

Short communication

Motor-related oscillations reveal the involvement of sensorimotor processes during recognition memory

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ABSTRACT

Certain object properties may render an item as more memorable than others. One such property is manipulability, or the extent to which an object can be interacted with using our hands. This study sought to determine if the manipulability of an item modulates memory task performance on both a behavioural and neural level. We recorded electroencephalography (EEG) from a large sample of right-handed individuals ($N = 53$) during a visual item recognition memory task. The task contained stimuli of both high and low manipulability. Analysis focused on activity in the theta rhythm (3.5–7 Hz), which has been implicated in sensorimotor integration, and the mu rhythm (8–14 Hz), the primary oscillation associated with sensorimotor related behaviours. At both encoding and retrieval, theta oscillations were greater over the left motor region for high manipulability stimuli, suggesting that an item's sensorimotor properties are assessed immediately upon presentation. Manipulability did not affect activity in the mu rhythm. However, mu oscillations over the left motor region were lower during the retrieval of old versus new items and response time was faster for old items, aligning with the cortical reinstatement hypothesis. These results collectively reveal an association between motor oscillations and memory processes, highlight the involvement of sensorimotor processing at both encoding and retrieval.

1. Introduction

Manipulability is the extent to which an item must be manually interacted with to achieve its intended purpose. The processing of manipulable items activates the sensorimotor network, which appears to impact memory processes (Beauchamp & Martin, 2007; Mecklinger et al., 2002). For example, crossing hands behind one's back, a position incongruent to manipulating items, disrupts retrieval of manipulable stimuli (Dutriaux & Gyselincx, 2021; Onishi, Tobita & Makioka, 2020). Memory for manipulable items improves when items are presented as photographs or pantomimes versus verbal labels, the latter of which provides the least direct activation of the sensorimotor network (Daprti et al., 2022).

Various neuroimaging studies support the sensorimotor network's involvement in processing manipulable items (Beauchamp & Martin, 2007; Mecklinger et al., 2002; Rueschemeyer et al., 2010). Madan et al.

(2016) investigated the electroencephalographic (EEG) correlates of item manipulability in the context of event-related potentials. Participants, all of whom were right-handed, studied images of items under one of two conditions: their recent personal experience with the item, or the item's manipulability. Manipulable items elicited a more positive P300 component over the left motor region regardless of encoding strategy.

Oscillations provide an alternative approach to examining the relationship between motor region activity and item manipulability. The mu rhythm is a variant of the alpha band and the primary oscillation associated with human sensorimotor behaviour (Pineda, 2005). This rhythm consistently desynchronizes during movement over the motor region contralateral to the executed action. A similar, albeit less intense, pattern occurs during the observation and imagination of movements. Desynchronization of the mu rhythm may also reflect sensorimotor contributions during working memory (Jenson & Saltuklaroglu, 2021).

Another oscillation of interest is the theta rhythm (3.5–7 Hz), which

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is widely studied in the context of memory (see Herweg et al. 2020 for a review). While less studied in the context of sensorimotor behaviour, theta oscillations were proposed by Bland et al. (2001) to operate as a carrier signal, enabling communication between the sensory and motor systems. Indeed, Cruikshank et al. (2012) found that theta oscillations increased over the cortical motor region during the initiation and execution of visually guided pointing, a task that relies on sensorimotor integration.

The aim of this study was twofold. First, we examined whether item manipulability affected theta and mu oscillations in a recognition memory task. We anticipated an increase in theta oscillations and decrease in mu oscillations for high versus low manipulability items. Second, we hypothesized that these oscillations would support memory performance, with faster and more accurate responses to high manipulability items. Additionally, we chose the Better Oscillation Detection Method (BOSC) (Caplan et al., 2001; Whitten et al., 2011) to detect oscillations. In contrast to conventional approaches of quantifying oscillations by power or amplitude, BOSC provides a measure of duration by capturing the proportion of time occupied by oscillations.

2. Methods

We reanalyzed data collected by Madan et al. (2016), which was approved by the University of Alberta Research Ethics Board. Eighty students (M age = 19.43 ± 2.62 years; 58 female) participated for partial course credit. Participants were right-hand dominant, had normal or corrected-to-normal vision, and self-reported no major neurological conditions. Data from 27 participants were excluded due to either equipment malfunction ($n = 14$), ambidexterity ($n = 2$), or excessive EEG artifacts ($n = 11$), leaving a total of 53 included participants. Participants provided written informed consent prior to participation.

2.1. Procedure

We followed a visual recognition memory procedure, using 240 gray-scale images that depicted either high ($n = 120$) or low ($n = 120$) manipulability items as stimuli (Salmon et al., 2014). See Madan et al. (2016) for a detailed description of stimulus selection. Participants randomly received one of two orienting instructions. The Personal Experience group judged if they had seen the item in the previous 3 days while the Functionality group judged if the item was easy to interact with using their hands. Each participant was presented with a randomized subset of 120 images (60 high manipulability, 60 low manipulability). All trials began with a 500 ms fixation cross. The object image resized to 300×300 pixels then appeared onscreen for 3000 ms. Responses were not permitted until the words “YES” and “NO” appeared onscreen 1500 ms later. Participants had another 1500 ms to input their judgment using foot presses to a response pad. The end-of-encoding distraction task contained ten equations following the form of $A (+ \text{ or } -) B (+ \text{ or } -) C = []$, where all digits represented by A, B, and C fell between 1 and 9. Both the digits and the addition versus subtraction operations were randomly selected. Participants typed out their response to each equation. Upon completing the distractor task, participants were presented with all 240 images at random. Each image appeared onscreen accompanied by the words “YES” and “NO”. Participants judged if the image appeared at encoding, again using foot presses to input their judgment. See Fig. 1A for the full procedure.

2.2. Electroencephalography recording

The task occurred in an electrically shielded, sound attenuated chamber, with EEG data collected using a high-density 256 channel array net. The signal was sampled at 250 Hz and amplified at a gain of 100. Impedances were kept below $50\text{k}\Omega$. The vertex electrode Cz served as the initial recording reference. Data was analyzed using a

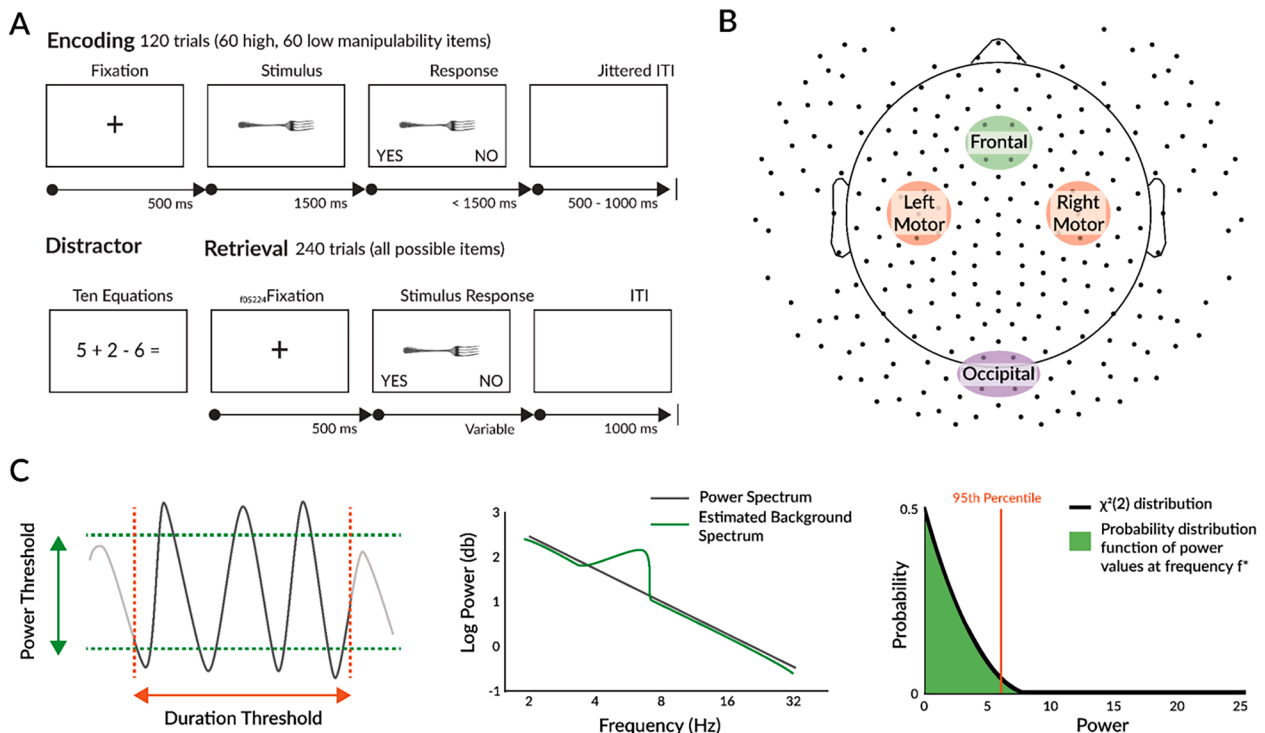


Fig. 1. Experiment methods. A) Trial procedure for the encoding, distractor, and retrieval tasks. B) High-density electroencephalography electrode map, with the four electrode clusters of interest (frontal, left motor, right motor, and occipital regions) highlighted. C) A schematic representation of the BOSC method, adapted from Whitten et al. (2011). Using this method, an epoch is classified as oscillatory if it exceeds both a power and duration threshold. To establish a power threshold, an estimated background spectrum is first modeled using linear regression methods. The probability of power values at a given frequency is then estimated using a $\chi^2(2)$ distribution, with the power threshold set at the 95th percentile of this $\chi^2(2)$ distribution for each frequency.

combination of the EEGLab open-source toolbox and in-house MATLAB scripts. The signal was bandpass filtered from 0.1 – 50 Hz and average re-referenced. Independent component analysis was implemented for artifact corrections. Components were selected through visual inspection of power spectrums, time courses, and spatial topographies.

2.3. Oscillation detection

The preprocessed data were analyzed using the BOSC method, which classifies signals as oscillatory based on both power and duration thresholds (Caplan et al., 2001; Hughes et al., 2012; Whitten et al., 2011). Establishing the power threshold involves modeling the coloured-noise background of the signal, generating a probability distribution of power values as if the entire signal were generated by this background noise. The power threshold is set at the 95th percentile of this probability distribution for each frequency. The duration threshold is set to three complete wavelet cycles. The resulting measure, P_{episode} , represents the proportion of time occupied by oscillations at a given frequency (Whitten et al., 2011; see Fig. 1C). Previous studies using BOSC have successfully detected event-related mu and theta oscillations (e.g., Chen & Caplan, 2017; Chen et al., 2021; Cruikshank et al., 2012; Lambert et al., 2023). We selected the 500 ms immediately following stimulus presentation as our time window. With reference to previous works, we chose electrodes C3 and C4 to capture motor region activity (Cruikshank et al., 2012; Pfurtscheller et al., 2006). As theta and alpha oscillations are commonly reported at frontal regions and occipital regions, respectively, we analyzed activity at Fz to capture oscillations at the frontal region and Oz to capture oscillations at the occipital region (Chen & Caplan, 2017; Hohaia et al. 2022; Pfurtscheller et al. 1994). Clusters of six electrodes were selected for each region (Cruikshank et al., 2012; see Fig. 1B).

3. Results

3.1. Behaviour

Accuracy and response time at retrieval were taken as measures of memory performance (Table 1). We implemented separate linear mixed effect models to examine the effects of different task factors on accuracy and response time from correct trials. Both models included group (Functionality versus Personal Experience), memory contrast (Old versus New), and stimulus manipulability (High versus Low) as fixed effects and subject as a random effect (Satterthwaite approximations used for significance of model coefficients). A total of 10 829 correct trials were included in the final model: (1) Hits (high): 2756, (2) Hits (low): 2666, (3) Correct Rejections (high): 2675, and (4) Correct Rejections (low): 2732.

The accuracy model revealed no effects for group (Functionality

versus Personal Experience: $t(52) = -1.419, p = 0.162$), manipulability (High versus Low: $t(156) = -0.450, p = 0.654$), or memory contrast (Old versus New: $t(156) = 0.204, p = 0.838$). An alternative model using discrimination index scores (d') in place of correct responses (%) generated similar results. The response time model revealed a significant effect of memory contrast (Old versus New: $t(156) = 2.485, p = 0.014$). In particular, participants responded faster to old versus new items. There was no effect of group (Functionality versus Personal Experience: $t(52) = 0.728, p = 0.470$) or manipulability (High versus Low: $t(156) = 0.107, p = 0.915$).

3.2. Oscillations

To understand the effects of task factors on theta and mu oscillations, we conducted linear mixed effect modeling for each electrode cluster and rhythm. At encoding, we implemented separate models with the factors of group (Functionality versus Personal Experience) and stimulus manipulability (High versus Low), with subject as a random effect. At retrieval, we implemented models with the factors of group (Functionality versus Personal Experience), stimulus manipulability (High versus Low), and memory contrast (Old versus New), with subject as a random effect.

3.3. Encoding

We first examined activity at item encoding in the theta rhythm in four clusters of interests: frontal, left/right motor, and occipital (Fig. 2A). At the frontal region, there was no effect of manipulability (High versus Low: $t(52) = -1.575, p = 0.121$) or group (Functionality versus Personal Experience: $t(52) = -0.328, p = 0.744$). For the left motor cluster, we found a main effect of manipulability (High versus Low: $t(52) = -2.266, p = 0.028$), with more theta activity observed at high manipulability trials. There was no effect of group (Functionality versus Personal Experience: $t(52) = -0.070, p = 0.945$). At the right motor cluster, we found no main effect of group (Functionality versus Personal Experience: $t(52) = 0.085, p = 0.933$) or manipulability (High versus Low: $t(52) = -1.500, p = 0.140$). Finally, at the occipital cluster, there was no main effect of group (Functionality versus Personal Experience: $t(52) = 0.016, p = 0.987$) or manipulability (High versus Low: $t(52) = -1.370, p = 0.177$).

We next examined activity in the mu/alpha frequency band. First, we investigated mu activity at the motor clusters (Fig. 2B). At the left motor region, we found no effect of manipulability (High versus Low: $t(52) = -1.389, p = 0.171$) or group (Functionality versus Personal Experience: $t(52) = 0.083, p = 0.934$). Similar results were observed for the right motor cluster, with no effect of manipulability (High versus Low: $t(52) = -1.305, p = 0.198$) or group (Functionality versus Personal Experience: $t(52) = -0.563, p = 0.5762$). We then investigated alpha activity at

Table 1

Mean accuracy (Percentage) RT (msec), and discrimination index (d') scores, along with their Standard Deviations across participants in parentheses.

Conditions		Manipulability		Personal experience	
		High	Low	High	Low
Hits	Accuracy (%)	91.944 (8.451)	90.486 (11.810)	85.238 (20.396)	81.131 (24.212)
	RT (ms)	703.945 (240.868)	767.133 (308.008)	780.007 (290.249)	757.370 (243.192)
Misses	Accuracy (%)	8.056 (8.451)	9.514 (11.810)	14.762 (20.396)	18.869 (24.212)
	RT (ms)	1007.783 (452.950)	891.948 (348.221)	1511.806 (944.936)	1180.735 (649.956)
Correct rejections	Accuracy (%)	89.097 (13.495)	89.028 (10.494)	82.857 (24.907)	86.310 (16.657)
	RT (ms)	759.788 (249.429)	788.180 (307.467)	866.705 (383.274)	820.007 (316.218)
False Alarms	Accuracy (%)	10.903 (13.495)	10.972 (10.494)	17.143 (24.907)	13.690 (16.657)
	RT (ms)	1638.533 (2795.996)	1061.973 (742.903)	1337.525 (727.126)	1124.793 (643.097)
d'		2.992 (0.926)	2.851 (0.855)	2.696 (1.702)	2.590 (1.576)

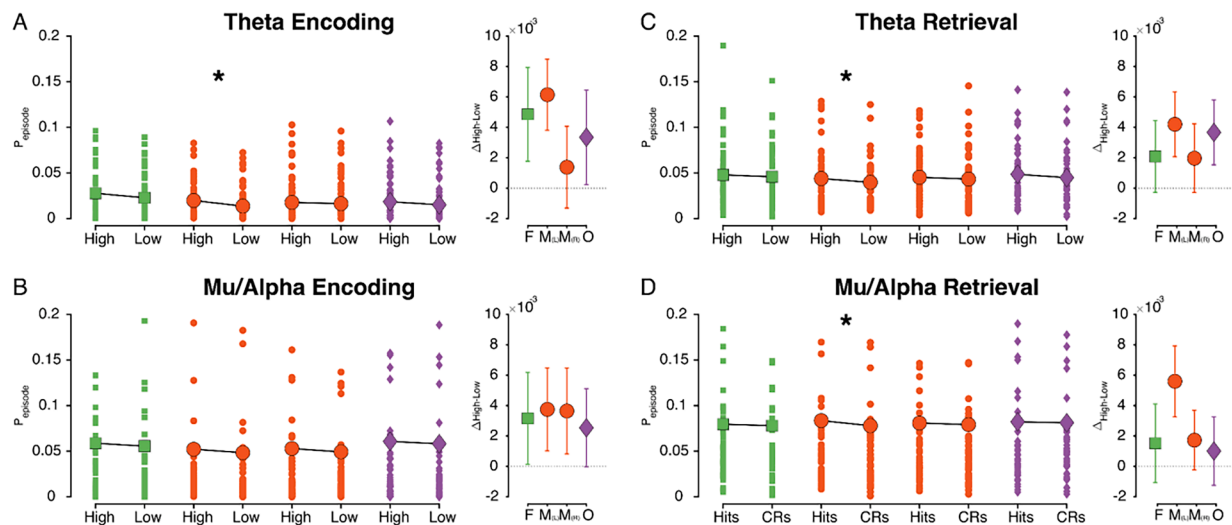


Fig. 2. Oscillation activity at four clusters of interest (frontal, left/right motor and occipital) during encoding for theta (A) and mu/alpha (B) and during retrieval for theta (C) and alpha/mu (D). Notably, more theta activity was observed at high manipulability trials compared to low manipulability trials at both encoding and retrieval. During retrieval, less mu activity was observed at hit trials compared to correct rejection (CR) trials.* denotes significant ($p < 0.05$) differences between conditions.

both the frontal and occipital clusters. At the frontal cluster, we found no effect of manipulability (High versus Low: $t(52) = -1.056$, $p = 0.296$) or group (Functionality versus Personal Experience: $t(52) = -0.028$, $p = 0.978$). A similar pattern was observed at the occipital cluster, with no effect of manipulability (High versus Low: $t(52) = -0.986$, $p = 0.329$) or group (Functionality versus Personal Experience: $t(52) = -0.275$, $p = 0.785$).

3.4. Retrieval

As with encoding, we first examined theta activity at retrieval (Fig. 2C). At the frontal cluster, there was no effect of group (Functionality versus Personal Experience: $t(52) = -0.947$, $p = 0.348$), manipulability (High versus Low: $t(52) = -0.660$, $p = 0.510$), or memory contrast (Old versus New: $t(52) = -0.240$, $p = 0.810$). Similar to encoding, we observed a significant effect of manipulability (High versus Low: $t(156) = 2.139$, $p = 0.034$) at the left motor cluster, with high manipulability items accompanied by more theta oscillations (Fig. 2b). There was no effect of group (Functionality versus Personal Experience: $t(52) = 1.040$, $p = 0.303$) or memory contrast (Old versus New: $t(156) = 0.370$, $p = 0.712$). At the right motor cluster, no effects emerged for group (Functionality versus Personal Experience: $t(52) = -1.797$, $p = 0.078$), manipulability (High versus Low: $t(156) = -0.635$, $p = 0.526$) or memory contrast (Old versus New: $t(156) = -0.001$, $p = 0.656$). Finally, we found no main effect of group (Functionality versus Personal Experience: $t(52) = -1.758$, $p = 0.085$), manipulability (High versus Low: $t(156) = -1.236$, $p = 0.218$) or memory (Old versus New: $t(156) = 0.906$, $p = 0.367$) on theta activity at the occipital cluster.

Outside of the theta rhythm, we observed a significant effect of memory contrast on mu activity at the left motor cluster (Old versus New: $t(156) = 2.495$, $p = 0.014$), but there was no effect of group (Functionality versus Personal Experience: $t(52) = -0.319$, $p = 0.751$) or manipulability (High versus Low: $t(156) = -0.820$, $p = 0.413$). Therefore, old items were accompanied by less mu oscillations at retrieval (Fig. 2c). At C4, there was no effect for group (Functionality versus Personal Experience: $t(52) = -0.947$, $p = 0.348$), manipulability (High versus Low: $t(156) = 0.387$, $p = 0.699$) or memory contrast (Old versus New: $t(156) = 0.814$, $p = 0.417$). For the alpha rhythm, we found no effect of group (Functionality versus Personal Experience: $t(52) = -0.160$, $p = 0.874$), manipulability (High versus Low: $t(52) = -0.855$, $p = 0.394$), or memory contrast (Old versus New: $t(52) = 0.680$, $p =$

0.497) at the frontal cluster. A similar pattern was observed for alpha activity at the occipital cluster, with no effect of group (Functionality versus Personal Experience: $t(52) = -0.500$, $p = 0.619$), manipulability (High versus Low: $t(52) = -1.029$, $p = 0.305$), or memory (Old versus New: $t(52) = 0.353$, $p = 0.725$).

4. Discussion

In this study, we reanalysed data from a previous study to examine the relationship between motor oscillations and item manipulability during recognition memory. To this aim, we analysed theta and mu activity at encoding and retrieval of high versus low manipulability items. The analysis revealed an effect of manipulability on theta oscillations at the left motor region, while both mu oscillations and memory behaviour were affected by the factor of memory contrast (hits versus correct rejections) at retrieval. No effects were found at frontal or occipital regions, indicating that our motor findings did not result from contamination from other regional activity.

The results support theta's proposed role in sensorimotor integration. At the left motor cluster, more theta oscillations were detected for high versus low manipulability items. This effect occurred at both encoding and retrieval. According to Bland et al. (2001), theta oscillations provide an avenue for sensory and motor systems to update one another and coordinate activity. It is possible that the immediate processing of an item involves an appraisal of its motor affordances. If the item is manipulable, this information is communicated from the sensory to motor system, priming the motor system for potential action. An increase of theta activity over the left motor cluster would then reflect this inter-system communication.

In contrast, no effect of manipulability was observed at the right motor cluster. All participants in the present study were right handed and therefore more likely to interact with manipulable items using this hand. Given the contralateral organization of the motor system, sensorimotor integration occurred at the brain region for which the communicated information was most relevant. The asymmetric finding may also result from hemispheric specialization, with the processing of manipulable items shown to rely on networks in the left hemisphere (Johnson-Frey, 2004; Johnson-Frey et al., 2005; Chang et al., 2018; Proverbio et al., 2013). This hemisphere is proposed to play a crucial role in goal-directed actions, making it key to sensorimotor integration processes (Gonzalez et al., 2006; Lavrysen et al., 2012).

Surprisingly, greater mu suppression did not accompany high manipulability items. The lack of effect across task stages and groups suggests that this finding is not solely attributable to task instructions. Instead, it may be a function of both task and stimuli. Mu suppression is greater for manipulable items when the stimuli are real objects as opposed to images (Fairchild et al., 2021). Further, Wamain et al. (2016) found that mu suppression during processing of manipulable items in a virtual reality setting varied according to task instruction and object location. However, correctly identified old items were accompanied by fewer mu oscillations at retrieval over the left motor region. It is possible that when participants encoded items, they imagined interacting with the item. The neural correlates of this encoding strategy were then reactivated at retrieval (Ruther et al., 2014). As participants would most likely imagine interacting with the item using their right hand, this led to decreased mu activity over the left motor region (Nam et al., 2011; Pfurtscheller et al., 2006; Takemi et al., 2013).

Response time was also affected by memory contrast. When considering only correct trials, participants responded faster to old versus new items. This finding is consistent with previous recognition memory paradigms (Cox & Shiffrin, 2017) and can be interpreted in the context of our mu results. According to the cortical reinstatement hypothesis, neural activity during retrieval overlaps with that during encoding (Alvarez and Squire, 1994; Norman and O'Reilly, 2003). Studies have shown that reinstatement reflects the quality of retrieved information (Favila et al., 2018; Kuhl and Chun, 2014; Polyn et al., 2005; Ritchey et al., 2013). When presented with an old item at retrieval, the reactivation of the network used to encode the item results in higher confidence at retrieval and faster response times (Weidemann & Kahana, 2016).

In conclusion, this study examined how item manipulability affects recognition memory and its neural correlates. Theta oscillations at the left motor region were sensitive to manipulability at both encoding and retrieval, supporting the rhythm's proposed involvement in sensorimotor integration. Mu oscillations decreased for old versus new items, suggesting that retrieval of familiar items may reactivate imagery processes used to encode items. This reactivation may support memory behaviour as participants responded faster to old items. Taken together, our findings reveal the impact of sensorimotor processes on recognition memory, shedding light on the interplay between motor oscillations and memory behavior. A consideration for future research is whether sleep and physical activity, factors shown to affect memory behaviour and theta oscillations, impact these sensorimotor processes (Hillman et al., 2008; Snipes et al., 2022).

CRedit authorship contribution statement

Yvonne Y. Chen: Writing – original draft, Visualization, Software, Project administration, Methodology, Formal analysis, Data curation, Conceptualization. **Kathryn J.M. Lambert:** Writing – original draft, Visualization, Project administration, Methodology, Formal analysis, Data curation. **Christopher R. Madan:** Methodology, Conceptualization. **Anthony Singhal:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization.

Declaration of Competing Interest

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

Data availability

Data will be made available on request.

References

- Alvarez, P., & Squire, L. R. (1994). Memory consolidation and the medial temporal lobe: A simple network model. *Proceedings of the National Academy of Sciences of the United States of America*, 91(15), 7041–7045. <https://doi.org/10.1073/pnas.91.15.7041>
- Beauchamp, M. S., & Martin, A. (2007). Grounding object concepts in perception and action: Evidence from fMRI studies of tools. *Cortex*, 43(3), 461–468. [https://doi.org/10.1016/s0010-9452\(08\)70470-2](https://doi.org/10.1016/s0010-9452(08)70470-2)
- Bland, B. H., & Oddie, S. D. (2001). Theta band oscillation and synchrony in the hippocampal formation and associated structures: The case for its role in sensorimotor integration. *Behavioural Brain Research*, 127(1–2), 119–136. [https://doi.org/10.1016/s0166-4328\(01\)00358-8](https://doi.org/10.1016/s0166-4328(01)00358-8)
- Caplan, J. B., Madsen, J. R., Raghavachari, S., & Kahana, M. J. (2001). Distinct patterns of brain oscillations underlie two basic parameters of human maze learning. *Journal of Neurophysiology*, 86(1), 368–380. <https://doi.org/10.1152/jn.2001.86.1.368>
- Chang, Y. T., Chen, H. Y., Huang, Y. C., Shih, W. Y., Chan, H. L., Wu, P. Y., Meng, L. F., Chen, C. C., & Wang, C. I. (2018). Left centro-parieto-temporal response to tool-gesture incongruity: An ERP study. *Behavioral and Brain Functions*, 14(1), 6. <https://doi.org/10.1186/s12993-018-0138-7>
- Chen, Y. Y., & Caplan, J. B. (2017). Rhythmic Activity and Individual Variability in Recognition Memory: Theta Oscillations Correlate with Performance whereas Alpha Oscillations Correlate with ERPs. *Journal of Cognitive Neuroscience*, 29(1), 183–202. https://doi.org/10.1162/jocn_a_01033
- Chen, Y. Y., Lambert, K. J. M., Madan, C. R., & Singhal, A. (2021). Mu oscillations and motor imagery performance: A reflection of intra-individual success, not inter-individual ability. *Human Movement Science*, 78, Article 102819. <https://doi.org/10.1016/j.humov.2021.102819>
- Cox, G. E., & Shiffrin, R. M. (2017). A dynamic approach to recognition memory. *Psychological Review*, 124(6), 795–860. <https://doi.org/10.1037/rev0000076>
- Cruikshank, L. C., Singhal, A., Hueppelsheuser, M., & Caplan, J. B. (2012). Theta oscillations reflect a putative neural mechanism for human sensorimotor integration. *Journal of Neurophysiology*, 107(1), 65–77. <https://doi.org/10.1152/jn.00893.2010>
- Daprati, E., Balestrucci, P., & Nico, D. (2022). Do graspable objects always leave a motor signature? A study on memory traces. *Experimental brain research*, 240(12), 3193–3206. <https://doi.org/10.1007/s00221-022-06487-4>
- Dutriaux, L., & Gyselinck, V. (2021). The Postural Effect on the Memory of Manipulable Objects. *Experimental psychology*, 68(6), 333–339. <https://doi.org/10.1027/1618-3169/a000537>
- Fairchild, G. T., Marini, F., & Snow, J. C. (2021). Grasability Modulates the Stronger Neural Signature of Motor Preparation for Real Objects vs. Pictures. *Journal of Cognitive Neuroscience*, 33(12), 2477–2493. https://doi.org/10.1162/jocn_a_01771
- Favila, S. E., Samide, R., Sweigart, S. C., & Kuhl, B. A. (2018). Parietal Representations of Stimulus Features Are Amplified during Memory Retrieval and Flexibly Aligned with Top-Down Goals. *The Journal of neuroscience*, 38(36), 7809–7821. <https://doi.org/10.1523/JNEUROSCI.0564-18.2018>
- Gonzalez, C. L., Ganel, T., & Goodale, M. A. (2006). Hemispheric specialization for the visual control of action is independent of handedness. *Journal of neurophysiology*, 95(6), 3496–3501. <https://doi.org/10.1152/jn.01187.2005>
- Herweg, N. A., Solomon, E. A., & Kahana, M. J. (2020). Theta Oscillations in Human Memory. *Trends in Cognitive Science*, 24(3), 208–227. <https://doi.org/10.1016/j.tics.2019.12.006>
- Hillman, C. H., Erickson, K. I., & Kramer, A. F. (2008). Be smart, exercise your heart: Exercise effects on brain and cognition. *Nature reviews. Neuroscience*, 9(1), 58–65. <https://doi.org/10.1038/nrn2298>
- Hohaia, W., Saurels, B. W., Johnston, A., Yarrow, K., & Arnold, D. H. (2022). Occipital alpha-band brain waves when the eyes are closed are shaped by ongoing visual processes. *Scientific reports*, 12(1), 1194. <https://doi.org/10.1038/s41598-022-05289-6>
- Hughes, A. M., Whitten, T. A., Caplan, J. B., & Dickson, C. T. (2012). BOSC: A better oscillation detection method, extracts both sustained and transient rhythms from rat hippocampal recordings. *Hippocampus*, 22(6), 1417–1428. <https://doi.org/10.1002/hipo.20979>
- Jenson, D., & Saltuklaroglu, T. (2021). Sensorimotor contributions to working memory differ between the discrimination of Same and Different syllable pairs. *Neuropsychologia*, 159, Article 107947. <https://doi.org/10.1016/j.neuropsychologia.2021.107947>
- Johnson-Frey, S. H. (2004). The neural bases of complex tool use in humans. *Trends in cognitive sciences*, 8(2), 71–78. <https://doi.org/10.1016/j.tics.2003.12.002>
- Johnson-Frey, S. H., Newman-Norlund, R., & Grafton, S. T. (2005). A distributed left hemisphere network active during planning of everyday tool use skills. *Cerebral cortex (New York, N.Y.: 1991)*, 15(6), 681–695. <https://doi.org/10.1093/cercor/bhh169>
- Kuhl, B. A., & Chun, M. M. (2014). Successful remembering elicits event-specific activity patterns in lateral parietal cortex. *The Journal of neuroscience*, 34(23), 8051–8060. <https://doi.org/10.1523/JNEUROSCI.4328-13.2014>
- Lambert, K. J. M., Chen, Y. Y., Donoff, C., Elke, J., Madan, C. R., & Singhal, A. (2023). Handedness effects on imagery of dominant- versus non-dominant-hand movements: An electroencephalographic investigation. *The European journal of neuroscience*, 58(5), 3286–3298. <https://doi.org/10.1111/ejn.16096>
- Lavrysen, A., Heremans, E., Peeters, R., Wenderoth, N., Feys, P., Swinnen, S. P., & Helsen, W. F. (2012). Hemispheric asymmetries in goal-directed hand movements are independent of hand preference. *NeuroImage*, 62(3), 1815–1824. <https://doi.org/10.1016/j.neuroimage.2012.05.033>
- Madan, C. R., Chen, Y. Y., & Singhal, A. (2016). ERPs differentially reflect automatic and deliberate processing of the functional manipulability of objects. *Frontiers in Human Neuroscience*, 10, 360. <https://doi.org/10.3389/fnhum.2016.00360>

- Mecklinger, A., Gruenewald, C., Besson, M., Magnié, M. N., & Von Cramon, D. Y. (2002). Separable neuronal circuitries for manipulable and non-manipulable objects in working memory. *Cerebral Cortex*, *12*(11), 1115–1123. <https://doi.org/10.1093/cercor/12.11.1115>
- Nam, C. S., Jeon, Y., Kim, Y. J., Lee, I., & Park, K. (2011). Movement imagery-related lateralization of event-related (de)synchronization (ERD/ERS): Motor-imagery duration effects. *Clinical Neurophysiology*, *122*(3), 567–577. <https://doi.org/10.1016/j.clinph.2010.08.002>
- Norman, K. A., & O'Reilly, R. C. (2003). Modeling hippocampal and neocortical contributions to recognition memory: A complementary-learning-systems approach. *Psychological review*, *110*(4), 611–646. <https://doi.org/10.1037/0033-295X.110.4.611>
- Onishi, S., Tobita, K., & Makioka, S. (2022). Hand constraint reduces brain activity and affects the speed of verbal responses on semantic tasks. *Scientific reports*, *12*(1), 13545. <https://doi.org/10.1038/s41598-022-17702-1>
- Pfurtscheller, G., Brunner, C., Schlögl, A., & Lopes da Silva, F. H. (2006). Mu rhythm (de) synchronization and EEG single-trial classification of different motor imagery tasks. *NeuroImage*, *31*(1), 153–159. <https://doi.org/10.1016/j.neuroimage.2005.12.003>
- Pfurtscheller, G., Neuper, C., & Mohl, W. (1994). Event-related desynchronization (ERD) during visual processing. *International journal of psychophysiology: official journal of the International Organization of Psychophysiology*, *16*(2–3), 147–153. [https://doi.org/10.1016/0167-8760\(89\)90041-x](https://doi.org/10.1016/0167-8760(89)90041-x)
- Pineda, J. A. (2005). The functional significance of mu rhythms: Translating “seeing” and “hearing” into “doing”. *Brain research. Brain research reviews*, *50*(1), 57–68. <https://doi.org/10.1016/j.brainresrev.2005.04.005>
- Polyn, S. M., Natu, V. S., Cohen, J. D., & Norman, K. A. (2005). Category-specific cortical activity precedes retrieval during memory search. *Science (New York, N.Y.)*, *310*(5756), 1963–1966. <https://doi.org/10.1126/science.1117645>
- Proverbio, A. M., Azzari, R., & Adorni, R. (2013). Is there a left hemispheric asymmetry for tool affordance processing? *Neuropsychologia*, *51*(13), 2690–2701. <https://doi.org/10.1016/j.neuropsychologia.2013.09.023>
- Ritchey, M., Wing, E. A., LaBar, K. S., & Cabeza, R. (2013). Neural similarity between encoding and retrieval is related to memory via hippocampal interactions. *Cerebral cortex (New York, N.Y.: 1991)*, *23*(12), 2818–2828. <https://doi.org/10.1093/cercor/bhs258>
- Rueschemeyer, S. A., van Rooij, D., Lindemann, O., Willems, R. M., & Bekkering, H. (2010). The function of words: distinct neural correlates for words denoting differently manipulable objects. *Journal of cognitive neuroscience*, *22*(8), 1844–1851. <https://doi.org/10.1162/jocn.2009.21310>
- Rüther, N. N., Brown, E. C., Klepp, A., & Bellebaum, C. (2014). Observed manipulation of novel tools leads to mu rhythm suppression over sensory-motor cortices. *Behavioural Brain Research*, *261*, 328–335. <https://doi.org/10.1016/j.bbr.2013.12.033>
- Salmon, J. P., Matheson, H. E., & McMullen, P. A. (2014). Photographs of manipulable objects are named more quickly than the same objects depicted as line-drawings: Evidence that photographs engage embodiment more than line-drawings. *Frontiers in Psychology*, *5*, 1187. <https://doi.org/10.3389/fpsyg.2014.01187>
- Snipes, S., Krugliakova, E., Meier, E., & Huber, R. (2022). The Theta Paradox: 4–8 Hz EEG Oscillations Reflect Both Sleep Pressure and Cognitive Control. *The Journal of Neuroscience*, *42*(45), 8569–8586. <https://doi.org/10.1523/JNEUROSCI.1063-22.2022>
- Takemi, M., Masakado, Y., Liu, M., & Ushiba, J. (2013). Event-related desynchronization reflects downregulation of intracortical inhibition in human primary motor cortex. *Journal of Neurophysiology*, *110*(5), 1158–1166. <https://doi.org/10.1152/jn.01092.2012>
- Wamain, Y., Gabrielli, F., & Coello, Y. (2016). EEG μ rhythm in virtual reality reveals that motor coding of visual objects in peripersonal space is task dependent. *Cortex*, *74*, 20–30. <https://doi.org/10.1016/j.cortex.2015.10.006>
- Weidemann, C. T., & Kahana, M. J. (2016). Assessing recognition memory using confidence ratings and response times. *Royal Society open science*, *3*(4), Article 150670. <https://doi.org/10.1098/rsos.150670>
- Whitten, T. A., Hughes, A. M., Dickson, C. T., & Caplan, J. B. (2011). A better oscillation detection method robustly extracts EEG rhythms across brain state changes: The human alpha rhythm as a test case. *NeuroImage*, *54*(2), 860–874. <https://doi.org/10.1016/j.neuroimage.2010.08.064>