

THETA-BAND POWER CHANGES ASSOCIATED WITH CONFIGURAL THREAT LEARNING IN THE COURSE OF MEMORY CONSOLIDATION: A MEG STUDY

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Изменение мощности осцилляций в тета-диапазоне, ассоциированное с конфигурационным научением угрозе, в ходе консолидации памяти: МЭГ-исследование

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Abstract

Configural learning is essential for generating adaptive behavior in complex environments; however, the neurophysiological mechanisms underlying configural processing and the consolidation of configural memory remain poorly understood. The present study aimed to characterize the spatiotemporal dynamics of

Резюме

Конфигурационное обучение необходимо для формирования адаптивного поведения в сложной среде, однако нейрофизиологические механизмы конфигурационного процессинга и консолидации конфигурационной памяти остаются недостаточно изученными. Целью настоящего исследования было изучение изменений мощности тета-осцилляций после

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theta-band power during configural and elemental associative learning and to assess their reorganization following a one-week consolidation interval. Thirty-seven healthy volunteers participated in a multi-modal aversive learning paradigm in which auditory, visual, and audiovisual stimuli were associated with electrocutaneous stimulation. Source-level theta power (4–7 Hz) was analyzed in the 0–400 ms post-stimulus interval using linear mixed-effects models. During the initial acquisition phase, reinforced configural stimuli elicited increased theta power in higher-tier associative cortical areas. To a lesser extent, this effect was observed also for constituent elements of the configural stimuli. Following a one-week systems consolidation interval, this response pattern disappeared, and we observed an increase in theta power for all stimuli involved in binding (including the association of both complex and elemental stimuli with reinforcement, as well as cross-modal association between elements within the non-reinforced complex stimulus). Yet no such increase was observed for non-reinforced elements themselves. Differences of the neural response between groups of stimuli are consistent with the transformational hypothesis of memory.

Keywords: associative learning, configural processing, memory consolidation, magnetoencephalography.

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консолидации памяти при конфигурационном и элементарном ассоциативном обучении. 37 здоровых добровольцев приняли участие в эксперименте, основанном на парадигме мультимодального авersive обучения, в которой формировалась ассоциативная связь между зрительными, слуховыми стимулами, а также аудиовизуальными комплексами и электрокожной стимуляцией. Тета-мощность (4–7 Гц) в пространстве источников в интервале 0–400 мс после предъявления стимула анализировалась с использованием линейных смешанных моделей. На этапе первоначального обучения в первый день эксперимента увеличение тета-мощности в высокоуровневых ассоциативных областях было выявлено для подкрепляемого конфигурационного стимула и, в меньшей степени, составляющих его элементов. После семидневного периода системной консолидации конфигурационный профиль ответа исчез, и при этом наблюдался рост тета-мощности для всех стимулов, вовлеченных в ассоциативное связывание (включая ассоциацию как комплексных, так и элементарных стимулов с подкреплением, а также кросс-модальную ассоциацию между элементами в составе неподкрепляемого комплексного стимула). В то же время, для неподкрепляемых элементов такого эффекта не наблюдалось. Различия в характере нервного ответа между группами стимулов согласуются с трансформационной гипотезой памяти.

Ключевые слова: ассоциативное обучение, конфигурационный процессинг, консолидация памяти, магнитоэнцефалография.

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Introduction

Configural learning is a form of associative learning in which reinforcement is predicted not by separate stimulus elements, but rather by their conjunctions and the structure of the relationships between the elements. Such learning in its simplest form is typically studied using nonadditive discrimination paradigms, including positive patterning (A[−], B[−], AB⁺) and negative patterning (A⁺, B⁺, AB[−]), in which the predictive value of individual elements differs from that of the compound stimulus.

Classical elemental theories of associative learning, such as the early formulation of Rescorla–Wagner model (Rescorla & Wagner, 1972), assume that associative strength accumulates across individual elements of a stimulus. While this framework successfully explains many forms of compound conditioning, it has difficulty

accounting for patterning discriminations, because in these tasks the individual elements themselves are ambiguous predictors of reinforcement. For example, in a positive patterning task (A−, B−, AB+), stimulus A predicts reinforcement and non-reinforcement with equal probability depending on whether it is presented alone or in conjunction with B. Therefore, successful performance cannot rely solely on elemental associations.

To account for such phenomena, configural theories propose that compound stimuli give rise to integrated conjunctive representations that are processed as distinct entities (i.e., configurations) rather than as a straightforward sum of their constituent elements (Pearce, 2002). In this framework, learning about the reinforced compound AB depends on the formation of a unified representation of the stimulus complex itself. Empirically, the formation of such configurations can be inferred from successful discrimination between configurations and individual elements.

As numerous empirical studies show, the hippocampus serves as a key hub in processing configural information in all types of configural learning tasks (Cashdollar et al., 2009; Duncan et al., 2018; Ivashkina et al., 2020; Poch et al., 2011; Stout et al., 2019; Sutherland & Rudy, 1989). Yet, while the critical role of the hippocampus in configural learning is well established, the Complementary Learning Systems framework assumes involvement of both the hippocampus and the neocortex in configural learning tasks (McClelland et al., 1995; O'Reilly et al., 2014). According to this theoretical framework, the brain requires two learning and memory systems with distinct functions, with the hippocampus being a sparse, pattern-separated system capable of rapidly acquiring episodic memories, and the neocortex being a distributed, overlapping system that gradually integrates across episodes to extract hidden semantic structure.

Indeed, numerous recent fMRI studies have revealed engagement of the dorsal hippocampus in configural learning (e.g., Duncan et al., 2018; Stout et al., 2019). Moreover, substantial cortical recruitment has also been demonstrated in neuroimaging studies (Chernyshev et al., 2025; Stout et al., 2019), as well as in animal data (Ivashkina et al., 2023).

Theta oscillations seem to be strongly and specifically associated with configural processing. For example, several studies have shown theta power increase during transverse patterning task (Meltzer et al., 2009) and relational memory retrieval (Nikolaev et al., 2025). Specific hippocampus-dependent theta network was revealed during a delayed matching-to-sample (DMS) configural task (Cashdollar et al., 2009), and there was also evidence obtained that theta oscillations modulate periodic replay of configural-relational information (Poch et al., 2011). Recently, we have observed robust increases in the early theta-band synchronization (0–400 ms) specifically in response to the reinforced configural stimuli within a large network of cortical associative areas (Chernyshev et al., 2025).

Yet, a very important aspect of configural learning has been overlooked: to our knowledge, there have been no neuroimaging studies addressing systems consolidation in relation to configural learning. Moreover, as far as we know, there have been no attempts to compare the dynamics of systems consolidation for configural and elemental stimuli in neuroimaging studies.

There is broad consensus that newly formed memory traces undergo systems consolidation¹, a large-scale reorganization process in which initially hippocampus-dependent memories gradually become supported by distributed neocortical networks. The Standard Consolidation Theory (SCT) proposes an obligatory but time-limited involvement of the hippocampus. SCT can explain why hippocampal damage may cause severe anterograde amnesia and temporally graded retrograde amnesia, when older memories are more likely to stay intact. Multiple Trace Theory (MTT) offers a different view (Nadel & Moscovitch, 1997), in which the hippocampus is engaged every time during memory recall and adds a new trace resulting in a set of multiple representations. A more recent Transformation Hypothesis, based on MTT, explicitly proposes a transition from a hippocampal, context-rich, vivid memory to a semantic neocortical memory, while suggesting that both types of memory coexist and dynamically interact. If SCT assumes that every type of memory undergoes the uniform process, later views allow for a variety of possible scenarios: for example, vivid, episodically rich memories remain hippocampus-dependent over extended periods of time (Sekeres et al., 2018; Winocur et al., 2010). In a similar vein, we can expect that consolidation will take different courses for configural and elemental stimuli, since only the former necessarily involve the hippocampus, while the latter may be less dependent on it.

The experimental design we used is an expanded version of patterning tasks, which included complex stimuli and elemental stimuli, both reinforced and non-reinforced (Chernyshev et al., 2025). Such a design allowed us to compare brain responses in dependence on two factors orthogonally: whether a stimulus was complex or elemental, and whether it was reinforced or non-reinforced. While the interaction between the two factors indicates non-additive relationships beyond the main effects of Reinforcement and Stimulus Type, this effect may be attributed to configural processing, which is thought to recruit additional mechanisms beyond those underlying sensory feature binding or stimulus–reinforcement learning alone. Following a predominant body of literature on configural learning (e.g., Stout et al., 2019), we paired some of the stimuli with an aversive (negative) reinforcement (a mild electric shock). Thus, we used a paradigm of discriminative threat learning, with aversive stimulation making respective stimuli significant and well-remembered by inducing threat anticipation. We used the power of theta oscillations as a relevant physiological measure, which have been implicated in memory consolidation and is sensitive to configural vs. elemental processing.

This work continues our previous study (Chernyshev et al., 2025) on an augmented sample of participants. So far, we have replicated our previous findings and partly extended them concerning the effects observed on the first day of learning. Yet, the main goal of this study was to probe into the changes that could occur after a period of systems consolidation. Thus, we included the data collected during the second recording session, which followed the first one after an approximately

¹ It is necessary to distinguish between systems consolidation, which occurs at the level of the whole brain on a time scale of days and weeks, and synaptic consolidation, which occurs at the level of individual neurons/synapses and requires significantly less time on a time scale of hours.

seven-day period — an interval sufficient for systems consolidation (Ivashkina et al., 2020, 2023; Sekeres et al., 2018). In particular, a comparable associative learning paradigm in mice demonstrated that neural responses did not differ between retrieval tested at 3 days and at 30 days post-learning, suggesting that the major consolidation-related changes had already plateaued by the earlier time point (Ivashkina et al., 2020). This supports the assumption that an approximately 7-day interval likely falls within the period in which consolidation-related effects have largely stabilized. This allowed us to compare how consolidation affects theta-power changes during multimodal configural and elemental processing during an associative task, and to address whether different types of memories undergo transformations uniformly as posited by Standard Consolidation Theory (SCT) — or instead follow distinct trajectories, as proposed by the Transformation Hypothesis.

Thus, we could expect an overall increase in theta-power after a one-week period, consistent with SCT and previous evidence of increased neocortical activity (Takashima et al., 2006, 2009). However, we also expected that this change in theta power would not be equally expressed across stimulus groups. Given that configural stimuli exhibit distinct processing characteristics already during the initial learning, and because configural memories may remain persistently hippocampus-dependent, we could expect a weaker increase in cortical theta activity for complex stimuli compared with elemental stimuli. Alternatively, we could expect that after the period of systems consolidation cortical theta response would increase specifically for configural stimuli (compared with elemental ones), since the initial memory for them is critically hippocampus-dependent, and the process of systems consolidation would transfer the learning to cortical circuits, establishing higher synchronization within them.

Methods

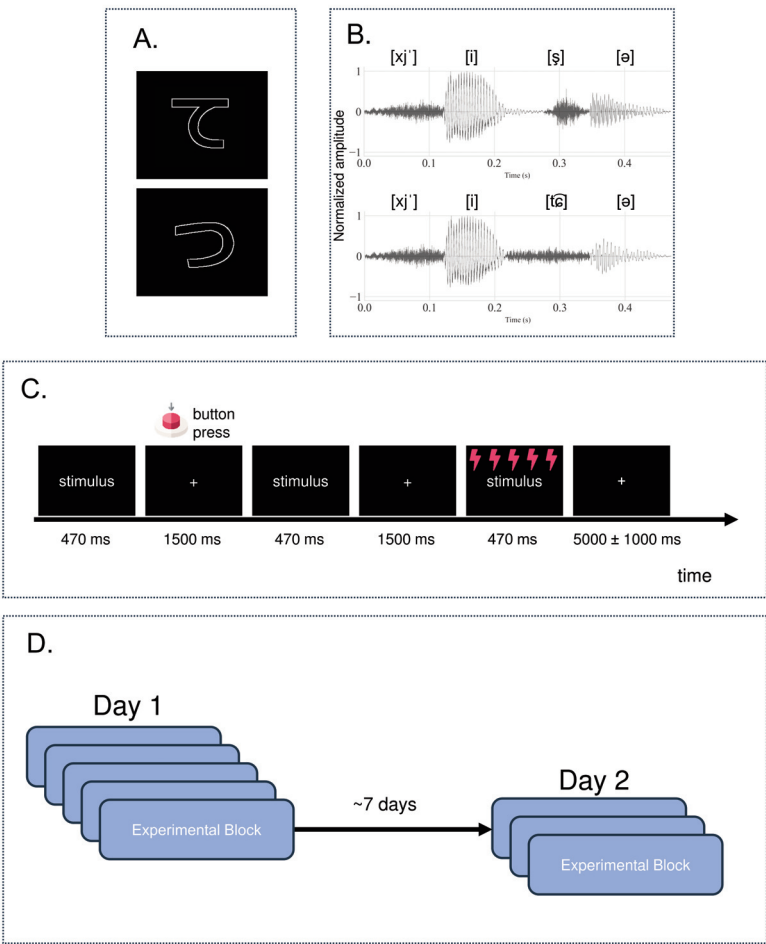
Here, we provide only a brief description of the methods; detailed methodological information is available on the project's OSF page (<https://osf.io/bp3n4/overview>).

Thirty-seven volunteers aged 18–42 years (28.1 ± 8.0 ; 18 females) participated in the study. All had normal hearing and normal or corrected-to-normal vision, were right-handed according to the Edinburgh Handedness Inventory (Oldfield, 1971), and had no history of neurological or psychiatric disorders. The study followed the Helsinki Declaration and was approved by the Ethics Committee of the Moscow State University of Psychology and Education. All participants provided written informed consent.

Six stimuli were presented in a sequential pseudorandom order: two auditory, two visual, and two bimodal audiovisual combinations (Figure 1A, B). Two stimuli (one elemental and one complex) were paired with electrocutaneous stimulation (mild electric shock), with counterbalancing across four participant groups (Table S1). Stimuli were organized into two sets, each containing an auditory (A), a visual (V), and a bimodal audiovisual stimulus (AV). One set served as an elemental set (reinforcement paired with a single-modality stimulus), and the other as a configural set (reinforcement paired with the audiovisual combination). For

Figure 1

Stimuli and Experimental Procedure



Note. A. Visual Stimuli. B. Auditory Stimuli. C. Trial Timeline. Trial consisted of three consecutive presentations of the same stimulus (either visual, or auditory or bimodal complex); on reinforced trials (see text), the last one of the three presentations was paired with five pulses of an electric shock. Participants were instructed to rate their anticipation of an upcoming electrical stimulation using one of three buttons ("I expect", "I don't know", "I do not expect"). D. Experiment timeline.

example, for the first of the four counterbalanced groups, the elemental set included one visual (V1–), one auditory (A1+) and one complex stimulus composed of these two elements presented together (A1V1–); of these three stimuli, only the auditory element was reinforced (A1+). The configural set included one visual (V2–), one auditory (A2–) and one complex stimulus composed of these two elements presented together (A2V2+); of these three stimuli, only the complex stimulus was reinforced (A2V2+).

Each trial included three consecutive presentations of the same stimulus. On reinforced trials, the final presentation was paired with five pulses of electrocutaneous stimulation (mild electric shock). Participants rated their expectation of the stimulation using three response buttons (“I expect”, “I don’t know”, “I do not expect”) (Figure 1C). The experiment consisted of two sessions separated by 6–10 days. On Day 1, participants completed five learning blocks, and on Day 2, three blocks (Figure 1D). Behavioral measures included percentage of correct responses and response latency, averaged across trials within each experimental block. Electrodermal activity (EDA) was measured during the 1000-ms time window preceding electrocutaneous stimulation as an index of implicit shock expectation.

MEG data were recorded in a magnetically shielded room using a dc-SQUID Neuromag VectorView system (Elekta, Finland). Source-level analysis focused on theta-band oscillations (4–7 Hz) within the early post-stimulus time window (0–400 ms). Power was estimated for cortical parcels defined by the HCPMMP1 parcellation (180 regions per hemisphere) (Glasser et al., 2016).

Statistical analysis used linear mixed-effects models implemented in the R package lme4 (Bates et al., 2015). Regions of interest were identified using a model including Stimulus Type (elemental vs. complex) and Reinforcement (CS+, CS–) for each parcel:

$$\text{theta power} \sim \text{Stimulus_type} * \text{Reinforcement} + (1|\text{subject}) \quad (1)$$

Parcels showing a significant FDR-corrected interaction in the Day 1 data were selected as regions of interest (ROIs), assuming an additional configural processing unit would produce a non-additive effect. For analyses concerning Day 2, we used the ROIs obtained for Day 1, as we were interested in events within those brain areas that manifested some configural effects during the initial learning.

Further analysis included Stimulus (AV+, AV–, A+, A–, V+, V–) and experimental Day (D1, D2) and was performed within previously identified ROIs:

$$\text{theta power} \sim \text{Stimulus} * \text{Day} + (1|\text{subject}) \quad (2)$$

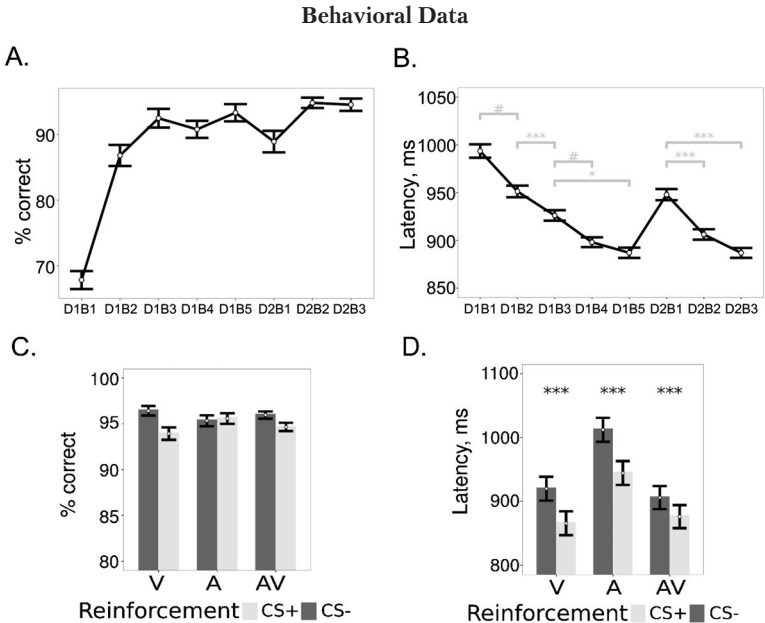
Pairwise comparisons were performed using the Tukey HSD test.

Results

Behavioral Analysis

Participants demonstrated high learning performance (Figure 2A, Supplementary Materials Table S2). Response latencies decreased with each successive block in the course of each experimental day, indicating an ongoing process of learning ($F(4, 140) = 25.56, p < .001$; $F(2, 70) = 21.24, p < .001$) (Figure 2B, Supplementary Materials Table S3). Since performance in the first block (D1B1) was low due to the novelty of the task, we excluded this block from the further analyses.

Figure 2



Note. A. Behavioral learning curve. B. Average response latencies over the course of the experiment. C. Average accuracy for each of the stimuli. D. Average response latencies for each of the stimuli. "D...B..." indicate day and block within day. "V", "A" and "AV" stand for visual elemental stimuli, auditory elemental stimuli and complex audio-visual stimuli. Whiskers represent the standard error of the mean between participants. # – $p < .01$; * – $p < .05$; *** – $p < .001$.

As can be seen in Figure 2C, performance was equally near-ceiling for all stimuli (all p 's $> .05$). Response latency was significantly shorter for reinforced stimuli (for all "V", "A" and "AV" conditions, $t(8034.36) > 5.80$, $p < .001$) (Figure 2D).

Implicit autonomic responses also testified successful learning: there was a highly significant difference in the amplitude of the anticipatory EDA between CS+ and CS- stimuli ($F(1, 8837.020) = 138.63$, $p < .001$; $F(1, 6623.074) = 68.23$, $p < .001$ for Day 1 and Day 2 correspondingly) (Figure 3).

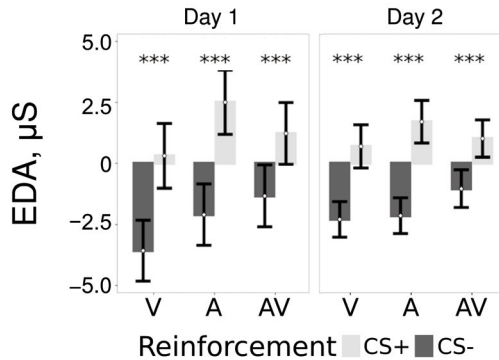
No significant differences were observed between Day 1 and Day 2 in response accuracy ($F(1, 961) = .01$, $p = .919$), response latency ($F(1, 960) = .018$, $p = .893$), or anticipatory EDA ($F(1, 17718) = .404$, $p = .525$).

MEG Analysis: Configural Processing

Within Day 1, using a data-driven approach, we identified regions of interest (ROIs) defined as parcels showing a significant Stimulus Type $\times$ Reinforcement interaction (for all ROIs, $F(1, 4371.60) > 7.33$, $p < .05$, FDR-corrected) (Supplementary Materials Table S4). The resulting ROIs (Figure 4A) were distrib-

Figure 3

EDA data. Average Anticipatory Electrodermal Activity (EDA) at Each Experimental Day



Note. V – visual, A – auditory, AV – bimodal stimuli. Whiskers represent standard error between participants. *** – $p < .001$.

uted through the inferior parietal and temporal cortices, the temporo-parietal-occipital junction ($F(2, 4547.07) = 19.66, p < .001$), the left medial temporal lobe (including the parahippocampal region) ($F(2, 4539.67) = 6.78, p = .001$), posterior cingulate cortex (including retrosplenial cortex) ($F(2, 4545.00) = 9.37, p < .001$), and several medial and lateral prefrontal regions such as dorsolateral and orbitofrontal cortices ($F(2, 4547.32) = 19.32, p < .001$) (Supplementary Materials Figure S1). All subsequent analyses were restricted to these ROIs.

For theta power averaged across ROIs, as expected, there was a significant Stimulus type $\times$ Reinforcement interaction ($F(2, 4546.45) = 25.00, p < .001$). Both main effects were significant as well, for Stimulus type ($F(2, 4573.49) = 100.93, p < .001$) and for Reinforcement ($F(1, 4546.44) = 10.01, p = .002$).

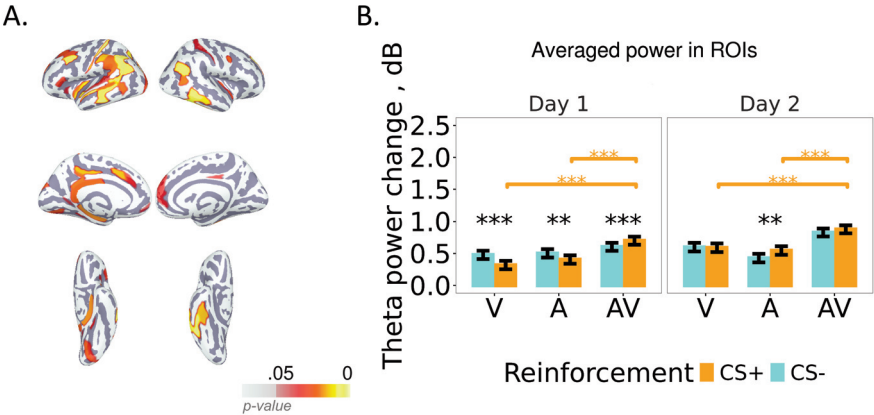
Post-hoc Tukey HSD comparisons revealed several significant contrasts (Figure 4B, left panel). Theta power was higher for reinforced complex stimuli (AV+) than for non-reinforced complex stimuli (AV-) ($t(4545.93) = -4.16, p < .001$). This effect reached significance in a substantial proportion of ROI parcels (25 out of 52 passed FDR correction), whereas no parcel showed the opposite pattern. The dominance of the reinforced configural stimuli was particularly evident in inferior parietal cortex, middle and inferior temporal regions, and dorsolateral prefrontal cortex (Figure 5C, Supplementary Materials Table S5).

Furthermore, the AV+ condition produced significantly stronger theta power than both V+ ($t(4576.98) = 12.79, p < .001$) and A+ ($t(4577.72) = 9.68, p < .001$) (Figure 4B, left panel).

In contrast, non-reinforced elemental stimuli (i.e., belonging to the configural set) evoked stronger theta responses than reinforced elemental stimuli (i.e., belonging to the elemental set). Particularly, V- elicited stronger theta power than V+ ($t(4547.20) = 5.00, p < .001$) (Figure 4B, left panel), and A- showed greater theta power than A+ ($t(4546.00) = 2.98, p = .003$) (Figure 4B, left panel).

Figure 4

Statistical Analysis of Mean Theta Power during 0–400 ms Time Window, within the First Experimental Day



Note. A. Topographical map of significant interaction between Stimulus type $\times$ Reinforcement factors. Color scale indicates p-values (FDR-corrected on the total number of parcels). B. Mean theta power averaged across all cortical parcels with significant interaction between Stimulus type $\times$ Reinforcement factors. Whiskers represent standard error across subjects. Other abbreviations as in Figure 3.

** – $p < .01$; *** – $p < .001$.

Respective topography of the effects is shown in Figure 5A and B. Note that all significant effects had the same sign within a particular comparison, while no significant parcels with opposite effects were detected (Supplementary Materials Tables S6, S7).

MEG Analysis for Day 2: Memory Consolidation

No significant Stimulus type $\times$ Reinforcement interaction was observed in any parcel on Day 2 (for all ROIs, $F(1, 3160.77) < 11.31$, $p > .28$, FDR-corrected), which is in sharp contrast with Day 1. So far, we aimed to describe the dynamics within the topography that we identified for Day 1.

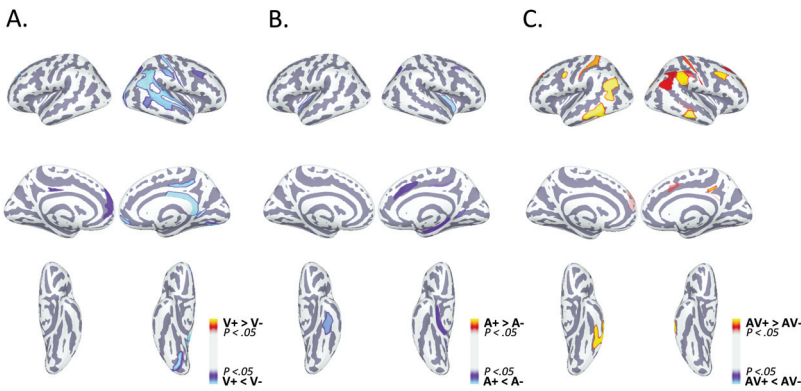
The theta power on Day 2 did not replicate the pattern observed on Day 1 (Figure 4B, right panel; Figure 6). Statistical analysis of data averaged across ROIs revealed no significant Stimulus type $\times$ Reinforcement interaction ($F(2, 3295.84) = 2.56$, $p = .077$). However, both main effects were significant, for Stimulus type ($F(2, 3288.55) = 126.57$, $p < .001$) and for Reinforcement ($F(1, 3295.80) = 6.19$, $p = .013$).

Post-hoc comparisons showed that on Day 2 the reinforced complex stimulus (AV+) continued to elicit greater theta power than the reinforced elements in each modality, both auditory ($t(3329.66) = 8.88$, $p < .001$) and visual ($t(3327.98) = 7.68$, $p < .001$) (Figure 4B, right panel).

In contrast, on Day 2 no significant difference was found between the reinforced and non-reinforced complex stimuli ($t(3295.69) = -1.72$, $p = .085$). Within the visual

Figure 5

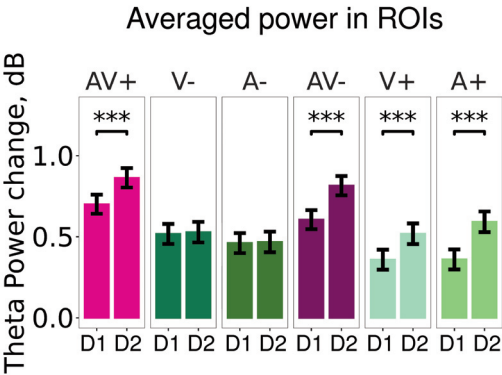
Topography of Paired Contrasts in Theta Power over The 0–400 Time Window



Note. Color scale indicates p-values and the sign of the effect. A. V+ less than V- (blue). B. A+ less than A- (blue). C. AV+ more than AV- (orange).

Figure 6

Mean Theta Power across ROIs on Day 1 and Day 2



Note. Whiskers represent standard error across subjects. *** – $p < .001$.

modality, there was likewise no effect of reinforcement ($t(3295.00) = -.24, p = .81$). The auditory modality, however, showed a significant difference, with greater theta power for A+ than for A- ($t(3296.74) = -2.97, p = .003$) (Figure 4B, right panel). Power of theta oscillations increased on Day 2 compared with Day 1 ($F(1, 7883.73) = 90.11, p < .001$). However, this increase was not uniform across stimulus categories, as is implied by a significant Day $\times$ Stimulus interaction ($F(5, 7878.74) = 8.11, p < .001$) (Figure 6). Relative to Day 1, theta power increased for complex stimuli, both reinforced ($t(7879.77) = -6.25, p < .001$) and non-reinforced ($t(7879.36) = -8.13, p < .001$). Likewise, theta power also increased for reinforced

elemental stimuli in both visual ($t(7881.29) = -4.34, p < .001$) and auditory ($t(7878.80) = -6.32, p < .001$) modalities. Only non-reinforced elemental stimuli in either modality showed no increase in theta power.

Discussion

The experimental design used in this study allowed us to compare brain activity for complex and elemental stimuli, each of which could be reinforced and non-reinforced, and to assess the respective dynamics over the period of systems consolidation.

Behavioral results confirm that participants successfully acquired and retained the learned associations. The absence of significant differences between Day 1 and Day 2 indicates that the acquired associations remained stable across the one-week consolidation interval.

Our data-driven strategy that we used to find regions specifically involved in configural processing was based on the assumption that a conjunctive representation is formed for a reinforced configural stimulus (Pearce, 2002). Thus, we searched for areas with significant Stimulus type $\times$ Reinforcement interaction in the Day 1 data in order to find an additional increase beyond the linear sum of the independent contributions of Stimulus type (complex vs. elemental) and Reinforcement (CS+ vs. CS-). Surprisingly, all regions identified showed homogeneous properties in the expected direction, across all of our theta power analyses — despite being located in anatomically different brain regions.

We replicated the previous findings as far as the first experimental day was concerned (Chernyshev et al., 2025). Particularly, theta power was greater for the reinforced configural stimuli (AV+) compared with the non-reinforced configural stimuli (AV-). Importantly, according to our data, the areas specifically engaged in configural processing were higher-tier associative cortical areas (Figure 5C). This finding suggests that integrative processes may underlie the specific computational demands of configural stimulus processing.

This study allowed us to obtain even more interesting new findings regarding the first day of the experiment. In many ROIs, non-reinforced elements belonging to the configural set (i.e., those that were also presented as part of the reinforced complex) induced higher theta power than the reinforced elemental stimuli of the same modality, which belonged to the elemental set (i.e. those that were never presented within the reinforced complex) (Figure 5A, B). In other words, not only the reinforced complex stimulus, but also its elements, presented alone and not reinforced, induced stronger theta response. This observation hints that even single elements belonging to the reinforced complex undergo some additional processing in the brain. These findings are in alignment with Pearce's model, which assumes that elemental information is embedded within configural representations. This effect may reflect reactivation of the integrated configural representation or the recruitment of configural processing mechanisms when individual components are presented.

In the present study, an overall increase in theta power was observed after a seven-day period of memory consolidation. This finding indicates that the neocortex

exhibits increased activity in the theta band a week after initial encoding. This result is consistent with the literature. First, theta rhythm is generally associated with successful memory encoding and retrieval (Heib et al., 2015; Herweg et al., 2020; Klimesch et al., 1996). Second, several fMRI studies have reported enhanced cortical activity following a consolidation period (Takashima et al., 2006, 2009), which agrees with the standard systems consolidation theory proposing a gradual transfer of memory traces from the hippocampus to the neocortex, accompanied by an increased contribution of the latter. There was also a report that theta power recorded using MEG increased following consolidation, at least in one task-specific brain region (Bakker-Marshall et al., 2018). All of these studies were based on tasks that did not aim at studying configural learning per se but were still rather complex to engage configural mechanisms to some extent.

We observed a substantial reorganization in stimulus processing after a period of systems consolidation. The data indicate that memory transformation was accompanied by increased theta power for complex stimuli, both reinforced and non-reinforced (the effect being much more pronounced for non-reinforced complexes AV–), as well as for reinforced elemental stimuli (A+ and V+). The most parsimonious explanation is that increased theta activity on Day 2 compared with Day 1 occurs whenever some form of associative binding is required, including cross-modal sensory to sensory binding between sensory representations even in the absence of reinforcement in the case of complex stimuli (AV–), and also binding between the reinforced elemental stimulus and its reinforcement (A+ and V+). Indeed, for the non-reinforced elements belonging to an configural set, there was virtually no increase in theta power after a one-week period – possibly, because such stimuli were not involved in any imaginable associations.

Thus, the findings suggest that memory trace formation may differ depending on the type of stimulus within the current experimental design. This result is consistent with the transformation theory of memory (Winocur et al., 2010), which posits that consolidation processes vary as a function of memory content. In particular, vivid, episodically rich memories have been shown to retain hippocampal dependence over extended periods (Sekeres et al., 2018).

As hypothesized, the regions of interest showed a significant increase in theta power. As we expected, this effect was not present uniformly across all stimulus types. Yet, the border-line of the effect being present was not exactly where we predicted. After consolidation we observed a strong and very significant increase in theta power for all stimuli associated with some form of binding (between auditory and visual stimuli, or between any of them and the reinforcement). This included not only complex stimuli (both reinforced and non-reinforced), but also reinforced elemental stimuli. These dramatic increases were in sharp contrast with the absence of any increase for the non-reinforced elemental stimuli.

Thus, the process of consolidation increased theta-activity for all stimuli that imaginably were involved in any learning and feature binding – on a much larger scale than we could imagine. We can speculate that all of such stimuli induced vivid episodic memory, that prolonged the engagement of the hippocampus (Sekeres et al., 2018; Winocur et al., 2010) and necessitated intense communication between

the hippocampus and the neocortex, as well as within the neocortex.

Conclusion

The present findings provide converging evidence that configural learning is associated with distributed cortical recruitment and systematic increase of theta power. During initial acquisition, the observed non-additive neural response patterns provide evidence for distributed cortical engagement in configural processing and are consistent with Pearce's configural theory. Importantly, even individual elements belonging to the reinforced complex underwent additional neural processing compared with elements that were never part of the reinforced stimulus.

Following a one-week interval, the overall theta power increased. This increase was observed for all complex stimuli — both reinforced and non-reinforced, and also for reinforced elemental stimuli. Yet for those non-reinforced elements that were compounds of the reinforced complex, there was no increase in theta power after the consolidation period. Thus, the increase was observed only for those stimuli, for which we can assume any kind of feature binding. As a result of such dramatic changes, we observed disappearance of non-additive encoding of reinforced configural stimuli.

Although the precise mechanisms underlying this shift cannot be determined within the scope of the present study, the results are compatible with the possibility that memory representations undergo reorganization over time, reflecting systems-level consolidation.

Taken together, these findings contribute to a better understanding of how configural memories are reorganized in the course of memory consolidation in humans.

Study limitations

The time window and frequency range were selected based on the previous literature and our earlier findings, as discussed above. However, the present analysis does not exclude the possibility of additional effects in other time intervals or frequency ranges.

References

- Bakker-Marshall, I., Takashima, A., Schoffelen, J. M., Van Hell, J. G., Janzen, G., & McQueen, J. M. (2018). Theta-band oscillations in the middle temporal gyrus reflect novel word consolidation. *Journal of Cognitive Neuroscience*, 30(5), 621-633. https://doi.org/10.1162/jocn_a_01240
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67(1), 1-48. <https://doi.org/10.18637/jss.v067.i01>
- Cashdollar, N., Malecki, U., Rugg-Gunn, F. J., Duncan, J. S., Lavie, N., & Duzel, E. (2009). Hippocampus-dependent and -independent theta-networks of active maintenance. *Proceedings of the National Academy of Sciences*, 106(48), 20493-20498. <https://doi.org/10.1073/pnas.0904823106>

- Chernyshev, B. V., Pozniak, L. A., Pulstina, K. I., Prokofyev, A. O., Kryuchkova, A. G., & Ushakov, V. L. (2025). Theta power increases during intermodal configural learning: A possible mechanism for establishing network communication during stimulus encoding and feature binding. *Cognitive Systems Research*, 94, Article 101415. <https://doi.org/10.1016/j.cogsys.2025.101415>
- Duncan, K., Doll, B. B., Daw, N. D., & Shohamy, D. (2018). More than the sum of its parts: A role for the hippocampus in configural reinforcement learning. *Neuron*, 98(3), 645–657. <https://doi.org/10.1016/j.neuron.2018.03.042>
- Glasser, M. F., Coalson, T. S., Robinson, E. C., Hacker, C. D., Harwell, J., Yacoub, E., Ugurbil, K., Andersson, J., Beckmann, C. F., Jenkinson, M., Smith, S. M., & Van Essen, D. C. (2016). A multi-modal parcellation of human cerebral cortex. *Nature*, 536(7615), 171–178. <https://doi.org/10.1038/nature18933>
- Heib, D. P. J., Hoedlmoser, K., Anderer, P., Gruber, G., Zeitlhofer, J., & Schabus, M. (2015). Oscillatory theta activity during memory formation and its impact on overnight consolidation: A missing link? *Journal of Cognitive Neuroscience*, 27(8), 1648–1658. https://doi.org/10.1162/jocn_a_00804
- Herweg, N. A., Solomon, E. A., & Kahana, M. J. (2020). Theta oscillations in human memory. *Trends in Cognitive Sciences*, 24(3), 208–227. <https://doi.org/10.1016/j.tics.2019.12.006>
- Ivashkina, O. I., Toropova, K. A., & Anokhin, K. V. (2023). Engram for the complex signals in the mouse brain: Distinct neuronal ensembles for compound conditioning stimulus and its components. *Genes & Cells*, 18(4), 710–712. <https://doi.org/10.17816/gc623248>
- Ivashkina, O. I., Toropova, K. A., Roshchina, M. A., & Anokhin, K. V. (2020). Formation and retrieval of associative memory for a complex signal in mice: Specific involvement of hippocampal field CA1 neurons. *Neuroscience and Behavioral Physiology*, 50(9), 1185–1194. <https://doi.org/10.1007/s11055-020-01020-y>
- Klimesch, W., Doppelmayr, M., Russegger, H., & Pachinger, T. (1996). Theta band power in the human scalp EEG and the encoding of new information. *NeuroReport*, 7(7), 1235–1240. <https://doi.org/10.1097/00001756-199605170-00002>
- McClelland, J. L., McNaughton, B. L., & O'Reilly, R. C. (1995). Why there are complementary learning systems in the hippocampus and neocortex: Insights from the successes and failures of connectionist models of learning and memory. *Psychological Review*, 102(3), 419–457. <https://doi.org/10.1037/0033-295X.102.3.419>
- Meltzer, J. A., Fonzo, G. A., & Constable, R. T. (2009). Transverse patterning dissociates human EEG theta power and hippocampal BOLD activation. *Psychophysiology*, 46(1), 153–162. <https://doi.org/10.1111/j.1469-8986.2008.00719.x>
- Nadel, L., & Moscovitch, M. (1997). Memory consolidation, retrograde amnesia and the hippocampal complex. *Current Opinion in Neurobiology*, 7(2), 217–227. [https://doi.org/10.1016/S0959-4388\(97\)80010-4](https://doi.org/10.1016/S0959-4388(97)80010-4)
- Nikolaev, A. R., Johansson, R., Bramão, I., & Johansson, M. (2025). Neural dynamics of relational memory retrieval across eye movements. *Psychophysiology*, 62(11), Article 70185. <https://doi.org/10.1111/psyp.70185>
- O'Reilly, R. C., Bhattacharyya, R., Howard, M. D., & Ketz, N. (2014). Complementary learning systems. *Cognitive Science*, 38(6), 1229–1248. <https://doi.org/10.1111/j.1551-6709.2011.01214.x>
- Pearce, J. M. (2002). Evaluation and development of a connectionist theory of configural learning. *Animal Learning & Behavior*, 30, 73–95. <https://doi.org/10.3758/BF03192911>
- Poch, C., Fuentemilla, L., Barnes, G. R., & Düzel, E. (2011). Hippocampal theta-phase modulation of replay correlates with configural-relational short-term memory performance. *Journal of Neuroscience*, 31(19), 7038–7042. <https://doi.org/10.1523/JNEUROSCI.6305-10.2011>

- Rescorla, R., & Wagner, A. (1972). A theory of Pavlovian conditioning: Variations in the effectiveness of reinforcement and nonreinforcement. In A. H. Black & W. F. Prokasy (Eds.), *Classical conditioning II: Current research and theory* (pp. 64–99). Appleton-Century-Crofts.
- Sekeres, M. J., Winocur, G., & Moscovitch, M. (2018). The hippocampus and related neocortical structures in memory transformation. *Neuroscience Letters*, 680, 39–53. <https://doi.org/10.1016/j.neulet.2018.05.006>
- Stout, D. M., Glenn, D. E., Acheson, D. T., Simmons, A. N., & Risbrough, V. B. (2019). Characterizing the neural circuitry associated with configural threat learning. *Brain Research*, 1719, 225–234. <https://doi.org/10.1016/j.brainres.2019.06.003>
- Sutherland, R. J., & Rudy, J. W. (1989). Configural association theory: The role of the hippocampal formation in learning, memory, and amnesia. *Psychobiology*, 17(2), 129–144. <https://doi.org/10.3758/BF03337828>
- Takashima, A., Nieuwenhuis, I. L. C., Jensen, O., Talamini, L. M., Rijpkema, M., & Fernández, G. (2009). Shift from hippocampal to neocortical centered retrieval network with consolidation. *Journal of Neuroscience*, 29(32), 10087–10093. <https://doi.org/10.1523/JNEUROSCI.0799-09.2009>
- Takashima, A., Petersson, K. M., Rutters, F., Tendolkar, I., Jensen, O., Zwarts, M. J., McNaughton, B. L., & Fernández, G. (2006). Declarative memory consolidation in humans: A prospective functional magnetic resonance imaging study. *Proceedings of the National Academy of Sciences*, 103(3), 756–761. <https://doi.org/10.1073/pnas.0507774103>
- Winocur, G., Moscovitch, M., & Bontempi, B. (2010). Memory formation and long-term retention in humans and animals: Convergence towards a transformation account of hippocampal-neocortical interactions. *Neuropsychologia*, 48(8), 2339–2356. <https://doi.org/10.1016/j.neuropsychologia.2010.04.016>