Vogel & Machizawa, 2004; Vogel et al., 2005; Woodman et al., 2013). Components related to long-term memory (P170 and N400) were evaluated at frontal (Fz), central (Cz), and parietal (Pz) midline sites, consistent with previous work (e.g., Carlisle et al., 2011; Reinhart & Woodman, 2014; Voss, Schendan, & Paller, 2010). Although we sought to measure the P170, the N400 is a far larger component with a better signal-to-noise ratio such that the N400 dominated our measurement intervals. As shown in all our experiments, P170 potentials are masked by the rising slope of the N400. Consequently, we restricted our long-term memory ERP analyses to the N400.

Unless specified, statistical tests were performed by means of repeated-measures analyses of variance (ANOVAs). The assumption of sphericity was tested by Mauchly's test (Mauchly, 1940). When sphericity was violated, degrees of freedom were adjusted according to the procedure developed by Greenhouse and Geisser (1959). Be-

havioral responses due to anticipations (RT $<$ 100 ms; 0.06% of data) and misses (0.8%) were discarded from all analyses.

Results

Learning phase. Experiment 1 used a true consistent mapping procedure and massed practice. We begin by reporting behavioral and ERP results from the learning phase, which constituted the main part of the experiment.

Behavior. Figure 2 (left column) shows mean RT and accuracy for targets versus distractors across the 8 consecutive memory set repetitions. An ANOVA on mean RT with display (target vs. distractor) and memory set repetition (1–8) as factors revealed a main effect of display, $F(1, 14) = 43.03$, $MSE = 4221.40$, $p <$ .001, $\eta_p^2 = .75$. Responses to targets were generally faster than responses to distractors. In addition, we found a main effect of repetition, $F(7, 98) = 8.71$, $MSE = 411.60$, $p < .001$, $\eta_p^2 = .38$, and a Display × Repetition interaction, $F(7, 98) = 3.83$, $MSE = 578.34$, $p = .001$, $\eta_p^2 = .22$. The effect of repetition reached significance only when subjects responded to targets, $F(7, 98) = 9.44$, $MSE = 516.22$, $p < .001$, $\eta_p^2 = .4$; distractors: $F(3.64, 50.97) = 1.96$, $MSE = 910.89$, $p = .12$, $\eta_p^2 = .12$. Mean RT to targets decreased from the first to the second memory set repetition, and plateaued afterward, which is not typical of automaticity studies. An ANOVA on error rates also revealed a significant Display × Repetition interaction, $F(7, 98) = 2.11$, $MSE = .001$, $p = .049$, $\eta_p^2 = .13$. Accuracy increased as a function of practice only when a target was presented, $F(7, 98) = 2.10$, $MSE = .001$, $p = .051$, $\eta_p^2 = .13$; distractors: $F(7, 98) = 0.79$, $MSE = .001$, $p = .6$, $\eta_p^2 = .05$.

ERPs. Figure 3 (left panel) displays grand-averaged CDA waveforms in response to the memory set for each repetition. The shaded area represents the time window used for the CDA analysis

(300–1,000 ms). An ANOVA on mean CDA amplitudes with electrode (PO3/4, T5/6, O1/2, OL/R and memory set repetition (1–8) as factors revealed a main effect of memory set repetition, $F(4.09, 57.21) = 4.66$, $MSE = 2.26$, $p = .002$, $\eta_p^2 = .25$. The amplitude of the CDA decreased from the first to the second memory set repetition, and plateaued afterward. In addition, we found a main effect of electrode, $F(3, 42) = 10.42$, $MSE = .48$, $p < .001$, $\eta_p^2 = .43$, reflecting a larger CDA amplitude at OL/R and T5/6 electrode sites (see Figure 3, topographical map of scalp voltages), similar to previous work (e.g., Carlisle et al., 2011). The interaction between electrode and memory set repetition was not significant, $F(21, 294) = .91$, $MSE = .14$, $p = .58$, $\eta_p^2 = .06$.

Figure 4 (left column) shows grand-averaged waveforms elicited at frontal (Fz) central (Cz) and parietal (Pz) midline sites in response to the memory set for each repetition. Massed practice modulates the amplitude of the N400 component in the 200- to 600-ms poststimulus-onset window (shaded area). An ANOVA on mean N400 amplitudes (computed in the 200- to 600-ms window) with electrode (Fz, Cz, Pz) and memory set repetition (1–8) as factors disclosed a main effect of electrode, $F(1.32, 18.43) = 16.01$, $MSE = 37.50$, $p < .001$, $\eta_p^2 = .53$, and a main effect of repetition, $F(3.25, 45.56) = 2.76$, $MSE = 7.68$, $p = .049$, $\eta_p^2 = .16$. The amplitude of the N400 became more positive from the first to the second memory set repetition, and plateaued afterward. Although the N400 effect was maximal at central midline site Cz (Figure 4, topographic map), the Repetition × Electrode interaction failed to reach significance, $F(5.09, 71.24) = 1.32$, $MSE = 1.02$, $p = .26$, $\eta_p^2 = .09$.

Power function fits. ERPs results show that the decrease in working memory load as a function of practice, as indexed by a decrease in the amplitude of the CDA, is accompanied by an increase in activity in long-term memory, as reflected by a more positive potential during the N400. ERP modulations seem to be related to the
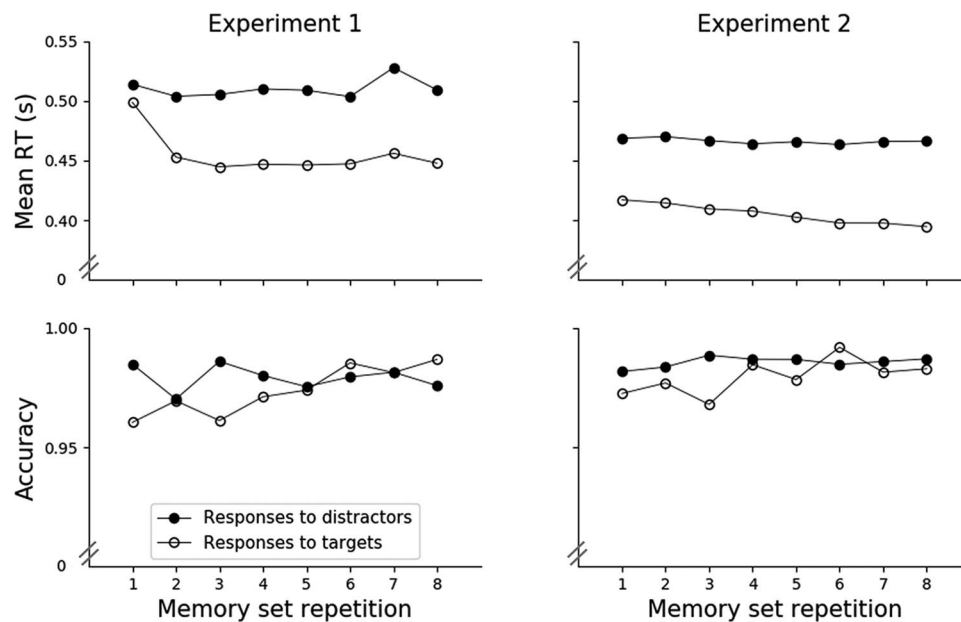

Figure 2. Mean response time (RT) and accuracy data from the learning phase of Experiment 1 (massed practice, left column) and Experiment 2 (spaced practice, right column).
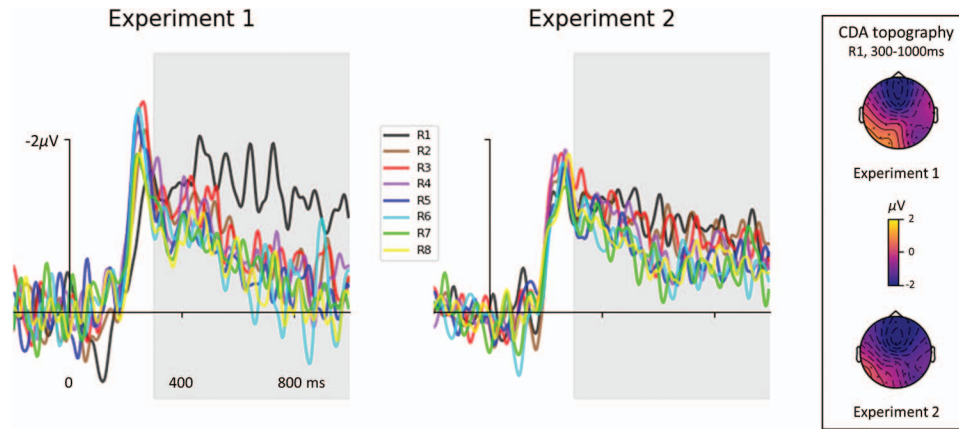
Figure 3. Contralateral delay activity (CDA) data from the learning phase of Experiment 1 (left column) and Experiment 2 (right column) for each memory set repetition (R1-R8). The CDA component is computed as the difference between grand-averaged waveforms averaged over posterior parietal, temporal and occipital sites contralateral versus ipsilateral to the location of the memory set. The shaded area represents the time window used for the CDA analysis (300–1,000 ms poststimulus onset). The inset displays the topographic voltage map (spline interpolation) of the CDA for the first memory set presentation (R1), averaged over the 300- to 1,000-ms window.

behavioral indices of learning. To test this hypothesis, we fit power functions to data with the exponent parameter (c) constrained to be identical across the three dependent variables (mean RT, CDA and N400 amplitude; referred to as Model 1) versus free to vary (Model 2). Notice that Model 1 is nested within Model 2. We then computed Fisher tests for nested models (e.g., Kerlinger & Pedhazur, 1973, p. 71) to evaluate whether the improvement in goodness-of-fit associated with Model 2 was significant given the additional degrees of freedom. If memory ERP components are related to the behavioral indices of learning, Model 2 should not fit the data significantly better than Model 1.

Power functions were fit to data by minimizing the root-mean square deviation (RMSD) between observed and predicted values with a Simplex routine (Nelder & Mead, 1965). One hundred starting points were used to reduce the likelihood of reaching a local minimum. The values of the best-fitting parameters for each model and measures of goodness-of-fit (RMSD and the product-moment correlation between observed and predicted values across the three dependent variables) are shown in Table 1. Predictions from Model 1 are plotted against data in Figure 5 (left column). The goodness-of-fit of the model is very good. The improvement in goodness-of-fit for Model 2 over Model 1 was not significant ($p = .64$), demonstrating that working memory and long-term memory ERPs are related to the behavioral indices of learning. The best-fitting exponent parameter (c) from Model 1 was high ($c = 1.566$; see Table 1), showing that practice mainly modulates brain activity and behavioral performance during the two first memory set repetitions.

Retention test. To probe long-term memory traces, a retention test was incorporated after the learning phase. We now report behavioral and ERP results from this retention test.

Behavior. Figure 6 (left column) shows mean RT and accuracy for targets versus distractors as a function of memory status (old vs. new). An ANOVA on mean RT with display (target vs. distractor) and memory status (old vs. new) as factors revealed a main effect of memory status, $F(1, 14) = 10.79$, $MSE = 567.12$, $p = .005$, $\eta_p^2 = .44$, a main effect of display, $F(1, 14) = 21.56$,

$MSE = 1125.76$, $p < .001$, $\eta_p^2 = .61$, and a Memory Status × Display interaction, $F(1, 14) = 9.07$, $MSE = 380.7$, $p = .009$, $\eta_p^2 = .39$. Responses to old memory sets were faster than responses to new memory sets only when a target was presented, $F(1, 14) = 18.15$, $MSE = 516.69$, $p < .001$, $\eta_p^2 = .57$; distractors: $F(1, 14) = 0.44$, $MSE = 431.12$, $p = .52$, $\eta_p^2 = .03$. An ANOVA on error rates did not reveal any significant effect (all $ps > .1$).

ERPs. Figure 7 (left column) shows grand-averaged waveforms elicited at frontal (Fz) central (Cz) and parietal (Pz) midline sites in response to old versus new memory sets. An ANOVA on mean N400 amplitudes (computed in the 200- to 600-ms window) with electrode (Fz, Cz, Pz) and memory status (old vs. new) as factors showed a main effect of electrode, $F(1.30, 18.21) = 16.99$, $MSE = 14.98$, $p < .001$, $\eta_p^2 = .55$, and a main effect of memory status, $F(1, 14) = 4.89$, $MSE = 1.84$, $p = .044$, $\eta_p^2 = .26$. The amplitude of the N400 was more positive for old compared with new memory items, suggesting that old items were stored in long-term memory, consistent with behavioral results. Figure 7 shows that the N400 old-new effect persisted until ~900 ms poststimulus onset. Although the interaction between electrode and memory set was not significant, $F(1.12, 15.74) = .79$, $MSE = .98$, $p = .79$, $\eta_p^2 = .007$, the topographic voltage map of the old-new effect in the 200- to 600-ms window suggests that this distribution is due to the averaging of two distinct waveforms. We shall come back to this point later.

Figure 8 (left panel) shows grand-averaged CDA waveforms in response to old versus new memory items. An ANOVA on mean CDA amplitudes with electrode (PO3/4, T5/6, O1/2, OL/R), and memory status (old vs. new) as factors revealed a main effect of electrode, $F(3, 42) = 14.51$, $MSE = .27$, $p < .001$, $\eta_p^2 = .51$, reflecting a larger CDA amplitude at OL/R and T5/6 electrode sites, consistent with the CDA topography observed in the learning phase. The main effect of memory status and the interaction between memory status and electrode were not significant ($F(1, 14) = .52$, $MSE = .91$, $p = .48$, $\eta_p^2 = .04$ and $F(1.77, 24.78) = .22$,
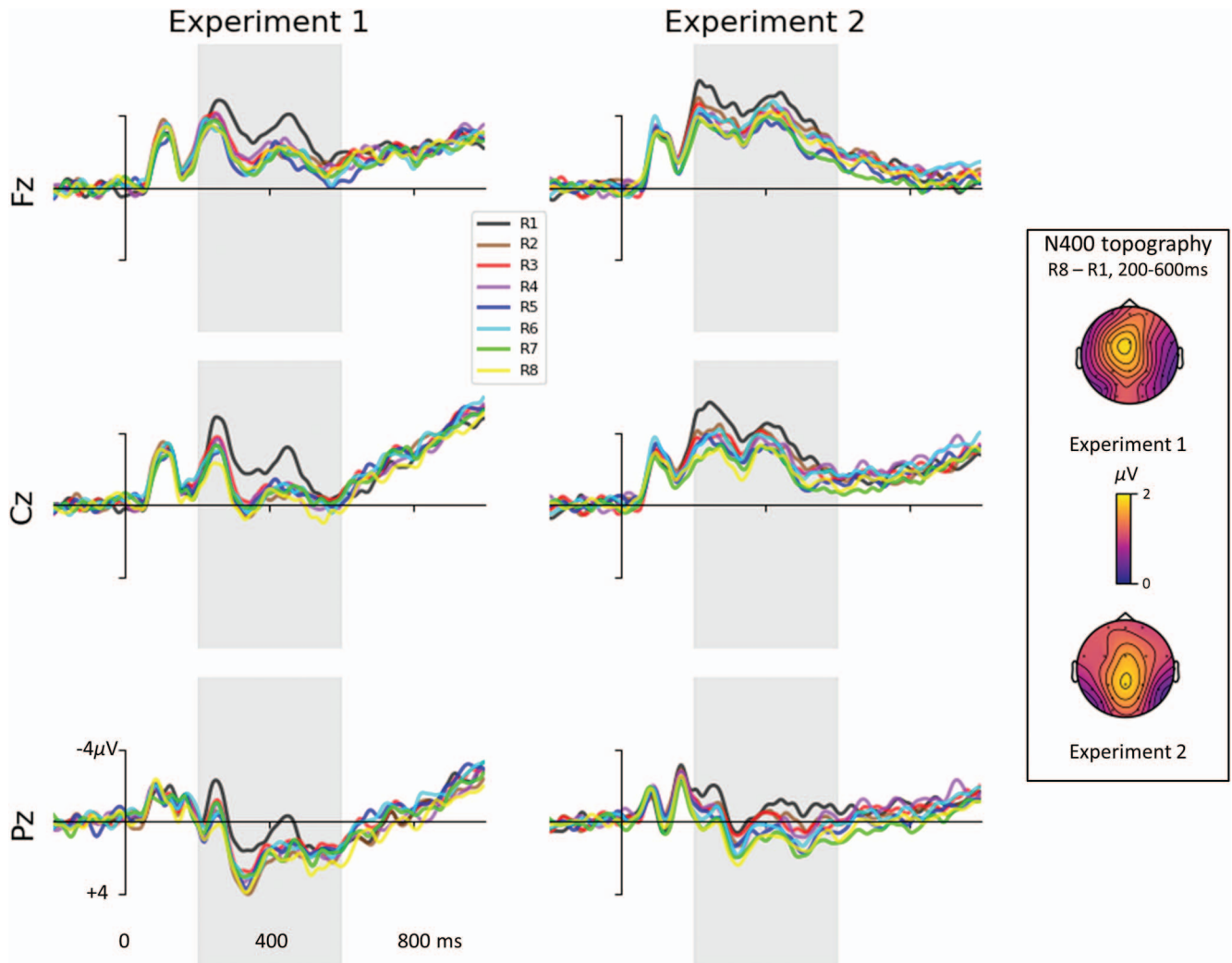
Figure 4. N400 data from the learning phase of Experiment 1 (left column) and Experiment 2 (left column). Grand-averaged waveforms elicited at frontal (Fz) central (Cz) and parietal (Pz) midline sites in response to the memory set for each repetition (R1-R8). The shaded area represents the time window used for the N400 analysis (200- to 600-ms poststimulus onset). The inset displays the topographic voltage map (spline interpolation) of the N400 repetition effect (R8 minus R1) averaged over the 200- to 600-ms window.

$MSE = .18$, $p = .78$, $\eta_p^2 = .02$, respectively), showing that the amplitude of the CDA was similar for old and new memory items.

Discussion

Behavioral and ERPs results from the learning phase of Experiment 1 showed a strong convergence. The speed-up of RT as a function of practice was accompanied by a reduction in CDA amplitude (reflecting a reduction in working memory activity) and an increase in positivity during the N400 (reflecting an increase of activity in long-term memory). All of these modulations occurred at the same rate, suggesting that the interplay between working memory and long-term memory underlies learning, consistent with theories of automaticity.[2] These findings extend results of Woodman and colleagues (Carlisle et al., 2011; Reinhart & Woodman, 2014; Woodman et al., 2013) to a true consistent mapping procedure.

Behavioral results from the retention test showed faster responses to targets for old than news items. Old items were also associated with a more positive potential during the N400. These results provide strong converging evidence that the stimulus–response associations acquired during learning were stored in

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[2] Given that the observed modulations of mean RT and CDA amplitude mainly occur between the first and the second memory set presentation, one could argue that these modulations simply reflect loading into working memory during the first memory set presentation. Retrieval from working memory is known to be faster than retrieval from long-term memory, so a working memory performance strategy would seem adaptive. However, a pure working memory account is hard to reconcile with our modeling findings. If encoding in long-term memory had no impact on behavioral performance, why would N400 and mean RT modulations as a function of memory set repetitions occur at the same rate?

Table 1

Best-Fitting Parameters and Measures of Goodness-of-Fit for Each Power Function Model and Each Experiment

Experiment and model	Power function best-fitting parameter estimates									Measures of goodness-of-fit	
	a			b			c				
	Mean RT	CDA	N400	Mean RT	CDA	N400	Mean RT	CDA	N400	*RMSD*	*r*
Experiment 1											
Model 1	0.443	−0.495	−.196	0.052	−0.938	−1.304	1.566	1.566	1.566	0.279	.979
Model 2	0.458	−0.383	−.308	0.051	−1.025	−1.238	3.979	1.067	2.790	0.267	.981
Experiment 2											
Model 1	0	7.502	24.561	0.420	−8.618	27.514	0.027	0.027	0.027	0.236	.994
Model 2	0	221.508	14.698	0.420	−222.623	−17.654	0.028	0.001	0.043	0.235	.995
Experiment 3, massed practice											
Model 1	0.441	−0.602	−0.540	0.053	−0.676	−2.989	1.317	1.317	1.317	0.300	.991
Model 2	0.442	49.672	−0.653	0.060	−50.902	−2.901	1.753	0.007	1.516	0.261	.993
Model 3	0.446	−0.630	−0.358	0.057	−1.202	−3.085	1.057	1.057	1.057	0.322	.990
Experiment 3, spaced practice											
Model 1	0.406	−0.319	0.328	0.071	−1.073	−3.377	0.306	0.306	0.306	0.149	.998
Model 2	0.020	162.693	−0.379	0.457	−164.070	−2.696	0.037	0.002	0.429	0.136	.999
Model 3	0.444	−1.188	−1.400	0.034	−0.665	−1.763	1.057	1.057	1.057	0.269	.995

Note. RT = reaction time; CDA = contralateral delay activity; RMSD = root-mean square deviation.

long-term memory. We also found that the amplitude of the CDA was not affected by memory status, suggesting that subjects relied on working memory throughout the retention test. Old and new items were presented with equal frequency in the retention test, so the odds of long-term memory being useful were lower than during the training phase. Subjects may thus have relied on working memory strategically because new items were more common compared with the learning phase. These findings are consistent with the idea that people can strategically choose to rely on working memory if they deem long-term memory to be insufficient for the current demands of the task (see also Reinhart & Woodman, 2014; Reinhart et al., 2016). This is an idea initially discussed in instance theory (Logan, 1988, p. 495, 496–499) and here we appear to have found additional support for the idea that people can revert to using working memory representations when the task demands it.

Experiment 2

Skill acquisition typically involves spaced practice. Accordingly, automaticity studies have used spaced practice procedures. Results from Experiment 1 show that the tradeoff between working memory and long-term memory ERP components is observed when a true consistent mapping procedure is used, in line with theories of automaticity. However, practice was massed, and the extent to which these results generalize to spaced practice conditions is unknown.

Learning curves observed in Experiment 1 were steep, and might be a consequence of massed practice. As outlined in the introduction section, the instance theory of automaticity (Logan, 1988) assumes that the exponent of the power function is determined by the retrieval of traces from long-term memory along with the subjects' choice to rely on working memory versus long-term memory systems. The steep learning curves observed in Experi-

ment 1 may reflect fast learning within long-term memory (Hypothesis 1). Alternatively, the steep learning curves may be largely determined by the choice strategy (Hypothesis 2). Subjects might have rapidly shifted to long-term memory because they learned that memory sets repeat for 8 consecutive trials.

To tell apart these competing hypotheses, we introduced a variable lag between each presentation of the same memory set. Spaced practice has been shown to lead to stronger long-term memory traces and better recall performance than massed practice (e.g., Cepeda et al., 2006). If Hypothesis 1 holds, then learning curves should be steeper in Experiment 2 compared with Experiment 1. Alternatively, if Hypothesis 2 holds, learning curves should be shallower in Experiment 2 compared with Experiment 1. Spaced practice should discourage the reliance on long-term memory traces, thus modulating the choice strategy. The long-term memory strengthening may be the same as in Experiment 1, but subjects would rely more on working memory across memory set repetitions.

Materials and Method

Participants. Sixteen right-handed volunteers (20–32 years of age) participated in the experiment in exchange for monetary compensation. Six were male, and all had normal or corrected-to-normal vision and no history of neurological problems. None of these subjects participated in Experiment 1. One subject was excluded due to an excessive number of ocular artifacts in the EEG. Informed consent was obtained prior to the beginning of the experiment. All procedures were approved by the Vanderbilt Institutional Review Board.

Stimuli. Stimuli were identical to Experiment 1. Memory (μ) and distractor (δ) ensembles contained $\mu = 120$ and $\delta = 480$ pictures respectively.
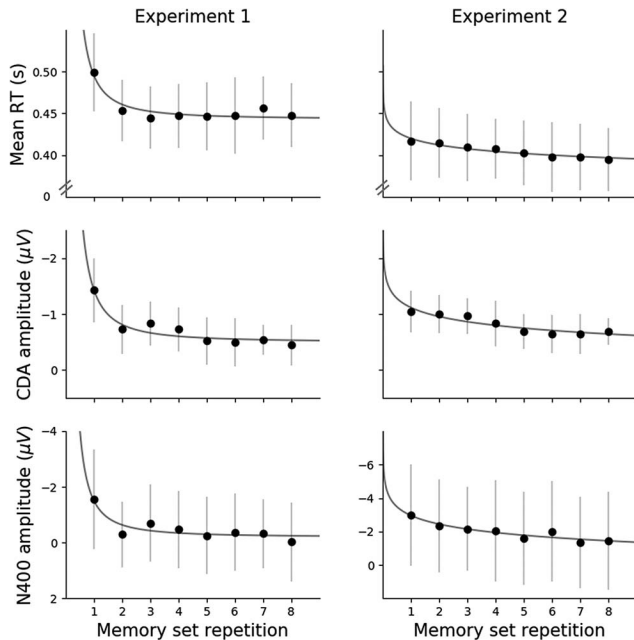
Figure 5. Power function fits to response time (RT) data (upper row), contralateral delay activity (CDA) amplitude (middle row) and N400 amplitude (lower row) from the learning phase of Experiment 1 (left column) and Experiment 2 (right column). For each experiment, the exponent parameter (*c*) is constrained to be identical across the three dependent variables (see text for modeling details). RT data only considers responses to targets. CDA amplitude is averaged over posterior parietal (PO3/4), temporal (T5/6) and occipital (O1/2 and OL/R) lateral electrode sites. N400 amplitude is averaged over frontal (Fz), central (Cz), and parietal (Pz) midline electrode sites. Each data point is accompanied by a 95% confidence interval assuming a Student's *t* distribution.

Procedure. The experimental procedure and task instructions were similar to Experiment 1, except that practice was spaced during the learning phase. Subjects completed 2 sets of trials, each one containing 5 blocks of 96 trials. A short rest break was given after each block. Spaced practice was manipulated within each block. Each block featured 12 memory sets, each one being repeated 8 times. Critically, the 12×8 vector of trials within each block was randomized, resulting in a variable lag between two presentations of the same memory set (with a mean lag $\approx$ 7 items).

After completion of the 960 trials (learning phase), participants performed a retention test that was identical to the retention test of Experiment 1. The memory ensemble (μ') for the retention test contained the 120 previously learned (old) pictures (ensemble μ) plus 120 new pictures that never appeared during the learning phase.

ERP recording and analysis. EEG recordings and analyses were similar to Experiment 1, except that vertical eye movements were measured by means of two electrodes placed below and above the left eye. The resulting bipolar derivation has a better signal-to-noise ratio than the monopolar montage used in Experiment 1, and showed better efficiency in detecting vertical eye movements and blinks. One subject was excluded from all analyses due to excessive eye movements ($>35\%$). On average, the proportion of rejected trials was 4.3%, (max = 16.2%) in

the learning phase and 5.8% (max = 15.7%) in the retention test. Behavioral responses due to anticipations (RT <100 ms; 0.03% of data) and misses (0.8%) were discarded from all analyses.

Results

Learning phase. Experiment 2 used a true consistent mapping procedure and spaced practice. Behavioral and ERP results from the learning phase are reported below.

Behavior. Figure 2 (right column) shows mean RT and accuracy for targets versus distractors across the 8 spaced repetitions. An ANOVA on mean RT with display (target vs. distractor) and memory set repetition (1–8) as factors showed a main effect of display, $F(1, 14) = 61.74$, $MSE = 3639.36$, $p < .001$, $\eta_p^2 = .82$. Responses to targets were generally faster than responses to distractors, similar to Experiment 1. In addition, we found a main effect of memory set repetition, $F(7, 98) = 2.30$, $MSE = 321.67$, $p = .033$, $\eta_p^2 = .14$. Mean RT monotonically decreased as a function of practice. The interaction between the 2 factors was not significant, $F(7, 98) = 1.36$, $MSE = 277.08$, $p = .23$, $\eta_p^2 = .09$.

An ANOVA on error rates revealed a significant Display $\times$ Memory Set interaction, $F(7, 98) = 2.60$, $MSE = .0002$, $p = .017$, $\eta_p^2 = .16$. Accuracy slightly increased as a function of practice only when a target was presented, $F(3.05, 42.69) = 2.65$, $MSE = .0003$, $p = .06$, $\eta_p^2 = .16$; distractors: $F(3.99, 55.89) = .38$, $MSE = .0003$, $p = .82$, $\eta_p^2 = .03$. However, Figure 2 shows that performance is near ceiling across repetitions for both targets and distractors that may have limited our ability to observe accuracy effects.

ERPs. Figure 3 (right panel) shows grand-averaged CDA waveforms in response to the memory set for each repetition. The shaded area represents the time window used for the CDA analysis (300–1,000 ms). An ANOVA on mean CDA amplitudes with electrode (PO3/4, T5/6, O1/2, OL/R) and memory set repetition (1–8) as factors revealed a main effect of memory set repetition, $F(7, 98) = 3.05$, $MSE = .59$, $p = .006$, $\eta_p^2 = .18$. The amplitude of the CDA decreased as memory set repetition increased. In addition, we found a main effect of electrode, $F(1.34, 18.74) = 12.01$, $MSE = 1.29$, $p = .001$, $\eta_p^2 = .46$, reflecting a larger CDA amplitude at OL/R and T5/6 electrode sites, consistent with the topography of the CDA observed in Experiment 1 (see Figure 3, topographic voltage maps). The interaction between electrode and memory set repetition was not significant, $F(21, 294) = 1.16$, $MSE = .07$, $p = .28$, $\eta_p^2 = .08$.

Figure 4 (right column) shows grand-averaged waveforms elicited at frontal (Fz) central (Cz) and parietal (Pz) midline sites in response to the memory set for each repetition. Spaced practice modulates the amplitude of the N400 component in the 200- to 600-ms poststimulus-onset window (shaded area). An ANOVA on mean N400 amplitudes (computed in the 200- to 600-ms window) with electrode (Fz, Cz, Pz) and memory set repetition (1–8) as factors revealed a main effect of electrode, $F(1.31, 18.27) = 23.07$, $MSE = 31.52$, $p < .001$, $\eta_p^2 = .62$, and a main effect of repetition, $F(7, 98) = 4.91$, $MSE = 2.71$, $p < .001$, $\eta_p^2 = .26$. The N400 exhibited a monotonically more positive potential as a function of practice. The topography of this effect had a slightly more posterior distribution compared with that observed in Experiment 1 (Figure 4, topographic map). The interaction between electrode

Figure 6. Mean response time (RT) and accuracy data from the retention test of Experiment 1 (left column) and Experiment 2 (right column).

and repetition, however, was not significant, $F(4.71, 65.89) = 1.30$, $MSE = .80$, $p = .28$, $\eta_p^2 = .09$.

Power function fits. Behavioral and ERP results from Experiment 2 show modulations of mean RT, working memory and long-term memory ERP components by practice. Learning curves associated with spaced practice are shallower than learning curves observed with massed practice in Experiment 1. We fit power functions to data using the same method as for Experiment 1. That is, we fit power functions to data with the exponent parameter (c) constrained to be identical across the three dependent variables (mean RT, CDA and N400 amplitude; referred to as Model 1) versus free to vary (Model 2). The values of the best-fitting parameters for each model and measures of goodness-of-fit (RMSD and the product-moment correlation between observed and predicted values across the three dependent variables) are shown in Table 1. Predictions from Model 1 are plotted against data in Figure 5 (right column). The goodness-of-fit of the model is very good. The improvement in goodness-of-fit for Model 2 over Model 1 was not significant ($p = .98$), demonstrating that working memory and long-term memory ERPs are related to the behavioral indices of learning, consistent with Experiment 1. However, the best-fitting exponent parameter (c) from Model 1 ($c = 0.027$; see Table 1) was much smaller compared with Experiment 1 ($c = 1.566$), showing that the power function approaches a linear function. Small exponents under spaced practice conditions are generally observed for a small number of presentation of items (Logan & Klapp, 1991), consistent with the present study.

Retention test. Similar to Experiment 1, participants completed a retention test after the learning phase. Behavioral and ERP results from this retention test are reported below.

Behavior. An ANOVA on mean RT with display (target vs. distractor) and memory status (old vs. new) as factors revealed a main effect of display, $F(1, 14) = 42.13$, $MSE = 1311.32$, $p <$

.001, $\eta_p^2 = .75$. Responses to targets were generally faster than responses to distractors. The main effect of memory status and the interaction between memory status and display failed to reach significance, $F(1, 14) = 0.61$, $MSE = 285.58$, $p = .45$, $\eta_p^2 = .04$ and $F(1, 14) = 1.44$, $MSE = 336.64$, $p = .25$, $\eta_p^2 = .09$, respectively. At first glance, this result suggests that learned memory sets were not stored in long-term memory.

Instance theory assumes that automaticity is specific to stimuli and context experienced during the learning phase, with poor transfer to new stimuli (Logan, 1988, 1990). However, approximately half of the learned memory sets were not presented on the same side in the retention test. Although the side of the memory set was reversed in the same way across the two sets of trials for learning and retention phases, old and new items were randomized, resulting in approximately half of the old items being presented on the opposite side. Figure 6 (right column) shows behavioral data for old items presented on the same side versus the opposite side. An ANOVA[3] on mean RT with memory status (old same side vs. old opposite side vs. new) and display (target vs. distractor) as factors revealed a main effect of memory status, $F(2, 28) = 3.71$, $MSE = 550.86$, $p = .037$, $\eta_p^2 = .21$, and a trend for a Memory Status × Display interaction, $F(2, 28) = 2.82$, $MSE = 393.19$, $p = .076$, $\eta_p^2 = .17$. The effect of memory status reached significance only for responses to targets, $F(2, 28) = 5.63$, $MSE = 501.19$, $p = .009$, $\eta_p^2 = .29$; distractors: $F(2, 28) = 0.75$, $MSE = 442.86$, $p = .48$, $\eta_p^2 = .05$. Post hoc pairwise comparisons (adjusted with the Bonferroni correction) revealed that RT to targets were signifi-

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[3] This analysis could not be performed for Experiment 1, because we did not keep track of the identity of old items. Consequently, we could not determine whether a given old item was presented on the same versus opposite side.
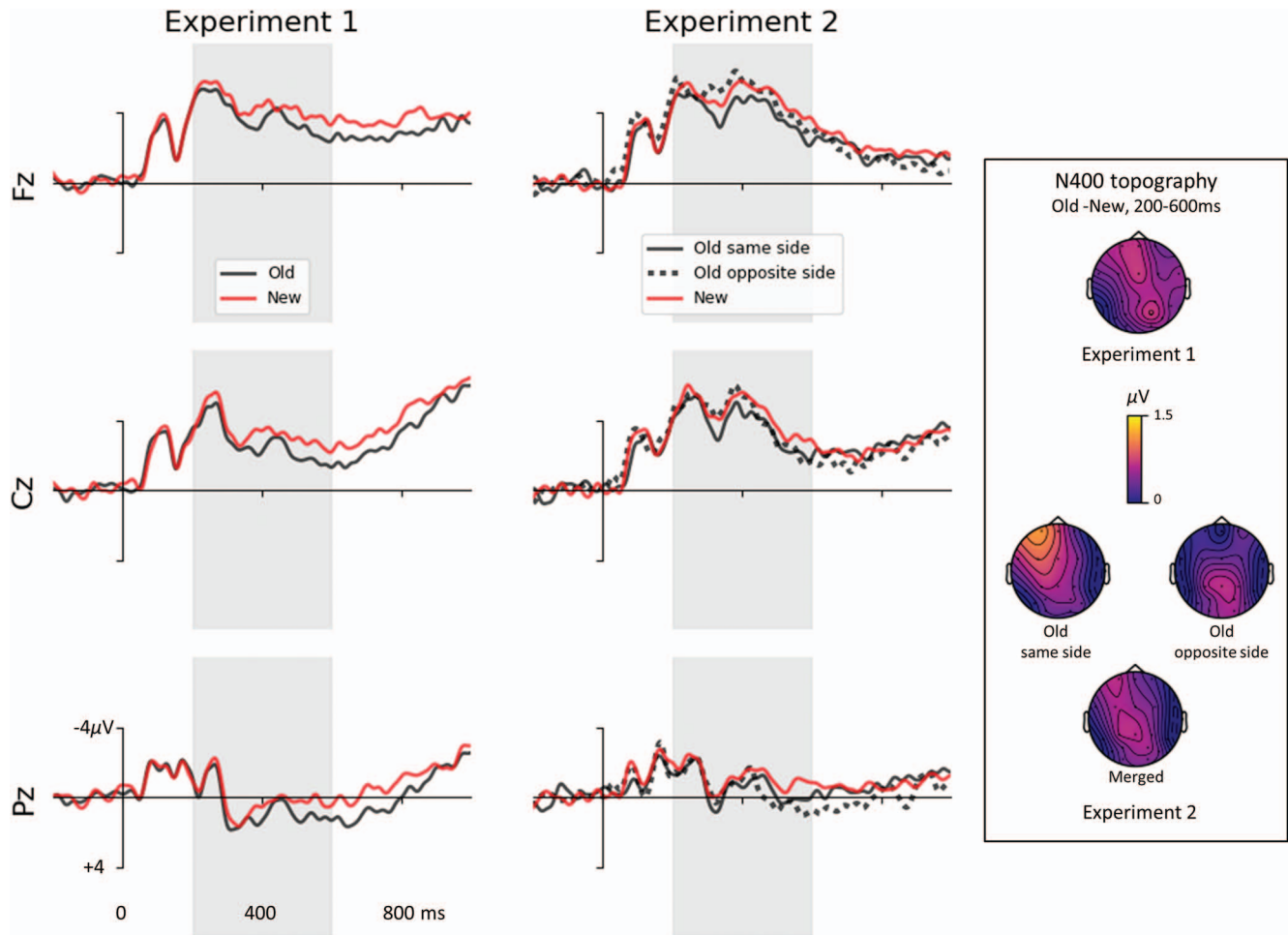
Figure 7. N400 data from the retention test of Experiment 1 (left column) and Experiment 2 (right column). Conventions are the same as in Figure 4. N400 data from the retention test of Experiment 2 incorporates the dissociation between old memory sets presented on the side attended during learning (plain black lines) versus the opposite side (dashed black lines).

cantly faster for old same side ($M = 391$ms) than old opposite side items ($M = 417$ms; $p = .036$), and faster for old same side than new items ($M = 414$ms; $p = .029$). RT to old opposite side and new items were not significantly different, $p = 1$. These findings demonstrate that automaticity only develops for old same side memory sets. Automaticity is thus highly item-specific, consistent with predictions of instance theory.

An ANOVA on error rates with memory status (old same side, old opposite side, new) and display (target vs. distractor) as factors disclosed a trend for a main effect of memory status, $F(1.23, 17.27) = 3.40$, $MSE = .002$, $p = .076$, $\eta_p^2 = .19$. Although post hoc pairwise comparisons did not reveal any significant difference between old same side, old opposite side, and new memory items (all $ps > .1$), error rate was numerically highest for old opposite side items. No other effect reached significance.

ERPs. Figure 7 (right column) shows grand-averaged waveforms elicited at frontal (Fz) central (Cz) and parietal (Pz) midline sites in response to old same side, old opposite side, and new items. An ANOVA on mean N400 amplitudes (computed in the 200- to 600-ms window) with electrode (Fz, Cz, Pz) and memory status (old same side, old opposite side, new) as factors revealed a main effect of electrode, $F(1.37, 19.12) = 23.46$, $MSE = 12.60$, $p < .001$, $\eta_p^2 = .63$, and a Memory Status × Electrode interaction, $F(4, 56) = 2.7$, $MSE = .33$, $p = .04$, $\eta_p^2 = .16$. Although separate ANOVAs for each electrode did not reveal any significant effect of memory status (all $ps > .1$), topographic voltage maps illustrated in Figure 7 show that the old same side-new effect has a frontocentral distribution with a left hemisphere bias, whereas the old opposite side-new effect has a parietal distribution. In addition, the old opposite side-new parietal effect develops later (400–900 ms) than the old same side-new frontocentral effect (200–600 ms; see Appendix, Figure A1).[4] Behavioral results suggest that automatic-

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[4] The partial temporal overlap of the two components explains the mixture observed in the topographical voltage map of the N400 old-new effect from the retention test of Experiment 1 (see Figure 7, topographic voltage map merged across old same side and old opposite side items).
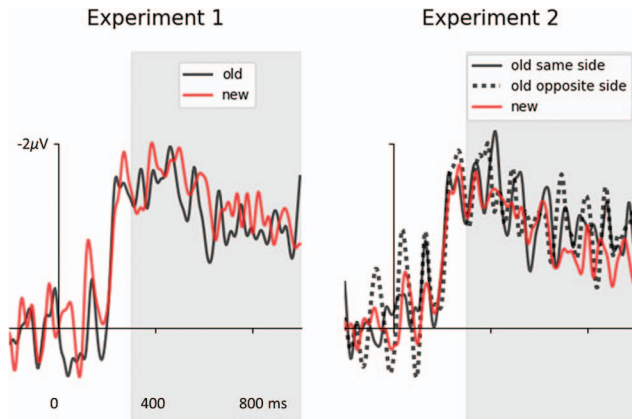
Figure 8. Contralateral delay activity (CDA) data from the retention test of Experiment 1 (left column) and Experiment 2 (right column). Conventions are the same as in Figure 3. CDA data from the retention test of Experiment 2 incorporates the dissociation between old memory sets presented on the side attended during learning (plain black line) versus the opposite side (dashed black line).

ity builds upon the fronto-central component. This analysis, however, should be considered with caution, given that the number of trials per cell (after artifact rejection) is small (range 22–35 for old same side and old opposite side conditions).

Figure 8 (right panel) shows grand-averaged CDA waveforms in response to old same side, old opposite side, and new items. An ANOVA on mean CDA amplitudes with electrode (PO3/4, T5/6, O1/2, OL/R) and memory status (old same side vs. old opposite side vs. new) as factors revealed a main effect of electrode, $F(1.74, 24.32) = 12.25$, $MSE = .75$, $p < .001$, $\eta_p^2 = .47$, reflecting a larger CDA amplitude at OL/R and T5/6 electrode sites, consistent with CDA topographies previously observed. The main effect of memory status and the interaction between memory status and electrode were not significant ($F(2, 28) = .75$, $MSE = 1.06$, $p = .48$, $\eta_p^2 = .05$ and $F(2.67, 37.32) = 1.22$, $MSE = .46$, $p = .31$, $\eta_p^2 = .08$, respectively), indicating that the amplitude of the CDA was similar for old same side, old opposite side, and new items.

Discussion

Behavioral and ERP results from Experiment 2 showed a progressive switch from working memory to long-term memory as a function of practice, consistent with Experiment 1. Power function fits to mean RT and ERP data from Experiments 1 and 2 showed a much smaller exponent parameter for spaced (0.027) than massed practice (1.566). These findings refute the hypothesis that the observed modulations in the exponent parameter reflect modulations in the strength of long-term memory representations, given that spaced practice has been shown to lead to stronger long-term memory traces than massed practice (Cepeda et al., 2006). They are fully consistent with the hypothesis that memory systems are used in a strategic manner (Logan, 1988; Rickard, 1997; Siegler, 1987). In other words, the choice to rely on working memory versus long-term memory is largely modulated by context. Further evidence for this hypothesis comes from the CDA data in the retention tests of Experiments 1 and 2. The odds of long-term memory being useful were lower in the retention test

than during the training phase (because of the new items). In addition, long-term memory might be less reliable because of forgetting. Accordingly, subjects relied on working memory throughout the retention test, as reflected by large and similar CDA amplitudes between old and new items.

Behavioral data from the retention test of Experiment 2 showed that automaticity vanished when learned memory sets were presented on the opposite side. This finding suggests that automaticity is item specific, consistent with instance theory. The dissociation between old same side and old opposite side memory items allowed us to further isolate ERP components underlying automaticity. Compared with new items, old same side items were associated with a more positive potential during the N400. Although the fronto-central topography of this N400 effect appears more anterior than classically observed, the topography of the N400 has proven sensitive to paradigmatic differences (Kutas & Federmeier, 2011). In particular, the N400 exhibits a fronto-central distribution in recognition memory experiments, particularly when pictures are used as stimuli (Johnson, Kreiter, Russo, & Zhu, 1998; Paller, Voss, & Boehm, 2007; Voss & Federmeier, 2011; Voss, Lucas, & Paller, 2010; Voss & Paller, 2006, 2007, 2009; Voss, Schendan, & Paller, 2010; but see Bridger, Bader, Kriukova, Unger, & Mecklinger, 2012). By contrast, old opposite side items were associated with an old-new effect that developed later over the course of processing (400- to 900-ms poststimulus onset), with a peak over parietal midline site Pz. The time course and topography of this effect resemble the late parietal old-new effect observed in recognition memory experiments (e.g., Roberts, Tsivilis, & Mayes, 2013; Vilberg, Moosavi, & Rugg, 2006; Wilding, 2000). The late parietal old-new effect has been linked to the recollection of episodic information (reviewed by Rugg & Curran, 2007). The change of side for old opposite side items might have triggered some recollective memory processing. The absence of a late parietal old-new effect for old same side memory items suggests that late parietal potentials play little role in automaticity.

Recollective memory processing might have also occurred during the learning phase, particularly when a variable lag was introduced between two presentations of the same memory set. This would explain the slightly more posterior distribution of the N400 practice effect in Experiment 2 (due to the partial temporal overlap between N400 and late parietal potentials). To test this hypothesis, we plotted the topography of practice effects from 200 to 900 ms poststimulus onset in bins of 100 ms. Results are shown in the Appendix, Figure A1. The massed practice effect observed in Experiment 1 is associated with a central scalp voltage distribution in the 200- to 600-ms window. The spaced practice effect observed in Experiment 2 shows a similar central distribution in the 200- to 400-ms window, and shifts toward a more posterior locus afterward, presumably due to the engagement of recollective memory processes.

Experiment 3

In Experiment 3 we had two goals. The first goal was to replicate the results from the first two experiments in a within-subject design. We found steeper learning curves in Experiment 1 compared to Experiment 2, and we wanted to verify these differences in a within-subject design. The second goal was to provide further evidence for item-specific learning by comparing old same

side, old opposite side, and new items in the retention test of Experiment 3. We also examined whether the item-specific learning we found in Experiment 2 is modulated by the temporal distribution of practice.

Materials and Method

Participants. Twenty-eight right-handed volunteers (19–30 years of age) participated in the experiment in exchange for monetary compensation. The sample size was increased to compensate for the loss of power induced by the fewer number of trials per condition compared with Experiments 1 and 2 (see below). Six subjects were male, and all had normal or corrected-to-normal vision and no history of neurological problem. None of these subjects participated in Experiment 1 and 2. One subject was excluded due to an excessive number of ocular artifacts in the EEG. Informed consent was obtained prior to the beginning of the experiment. All procedures were approved by the Vanderbilt Institutional Review Board.

Stimuli. Stimuli were identical to Experiments 1 and 2. Memory (μ_m) and distractor (δ_m) ensembles for the massed practice condition contained $\mu_m = 72$ and $\delta_m = 288$ pictures. Memory (μ_s) and distractor (δ_s) ensembles for the spaced practice condition contained $\mu_s = 72$ and $\delta_s = 288$ pictures. The ensembles μ_m, δ_m, μ_s, δ_s did not overlap.

Procedure. The experimental procedure and task instructions were similar to Experiments 1 and 2, except that the temporal distribution of practice was treated as a within-subject factor. Subjects completed two sets of trials, each one containing 6 blocks of 96 trials. A short rest break was given after each block. The temporal distribution of practice (massed vs. spaced) was manipulated between blocks. Massed versus spaced blocks were alternated, with the type of practice in the first block being counterbalanced across subjects. In each practice condition, memory sets were repeated 8 times. Spaced practice was manipulated in the

same way as in Experiment 2. The side of the memory set and the stimulus-response mapping were reversed between the two sets of trials, and fully counterbalanced across sets of trials and participants (similar to Experiments 1 and 2).

After completion of the 1152 trials (learning phase), participants performed a retention test similar to Experiments 1 and 2. The memory ensemble (μ') for the retention test contained the 72 memory sets learned under massed practice (ensemble μ_m), the 72 memory sets learned under spaced practice (ensemble μ_s), and 72 new pictures that never appeared during the learning phase.

ERP recording and analysis. EEG recordings and analyses were similar to Experiment 2. One subject was excluded from all analyses due to excessive eye movements (>35%). On average, the proportion of rejected trials was 7.5%, (max = 12.8%) in the learning phase and 5.7% (max = 16.8%) in the retention test. Behavioral responses due to anticipations (RT <100 ms; 0.2% of data) and misses (0.6%) were discarded from all analyses.

Results

Learning phase. In Experiment 3, we manipulated the temporal distribution of practice (massed versus spaced) in a within-subject design. Behavioral and ERP results are reported below.

Behavior. Figure 9 shows mean RT and accuracy for responses to targets versus distractors as a function of practice type and memory set repetition. An ANOVA on mean RT with display (target vs. distractor), practice type (massed vs. spaced) and memory set repetition (1–8) as factors revealed a main effect of display, $F(1, 26) = 52.76$, $MSE = 6028.28$, $p < .001$, $\eta_p^2 = .67$, a main effect of repetition, $F(3.18, 82.59) = 10.85$, $MSE = 1865.38$, $p < .001$, $\eta_p^2 = .29$, and a significant Display × Repetition interaction, $F(7, 182) = 4.96$, $MSE = 683.97$, $p < .001$, $\eta_p^2 = .16$, showing that practice had a selective effect on responses to targets. This interaction was modulated by practice type, $F(7, 182) = 2.98$, $MSE = 617.86$, $p = .006$,
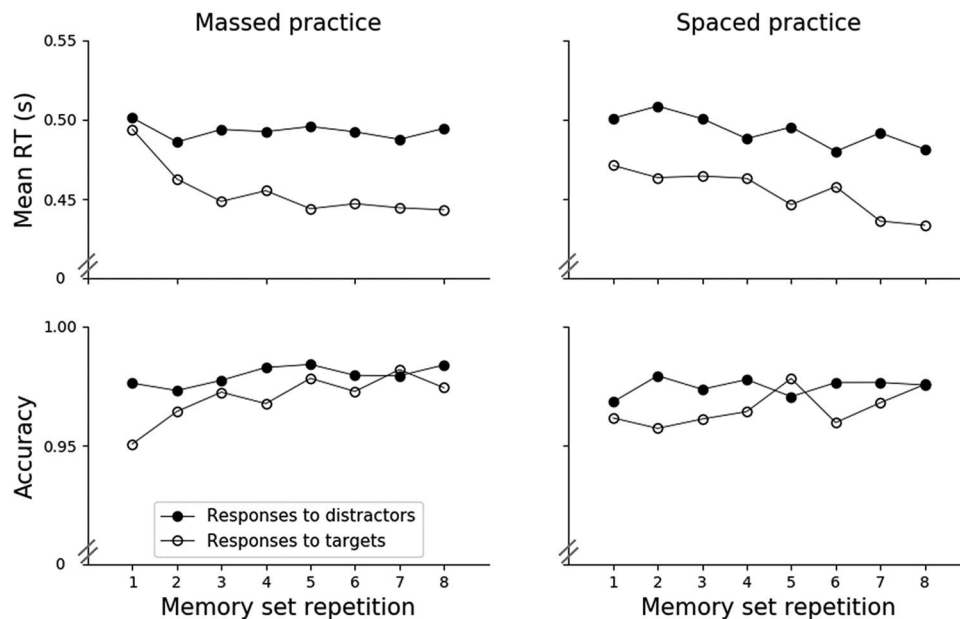

Figure 9. Mean response time (RT) and accuracy data from the learning phase of Experiment 3.

$\eta_p^2 = .1$. The learning curve was shallower for spaced than massed practice (see power function fits), consistent with behavioral results obtained in Experiments 1 and 2.

An ANOVA on error rates revealed a main effect of repetition, $F(7, 182) = 3.55$, $MSE = .001$, $p = .001$, $\eta_p^2 = .12$, showing that accuracy generally improved as a function of practice. Accuracy was also slightly higher for responses to distractors than responses to targets, as revealed by a main effect of display, $F(1, 26) = 5.43$, $MSE = .003$, $p = .028$, $\eta_p^2 = .17$. We also found a trend for a main effect of practice type, $F(1, 26) = 3.92$, $MSE = .001$, $p = .058$, $\eta_p^2 = .13$, with slightly higher accuracy for massed than spaced practice. None of the interactions reached significance (all $ps > .1$), possibly because accuracy is at ceiling.

ERPs. An ANOVA on mean CDA amplitudes with electrode (PO3/4, T5/6, O1/2, OL/R), memory set repetition (1–8), and practice type (massed vs. spaced) as factors revealed a main effect of practice type, $F(1, 26) = 8.68$, $MSE = 3.52$, $p = .007$, $\eta_p^2 = .25$, and a main effect of memory set repetition, $F(3.99, 103.80) = 7.43$, $MSE = 2.40$, $p < .001$, $\eta_p^2 = .22$. The amplitude of the CDA decreased as a function of practice, consistent with previous findings. The analysis also revealed a significant Repetition × Electrode interaction, showing that the effect of repetition was largest at lateral occipital electrode sites OL/R, $F(8.56, 223.04) = 2.79$, $MSE = .51$, $p = .005$, $\eta_p^2 = .1$. Neither the Practice Type × Repetition nor the Practice Type × Repetition × Electrode interaction reached significance, $F(7, 182) = .69$, $MSE = 1.15$, $p = .68$, $\eta_p^2 = .03$ and $F(5.44, 141.55) = .79$, $MSE = 1.27$, $p = .57$, $\eta_p^2 = .03$, respectively. Caution is required with this analysis for two reasons. (i) Figure 10 displays grand-averaged CDA waveforms in response to the memory set for each repetition and practice condition at electrode sites OL/R (where the repetition effect is the largest). CDA waveforms strongly resemble those ob-

tained in Experiments 1 and 2, with a shallower decrease in CDA amplitude for spaced practice (compare Figure 3 to 10). The high number of conditions in Experiment 3 might have hurt our ability to detect a high-level three-way interaction between electrode, practice, and repetition, if it does exist. (ii) The joint modeling of CDA, N400, and mean RT data will indeed demonstrate that these dependent variables are modulated at different rates by massed versus spaced practice across memory set repetitions (see power function fits below).

Figure 11 shows grand-averaged waveforms elicited at frontal (Fz) central (Cz) and parietal (Pz) midline sites in response to the memory set for each repetition and practice condition. An ANOVA on mean N400 amplitudes (computed in the 200- to 600-ms window) with electrode (Fz, Cz, Pz), memory set repetition (1–8), and practice type (massed vs. spaced) as factors revealed a significant three-way interaction, $F(14, 364) = 4.73$, $MSE = .45$, $p < .001$, $\eta_p^2 = .15$. To decompose this interaction, we conducted separate ANOVAs for massed and spaced practice conditions. For massed practice, the analysis revealed a main effect of electrode, $F(1.37, 35.72) = 44.22$, $MSE = 27.71$, $p < .001$, $\eta_p^2 = .6$, and a main effect of repetition, $F(7, 182) = 18.09$, $MSE = 4.10$, $p < .001$, $\eta_p^2 = .41$. The amplitude of the N400 became more positive from the first to the second memory set repetition, and plateaued afterward, consistent with Experiment 1. The interaction between electrode and repetition reached significance, $F(6.63, 172.25) = 2.75$, $MSE = 1.10$, $p = .001$, $\eta_p^2 = .1$, reflecting the fronto-central distribution of the N400 massed practice effect (Figure 11, topographic voltage maps). The analysis for the spaced practice condition revealed similar statistical findings (main effect of electrode, $F(1.36, 35.32) = 51.02$, $MSE = 32.58$, $p < .001$, $\eta_p^2 = .66$; main effect of repetition, $F(7, 182) = 16.07$,
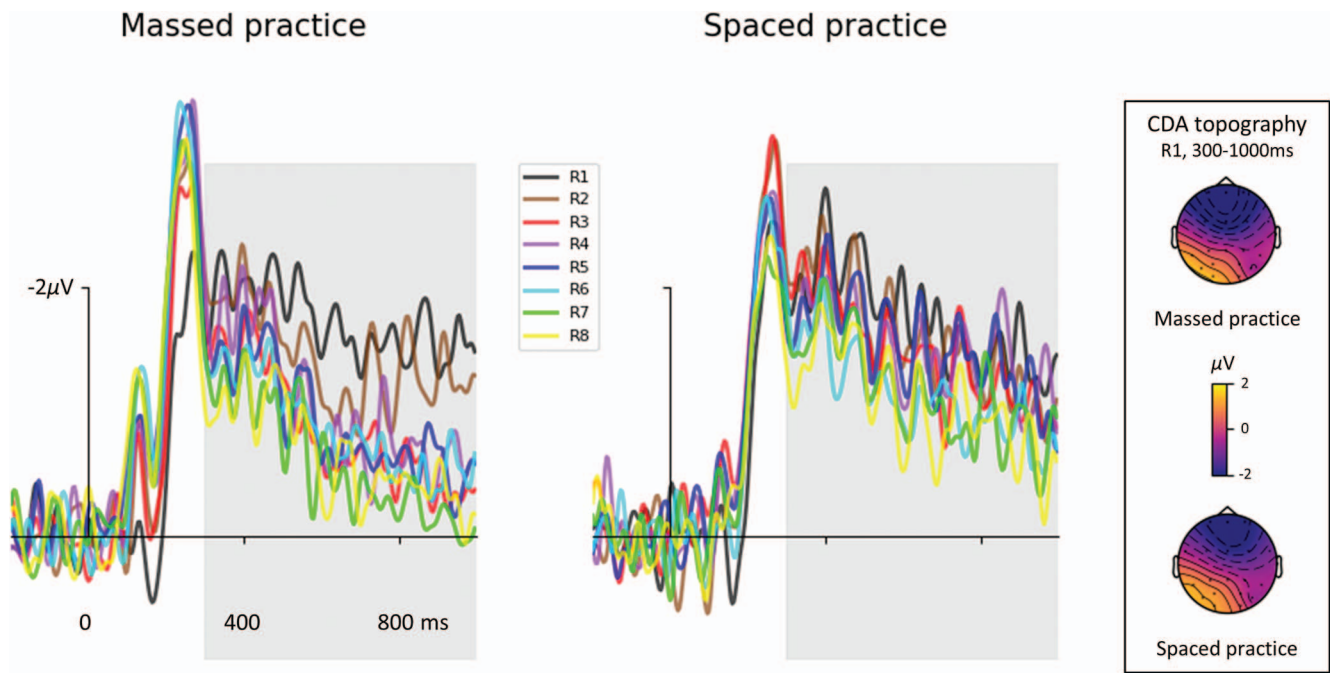

Figure 10. Contralateral delay activity (CDA) data from the learning phase of Experiment 3, measured at occipital lateral electrode sites OL/R (see text for details). Conventions are the same as in Figure 3.
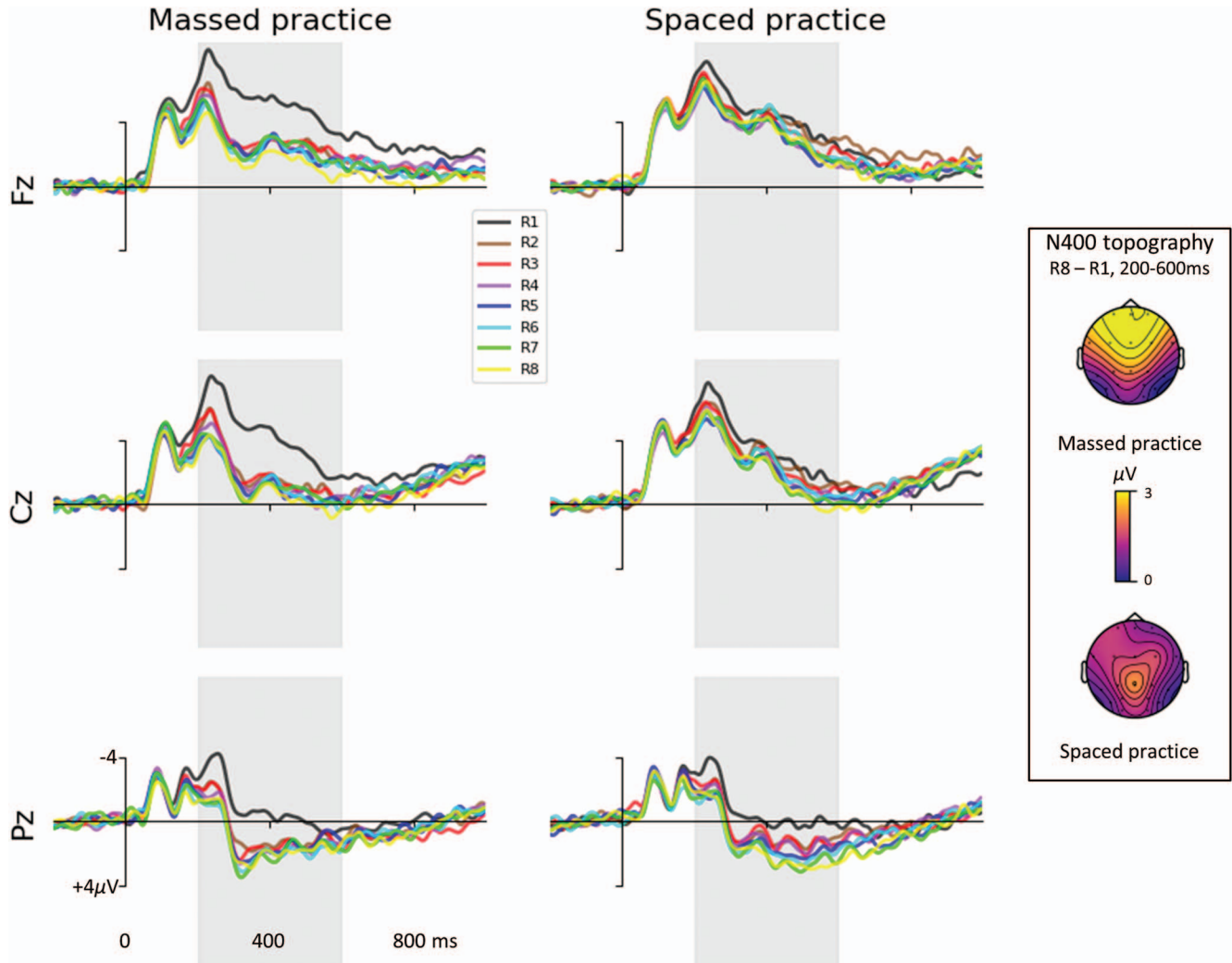
Figure 11. N400 data from the learning phase of Experiment 3. Conventions are the same as in Figure 4.

$MSE = 3.04$, $p < .001$, $\eta_p^2 = .38$; Electrode $\times$ Repetition interaction, $F(6.74, 175.15) = 3.55$, $p < .001$, $\eta_p^2 = .19$). However, the N400 spaced practice effect exhibited a more posterior distribution than the N400 massed practice effect (Figure 11, topographic voltage maps), consistent with previous observations. Figure A2 in the Appendix (topography of practice effects from 200 to 900 ms poststimulus onset in bins of 100 ms) shows that the more posterior topography of the N400 spaced practice effect is due to a contamination by late parietal potentials.

Power function fits. For each practice condition, power functions were fit to mean RT and CDA/N400 amplitudes using the method described in Experiment 1. That is, we fit power functions to data with the exponent parameter (c) constrained to be identical across the three dependent variables (mean RT, CDA and N400 amplitude; referred to as Model 1) versus free to vary (Model 2). The values of the best-fitting parameters for each model and measures of goodness-of-fit (RMSD and the product-moment correlation between observed and predicted values across the three dependent variables) are shown in Table 1. Predictions from Model 1 are plotted against data in Figure 12. The goodness-of-fit

of the model is good. For each practice condition, the improvement in goodness-of-fit for Model 2 over Model 1 was not significant (massed practice: $p = .18$; spaced practice: $p = .33$), demonstrating that working memory and long-term memory ERPs are related to the behavioral indices of learning.[5] The best-fitting exponent parameter (c) from Model 1 was larger for massed ($c = 1.317$) than spaced practice ($c = 0.306$), consistent with previous findings. To test whether this difference was significant or not, we compared the goodness-of-fit of Model 1 with a model in which the exponent parameter (c) was constrained to be similar across practice regimes (Model 3). Notice that Model 3 is nested into Model 1. We found that the improvement in goodness-of-fit for Model 1 over Model 3 was significant ($p = .008$), demonstrating that the exponent parameter of the power function is significantly

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[5] In Experiment 3, we modeled CDA amplitude measured at electrode sites OL/R (where the repetition effect was the largest). Fisher tests for nested models remained nonsignificant when considering CDA data averaged over electrode sites PO3/4, T5/6, O1/2 and OL/R (massed practice: $p = 17$; spaced practice: $p = .29$).
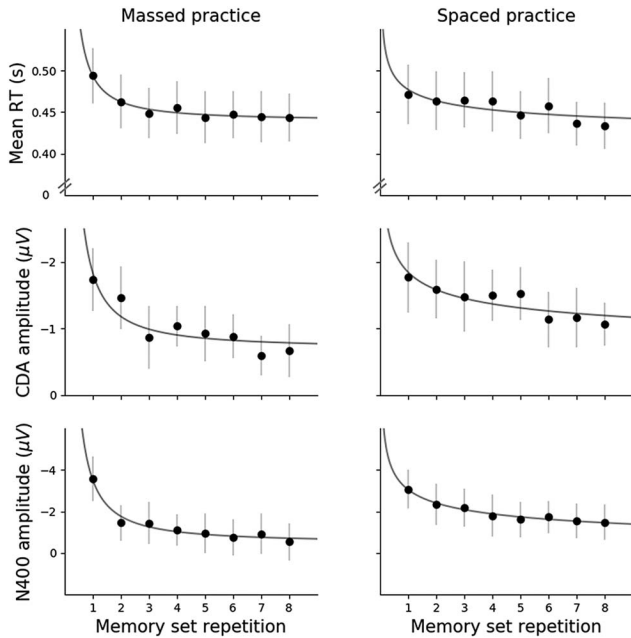
Figure 12. Power function fits to response time (RT) data (upper row), contralateral delay activity (CDA) amplitude (middle row) and N400 amplitude (lower row) from the learning phase of Experiment 3. For each practice condition, the exponent parameter (c) is constrained to be identical across the three dependent variables. Conventions are the same as in Figure 5, with the exception of CDA amplitude being computed at lateral occipital electrode sites OL/R (see text for details).

larger for massed than spaced practice. These analyses provide further support for our two main findings: (i) the switch between working memory and long-term memory underlies learning and (ii) this switch is under strategic control.

Retention test. Similar to Experiments 1 and 2, a retention test was incorporated after the learning phase to probe long-term memory traces. Behavioral and ERP results from this retention test are reported below.

Behavior. Figure 13 shows behavioral data for the retention test of Experiment 3. An ANOVA on mean RT with memory status (old massed same side vs. old massed opposite side vs. old spaced same side vs. old spaced opposite side vs. new) and display (target vs. distractor) revealed a main effect of display, $F(1, 26) = 19.56$, $MSE = 6066.34$, $p < .001$, $\eta_p^2 = .43$, and a main effect of memory status, $F(4, 104) = 4.89$, $MSE = 1263.44$, $p = .002$, $\eta_p^2 = .15$. The two factors did not interact, $F(2.90, 75.44) = .25$, $MSE = 1882.26$, $p = .85$, $\eta_p^2 = .01$. Post hoc pairwise comparisons showed that mean RTs were significantly faster for old massed same side ($M = 467$ms) than new items ($M = 485$ms; $p = .033$), and faster for old spaced same side ($M = 465$ms) than new items ($p = .019$). By contrast, old opposite side items were not significantly different than new items (old massed opposite side: $M = 485$ms, $p = 1$; old spaced opposite side: $M = 486$ms, $p = 1$). In addition, mean RT for old same side items and old opposite side items were not modulated by the temporal distribution of practice, $p = 1$ and $p = 1$, respectively.

An ANOVA on error rates with memory status (old massed same side, old massed opposite side, old spaced same side, old

spaced opposite side, new) and display (target vs. distractor) as factors disclosed a main effect of display, $F(1, 26) = 5.44$, $MSE = .003$, $p = .028$, $\eta_p^2 = .17$, showing that accuracy was slightly higher for responses to distractors than responses to targets. Neither the main effect of repetition nor the interaction between repetition and display reached significance, $F(3.12, 81.08) = .88$, $MSE = .003$, $p = .46$, $\eta_p^2 = .03$ and $F(2.79, 72.50) = 1.22$, $MSE = .003$, $p = .31$, $\eta_p^2 = .05$, respectively.

ERPs. Behavioral analyses show that performance for old same side and old opposite side items is not modulated by the temporal distribution of practice. Consequently, we merged old same side and old opposite side items across practice conditions to increase the power of our EEG analyses. Figure 14 shows grand-averaged waveforms elicited at frontal (Fz), central (Cz) and parietal (Cz) midline sites in response to old same side, old opposite side, and new items. An ANOVA on mean N400 amplitudes (computed in the 200- to 600-ms window) with electrode (Fz, Cz, Pz) and memory status (old same side vs. old opposite side vs. new) as factors revealed a main effect of electrode, $F(1.32, 34.22) = 52.18$, $MSE = 14.82$, $p < .001$, $\eta_p^2 = .67$, and a main effect of memory status, $F(2, 52) = 3.18$, $MSE = 3.31$, $p = .05$, $\eta_p^2 = .11$. The N400 was generally more positive for old than new items. Although the N400 was more positive for old same side ($M = -3.095$ μV) than old opposite side items ($M = -3.208$ μV), post hoc pairwise comparisons did not reveal a significant difference between the two categories of old items, $p = .18$. Although these analyses provide electrophysiological support for a storage of old items in long-term memory, they do not replicate the effect of item specificity on the N400 observed in the retention test of Experiment 2. In addition, topographic voltage maps of old-new effects in Experiments 2 (see Figure 7) and Experiments 3 (see Figure 14) appear dramatically different. This nonreplication could be due to the ERPs for massed and spaced practice being combined together in Experiment 3. Unfortunately, our experimental design precludes a reliable ERP analysis of old same side and old opposite side items for each practice condition separately, because the number of trials per cell (after artifact rejection) is very small (range 9–22 for old massed same side vs., massed opposite side, old spaced same side and old spaced opposite side conditions), resulting in a substantial amount of noise in the ERP averages. For completeness, we report results from an ANOVA on N400 amplitudes with memory status (old massed same side vs. old massed opposite side vs. old spaced same side vs. old spaced opposite side vs. new) and electrode (Fz, Cz, Pz) as factors. Not surprisingly, neither the main effect of memory status nor the Memory Status × Electrode interaction reached significance, $F(4, 104) = 1.03$, $MSE = 5.70$, $p = .39$, $\eta_p^2 = .04$ and $F(8, 208) = 1.19$, $MSE = .90$, $p = .30$, $\eta_p^2 = .044$, respectively. Grand-averaged waveforms elicited at frontal (Fz), central (Cz) and parietal (Cz) midline sites in response to old massed same side, old massed opposite side, old spaced same side, old spaced opposite side and new items are displayed in Figure A3 (Appendix), and associated topographic voltage maps of old-new effects are shown in Figure A2 (Appendix). Topographic voltage maps appear different than those observed in Experiments 1 and 2. Consequently, our analyses do not allow us to link the item specificity property of automaticity with a particular ERP component. In addition, they do not allow us to determine whether the neurocognitive mechanisms underlying item specify are modulated or not by practice type.
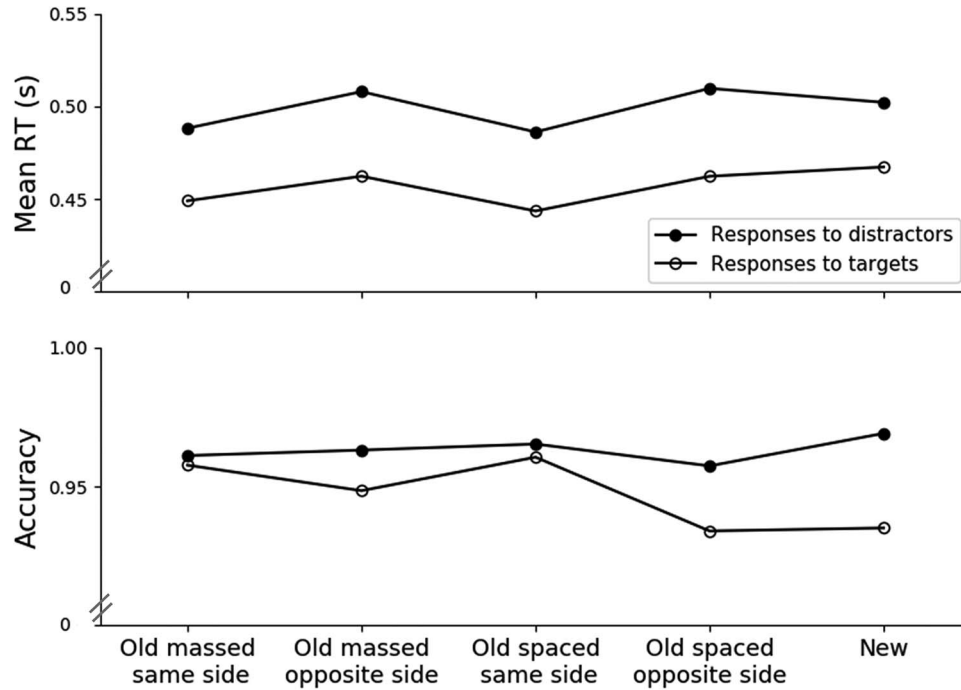
Figure 13. Mean response time (RT) and accuracy data from the retention test of Experiment 3.

Figure 15 shows grand-averaged CDA waveforms in response to old same side, old opposite side, and new memory items. An ANOVA on mean CDA amplitudes with electrode (PO3/4, T5/6, O1/2, OL/R) and memory status (old same side vs. old opposite side vs. new) as factors revealed a main effect of electrode, $F(1.77, 45.97) = 16.61$, $MSE = 1.08$, $p < .001$, $\eta_p^2 = .39$, reflecting a larger CDA amplitude at OL/R and T5/6 electrode sites, consistent with CDA topographies previously observed. The main effect of memory status and the interaction between memory status and electrode were not significant, $F(2, 52) = .90$, $MSE = 1.21$, $p = .41$, $\eta_p^2 = .03$ and $F(4.33, 112.63) = 1.96$, $MSE = .21$, $p = .1$, $\eta_p^2 = .07$, respectively, showing that the amplitude of the CDA was similar for old same side, old opposite side, and new items, consistent with previous results. Similar statistical findings were obtained when considering old same side and old opposite side items separately for massed and spaced conditions; main effect of memory status: $F(4, 104) = .57$, $MSE = 2.07$, $p = .67$, $\eta_p^2 = .02$; Memory Status $\times$ Electrode Interaction, $F(6.59, 171.21) = 1.73$, $MSE = .49$, $p = .11$, $\eta_p^2 = .06$; see Figure A4 (Appendix).

Discussion

Behavioral and ERP results from the learning phase of Experiment 3 globally replicate findings from Experiments 1 and 2 in a within-subject design. For each practice condition, the speed-up of RT as a function of practice was accompanied by a reduction in CDA amplitude (reflecting a reduction in working memory activity) and an increase in positivity during the N400 (reflecting an increase of activity in long-term memory). All of these modulations occurred at the same rate, suggesting that the interplay between working memory and long-term memory underlies learning, consistent with theories of automaticity. In addition, power function fits to mean RT data showed

a much smaller exponent parameter for spaced ($c = 0.306$) than massed practice ($c = 1.317$), providing further evidence for a strategic switch between the two memory systems (Logan, 1988; Rickard, 1997; Siegler, 1987).

Behavioral results from the retention test of Experiment 3 showed that automaticity vanished when learned memory sets were presented on the opposite side. This effect was not modulated by the temporal distribution of practice, suggesting that item specificity is a robust property of automaticity. The neurocognitive mechanisms underlying item specificity, however, are unclear. In Experiment 2, old same side items were associated with a more positive potential during the N400 compared with old opposite and new items. However, the N400 was more positive for both old same side and old opposite side items than new items in Experiment 3. In addition, topographic voltage maps of old–new effects differed between Experiments 2 and 3. These discrepancies might be explained by two factors. (i) The experimental design of Experiment 3 did not allow for a reliable analysis of retention ERPs separately for massed and spaced items, due to the very small number of trials per condition (range 9–22 for old massed same side, massed opposite side, old spaced same side and old spaced opposite side conditions). Experiment 3 involved ~3 hours of data collection per subject, and increasing the number of trials per condition would have been unreasonable. The neurocognitive mechanisms underlying item specificity might be modulated by the temporal distribution of practice. (ii) Consistent with a strategic use of memory systems, retention ERPs across the three experiments disclosed a large CDA and relatively small N400 effects. In addition, the CDA was not modulated by memory status. The strong reliance on working memory throughout the retention test impedes
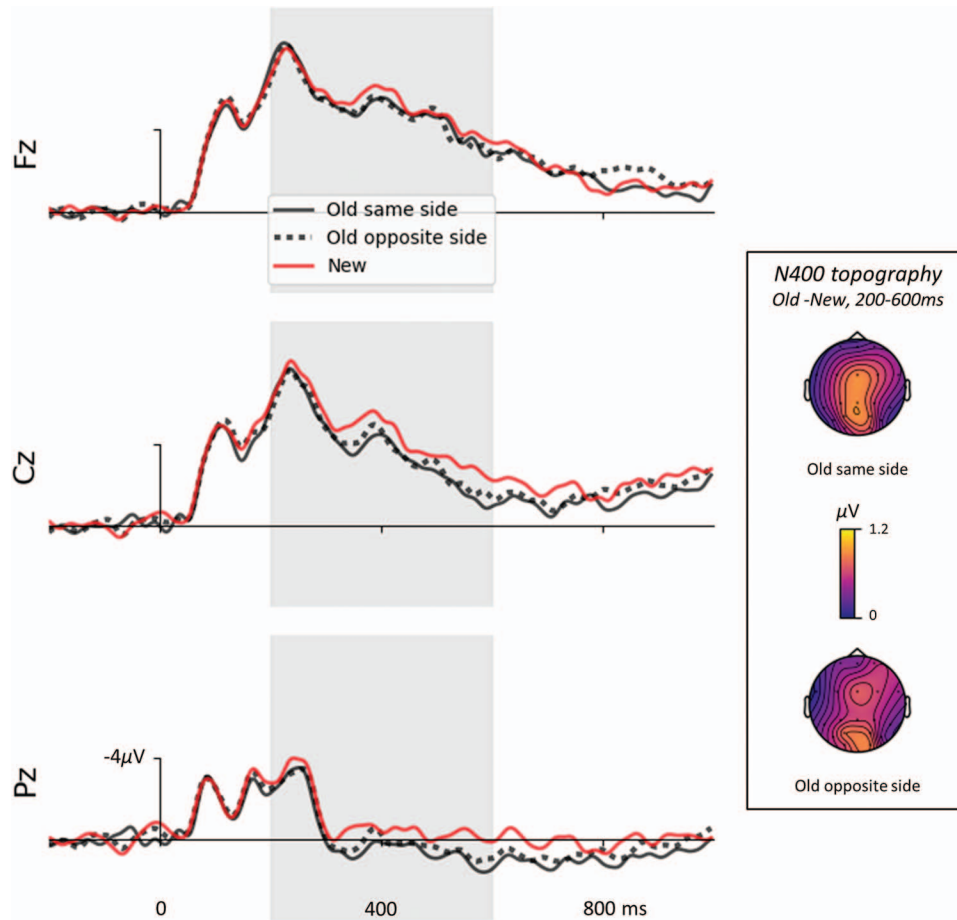
Figure 14. N400 data from the retention test of Experiment 3. Conventions are the same as in Figure 4.

electrophysiological analyses of item specificity and associated long-term memory effects.

General Discussion

The present work aimed to examine whether the practice-induced shift from working memory to long-term memory inferred from subjects' ERPs would be observed under the conditions in which automaticity is traditionally studied. We found that to be the case in three experiments. Using a search task with a consistent mapping procedure, we showed that working memory load, as reflected by the amplitude of the CDA (Vogel & Machizawa, 2004; Vogel et al., 2005), reduced as a function of practice. The reduction in CDA amplitude was accompanied by a more positive potential during the N400, reflecting increased access to long-term memory (Kutas & Federmeier, 2000, 2011). Modulations of CDA and N400 potentials as a function of practice mirrored the power-function speed-up of RT. These findings provide strong support for theories of automaticity (e.g., Logan, 1988; Palmeri, 1997; Rickard, 1997; Siegler, 1987).

Behavioral findings from our retention tests provided converging evidence that representations of learned items were stored in long-term memory. However, a speed-up of RT was only observed for old items presented in the attended spatial location during learning (and vanished for old items presented

in the opposite side; see Experiments 2 and 3). This result is consistent with predictions of the instance theory of automatization (Logan, 1988). Instance theory assumes that each encounter with a stimulus is encoded, stored and retrieved separately. Automatization is thus item specific, because it is based on the retrieval of specific instances from long-term memory (see also Logan, 1990). The neurocognitive mechanisms underlying item specificity, however, remain unclear. The N400 component was generally more positive for old compared with new items, providing electrophysiological evidence that the stimulus–response associations acquired during learning were stored in long-term memory. The N400 old-new effect was only present for old same side items in Experiment 2, suggesting that the N400 is linked to the retrieval of specific instances in long-term memory. However, both old same side and old opposite side items were associated with a more positive N400 in Experiment 3, possibly due to a modulation of neurocognitive mechanisms underlying item specificity by the temporal distribution of practice. However, the experimental design of Experiment 3 (combined with the small old-new N400 effects) precludes a reliable test of this hypothesis (see discussion of Experiment 3). The neural mechanisms of item specificity are in need of clarification.
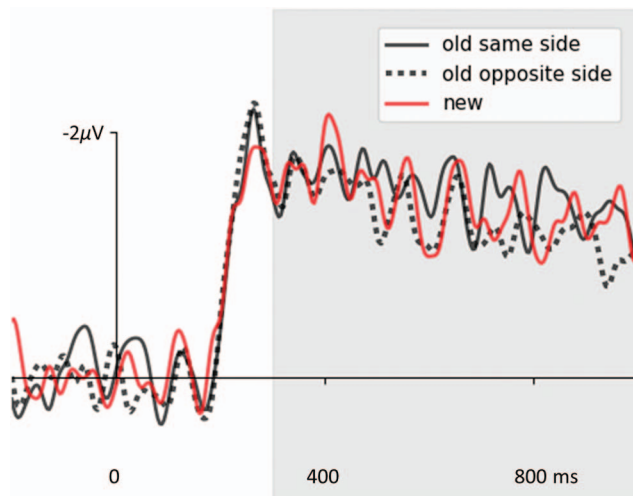
Figure 15. Contralateral delay activity (CDA) data from the retention test of Experiment 3. Conventions are the same as in Figure 3.

Although the fronto-central topography of N400 repetition effects observed in the present work appears more anterior than generally observed, the topography of the N400 has proven sensitive to differences in stimuli and paradigms. Notably, N400 repetition effects exhibit a more fronto-central distribution in recognition memory experiments (so-called FN400 potentials, the "F" indicating the more frontal distribution of the N400), particularly when pictures are used as stimuli (Johnson et al., 1998; Paller et al., 2007; Voss & Federmeier, 2011; Voss, Lucas, & Paller, 2010; Voss & Paller, 2006, 2007, 2009; Voss, Schendan, & Paller, 2010). There is an ongoing debate as to whether FN400 and N400 components reflect the same underlying mechanisms (Bridger et al., 2012; Mecklinger, Frings, & Rosburg, 2012; Paller et al., 2007; Voss & Federmeier, 2011). FN400 potentials observed in recognition memory experiments are generally modulated by factors thought to affect familiarity processes (Rugg & Curran, 2007). For example, the amplitude of the FN400 scales with the degree of confidence in familiarity-based memory judgments, and do not covary with the amount of episodic information retrieved (Curran, 2004; Woodruff, Hayama, & Rugg, 2006; Yu & Rugg, 2010). However, it has been shown that the amplitude of the FN400 old-new effect scales with the amount of perceived meaningfulness of the stimuli, questioning the functional dissociation between N400 and FN400 potentials (Voss & Federmeier, 2011; Voss, Lucas, & Paller, 2010; Voss & Paller, 2006, 2007; Voss, Schendan, & Paller, 2010). Some researchers have hypothesized that repetition priming effects might be at the origin of familiarity judgments (Jacoby & Dallas, 1981; Wagner, Gabrieli, & Verfaellie, 1997; Yonelinas, 2002). This hypothesis would suggest a common mechanism underlying automaticity, repetition priming effects and feelings of familiarity.

Behavioral and electrophysiological results from our three experiments suggest that across practice processing transitions from performance that is controlled by working memory to performance that is controlled by long-term memory retrieval. They also provide important insight into the mechanisms regulating the transition between the

two memory systems. Power function fits to learning curves showed a much smaller exponent for spaced than massed practice. This was demonstrated in both between- (Experiments 1 and 2) and within-subjects (Experiment 3) designs. Instance theory predicts that the exponent parameter of the power function is determined by the race of instances within long-term memory and the choice strategy to rely on working memory versus long-term memory systems (Logan, 1988). The former cannot explain our findings, as spaced practice generates stronger long-term memory traces than massed practice (Cepeda et al., 2006). The choice process, however, provides a straightforward account of the data. In the massed practice condition, subjects may have decided to shift rapidly to long-term memory, because they have learned that memory sets repeat for 8 trials consecutively. Spaced practice compromised the use of this strategy, resulting in shallower learning curves. Further evidence for a strategic use of working memory and long-term memory systems comes from the ERP data of our retention tests. Because old and new items were equally frequent, the odds of long-term memory being useful were lower in the retention test than during the training phase. In addition, long-term memory might be less reliable because of forgetting. Accordingly, we found small old-new N400 effects along with large and similar CDA amplitudes for old and new items.

These results suggest that participants strategically decide whether to represent targets in working memory. Their decision depends on their estimates of the reliability of long-term memory retrieval. If long-term memory is reliable (and predictable, as in massed practice), participants may strategically decide not to represent targets in working memory. Note that this is not saying that participants strategically decide whether to represent targets in long-term memory. Empirical evidence overwhelmingly indicates that encoding and retrieval from long-term memory is obligatory (reviewed by Logan, 1980, 1988). Rather, we assume that participants can decide whether to act on what they retrieve to perform the task. Our findings thus contribute to emerging electrophysiological evidence showing that working memory and long-term memory systems are used in a strategic manner. Reinhart et al. (2014, 2016 Experiment 1) used the visual search paradigm elaborated by Carlisle et al. (2011; see Introduction), and introduced a monetary incentive when automaticity had occurred. The ERP data showed the expected tradeoff between working memory and long-term memory potentials as a function of learning. However, high stakes triggered an increase in CDA amplitude, and the magnitude of this modulation predicted the reward-based speed-up of RT. This result suggests that subjects recruited additional representations of the target in working memory to supplement long-term memory and maximize reward rate. Similar modulations of behavioral and ERP data have been observed when participants are put under speed pressure when automatization has occurred (Reinhart et al., 2016, Experiment 2).[6]

In addition to our main findings, our ERP data showed a modulation of parietal potentials by spaced practice in the 400- to 900-ms

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[6] These observations also speak against the idea that the reduction in amplitude of the CDA that we observed across trials is simply due to more efficient use of working memory, with this storage efficiency mirroring RT decreases. If this idea were accounting for the reduction of CDA amplitude that we consistently observed in the present experiments, then it should decrease in these situations in which RT is speeded with reward or time pressure, as well as systematically decrease across the experiment. However, previous research has observed the opposite pattern (Reinhart et al., 2014, 2016; Woodman et al., 2013).

poststimulus onset window. Specifically, parietal potentials became more positive as memory set repeated. The late parietal component has been linked to the recollection of episodic information (reviewed by Rugg & Curran, 2007). The more positive the amplitude of this component, the larger the amount of episodic information recollected (e.g., Vilberg et al., 2006; Wilding, 2000). We did not find any modulation of late parietal potentials by massed practice. These findings appear consistent with the encoding variability theory of spaced practice (Glenberg, 1979; Melton, 1970; Raaijmakers, 2003). According to this theory, subjects form associations between the studied item and adjacent items. Consequently, spaced practice is inherently associated with more interitem associations than massed practice. These associations generate stronger memory traces as a function of practice, and explain the better recall performance for spaced than massed practice. The modulation of late parietal potentials by spaced practice provides electrophysiological support for the encoding variability theory.[7]

To summarize, behavioral and ERP results obtained in the present work show that across practice processing transitions from being controlled by working memory to being controlled by long-term memory retrieval, consistent with theories of automaticity. The transition is modulated by the temporal distribution of practice, suggesting that the use of working memory and long-term memory systems is under strategic control.

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[7] One might argue that the engagement of recollective processes is time-consuming, resulting in slower mean RTs for spaced than massed practice. However, Dewhurst and Conway (1994) showed that old decisions are generally faster for items judged to be remembered (recollection-based judgments) rather than known (familiarity-based judgments). Rotello and Zeng (2008) further demonstrated that this effect was due to a generally higher decision confidence for remember judgments. Behavioral data from our third experiment showed that massed and spaced practice resulted in similar RTs during the middle of the learning curves, but RTs were trending faster after 8 trials of spaced practice. In addition, power function fits across our three experiments consistently showed a faster asymptotic mean RT for the spaced practice condition. This prediction is consistent with the progressive engagement of recollective processes (and associated parietal ERP repetition effects), strengthening the confidence in decisions.

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Appendix

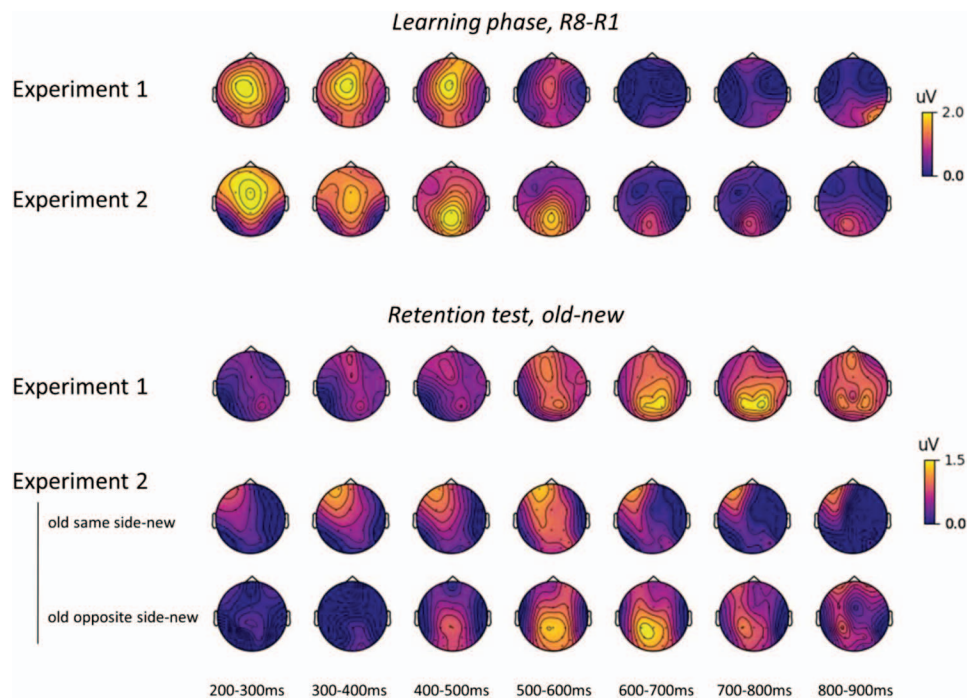## Additional Electrophysiological Analyses for Experiments 1, 2 and 3

Figure A1. Upper panel: topographic voltage maps (spline interpolation) of memory set repetition effects (R8 minus R1) from the learning phase of Experiment 1 and Experiment 2. Lower panel: topographic voltage maps (spline interpolation) of old-new effects from the retention test of Experiment 1 and Experiment 2. Each map represents the average over a 100 ms bin.
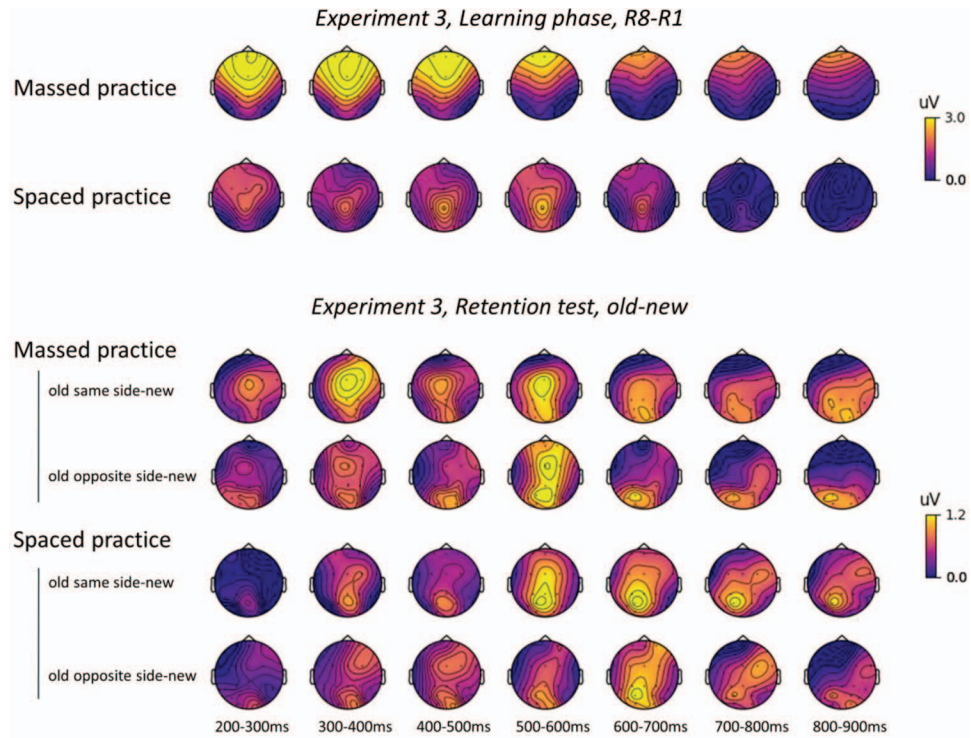
(*Appendix continues*)

Figure A2. Upper panel: topographic voltage maps (spline interpolation) of memory set repetition effects (R8 minus R1) for massed versus spaced practice conditions from the learning phase of Experiment 3. Lower panel: topographic voltage maps (spline interpolation) of old-new effects from the retention test of Experiment 3. Each map represents the average over a 100 ms bin.
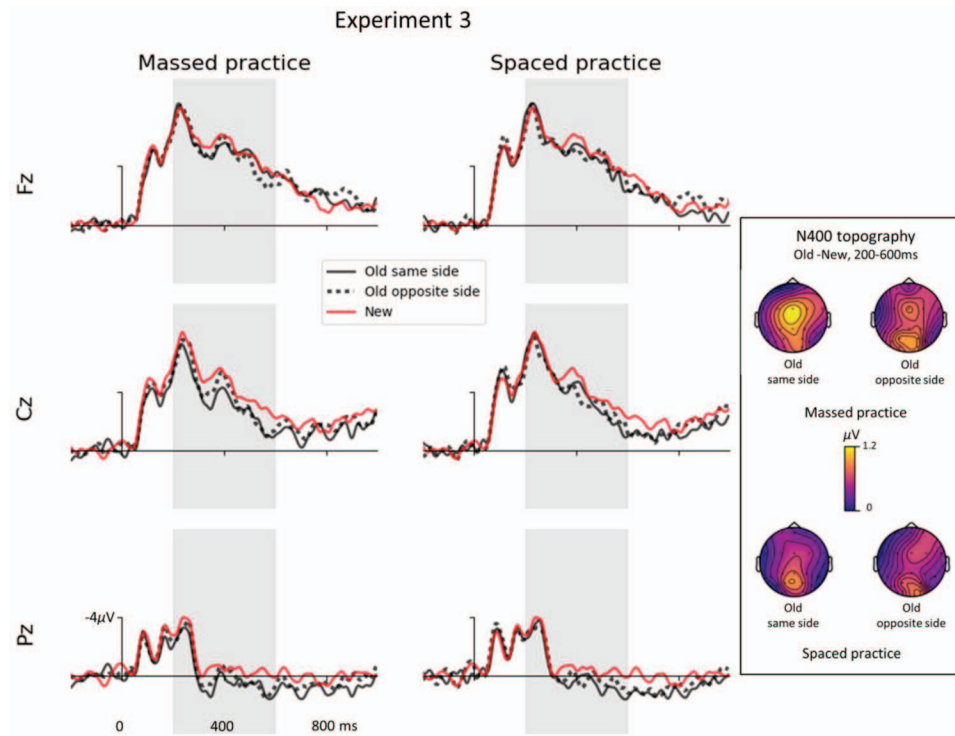
(*Appendix continues*)

Experiment 3

Massed practice   Spaced practice

Fz

Cz

Pz

-4μV

0   400   800 ms

N400 topography
Old -New, 200-600ms

Old same side   Old opposite side

Massed practice

μV
1.2

0

Old same side   Old opposite side

Spaced practice

— Old same side
····· Old opposite side
— New

Figure A3. N400 data from the retention test of Experiment 3 for each practice condition separately.

Experiment 3

Massed practice   Spaced practice

— old same side
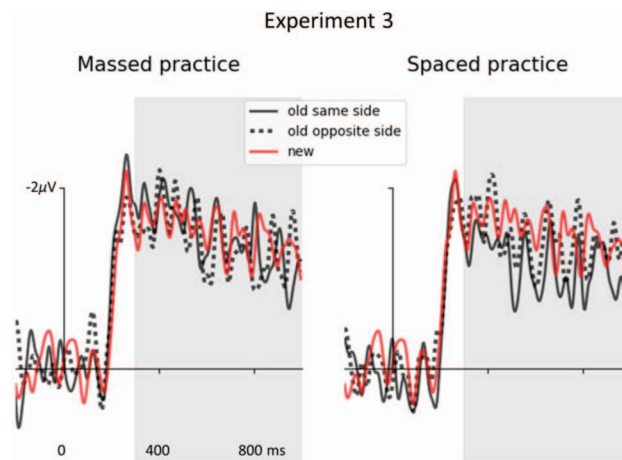····· old opposite side
— new

-2μV

0   400   800 ms

Figure A4. Conntralateral delay activity (CDA) data from the retention test of Experiment 3 for each practice condition separately.