

JYX



This is a self-archived version of an original article. This version may differ from the original in pagination and typographic details.

Author(s): Tu, Chia-An; Parviainen, Tiina; Hämäläinen, Jarmo A.; Hsu, Yi-Fang

Title: Alpha oscillations protect auditory working memory against distractors in the encoding phase

Year: 2025

Version: Published version

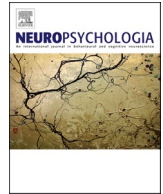
Copyright: © 2024 The Authors. Published by Elsevier Ltd.

Rights: CC BY-NC-ND 4.0

Rights url: <https://creativecommons.org/licenses/by-nc-nd/4.0/>

Please cite the original version:

Tu, C.-A., Parviainen, T., Hämäläinen, J. A., & Hsu, Y.-F. (2025). Alpha oscillations protect auditory working memory against distractors in the encoding phase. *Neuropsychologia*, 207, Article 109058. <https://doi.org/10.1016/j.neuropsychologia.2024.109058>



Alpha oscillations protect auditory working memory against distractors in the encoding phase

Chia-An Tu^a, Tiina Parviainen^b, Jarmo A. Hämäläinen^b, Yi-Fang Hsu^{a,c,*}

^a Department of Educational Psychology and Counselling, National Taiwan Normal University, Taipei, 106308, Taiwan

^b Jyväskylä Centre for Interdisciplinary Brain Research, Department of Psychology, University of Jyväskylä, Jyväskylä, 40014, Finland

^c Institute for Research Excellence in Learning Sciences, National Taiwan Normal University, Taipei, 106308, Taiwan

ARTICLE INFO

Keywords:

Alpha oscillations
Working memory
Sternberg paradigm
Electroencephalography (EEG)

ABSTRACT

Alpha oscillations are proposed to serve the function of inhibition to protect items in working memory from intruding information. In a modified Sternberg paradigm, alpha power was initially found to increase at the anticipation of strong compared to weak distractors, reflecting the active gating of distracting information from interfering with the memory trace. However, there was a lack of evidence supporting the inhibition account of alpha oscillations in later studies using similar experimental design with greater temporal disparity between the encoding phase and the presentation of the distractors. This temporal disparity might have dampened the demands for inhibition. To test the hypothesis that alpha inhibition takes place when distractors are temporally close to the encoding phase, here we designed a modified Sternberg paradigm where distractors were sandwiched between targets in the encoding phase to ensure that they compete for working memory resources. Using electroencephalography (EEG), we replicated the finding that alpha power increased for strong compared to weak distractors. The effect was present throughout the encoding phase, not only upon the presentation of distractors but also before and after the presentation of distractors, providing evidence for both proactive and reactive inhibition of distractors at the neuronal level. Meanwhile, the effect was restricted to the context of high but not low target-to-distractor ratio. The results suggest that the distractors being temporally close to the encoding phase of more targets might be a boundary condition of the generation of alpha oscillations for gating.

1. Introduction

To effectively resist distracting information is an important determinant of working memory capacity. The inhibition of task-irrelevant information is proposed to be reflected by neuronal oscillations in the alpha band (8–12 Hz) (for reviews see Klimesch et al., 2007; Jensen and Mazaheri, 2010; Weisz et al., 2011; Roux and Uhlhaas, 2014; Miller et al., 2018). In a seminal study, Bonnefond and Jensen (2012) used a modified Sternberg paradigm which consisted of visual presentation of a memory set of four consonants (in the encoding phase), followed by a strong or weak distractor (i.e., a consonant or a symbol; in the retention phase), and then a probe (in the retrieval phase). The distractor strength could be anticipated by the participants because the strong and weak distractors were grouped in blocks. Magnetoencephalography (MEG) recordings showed that alpha power in the left parieto-occipital region increased at the anticipation of strong compared to weak distractors and

that the increase in alpha power led to better distractor suppression at behavioural level. It was suggested that alpha oscillations might reflect functional inhibition of the sensory regions which prevents task-irrelevant processes from interfering with the memory trace (Bonnefond and Jensen et al., 2013).

Intriguingly, later research using similar block design of the modified Sternberg paradigm failed to provide converging results. Although the anticipatory activity in the alpha band was commonly reported, the direction of the alpha power change was inconsistent. Weisz et al. (2020) adapted the experiment of Bonnefond and Jensen, 2013 to the auditory modality, where participants listened to a memory set of four consonants (in the encoding phase), followed by a strong or weak distractor (i.e., a spoken consonant or a scrambled consonant; in the retention phase), and then a probe (in the retrieval phase). MEG results showed that alpha power in the left superior temporal gyrus (STG) decreased at the anticipation of strong compared to weak distractors,

* Corresponding author. Department of Educational Psychology and Counselling, National Taiwan Normal University, Taipei, 106308, Taiwan.

E-mail addresses: chiaantu@gmail.com (C.-A. Tu), tiina.m.parviainen@jyu.fi (T. Parviainen), jarmo.a.hamalainen@jyu.fi (J.A. Hämäläinen), yi-fang.hsu@cantab.net (Y.-F. Hsu).

<https://doi.org/10.1016/j.neuropsychologia.2024.109058>

Received 31 May 2024; Received in revised form 25 November 2024; Accepted 27 November 2024

Available online 28 November 2024

0028-3932/© 2024 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

which might reflect the top-down prioritisation of targets in the face of strong distractors and/or involuntary attention to strong distractors (i.e., failed gating). Sghirripa et al. (2021) adapted the experiment of Bonnefond and Jensen (2012) by changing the visual presentation mode of stimuli from sequential to simultaneous. Participants were shown a screen of a memory set of five consonants (in the encoding phase), followed by a screen of strong or weak distractors (i.e., three consonants or three hash symbols; in the retention phase), and then a screen of a probe (in the retrieval phase). Electroencephalography (EEG) results showed that alpha power in the right parieto-occipital region increased at the anticipation of the distractor, but did not differ between strong and weak distractors.

The lack of converging evidence might be related to the alteration of the modified Sternberg paradigm. In the study of Weisz et al. (2020), the time interval between the presentation of the memory set and the distractor doubled from 1000 ms to 2000 ms, creating a temporal gap between the two phases. In the study of Sghirripa et al. (2021), the simultaneous presentation of the memory set followed by the simultaneous presentation of the distractors resulted in the presentation of two discrete frames of stimuli. In these cases, there was a clear distinction between the encoding phase (when the memory set was presented) and the presentation of the distractor. As the encoding of the memory set was obviously over when the distractor appeared, there might be less need to suppress the distractor from competing for working memory resources. In other words, although previous studies all reported the presentation of the distractor in the retention phase, it is possible that in the initial study of Bonnefond and Jensen (2012) the distractor appeared in the encoding phase to compete for working memory resources, whereas in later studies where the experimental parameters changed, the distractor was pushed further away from the encoding phase into the retention phase (e.g., Weisz et al., 2020; Sghirripa et al., 2021).

To test the hypothesis that alpha inhibition takes place when distractors are temporally close to the encoding phase, here we designed a modified Sternberg paradigm where distractors were sandwiched between targets. This design would ensure that the distractors remained in the encoding phase to compete for working memory resources. To explore the boundary condition of the generation of alpha oscillations as a neuronal mechanism for gating, we also created two contexts, one containing more targets than distractors (which resembled the setup in most literature) and one containing fewer targets than distractors (which was less studied). We hypothesised that alpha power should increase at the anticipation of strong compared to weak distractors. Whether the result pattern would hold in both contexts was an open question.

2. Materials and methods

Participants. A total of 25 healthy volunteers participated in the study (19–23 years of age, 13 males, 23 right-handed), all reporting no history of neurological, neuropsychiatric, or visual/hearing impairments. Participants gave written informed consent and were paid for participation. Three participants were excluded from data analysis due to excessive sweating, environmental noise, and not following the instruction, leaving 22 participants in the sample (19–23 years of age, 11 males, 21 right-handed). The study was conducted in accordance with the Declaration of Helsinki and approved by the Research Ethics Committee at National Taiwan Normal University.

Stimuli. Stimuli consisted of Mandarin spoken digits from zero to nine (all of which were monosyllabic) from the Notevibes database (<http://notevibes.com/>) by a female voice (Mandarin Chinese-Yu Yan) to serve as targets and by a male voice (Mandarin Chinese-Chang) to serve as distractors. We used voices of different genders as targets and distractors to allow a clear distinction between them. We submitted all files (64 kbps/24 kHz) to a root-mean-square amplitude normalisation and removed the silent parts in the beginning and the end of each file (using a threshold of 0.035). For the manipulation of distractor strength, we

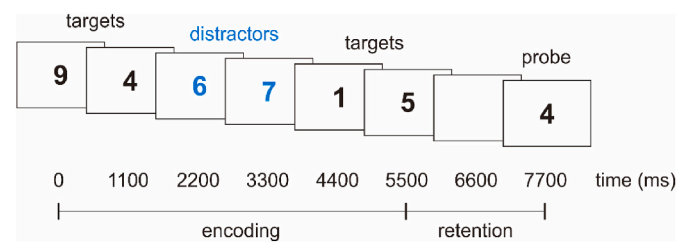


Fig. 1. A set of six spoken digits were presented sequentially at a rate of 1100 ms, where strong or weak distractors (corresponding to the original or scrambled male voice) were sandwiched between targets spoken by a female voice. The target-to-distractor ratio can be 4-to-2 (as shown here) or 2-to-4. Participants indicated by a button press whether the probe was part of the targets.

additionally generated a scrambled version of the male voice using the shufflewins function in Matlab (Ellis, 2010), which preserves the frequency content of the original sound but makes it unintelligible. Lastly, for all files the final 10 ms were edited with the Fade Out effect in Audacity to avoid audio artefacts. Overall, the duration of the spoken digits ranged from 305.083 to 437.667 ms for the female voice (mean: 367.387 ms) and 248.208–414.625 ms for the male voice (mean: 344.396 ms).

Procedures. Fig. 1 illustrates the modified Sternberg paradigm in which participants were presented with six spoken digits, where strong distractors (using the original male voice) or weak distractors (using the scrambled male voice) were sandwiched between targets spoken by a female voice, with a stimulus-onset asynchrony (SOA) of 1100 ms (i.e., the encoding phase). The target-to-distractor ratio can be 4-to-2 (where there were more targets than distractors) or 2-to-4 (where there were fewer targets than distractors). The encoding phase was followed by a silent interval of 2200 ms (i.e., the retention phase) and then a spoken digit as a probe to which participants had to press a key to indicate whether it was one of the targets presented earlier (i.e., the retrieval phase). While 50% of the probes called for a yes response, 50% of the probes called for a no response. The assignment of the response keys was counterbalanced across participants. Participants' response was followed by a jittered intertrial interval (ITI) of 900–1300 ms.

Participants were presented with 16 blocks, four blocks per each condition (i.e., block design), so that participants can anticipate the distractor (of different strength) and the context (of different target-to-distractor ratio). Each block contained one practice trial followed by 26 trials. Block order and trial order were randomised across participants. A black fixation cross against white background remained on the screen for the duration of each block, viewed from a distance of 120 cm. E-prime version 2.0 (Psychology Software Tools) was used for stimulus presentation. Stimulation was delivered binaurally via headphones (Sennheiser HD 2.30i) with an intensity of maximum 73 dB (65.4–73.7 dBA; 67.0–73.1 dBC).

Data recording and preprocessing. EEG was recorded from 32 active electrodes on a Brain Products actiCAP snap according to the extended 10–20 system. The ground electrode was placed at FPz and the reference electrode was placed at Fz. Eye movements were monitored by additional four electrodes placed above and below the left eye and at the outer canthi of both eyes, which were bipolarized online to yield vertical and horizontal electrooculography (EOG), respectively. All signals were amplified with the BrainVision actiCHamp Plus (Brain Products GmbH, Germany) and sampled at 500 Hz, and then filtered at 0.1–100 Hz offline in EEGLab 14_1_2b (Delorme and Makeig, 2004).

Ocular artefact correction was conducted with independent component analysis (ICA) using the runica algorithm. ICs capturing blinks and horizontal eye movements were determined by visual inspection, pruning out one to two components for each participant. Epochs extended from –1100 ms to 8800 ms relative to the onset of each correct trial (i.e., covering 1100 ms before the onset of the encoding phase and 1100 ms after the offset of the retention phase), using the average of the entire epoch as baseline (i.e., demean). Bad electrodes were identified (if

Table 1

Trial numbers after artefact rejection in each condition.

	4-target-2-distractor		2-target-4-distractor	
	Strong	Weak	Strong	Weak
Min	70	72	51	73
Max	98	100	98	97
Mean	87.591	87.227	87.227	86.955
SD	8.094	7.751	10.958	6.745

there were more than 25% of the epochs containing voltage deviations exceeding ± 100 μV relative to baseline) and interpolated using spherical interpolation. The data was recomputed to average reference. Epochs containing voltage deviations exceeding ± 100 μV relative to baseline at any of the electrodes were rejected. The trial numbers after artefact rejection in each condition are listed in Table 1.

Data analysis. To examine the time course of the frequency content, EEGLab 14_1_2b (Delorme and Makeig, 2004) was used to compute the event-related spectral perturbation (ERSP) which provides a time-frequency representation of the mean change in power spectra relative to baseline. To model ERSF, we applied a 3-cycle Morlet wavelet where the cycles linearly increased with frequency by a factor of 0.8 from 4 to 30 Hz, using the entire epoch and the baseline from -800 to -300 ms (i.e., 500-ms long). To estimate the effect of strong and weak distractors in different contexts, we performed one-way ANOVA using permutation statistics with FDR correction, with the p-value threshold set at 0.05 and randomization set at 2000. The topographical distribution of alpha activity (8-12 Hz) between strong and weak distractors in different contexts was respectively compared in the encoding phase (0-5500 ms as a whole and per 1100 ms corresponding to the onset of each spoken digits to delineate the development of alpha power before and after the presentation of distractors) as well as the retention phase (5500-7700 ms).

3. Results

Behavioural performance differed by context. For accuracy (Fig. 2A), there was no distractor \times context interaction ($F(1,21) = 0.522$, $p = 0.478$). Participants' accuracy did not differ between strong and weak distractors ($F(1,21) = 1.481$, $p = 0.237$), but was lower in 4-target-2-distractor than 2-target-4-distractor context ($F(1,21) = 6.277$, $p = 0.021$).

For RT (Fig. 2B), there was a significant distractor \times context interaction ($F(1,21) = 7.975$, $p = 0.010$). Post hoc comparisons showed that participants' RT did not differ between strong and weak distractors (4-target-2-distractor: $t(21) = 1.822$, $p = 0.083$; 2-target-4-distractor: $t(21) = -2.260$, $p = 0.035$), but was longer in 4-target-2-distractor than 2-

target-4-distractor context (strong distractor: $t(21) = 5.228$, $p < 0.001$; weak distractor: $t(21) = 4.203$, $p < 0.001$).

Inhibition-related alpha power was modulated by context. The time-frequency representations suggested that there was a difference between strong and weak distractors at frontal and central electrodes in the 4-target-2-distractor context but not in the 2-target-4-distractor context (Fig. 3).

We then compared the topographical distributions of alpha activity between strong and weak distractors per context. In the 4-target-2-distractor context, alpha power increased for strong compared to weak distractors in the encoding phase (Fig. 4A). We also examined the effect per 1100 ms, corresponding to the onset of one spoken digit until the onset of next spoken digit (i.e., 0-1100 ms, 1100-2200 ms, 2200-3300 ms, 3300-4400 ms, and 4400-5500 ms). Alpha power increased not only upon the presentation of distractors but also before and after the presentation of distractors (Fig. 4B). Notably, although alpha enhancement peaked at right temporal electrodes, the significant difference between strong and weak distractors was found beyond right temporal electrodes, across bilateral frontal and occipital electrodes.

In the 2-target-4-distractor context, alpha power did not differ between strong and weak distractors in the encoding phase (Fig. 4C and D).

No significant effect was found in the retention phase.

Exploratory analysis revealed a negative correlation between alpha power and RT. Since we found alpha enhancement for strong compared to weak distractors in the 4-target-2-distractor context, we further explored whether there is a correlation between alpha power and behavioural performance here. We averaged the alpha power on Cz (where significant effect can be seen before/during/after distractor presentation) per 1100 ms as before distractor presentation (1100-2200 ms), during distractor presentation (2200-3300 ms and 3300-4400 ms), and after distractor presentation (4400-5500 ms). An α level of $0.05/4 = 0.0125$ was used to correct for multiple comparisons. When strong distractors were presented, no significant correlation was found between alpha power and behavioural performance. When weak distractors were presented, a negative correlation was found between alpha power after distractor presentation and RT (Table 2). Given that no inhibition-related alpha power was found in the 2-target-4-distractor context, no correlation analysis was performed here.

4. Discussion

Alpha oscillations have been implicated in the gating of task-irrelevant information in working memory (Klimesch et al., 2007; Jensen and Mazaheri, 2010; Weisz et al., 2011; Roux and Uhlhaas, 2014; Miller et al., 2018), showing anticipatory enhancement for strong compared to weak distractors (Bonfond and Jensen, 2012). However, the lack of converging evidence in later research using similar

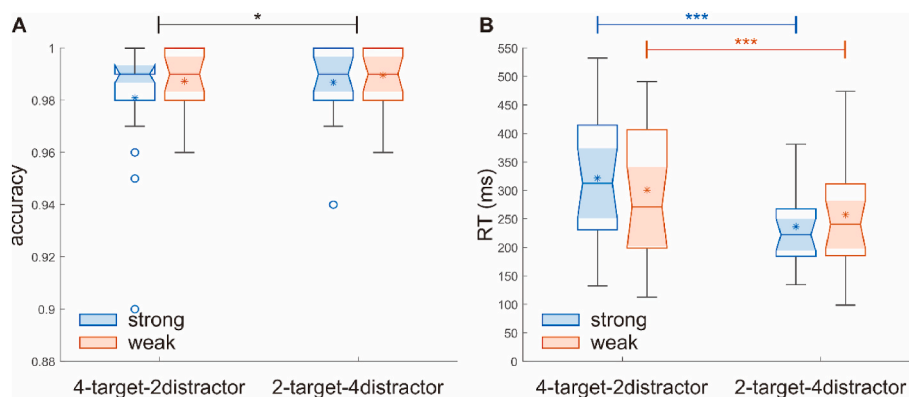


Fig. 2. The accuracy and RT to the probe. The accuracy was lower and the RT was longer in 4-target-2-distractor than 2-target-4-distractor context, independent of distractors. The asterisk indicates the mean, the central mark indicates the median, the edges of the box indicate the lower/upper quartiles, and the whisker indicates the nonoutlier min/max.

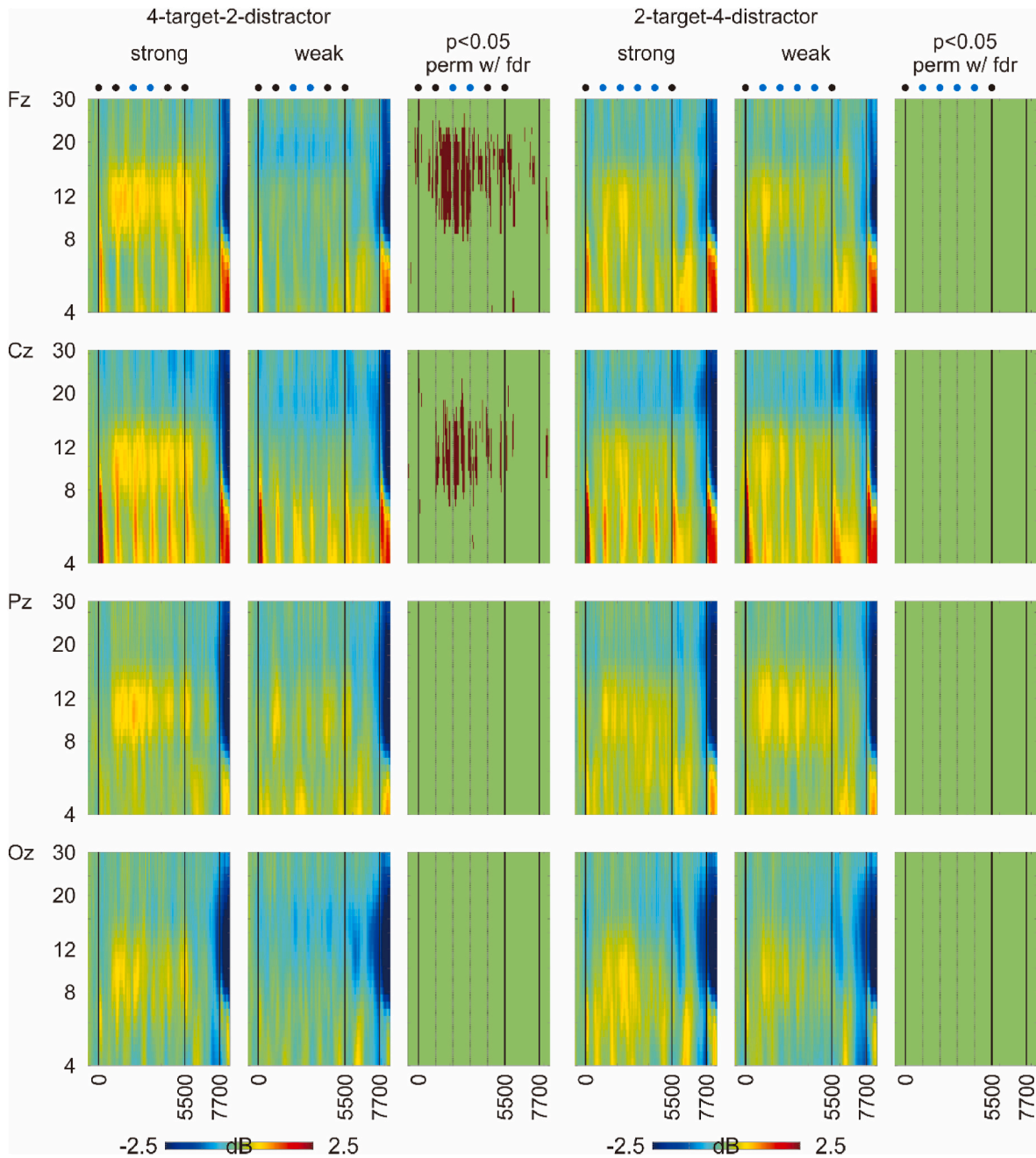


Fig. 3. Grand-averaged time-frequency representations on midline electrodes. The x-axis represents time (ms). The y-axis represents frequency (Hz). The vertical lines mark the beginning of the encoding phase (at 0 ms), the beginning of the retention phase (at 5500 ms), and the beginning of the retrieval phase (at 7700 ms). The black and blue dots respectively indicate when the targets and distractors occur in the encoding phase. The difference between strong and weak distractors can be seen in the alpha band at frontal and central electrodes in the 4-target-2-distractor context but not in the 2-target-4-distractor context.

experimental design (e.g., Weisz et al., 2020; Sghirripa et al., 2021) suggested that greater temporal disparity between the encoding phase and the presentation of the distractors might lessen the need to suppress the distractors from competing for working memory resources. Here we designed a modified Sternberg paradigm where distractors were sandwiched between targets to ensure that the distractors remained in the encoding phase to compete for working memory resources. We replicated the finding of Bonnefond and Jensen (2012) that alpha power increased for strong compared to weak distractors. The enhancement can be seen throughout the encoding phase, not only upon the presentation of distractors but also before and after the presentation of distractors. Moreover, the effect was seen in the 4-target-2-distractor context but not in the 2-target-4-distractor context. The results suggest

that the distractors being temporally close to the encoding phase when more targets than distractors are presented might be a boundary condition of the generation of alpha oscillations as a neuronal mechanism for gating.

Unlike previous research (e.g., Weisz et al., 2020; Sghirripa et al., 2021) which failed to replicate the finding of Bonnefond and Jensen (2012), we demonstrated the alpha enhancement for strong compared to weak distractors by placing the distractors in the middle of the encoding phase. It seems that alpha oscillations can serve a function of inhibiting task-irrelevant information in working memory as long as the distractors are temporally close to the targets in the processing stream. Importantly, the alpha enhancement for strong compared to weak distractors cannot be explained by the perceptual difference between distractors, as the

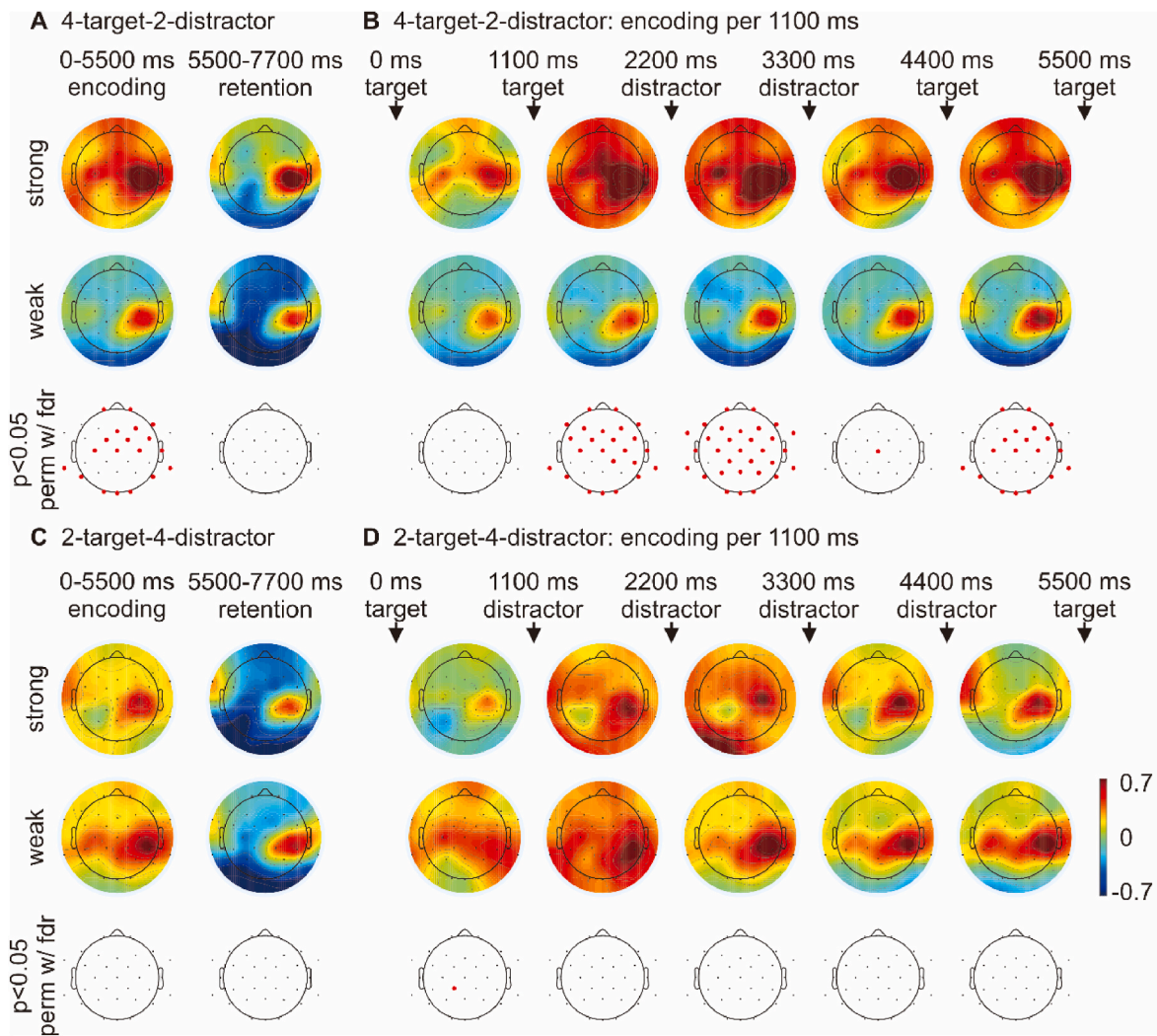


Fig. 4. Topographical distributions of alpha activity (8-12 Hz) in strong and weak distractors per context. Electrodes showing significant differences between conditions are marked as red dots. (A) In the 4-target-2-distractor context, alpha power increased for strong compared to weak distractors in the encoding phase but not in the retention phase. (B) The comparison between strong and weak distractors per 1100 ms of the encoding phase in the 4-target-2-distractor context. (C) In the 2-target-4-distractor context, alpha power did not differ between strong and weak distractors. (D) The comparison between strong and weak distractors per 1100 ms of the encoding phase in the 2-target-4-distractor context.

Table 2
Correlation between alpha power and behavioural performance in the 4-target-2-distractor context.

			Before	During	During	After
			distractor	distractor	distractor	distractor
			1100-2200	2200-3300	3300-4400	4400-
			ms	ms	ms	5500 ms
Strong	accuracy	r	-0.003	-0.268	-0.008	0.053
		p	0.990	0.228	0.970	0.815
	RT	r	-0.286	-0.275	-0.299	-0.367
		p	0.196	0.216	0.177	0.093
Weak	accuracy	r	0.066	0.166	0.103	0.033
		p	0.770	0.461	0.648	0.884
	RT	r	-0.400	-0.473	-0.500	-0.577
		p	0.065	0.026	0.018	0.005

strong and weak distractors were based on identical physical features (using the original and scrambled male voice). Moreover, the effect was significant not only upon the presentation of distractors but also before and after the presentation of distractors, providing evidence for both proactive and reactive inhibition of distractors at the neuronal level. The

proactive inhibition likely suppresses perception in anticipation of intruding information. Recent reviews further suggested that it can involve a direct mechanism (i.e., a selective inhibition arising from top-down connections) and/or a secondary mechanism (i.e., a non-specific inhibition as a consequence of target facilitation) (Noonan et al., 2018; Jensen, 2024); however, the current research cannot distinguish between these two mechanisms. The reactive inhibition, on the other hand, likely reflects the quick disengagement from task-irrelevant information (Fodor et al., 2020; Zhou et al., 2023).

The alpha enhancement for strong compared to weak distractors was found to peak at right temporal electrodes and extend across bilateral frontal and occipital electrodes. The topographic distribution of the alpha activity focusing near the temporal areas is not surprising given that speech stimuli are known to activate the auditory cortices. Its lateralization to the right hemisphere was also observed in earlier research using visual (Proskovec et al., 2019; Sghirripa et al., 2021) and auditory (Leiberg et al., 2006) verbal working memory tasks. Similar to our results, Leiberg et al. (2006) found alpha and beta activity to be lateralized to the right fronto-temporal sites, yet the effect of working memory load did not show hemispheric differences. While the interpretation of the spatial information of a 32-channel EEG should be treated with caution, the widespread effect supports the involvement of

an interactive network in distractor-filtering. For example, functional magnetic resonance imaging (fMRI) activity in the middle frontal gyrus and basal ganglia was reported to precede the filtering of task-irrelevant information in the encoding phase in working memory (McNab and Klingberg, 2008). It remains an open question how functional inhibition is reflected in alpha oscillations at different spatial scales.

Interestingly, the alpha enhancement for strong compared to weak distractors was significant in the 4-target-2-distractor context (which resembled the setup in most literature) but not in the 2-target-4-distractor context (which was less studied). If we use the load theory (Lavie, 2005; see also Jensen, 2024) to label the 4-target-2-distractor context to be of high load and the 2-target-4-distractor context to be of low load, the context dependency of our results seems to be in line with the reports of Gutteling et al. (2022). When they presented participants with targets of high/low load alongside strong/weak distractors (using salient/masked faces as stimuli), alpha enhancement for strong compared to weak distractors was observed with targets of high but not low load. According to Jensen (2024), alpha as an inhibition mechanism can be driven by the load of goal-relevant information. When there were many targets to be processed (i.e., high load), working memory capacity was nearly exhausted. This would necessitate the discriminating suppression of strong and weak distractors to optimise performance. When there were not many targets to be processed (i.e., low load), working memory capacity left for the distractors was abundant. It could then be that both types of distractors were properly processed by cognitive resources in surplus or that both types of distractors were properly suppressed. Either scenario would obscure the putative difference between strong and weak distractors, which might also explain why previous research using a simple-feature discrimination task failed to find alpha enhancement to distractors (Noonan et al., 2016). Notably, the load theory might favour the former scenario (that both strong and weak distractors were properly processed) (Jensen, 2024). However, the result pattern of the alpha power in the current research seemed to favour the latter scenario (that both strong and weak distractors were properly suppressed), as alpha enhancement did appear for both strong and weak distractors in the 2-target-4-distractor context. Indeed, given the antagonistic relation between the number of targets and distractors here, caution is needed in interpreting the dependence on context. Future research might consider using a factorial design to scrutinise how the number of targets and distractors respectively contribute to the dependence on context.

Moreover, the inhibition-related activity was not restricted to the alpha band but can be seen to spread to the beta band. Recent research suggested that both alpha and beta bursts filter information in and out of working memory but with partially distinct roles (Liljefors et al., 2024). While alpha bursts appear to suppress the sensory processing of unwanted information, beta bursts appear to bar information from sensory processing into working memory and proactively remove information already retained in working memory (Lundqvist et al., 2016, 2018). Future research should explore how alpha and beta activity contribute to different aspects of working memory control to orchestrate the flow of sensory information in working memory according to task demands.

Lastly, the current research used voices of different genders as targets and distractors to ensure a clear distinction between them. While it resembles the experience of group conversations with multiple speakers whose voices are of distinct pitch and timbre, it remains undetermined whether the result pattern of the alpha power can be generalised to settings where targets and distractors share similar characteristics. It will be of interest for future research to systematically examine how the ease to distinguish targets and distractors might modulate the neuronal mechanism for gating.

In conclusion, we showed that alpha oscillations as a neuronal mechanism for gating take place when the distractors are temporally close to the encoding phase. Moreover, this phenomenon seemed to be context-dependent, manifesting in the context of high but not low target-to-distractor ratio. The results extended the inhibition account of alpha oscillations, suggesting that an adaptive mechanism might underlie the

generation of alpha oscillations to protect working memory against distractors.

CRedit authorship contribution statement

Chia-An Tu: Writing – original draft, Visualization, Investigation, Formal analysis, Data curation, Conceptualization. **Tiina Parviainen:** Writing – review & editing, Conceptualization. **Jarmo A. Hämäläinen:** Writing – review & editing, Funding acquisition, Conceptualization. **Yi-Fang Hsu:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Investigation, Funding acquisition, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare no competing interests.

Acknowledgements

This work was supported by Taiwan National Science and Technology Council (Grant Number NSTC 112-2628-H-003-006 and NSTC 113-2628-H-003-001) and Taiwan Ministry of Education (Higher Education Sprout Project Grant Number 113J1E0503) to YFH and the Research Council of Finland (Grant Number 347903) to JAH.

Data availability

Data will be made available on request.

References

- Bonnefond, M., Jensen, O., 2012. Alpha oscillations serve to protect working memory maintenance against anticipated distractors. *Curr. Biol.* 22 (20), 1969–1974. <https://doi.org/10.1016/j.cub.2012.08.029>.
- Bonnefond, M., Jensen, O., 2013. The role of gamma and alpha oscillations for blocking out distraction. *Commun. Integr. Biol.* 6 (1), e22702. <https://doi.org/10.4161/cib.22702>.
- Delorme, A., Makeig, S., 2004. EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *J. Neurosci. Methods* 134 (1), 9–21. <https://doi.org/10.1016/j.jneumeth.2003.10.009>.
- Ellis, D.P.W., 2010. Time-domain scrambling of audio signals in Matlab. <https://www.ee.columbia.edu/~dpwe/resources/matlab/scramble/>.
- Fodor, Z., Marosi, C., Tombor, L., Csukly, G., 2020. Salient distractors open the door of perception: alpha desynchronization marks sensory gating in a working memory task. *Sci. Rep.* 10, 19179. <https://doi.org/10.1038/s41598-020-76190-3>.
- Gutteling, T.P., Sillekens, L., Lavie, N., Jensen, O., 2022. Alpha oscillations reflect suppression of distractors with increased perceptual load. *Prog. Neurobiol.* 214, 102285. <https://doi.org/10.1016/j.pneurobio.2022.102285>.
- Jensen, O., 2024. Distractor inhibition by alpha oscillations is controlled by an indirect mechanism governed by goal-relevant information. *Commun. Psychol.* 2, 36. <https://doi.org/10.1038/s44271-024-00081-w>.
- Jensen, O., Mazaheri, A., 2010. Shaping functional architecture by oscillatory alpha activity: gating by inhibition. *Front. Hum. Neurosci.* 4, 186. <https://doi.org/10.3389/fnhum.2010.00186>.
- Klimesch, W., Sauseng, P., Hanslmayr, S., 2007. EEG alpha oscillations: the inhibition–timing hypothesis. *Brain Res. Rev.* 53 (1), 63–88. <https://doi.org/10.1016/j.brainresrev.2006.06.003>.
- Lavie, N., 2005. Distracted and confused?: selective attention under load. *Trends Cognit. Sci.* 9, 75–82. <https://doi.org/10.1016/j.tics.2004.12.004>.
- Leiberg, S., Lutzenberger, W., Kaiser, J., 2006. Effects of memory load on cortical oscillatory activity during auditory pattern working memory. *Brain Res.* 1120 (1), 131–140.
- Liljefors, J., Almeida, R., Rane, G., Lundström, J.N., Herman, P., Lundqvist, M., 2024. Distinct functions for beta and alpha bursts in gating of human working memory. *Nat. Commun.* 15, 8950.
- Lundqvist, M., Rose, J., Herman, P., Brincat, S.L., Buschman, T.J., Miller, E.K., 2016. Gamma and beta bursts underlie working memory. *Neuron* 90, 152–164.
- Lundqvist, M., Herman, P., Warden, M.R., Brincat, S.L., Miller, E.K., 2018. Gamma and beta bursts during working memory readout suggest roles in its volitional control. *Nat. Commun.* 9, 394.
- McNab, F., Klingberg, T., 2008. Prefrontal cortex and basal ganglia control access to working memory. *Nat. Neurosci.* 11, 103–107. <https://doi.org/10.1038/nn2024>.
- Miller, E.K., Lundqvist, M., Bastos, A.M., 2018. Working memory 2.0. *Neuron* 100 (2), 463–475. <https://doi.org/10.1016/j.neuron.2018.09.023>.
- Noonan, M.P., Adamian, N., Pike, A., Printzlau, F., Crittenden, B.M., Stokes, M.G., 2016. Distinct mechanisms for distractor suppression and target facilitation. *J. Neurosci.* 36 (6), 1797–1807. <https://doi.org/10.1523/JNEUROSCI.2133-15.2016>.

- Noonan, M.P., Crittenden, B.M., Jensen, O., Stokes, M.G., 2018. Selective inhibition of distracting input. *Behav. Brain Res.* 355, 36–47. <https://doi.org/10.1016/j.bbr.2017.10.010>.
- Proskovec, A.L., Heinrichs-Graham, E., Wilson, T.W., 2019. Load modulates the alpha and beta oscillatory dynamics serving verbal working memory. *Neuroimage* 184, 256–265.
- Roux, F., Uhlhaas, P.J., 2014. Working memory and neural oscillations: alpha–gamma versus theta–gamma codes for distinct WM information? *Trends Cognit. Sci.* 18 (1), 16–25. <https://doi.org/10.1016/j.tics.2013.10.010>.
- Sghirripa, S., Graetz, L., Merkin, A., Rogasch, N.C., Ridding, M.C., Semmler, J.G., Goldsworthy, M.R., 2021. The role of alpha power in the suppression of anticipated distractors during verbal working memory. *Brain Topogr.* 34, 102–109. <https://doi.org/10.1007/s10548-020-00810-4>.
- Weisz, N., Hartmann, T., Müller, N., Obleser, J., 2011. Alpha rhythms in audition: cognitive and clinical perspectives. *Front. Psychol.* 2, 73. <https://doi.org/10.3389/fpsyg.2011.00073>.
- Weisz, N., Kraft, N.G., Demarchi, G., 2020. Auditory cortical alpha/beta desynchronization prioritizes the representation of memory items during a retention period. *Elife* 9, e55508. <https://doi.org/10.7554/eLife.55508>.
- Zhou, Y.J., Ramchandran, A., Haegens, S., 2023. Alpha oscillations protect working memory against distracters in a modality-specific way. *Neuroimage* 278, 120290. <https://doi.org/10.1016/j.neuroimage.2023.120290>.