Author(s): Hsu, Yi-Fang; Hämäläinen, Jarmo A.

Title: Load-dependent alpha suppression is related to working memory capacity for numbers

Year: 2022

Version: Accepted version (Final draft)

Please cite the original version:

Hsu, Y.-F., & Hämäläinen, J. A. (2022). Load-dependent alpha suppression is related to working memory capacity for numbers. Brain Research, 1791, Article 147994. https://doi.org/10.1016/j.brainres.2022.147994

Title

Load-dependent alpha suppression is related to working memory capacity for numbers

Running head

Alpha correlates with working memory

Author names and affiliations

Yi-Fang Hsu (yi-fang.hsu@cantab.net) [a,b]
Jarmo A. Hämäläinen (jarmo.a.hamalainen@jyu.fi) [c]

[a] Department of Educational Psychology and Counselling, National Taiwan Normal University, 106308 Taipei, Taiwan
[b] Institute for Research Excellence in Learning Sciences, National Taiwan Normal University, 106308 Taipei, Taiwan
[c] Jyväskylä Centre for Interdisciplinary Brain Research, Department of Psychology, University of Jyväskylä, 40014 Jyväskylä, Finland

Corresponding author: Yi-Fang Hsu (yi-fang.hsu@cantab.net) (+886-2-7749-3764)

Author contributions

Y-FH: Conceptualization, Investigation, Methodology, Formal Analysis, Writing-original draft, Writing-review & editing, Visualization, Funding acquisition.
JAH: Conceptualization, Methodology, Writing-review & editing.

Author notes

This work was supported by Taiwan Ministry of Science and Technology (grant number MOST110-2636-H-003-001 and MOST111-2636-H-003-001) to Y-FH. We thank Miss S-H Lee and Mr C-A Tu for assistance with EEG data collection.

The authors declare no competing financial interests.

Abstract

Alpha suppression is proposed to reflect a surge in cortical excitability to enhance stimulus processing in working memory. The attenuated state of alpha might reflect the prioritisation of behaviourally relevant information, making it a proxy for working memory functioning. Despite the growing interest in utilising the advancement of brain-based measures to evaluate individuals' cognitive processes, there was a lack of consistent evidence on the relationship between alpha suppression and working memory performance. To investigate whether interindividual differences in alpha suppression might be related to variability in working memory capacity, we recorded participants' electroencephalography (EEG) while they performed an arithmetic task of either low or high working memory load. Participants were required to calculate either the product of digits (i.e., low-load condition) or the difference between the product of digits (i.e., high-load condition). We found alpha suppression at parietal regions, which became more prominent as working memory load increased. The pattern was present in approximately 80% of the participants. Importantly, the more the alpha suppressed as working memory load increased, the larger the drops in behavioural performance and the lower the Digit Span score. That is, alpha suppression was more prominent in participants of poor working memory capacity. Our findings suggest that alpha activity, subject to interindividual differences in sensitivity, could serve as a brain-based measure of an individual's working memory functioning.

Keywords: neural oscillations; alpha; working memory; electroencephalography (EEG)

1. Introduction

Oscillatory activity in the alpha band (8-12 Hz) is one of the most prominent components of neural oscillations in the human brain. It is commonly reported to play an important role in the sensory engagement, as its power decreases in task-relevant areas (e.g., visual: Thut et al., 2006; auditory: Wöstmann et al., 2016, 2019; somatosensory: Haegens et al., 2011). It is therefore hypothesised that attenuated alpha power reflects the releases of task-relevant areas from inhibition (Roux et al., 2014; Klimesch, 2012). Electroencephalography (EEG) and magnetoencephalography (MEG) research further showed that pre-stimulus alpha power over posterior regions decreased in rhythmic relative to arrhythmic condition in a temporal attention task (Rohenkohl et al., 2011). Moreover, smaller amplitude in pre-stimulus alpha power seemed to be associated with better perceptual performance (visual: van Dijk et al., 2008; Grabot et al., 2020; somatosensory: Jones et al., 2010; van Ede et al., 2012). These findings suggest that the attenuated states of alpha oscillations reflect an anticipatory mechanism for resource allocation to prioritise task-relevant information in working memory (WM) (van Ede, 2018). The power decrease might reduce common noise fluctuations between neurons, which increases the coding capacity of the neuronal population (Zohary et al., 1994).

The idea that alpha oscillations are important for WM function received more direct support from studies using a variety of verbal and spatial tasks, which commonly found that posterior alpha decreased as WM load increased. For example, Gevins et al. (1997) used an n-back task where participants had to decide whether the letter stimulus on each trial matched with either the identity of a designated letter stimulus (i.e., 0-back, easy condition) or the identity of a letter stimulus occurring three trials back (i.e., 3-back, difficult condition). They found decreased centroparietal alpha as WM load increased. Pesonen et al. (2007) also used an n-back task of letter stimuli with varying WM load from 0-back to 3-back. They found event-related desynchronization in alpha across the scalp for all WM load conditions, which became steadily longer in time as WM load increased. Stipacek et al. (2003) examined participants' responses in a forward span task (where participants had to memorise sets of digits) and a counting span task (where participants had to count a specified subgroup of digits and memorise the answer), when set size varied from 3 to 5 items. They found that event-related desynchronization in the upper alpha band across the scalp (larger in posterior than anterior regions) showed further decrease as WM load increased in both tasks. Similar findings were demonstrated with spatial WM tasks (Gundel et al., 1992; Sauseng et al., 2005).

Partially converging results were reported in studies using a Sternberg-like task where participants were presented with a variable array of stimuli as a manipulation of WM (for encoding), a delay (for retention), and a probe when they had to decide whether the probe matched with the array of stimuli (Jensen et al., 2002; Meltzer et al., 2007; Tuladhar et al., 2007; Michels et al., 2008; Grimault et al., 2009; Crespo-Garcia et al., 2013; Proskovec et al., 2019a; Koshy et al., 2020). It was commonly reported that, during encoding, there was parietal alpha desynchronization which showed further decrease in power as WM load increased (Meltzer et al., 2007; Grimault et al., 2009; Proskovec et al., 2019a). Conversely, during retention, the effect of WM load seems less consistent (Meltzer et al., 2007). Some studies

demonstrated alpha power desynchronization which showed further decrease in power as WM load increased (Koshy et al., 2020). Some studies demonstrated alpha power synchronization which became either less pronounced (Crespo-Garcia et al., 2013) or more pronounced (Jensen et al., 2002; Tuladhar et al., 2007; Grimault et al., 2009; Proskovec et al., 2019a) as WM load increased. Michels et al. (2008) further reported both less and more pronounced alpha power synchronization during retention linked to individual variation. Specifically, there was a distinction between participants in two subgroups. In one half of the participants (showing relatively lower peak frequency of alpha), alpha power synchronization decreased with WM load. In another half of the participants (showing relatively higher peak frequency of alpha), alpha power synchronization increased with WM load.

Together, the aforementioned studies converged on the finding of load-dependent alpha suppression in a variety of WM tasks that combine encoding and retention phases as well as in a Sternberg-like task during encoding but not necessarily retention phase. Since decrease in alpha power was associated with increases in WM load, it is proposed that alpha suppression reflects a surge in cortical excitability to enhance stimulus processing. The attenuated state of alpha might reflect the prioritisation of behaviourally relevant information to support WM functioning (van Ede, 2018).

Nevertheless, it remains largely understudied whether there are interindividual differences in alpha suppression which potentially explains variability in WM performance. This is particularly intriguing considering there is an increased interest in utilising the advancement of brain-based measures, in parallel to standardized psychological tests, to evaluate individuals' cognitive processes. While a Sternberg-like task was commonly adopted to look into this issue, there was a lack of consistent evidence on the relationship between alpha suppression and WM performance. Some studies, on the one hand, failed to report significant load-related alpha suppression but still examined the relation between alpha suppression and WM performance. For example, Proskovec et al. (2019b) recruited 22 healthy adults and found significant clusters of alpha suppression (relative to baseline) peaking at posterior regions across WM loads throughout encoding and retention. Meanwhile, the stronger the alpha suppression at inferior frontal gyrus (IFG) from low-load to high-load trials (reflecting active recruitment of this region), the smaller the performance decrement from low-load to high-load trials. In other words, individuals who showed stronger alpha suppression in the IFG tended to have more preserved performance as WM load increased. The results suggested that load-sensitive alpha oscillations are central to successfully meeting the demands of WM task. In contrast, Pavlov et al. (2020) recruited 156 healthy adults as participants. They reported alpha suppression during encoding and alpha enhancement during retention (relative to baseline) across WM loads over posterior regions. However, alpha suppression during encoding was not explored further and alpha enhancement during retention was not related to participants' WM performance. Some studies, on the other hand, demonstrated significant load-related alpha suppression but cannot find the relation between alpha suppression and WM performance. Sghirripa et al. (2020) recruited 24 younger and 30 older adults as participants. During encoding and retention, they found that alpha suppression was modulated by WM load, showing decreased alpha power as

WM load increased. However, individual differences in alpha power did not predict participants' WM performance. Overall, despite the postulation that alpha suppression might actively support WM function, there seems to be a lack of link between the WM-related attenuation of alpha over posterior regions and individuals' WM performance when a Sternberg-like task was used, probably due to the inconsistent finding of load-related alpha suppression in the first place. Could we observe a correlation between alpha suppression and WM capacity using the WM tasks that combine encoding and retention phases, where the finding of load-dependent alpha suppression was more robust?

To investigate whether alpha suppression might be related to WM capacity, we recorded participants' EEG while they performed an arithmetic task, which is more similar to the WM tasks that combine encoding and retention phases than the Sternberg-like task. Participants were required to calculate either the product of digits (i.e., low-load condition) or the difference between the product of digits (i.e., high-load condition), the cognitive underpinnings of which are noted to heavily involve WM (Logie et al., 1994; Cragg et al., 2017; Zhang et al., 2017). On the basis of previous literature documenting robust effect of alpha suppression in WM tasks that combine encoding and retention phases, we expected to see load-related alpha suppression at posterior regions which correlates with WM capacity. Confirming our hypothesis, we found alpha suppression at parietal regions, which became more prominent as WM load increased. The pattern was present in approximately 80% of the participants. Importantly, the more the alpha suppressed as WM load increased, the larger the drops in behavioural performance and the lower the scores in the Digit Span subtest in Wechsler Adult Intelligence Scale-Fourth Edition (WAIS-IV). That is, alpha suppression was more prominent in participants of poor WM capacity. The results suggest that alpha oscillations, subject to interindividual differences in sensitivity, could serve as a brain-based measure to indicate individual's WM capacity.

2. Results

2.1. Behavioural performance

We detected and removed 3 outliers in either overall accuracy or overall RT (using the rmoutliers function in Matlab), leaving 35 participants in the sample. On accuracy, there was a significant load x probe interaction ($F(1,34) = 8.27$, $p < 0.01$, $\eta_p^2 = 0.20$). Nevertheless, paired samples t-test (using a Bonferroni-adjusted $p = 0.05/2 = 0.025$ for post hoc comparisons) showed that accuracy was higher in low-load than high-load for both same-probe ($t(34) = 6.57$, $p < 0.001$) and different-probe ($t(34) = 5.03$, $p < 0.001$). On RT, there was no load x probe interaction. However, there was a significant main effect of load ($F(1,34) = 60.63$, $p < 0.001$, $\eta_p^2 = 0.64$) where low-load < high-load and a significant main effect of probe ($F(1,34) = 11.81$, $p < 0.01$, $\eta_p^2 = 0.26$) where same-probe < different-probe (**Figure 1A**).

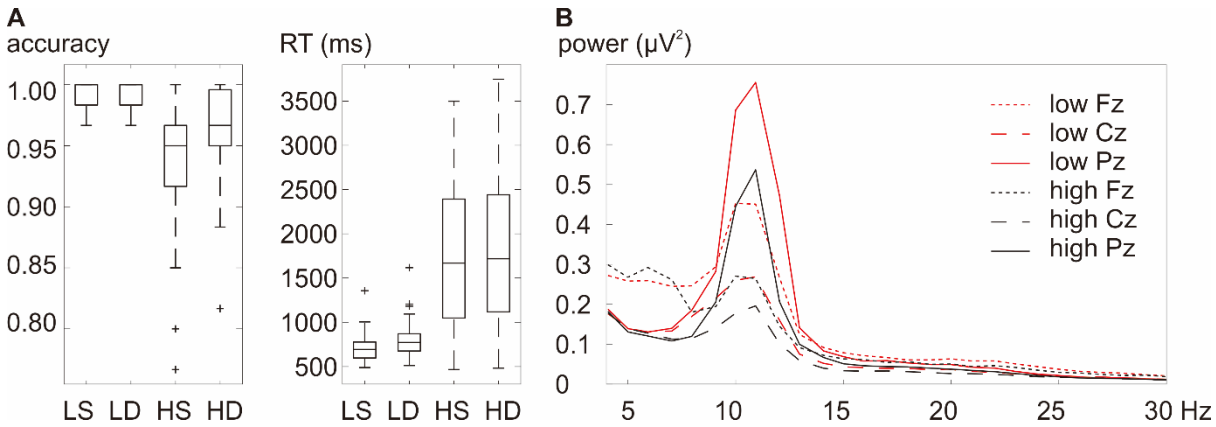

Figure 1. (A) Effects of WM load and same/different probe on participants' accuracy and RT. On each box, the central mark indicates the median, and the bottom and top edges of the box respectively indicate the 25th and 75th percentiles. The whiskers extend to the most extreme data points not considered outliers while the outliers are marked with the + symbol. LS: low-load same-probe; LD: low-load different probe; HS: high-load same-probe; HD: high-load different-probe. **(B)** Grand-averaged power spectra in low-load and high-load conditions on 3 midline electrodes (i.e., Fz, Cz, Pz) (N = 35).

2.2. EEG

2.2.1. Power spectra

Figure 1B shows the power spectra in low-load and high-load conditions on 3 midline electrodes (i.e., Fz, Cz, Pz) when participants' mental calculation took place. Relative to low-load condition, high-load condition was associated with attenuated alpha power.

2.2.2. Time-frequency representations

Time-frequency analysis revealed spectral power decrease across alpha and beta band (12-30 Hz) at parietal regions in both low-load and high-load conditions (**Figure 2A**). One-way analysis of variance (ANOVA) using permutation statistics with false discovery rate (FDR) correction showed that, relative to low-load condition, high-load condition was associated with more prominent spectral power decrease across upper (10-12 Hz) but not lower (8-10 Hz) alpha band over 1000-3000 ms, which can be seen in the left but not right parietal regions.

Therefore, we separately compared the topographical distributions of upper (**Figure 2B** upper panel) and lower (**Figure 2B** lower panel) alpha band activity in low-load and high-load conditions at 0-1000 ms, 1000-2000 ms, and 2000-3000 ms. The difference between conditions can be seen over 1000-3000 ms across upper alpha band at parietal regions, particularly on 3 parietal electrodes (i.e.,CP1, P3, P1).

Considering that time-frequency analysis also revealed spectral power decrease in the beta band, for exploratory purpose, we also compared its topographical distributions in low-load and high-load conditions at 0-1000 ms, 1000-2000 ms, and 2000-3000 ms. The difference between conditions can be seen over 1000-3000 ms around centroparietal regions (**Figure 2C**).

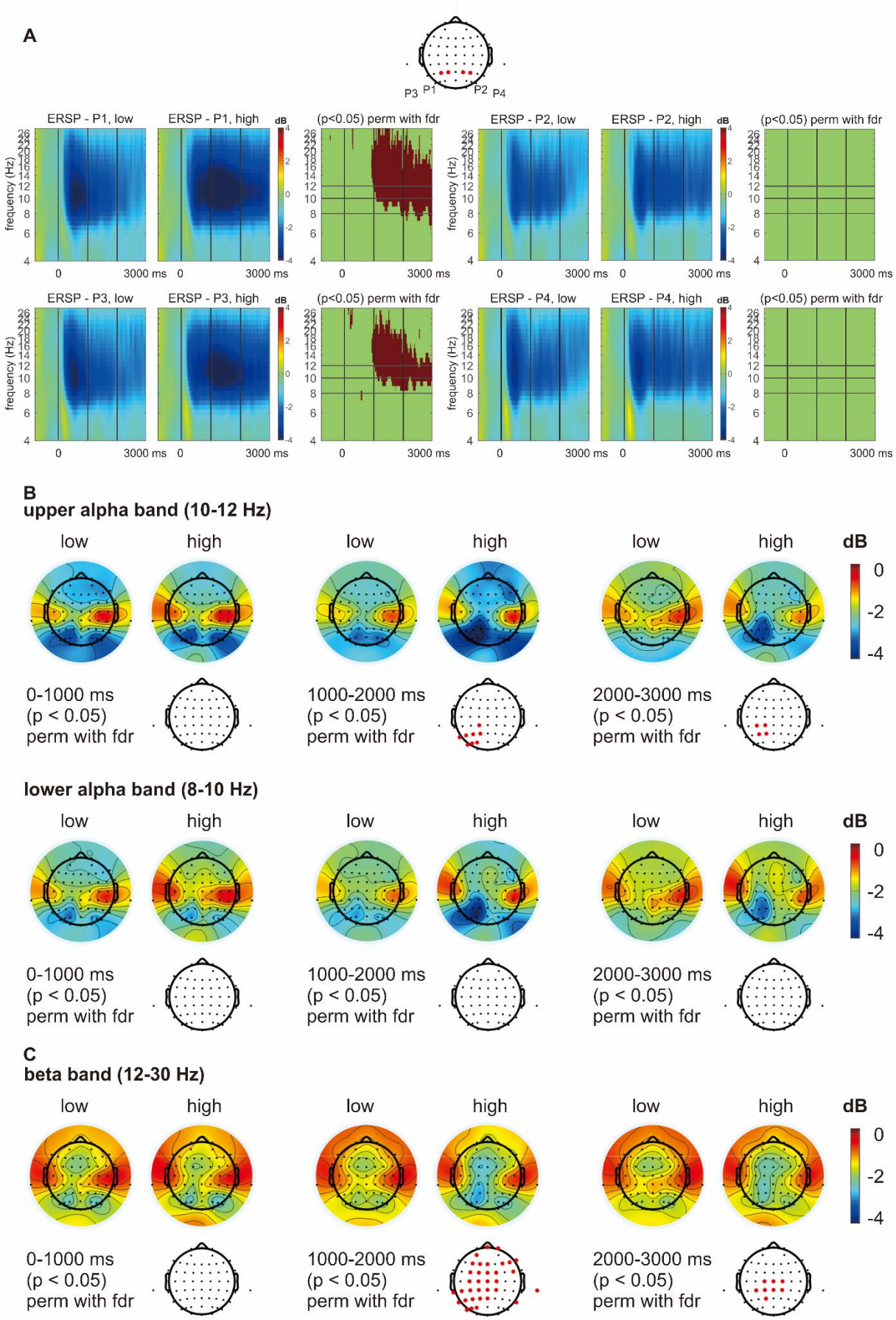
A
P3 P1 P2 P4
ERSP - P1, low
ERSP - P1, high
(p<0.05) perm with fdr
ERSP - P2, low
ERSP - P2, high
(p<0.05) perm with fdr
ERSP - P3, low
ERSP - P3, high
(p<0.05) perm with fdr
ERSP - P4, low
ERSP - P4, high
(p<0.05) perm with fdr
frequency (Hz)
dB
0
3000 ms
B
upper alpha band (10-12 Hz)
low
high
dB
0
-2
-4
0-1000 ms
(p < 0.05)
perm with fdr
1000-2000 ms
(p < 0.05)
perm with fdr
2000-3000 ms
(p < 0.05)
perm with fdr
lower alpha band (8-10 Hz)
C
beta band (12-30 Hz)

Figure 2. (A) Grand-averaged time-frequency representations on 4 parietal electrodes (i.e., P1, P3, P2, P4; marked as red dots) for low-load and high-load conditions. Spectral power decreases across alpha band in both low-load and high-load conditions. The difference between two conditions can be seen across upper (10-12 Hz) but not lower (8-10 Hz) alpha band and appears to be lateralised, showing significant difference at the left but not right parietal regions. **(B)** Topographical distributions of upper (upper panel) and lower (lower panel) alpha band activity in low-load and high-load conditions at 0-1000 ms, 1000-2000 ms, and 2000-3000 ms. Electrodes showing significant differences between conditions are marked as red dots. The difference between conditions can be seen over 1000-3000 ms across upper alpha band at parietal regions, particularly on 3 parietal electrodes (i.e.,CP1, P3, P1). **(C)** Exploratory analyses on the topographical distributions of beta band activity in low-load and high-load conditions at 0-1000 ms, 1000-2000 ms, and 2000-3000 ms. Electrodes showing significant differences between conditions are marked as red dots. The difference between conditions can be seen over 1000-3000 ms around centroparietal regions (N = 35).

2.2.3. Correlations between alpha power difference and WM

Since significant difference between conditions was identified over 1000-3000 ms across 3 parietal electrodes (i.e.,CP1, P3, P1) at upper alpha band, we calculated the power difference between conditions here (min = -2.59, max = 11.16, mean = 1.40, SD = 2.24), where 28/35 participants showed alpha suppression in both conditions, which became more prominent as WM load increased. We further detected and removed 1 outlier in alpha power difference (using the rmoutliers function in Matlab) and examined whether the alpha power difference between conditions might correlate with (1) participants' behavioural difference in the arithmetic task between low-load and high-load conditions and (2) participants' total raw score in the Digit Span subtest in a sample of 34 participants.

Alpha power difference significantly correlated with accuracy difference ($\rho = 0.41$, $p < 0.05$, **Figure 3 left**) and RT difference ($\rho = -0.40$, $p < 0.05$, **Figure 3 middle**) in the arithmetic task. Alpha power difference also significantly correlated with Digit Span score ($\rho = -0.55$, $p < 0.001$, **Figure 3 right**). The more the alpha power decreased with WM load, the larger the accuracy decrease from low-load to high-load condition, the larger the RT increase from low-load to high-load condition, and the lower the Digit Span score.

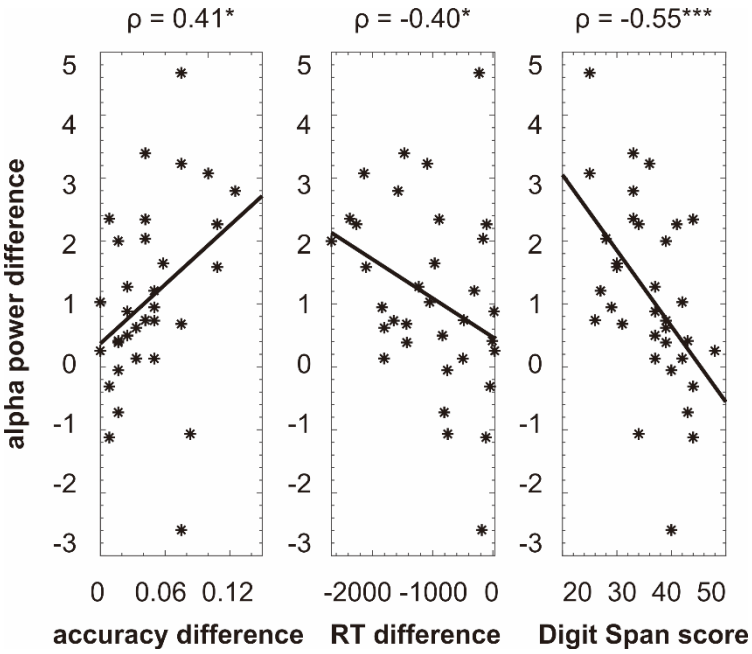

Figure 3. Scatterplots representing the correlation between alpha power difference and behavioural performance on the arithmetic task (including accuracy and RT difference) as well as Digits Span score (*p < 0.05, ***p < 0.001) (N = 34).

3. Discussion

Alpha suppression is proposed to reflect a surge in cortical excitability to enhance stimulus processing. To investigate whether interindividual differences in alpha suppression might be related to variability in WM capacity, we recorded participants' EEG while they performed an arithmetic task of either low or high WM load. We found alpha suppression at parietal regions, which became more prominent as WM load increased. The pattern was present in approximately 80% of the participants. Importantly, the more the alpha suppressed as WM load increased, the larger the drops in behavioural performance and the lower the scores in the Digit Span subtest in WAIS-IV. That is, alpha suppression was more prominent in participants of poor WM capacity.

3.1. Load-dependent alpha suppression in mental calculation

Earlier studies adopting a variety of WM tasks that combine encoding and retention phases commonly found that posterior alpha decreased as WM load increased (Gundel et al., 1992; Gevins et al., 1997 Stipacek et al., 2003; Sauseng et al., 2005; Pesonen et al., 2007). Later studies using a Sternberg-like task that differentiates between encoding and retention phases also found alpha suppression as WM load increased during encoding, while the effect of WM load during retention seems less consistent (Meltzer et al., 2007; Michels et al., 2008; Crespo-Garcia et al., 2013; Grimault et al., 2009; Proskovec et al., 2019a; Koshy et al., 2020). Our results that posterior alpha decreased as WM load increased replicated the aforementioned findings, confirming the idea that alpha suppression reflects the active support of WM function.

Interestingly, the load-dependent alpha suppression was found in the left but not right parietal regions, across upper but not lower alpha band. The lateralization of the effect was difficult to interpret due to the poor spatial resolution of EEG. On the other hand, the narrow-band responses can be interpreted within the framework of functional specialization of upper and lower alpha, where previous studies reported distinct patterns of alpha desynchronization when its broad frequency range was subdivided into sub-bands (Klimesch, 1999). While the upper alpha band was most sensitive to the encoding of task-specific information (Klimesch et al., 1997a, 1997b), the lower alpha band was found to reflect general task demands such as attentional processes (Klimesch et al., 1998). Therefore, our finding of the load-dependent alpha suppression across upper but not lower alpha band can be considered as reflecting task-specific processes such as numerical WM but not attentional demands such as alertness and expectancy.

3.2. Load-dependent alpha suppression as a proxy for WM capacity

Could alpha suppression be used as a proxy for cognitive test? In recent years there is an increased interest in utilising oscillatory activity as a measure to evaluate individuals' cognitive processes. However, the interindividual differences were relatively understudied. In the current research, we reported the interindividual differences on time-frequency representations. Specifically, approximately 80% of the participants showed alpha suppression in both conditions, which became more prominent as WM load increased. The existence of interindividual differences accords with two previous studies using a Sternberg-like task to examine the role of alpha activity in WM retention. Meltzer et al. (2007) found that, during retention, the effect of WM load on posterior alpha power manifested as decrease in one half and increase in another half of the participants. Michels et al. (2008) found that, during retention, there was a distinction between participants in two subgroups. In one half of the participants (showing relatively lower peak frequency of alpha), alpha decreased with WM load which might reflect the release of inhibition associated with attentional demands. In another half of the participants (showing relatively higher peak frequency of alpha), alpha increased with WM load which might reflect active inhibition of task-irrelevant areas. Together, these findings suggest that participants might express different types of alpha-related processes.

In addition to the interindividual differences on time-frequency representations, the current research further demonstrated a negative correlation between alpha suppression and individual's WM capacity. Alpha suppression was more prominent in participants showing larger drops in behavioural performance as WM load increased and lower scores in the Digit Span subtest, that is, in participants of poor WM capacity. The findings suggested that alpha suppression, subject to interindividual differences in sensitivity, could serve as a brain-based measure of an individual's WM functioning.

Intriguingly, the result pattern is in contrast with that in Proskovec et al. (2019b), which is to our knowledge the only report of significant correlation between alpha suppression and WM performance. Using MEG, they found that individuals who showed stronger alpha suppression

at IFG tended to have more preserved performance as WM load increased, suggesting that load-sensitive alpha activity is central to successfully meeting the demands of WM task. We speculate that the discrepancy can be attributed to at least three reasons.

First, the inconsistent findings might be related to the fact that we correlated parietal alpha suppression, whereas Proskovec et al. (2019b) correlated frontal alpha suppression with WM performance. It remains undetermined whether parietal and frontal alpha activity are interdependent phenomenon. In fact, alpha activity is thought to reflect a complex product of both thalamocortical and corticocortical interactions in visual cortex (Halgren et al., 2019). Therefore, alpha activity generated in different regions of the brain should not be considered as a singular phenomenon but might reflect a number of distinct neural processes (Clayton et al., 2018).

Second, the inconsistent findings might be related to the fact that we focused on verbal WM, whereas Proskovec et al. (2019b) focused on spatial WM. Indeed, significant load-related alpha suppression has been documented in studies using either verbal WM tasks (Gevins et al., 1997; Stipacek et al., 2003; Meltzer et al., 2007; Pesonen et al., 2007; Koshy et al., 2020; Michels et al., 2008; Proskovec et al., 2019a) or spatial WM tasks (Gundel et al., 1992; Sauseng et al., 2005; Crespo-Garcia et al., 2013; Grimault et al., 2009). Nevertheless, since verbal and spatial WM are associated with distinct theoretical conceptualization as well as separate neural structures (Smith & Koeppe, 1996), they might as well be supported by different alpha behaviours.

Third, the inconsistent findings might be related to the fact that we used an arithmetic task which is more similar to the WM tasks that combine encoding and retention phases, whereas Proskovec et al. (2019b) used a Sternberg-like task. Specifically, we utilised an arithmetic task to mimick how mental calculation takes place in everyday situations, when one would immediately start the numerical operations involving recursive phases of encoding and retention. Here, WM load was manipulated by changing the amount of numerical operations to perform. The low-load condition required participants to calculate the product of digits (entailing one multiplication, i.e., one set of numerical operations). The high-load condition required participants to calculate the difference between the product of digits (entailing two multiplications followed by one subtraction, i.e., three sets of numerical operations). Therefore, the low-load and high-load conditions likely contained different amounts of recursive encoding-retention cycle. In contrast, Proskovec et al. (2019b) presented participants with load-varying grids to encode and retain. In other words, WM load was manipulated by changing the amount of information within a single encoding-retention procedure. It is possible that the two types of processes are associated with different alpha responses.

3.3. Spectral power decrease in the beta band

Our time-frequency analysis showed that the load-dependent spectral power decrease also extended from the alpha to the beta band. In fact, spectral power decrease across alpha and beta band has been interpreted to reflect memory formation (Hanslmayr et al., 2009, 2011).

Hanslmayr et al. (2016) further suggested that such low-frequency desynchronization in the neocortex might serve to mediate the representation of different information during encoding, including nonverbal and verbal materials. While it remains an open question whether there are differential alpha and beta processes that support the prioritisation of different information in WM, we speculate that the concomitant power decrease across alpha and beta band might be related to the fact that mental calculation can involve a combination of nonverbal and verbal processing (Clearman et al., 2017).

3.4. Limitations and implications

One limitation of the current research is that it cannot distinguish between the effects of WM load and cognitive effort. While some studies equate the two concepts from a theoretical perspective, some studies suggested that WM load and cognitive effort to be separable, as participants have limited capacity in WM load but can exert cognitive effort in the absence of performance gains (Kardan et al., 2020). In order to delineate the relationship between WM load and cognitive effort in arithmetic task, one future direction is to have more levels of WM load to reveal whether alpha suppression plateaus (reflecting WM load) or continues (reflecting cognitive effort) as WM load increases. Nevertheless, as informative first steps, the current research with two levels of WM load is suitable for application in studies on the development of numerical skills in childhood, for example, to give indications on how alpha suppression might change in parallel to achievement level in arithmetic learning.

3.5. Conclusion

Overall, we demonstrated in an arithmetic task that alpha suppression at parietal regions became more prominent as WM load increased. Moreover, load-dependent modulation of alpha oscillations correlated with one's WM capacity. It seems that alpha activity, subject to interindividual differences in sensitivity, could serve as a brain-based measure of an individual's WM functioning. The results highlight the importance of devising new methods to further characterise the alpha-related WM processes in different individuals.

4. Experimental Procedure

4.1. Participants

A total of 38 healthy volunteers (age: mean = 22.89, SD = 3.71; 13 males; 36 right-handed) participated in the experiment with no history of neurological, neuropsychiatric, or visual/hearing impairments as indicated by self-report. Participants gave written informed consent and were paid for participation. The study was conducted in accordance with the Declaration of Helsinki and approved by the Research Ethics Committee at National Taiwan Normal University.

Their WM was measured with the Digit Span subtest in WAIS-IV. Participants were to repeat the numbers in the same order (digit span forward, DSF), repeat the numbers in reverse order (digit span backward, DSB), or repeat the numbers in numerical order (digit span sequencing, DSS). The sum of the DSF, DSB, and DSS raw scores serves as an index of WM capacity (**Table 1**).

Table 1. Range, mean, and SD of participants' raw scores in the Digit Span subtest (N = 38).

	DSF	DSB	DSS	Total
Min	11	5	6	25
Max	16	16	16	48
Mean	14.32	10.87	10.61	35.79
SD	1.76	3.17	2.14	5.96

4.2. Procedures

A total of 240 trials were presented in 6 blocks. Each trial contained a horizontally arranged list of four digits (e.g., 7 5 4 2) displayed in grey against black background at the centre of a computer monitor for 3000 ms (**Figure 4**). Participants were instructed at the beginning of each block the mental calculation to perform. In half of the blocks, participants had to calculate the product of the first and the last digits (e.g., 7 x 2 = 14) (i.e., low-load condition). In the other half of the blocks, participants had to calculate the difference between the product of the first two digits and the product of the last two digits (e.g., 7 x 5 - 4 x 2 = 27) (i.e., high-load condition). Block order was randomised across participants. The list of four digits was followed by a probe when participants were instructed to make a same-different judgement on whether their answer matched the probe. 50% of the probes called for a same response and 50% of the probes called for a different response. Participants' response was followed by a jittered ITI of 1200-1400 ms when a grey fixation cross against black background was shown. E-prime version 2.0 (Psychology Software Tools) was used for stimulus presentation. Stimulation was randomised individually for each participant.

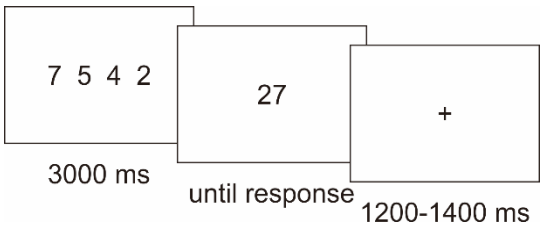

Figure 4. Schematic illustration of a trial. Each trial began with a horizontally arranged list of four digits presented for 3000 ms (i.e., the time window of interest). Participants had to calculate either the product of the first and the last digits (in low-load condition) or the difference between the product of the first two digits and the product of the last two digits (in high-load condition). The list was followed by a probe when participants were instructed to make a same-different judgement on whether their answer matched the probe. Participants' response was followed by a jittered ITI of 1200-1400 ms.

4.3. Data recording and analysis

4.3.1. EEG recording and pre-processing

EEG was recorded from 62 sintered Ag/AgCl electrodes on a Neuroscan quik-cap according to the extended 10-20 system. The ground electrode was placed at AFz and the reference electrode was placed between Cz and CPz. Eye movements were monitored by additional 4

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 electro-oculogram (EOG), respectively. All signals were amplified and online filtered at 0.1-100 Hz with the Neuroscan Synamps 2 amplifier (Compumedics Neuroscan, USA) and sampled at 500 Hz.

Ocular artefact correction was conducted with independent component analysis (ICA) in EEGlab (Delorme & Makeig, 2004). Epochs were extracted (from correct trials only) from -1200 to 4198 ms relative to the onset of the list, using the average of the entire epoch as baseline (i.e., demean). The epoch covered 1200 ms before and 1200 ms after the time window of interest (when a list of four digits was presented for 3000 ms) to avoid the effect of edge distortion in spectral analysis. Bad electrodes were identified (if 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 in each condition after all pre-processing are listed in **Table 2**.

Table 2. Range, mean, and SD of trial numbers after artefact rejection in each condition (N = 38).

	Low-load	High-load
Min	60	64
Max	120	115
Mean	98.97	94.26
SD	14.34	16.83

4.3.2. Spectral analysis

To examine the frequency content in the data, FieldTrip toolbox (Oostenveld et al., 2011) was used to estimate the power spectra on the 3000 ms segments when participants' mental calculation took place. Spectral power from 4 to 30 Hz was computed using a fast Fourier transform with a Hanning window.

To examine the time course of the frequency content, EEGlab (Delorme & 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 ERSP, 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 from -1200 to 4198 ms (i.e., 5398-ms long) and the baseline from -800 to -300 ms (i.e., 500-ms long). To estimate the effect of WM load (i.e., low-load versus high-load, collapsed across same/different probe), we performed one-way ANOVA using permutation statistics with FDR correction. The p-value threshold was set at 0.05 and randomization was set at 2000.

To examine the correlations between alpha suppression and WM capacity, we calculated the Spearman's correlation between alpha power difference (between conditions over significant

time window across significant electrodes) and (1) participants' behavioural difference in the arithmetic task between conditions and (2) participants' total raw score in the Digit Span subtest.

References

Clayton, M. S., Yeung, N., &Cohen Kadosh, R. (2018). The many characters of visual alpha oscillations. *European Journal of Neuroscience, 48*(7), 2498–2508). https://doi.org/10.1111/ejn.13747

Clearman, J., Klinger, V., &Szűcs, D. (2017). Visuospatial and verbal memory in mental arithmetic. *Quarterly Journal of Experimental Psychology, 70*(9), 1837–1855.

Cragg, L., Richardson, S., Hubber, P. J., Keeble, S., &Gilmore, C. (2017). When is working memory important for arithmetic? The impact of strategy and age. *PloS one, 12*(12), e0188693. https://doi.org/10.1371/journal.pone.0188693

Crespo-Garcia, M., Pinal, D., Cantero, J. L., Díaz, F., Zurrón, M., &Atienza, M. (2013). Working memory processes are mediated by local and long-range synchronization of alpha oscillations. *Journal of Cognitive Neuroscience, 25*(8), 1343–1357. https://doi.org/10.1162/jocn_a_00379

Delorme, A., &Makeig, S. (2004). EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods, 134*(1), 9–21. https://doi.org/10.1016/J.JNEUMETH.2003.10.009

Gevins, A., Smith, M. E., McEvoy, L., &Yu, D. (1997). High-resolution EEG mapping of cortical activation related to working memory: effects of task difficulty, type of processing, and practice. *Cerebral Cortex, 7*(4), 374–385.

Grabot, L., &Kayser, C. (2020). Alpha activity reflects the magnitude of an individual bias in human perception. *Journal of Neuroscience, 40*(17), 3443–3454. https://doi.org/10.1523/JNEUROSCI.2359-19.2020

Grimault, S., Robitaille, N., Grova, C., Lina, J. M., Dubarry, A. S., &Jolicoeur, P. (2009). Oscillatory activity in parietal and dorsolateral prefrontal cortex during retention in visual short-term memory: Additive effects of spatial attention and memory load. *Human Brain Mapping, 30*(10), 3378–3392. https://doi.org/10.1002/hbm.20759

Gundel, A., &Wilson, G. F. (1992). Topographical Changes in the Ongoing EEG Related to the Difficulty of Mental Tasks. *Brain Topography, 5*(1), 17–25.

Haegens, S., Händel, B. F., &Jensen, O. (2011). Top-down controlled alpha band activity in somatosensory areas determines behavioral performance in a discrimination task. *Journal of Neuroscience, 31*(14), 5197–5204. https://doi.org/10.1523/JNEUROSCI.5199-10.2011

Halgren, M., Ulbert, I., Bastuji, H., Fabó, D., Eröss, L., Rey, M., Devinsky, O., Doyle, W. K., Mak-Mccully, R., Halgren, E., Wittner, L., Chauvel, P., Heit, G., Eskandar, E., Mandell, A., &Cash, S. S. (2019). The generation and propagation of the human alpha rhythm. *Proceedings of the National Academy of Sciences of the United States of America, 116*(47), 23772–23782. https://doi.org/10.6084/m9.figshare.9927125.v2

Hanslmayr, S., Spitzer, B., Bäuml, K. H. (2009). Brain oscillations dissociate between semantic and nonsemantic encoding of episodic memories. *Cerebral Cortex, 19,* 1631–1640.

Hanslmayr, S., Staresina, B. P., Bowman, H. (2016). Oscillations and episodic memory: addressing the synchronization/desynchronization conundrum. *Trends in Neurosciences, 39*(1), 16–25. doi: 10.1016/j.tins.2015.11.004. PMID: 26763659; PMCID: PMC4819444.

Hanslmayr, S., Volberg, G., Wimber, M., Raabe, M., Greenlee, M. W., Bäuml, K. H. (2011). The relationship between brain oscillations and BOLD signal during memory formation:

a combined EEG-fMRI study. *Journal of Neuroscience, 31*(44), 15674–15680. doi: 10.1523/JNEUROSCI.3140-11.2011. PMID: 22049410; PMCID: PMC6623030.

Jensen, O., Gelfand, J., Kounios, J., &Lisman, J. E. (2002). Oscillations in the alpha band (9-12 Hz) increase with memory load during retention in a short-term memory task. *Cerebral Cortex, 12*(8), 877–882.

Jones, S. R., Kerr, C. E., Wan, Q., Pritchett, D. L., Hämäläinen, M., &Moore, C. I. (2010). Cued spatial attention drives functionally relevant modulation of the mu rhythm in primary somatosensory cortex. *Journal of Neuroscience, 30*(41), 13760–13765. https://doi.org/10.1523/JNEUROSCI.2969-10.2010

Kardan, O., Adam. K. C. S., Mance, I., Churchill, N. W., Vogel, E. K., &Berman, M. G. (2020). Distinguishing cognitive effort and working memory load using scale-invariance and alpha suppression in EEG. *Neuroimage,* 116622. doi: 10.1016/j.neuroimage.2020.116622

Klimesch, W. (1999). EEG alpha and theta oscillations reflect cognitive and memory performance: a review and analysis. *Brain Research Reviews, 29*(2-3), 169–195. doi: 10.1016/s0165-0173(98)00056-3. PMID: 10209231.

Klimesch, W. (2012). Alpha-band oscillations, attention, and controlled access to stored information. *Trends in Cognitive Sciences, 16*(12), 606–617. https://doi.org/10.1016/j.tics.2012.10.007

Klimesch, W., Doppelmayr, M., Pachinger, T., &Ripper, B. (1997a). Brain oscillations and human memory: EEG correlates in the upper alpha and theta band. *Neuroscience Letters, 238*(1-2), 9–12. doi: 10.1016/s0304-3940(97)00771-4

Klimesch, W., Doppelmayr, M., Pachinger, T., &Russegger, H. (1997b). Event-related desynchronization in the alpha band and the processing of semantic information. *Cognitive Brain Research, 6*(2), 83–94. doi: 10.1016/s0926-6410(97)00018-9

Klimesch, W., Doppelmayr, M., Russegger, H., Pachinger, T., &Schwaiger, J. (1998). Induced alpha band power changes in the human EEG and attention. *Neuroscience Letters, 244*(2), 73–76. doi: 10.1016/s0304-3940(98)00122-0

Koshy, S. M., Wiesman, A. I., Proskovec, A. L., Embury, C. M., Schantell, M. D., Eastman, J. A., Heinrichs-Graham, E., &Wilson, T. W. (2020). Numerical working memory alters alpha-beta oscillations and connectivity in the parietal cortices. *Human Brain Mapping, 41*(13), 3709–3719. https://doi.org/10.1002/hbm.25043

Logie, R. H., Gilhooly, K. J., &Wynn, V. (1994). Counting on working memory in arithmetic problem solving. *Memory & Cognition, 22,* 395–410. https://doi.org/10.3758/BF03200866

Meltzer, J. A., Negishi, M., Mayes, L. C., &Constable, R. T. (2007). Individual differences in EEG theta and alpha dynamics during working memory correlate with fMRI responses across subjects. *Clinical Neurophysiology, 118*(11), 2419–2436. https://doi.org/10.1016/j.clinph.2007.07.023

Michels, L., Moazami-Goudarzi, M., Jeanmonod, D., &Sarnthein, J. (2008). EEG alpha distinguishes between cuneal and precuneal activation in working memory. *NeuroImage, 40*(3), 1296–1310. https://doi.org/10.1016/j.neuroimage.2007.12.048

Oostenveld, R., Fries, P., Maris, E., &Schoffelen, J.-M. (2011). FieldTrip: Open Source Software for Advanced Analysis of MEG, EEG, and Invasive Electrophysiological Data.

Computational Intelligence and Neuroscience, 2011, 156869. https://doi.org/10.1155/2011/156869

Pavlov, Y. G., &Kotchoubey, B. (2020). The electrophysiological underpinnings of variation in verbal working memory capacity. *Scientific Reports, 10*(1). https://doi.org/10.1038/s41598-020-72940-5

Pesonen, M., Hämäläinen, H., &Krause, C. M. (2007). Brain oscillatory 4-30 Hz responses during a visual n-back memory task with varying memory load. *Brain Research, 1138*(1), 171–177. https://doi.org/10.1016/j.brainres.2006.12.076

Proskovec, A. L., Heinrichs-Graham, E., &Wilson, T. W. (2019a). Load modulates the alpha and beta oscillatory dynamics serving verbal working memory. *NeuroImage, 184*, 256–265. https://doi.org/10.1016/j.neuroimage.2018.09.022

Proskovec, A. L., Wiesman, A. I., Heinrichs-Graham, E., &Wilson, T. W. (2019b). Load effects on spatial working memory performance are linked to distributed alpha and beta oscillations. *Human Brain Mapping, 40*(12), 3682–3689. https://doi.org/10.1002/hbm.24625

Rohenkohl, G., &Nobre, A. C. (2011). Alpha oscillations related to anticipatory attention follow temporal expectations. *Journal of Neuroscience, 31*(40), 14076–14084. https://doi.org/10.1523/JNEUROSCI.3387-11.2011

Roux, F., &Uhlhaas, P. J. (2014). Working memory and neural oscillations: Alpha-gamma versus theta-gamma codes for distinct WM information? *Trends in Cognitive Sciences, 18*(1), 16–25. https://doi.org/10.1016/j.tics.2013.10.010

Sauseng, P., Klimesch, W., Doppelmayr, M., Pecherstorfer, T., Freunberger, R., &Hanslmayr, S. (2005). EEG alpha synchronization and functional coupling during top-down processing in a working memory task. *Human Brain Mapping, 26*(2), 148–155. https://doi.org/10.1002/hbm.20150

Sghirripa, S., Graetz, L., Merkin, A., Rogasch, N. C., Semmler, J. G., &Goldsworthy, M. R. (2021). Load-dependent modulation of alpha oscillations during working memory encoding and retention in young and older adults. *Psychophysiology, 58*(2). https://doi.org/10.1111/psyp.13719

Smith, E. E., Jonides, J., &Koeppe, R. A. (1996). Dissociating Verbal and Spatial Working Memory Using PET. *Cerebral Cortex, 6*(1), 11–20. https://doi.org/10.1093/cercor/6.1.11

Stipacek, A., Grabner, R. H., Neuper, C., Fink, A., &Neubauer, A. C. (2003). Sensitivity of human EEG alpha band desynchronization to different working memory components and increasing levels of memory load. *Neuroscience Letters, 353*(3), 193–196. https://doi.org/10.1016/j.neulet.2003.09.044

Thut, G., Nietzel, A., Brandt, S. A., &Pascual-Leone, A. (2006). α-Band electroencephalographic activity over occipital cortex indexes visuospatial attention bias and predicts visual target detection. *Journal of Neuroscience, 26*(37), 9494–9502. https://doi.org/10.1523/JNEUROSCI.0875-06.2006

Tuladhar, A. M., TerHuurne, N., Schoffelen, J. M., Maris, E., Oostenveld, R., &Jensen, O. (2007). Parieto-occipital sources account for the increase in alpha activity with working memory load. *Human Brain Mapping, 28*(8), 785–792. https://doi.org/10.1002/hbm.20306

VanDijk, H., Schoffelen, J. M., Oostenveld, R., &Jensen, O. (2008). Prestimulus oscillatory activity in the alpha band predicts visual discrimination ability. *Journal of Neuroscience, 28*(8), 1816–1823. https://doi.org/10.1523/JNEUROSCI.1853-07.2008

vanEde, F. (2018). Mnemonic and attentional roles for states of attenuated alpha oscillations in perceptual working memory: a review. *European Journal of Neuroscience, 48*(7), 2509–2515. https://doi.org/10.1111/ejn.13759

VanEde, F., Köster, M., &Maris, E. (2012). Beyond establishing involvement: quantifying the contribution of anticipatory-and-band suppression to perceptual improvement with attention. *Journal of Neurophysiology, 108,* 2352–2362. https://doi.org/10.1152/jn.00347.2012.-Systems

Wöstmann, M., Alavash, M., &Obleser, J. (2019). Alpha Oscillations in the Human Brain Implement Distractor Suppression Independent of Target Selection. *Journal of Neuroscience, 39*(49), 9797–9805. https://doi.org/10.1523/JNEUROSCI.1954-19.2019

Wöstmann, M., Herrmann, B., Maess, B., &Obleser, J. (2016). Spatiotemporal dynamics of auditory attention synchronize with speech. *Proceedings of the National Academy of Sciences of the United States of America, 113*(14), 3873–3878. https://doi.org/10.1073/pnas.1523357113

Zhang, X., Räsänen, P., Koponen, T., Aunola, K., Lerkkanen, M. K., &Nurmi, J. E. (2017). Knowing, applying, and reasoning about arithmetic: roles of domain-general and numerical skills in multiple domains of arithmetic learning. *Developmental Psychology, 53*(12), 2304–2318.

Zohary, E., Shadlen, M. N., &Newsome, W. T. (1994). Correlated neuronal discharge rate and its implications for psychophysical performance. *Nature, 370*(6485), 140–143. https://doi.org/10.1038/370140a0