Transcranial Static Magnetic Stimulation Dissociates the Causal Roles of the Parietal Cortex in Spatial and Temporal Processing

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Abstract

Accurate time estimation is essential for optimizing our perception and actions. Previous neuroimaging and transcranial magnetic stimulation (TMS) studies have suggested that the right inferior parietal lobule (IPL) and supplementary motor area (SMA) are involved in time perception. However, it remains inconclusive whether the activity in these regions is crucial for time perception, partly due to the possible spread of TMS effects across anatomically connected brain regions. Such a remote effect is less likely to happen with transcranial static magnet stimulation (tSMS), as the static magnetic field is expected to modulate the firing threshold of neurons rather than directly triggering an action potential. In this study, we aimed to determine the causal relevance of local activities in the right IPL and the SMA for temporal processing using tSMS. We measured duration discrimination thresholds, along with orientation discrimination thresholds as a control, using staircase methods before and during the administration of tSMS over the IPL/SMA. Our results indicated no significant changes in duration discrimination thresholds in either the IPL or SMA conditions. In contrast, we observed an improvement in orientation discrimination thresholds in the IPL condition. This improvement correlated with individual differences in the distance between the scalp and the IPL. Overall, our findings demonstrate a causal involvement of the IPL in orientation processing. The correlation between the effects of tSMS and the scalp-to-target distance suggests that the efficacy of tSMS may be sensitive to the strength of the magnetic field.

Introduction

Precise estimation of time is essential for adapting to an ever-changing environment and optimizing our actions. For instance, in daily activities such as conversation and dancing to a beat, the ability to accurately estimate and predict the timing of external events enables smooth and effective interactions [1–4].

Recent functional magnetic resonance imaging (fMRI) studies have shown that multiple brain regions are involved in temporal processing in the range of hundreds of milliseconds to about one second [5–7]. A meta-analysis of neuroimaging studies reported that perceptual, subsecond timing tasks engage a distributed network of brain regions, including the supplementary motor area (SMA), inferior parietal lobule (IPL), inferior frontal gyrus (IFG), and basal ganglia [5]. Among these areas, the right IPL and SMA have been highlighted as they seem to contain neural populations tuned for specific durations [8–10]. More recent research has associated activity in the right IPL with individual differences in time discrimination performance [11] and perceived duration [8], suggesting its relevance to our subjective experience of time.

Consistent with these neuroimaging findings, several studies have reported that transcranial magnetic stimulation (TMS) applied over the right IPL impairs time discrimination [12,13] or biases perceived durations [14,15]. However, it remains unclear whether the modulation of local activity in the area directly affects timing performances or operates through a remote effect, where TMS influences neuronal activity in anatomically connected regions (i.e., remote effect) [16–18]. This is of particular concern given that a recent functional connectivity study reported that the parietal cortex drives duration-selective activities in several brain regions, including the SMA, visual cortex, IFG, and cerebellum [19]. In line with this finding, a TMS-EEG study reported that

event-related potentials in frontocentral electrodes around the SMA were modulated by TMS

applied over the right IPL and correlated with changes in timing performance [14]. These studies

suggest that, even if TMS produces measurable behavioral effects, it may be premature to attribute

these effects to changes in local activity beneath the TMS coil.

A potentially useful neuromodulation technique for determining the causal role of specific

brain regions is transcranial static magnetic stimulation (tSMS) [20]. tSMS is a non-invasive brain

stimulation method that modulates the firing threshold of neurons in the cortex by placing a

neodymium magnet on the scalp [21]. Although the precise mechanism is not fully understood,

it is believed that a static magnetic field of approximately 120–200 mT affects sodium and

chloride ion channels, possibly by deforming the lipids in the cell membrane [21–23]. These

alternations in ion influx may lead to inhibitory effects on neural activity within the area exposed

to the static magnetic field. Since tSMS does not trigger action potential of neurons, it may offer

advantages over TMS in producing effects that are relatively localized and with minimal remote

influences on anatomically connected brain regions.

To determine whether the local activities of IPL and SMA are crucial for temporal processing,

here, we examined the influence of tSMS over these regions on the duration discrimination task.

If these areas contain duration-tuned neuronal populations that are crucial for subsecond timing,

we predicted that suppressing these areas through tSMS should alter duration discrimination

performance. Additionally, we used an orientation discrimination task as a control because our

previous neuroimaging study found that while duration information was decoded from the IPL

and, albeit less clearly, the SMA, orientation information was not evident in these areas [11].

Material and methods

Participants

A total of 48 healthy, right-handed adult volunteers participated in our experiments (22 females

and 26 males; age = 22.1 (mean) ± 1.4 (SD) years). Participants were recruited through the

institutional online recruitment system from July 15, 2021, to April 14, 2023. All participants had

normal or corrected-to-normal vision and no history of neurological and psychiatric disorders.

This study was conducted in accordance with the Declaration of Helsinki. Participants received

detailed written explanations of the experimental procedures and safety measures, and they

provided informed consent. The protocol was approved by the institutional ethics and safety

committees of the National Institute of Information and Communications Technology.

Task and stimuli

Visual stimuli were generated using MATLAB (MathWorks, Natick, MA, USA) and presented

on a gamma-corrected CRT monitor (Multiscan G520; Sony Inc., Tokyo, Japan) with a refresh

rate of 100 Hz. In each trial, a standard stimulus and a comparison stimulus were sequentially

presented at the center of the screen, with an inter-stimulus interval (ISI) of 1.0 s (Fig. 1).

Following the two visual stimuli, a red fixation point was presented to indicate the response period.

The red fixation point remained on the screen until the participant responded. The subsequent trial

began immediately after the response. Participants were instructed to maintain their gaze on the

fixation point throughout the experiments.

In the duration task, the standard and comparison stimuli were black disks (diameter 5.4

degrees), and participants judged whether the second stimulus was shorter or longer than the first.

103 In the orientation task, the standard and comparison stimuli were sinusoidal Gabor patches (100%

104 contrast, spatial frequency of 1.6 cycles/degree, Gaussian envelope SD of 2.0 degrees, diameter

105 ~12 degrees). Participants judged whether the second stimulus was rotated clockwise or

106 counterclockwise relative to the first.

107  A one-up-three-down staircase procedure was employed to measure participants' thresholds in

108 both the duration and orientation discrimination tasks. In the duration discrimination task, the

109 duration of the standard stimulus was set to 0.5 s, while the duration of the comparison stimulus

110 was 0.5 s + T (initial T = 0.4 s). In the orientation discrimination task, the standard orientation of

111 the sinusoidal Gabor patches was 45° from vertical while that for the comparison was 45° + T

112 (initial T = 12°). The stimulus duration for each Gabor patch was 0.06 s. The order of presentation

113 for the standard and comparison stimuli was randomized across trials.

114  Until the first three reversals, T was multiplied by 1.5 (increased) when the response was

115 incorrect and divided by 1.5 (decreased) when the response was correct for both tasks. After

116 obtaining three reversal points, T was multiplied by 1.3 when the response was incorrect or

117 divided by 1.3 when the response was correct for three consecutive trials. To mitigate any

118 potential confounds related to experiment duration (e.g., fatigue), the measurement durations

119 were fixed at 270 s for the duration task and 215 s for the orientation task based on pilot

120 experiments. Participants responded by pressing either the "J" key (for shorter or

121 counterclockwise) or the "K" key (for longer or clockwise) with their right index and middle

122 fingers, respectively. Participants were explicitly instructed to respond as accurately as possible

123 and not to count time during the duration task.

Fig. 1. Stimulus sequence. In the duration task (left), two visual stimuli (black disks) were

presented sequentially. Participants judged whether the duration of the second disk was shorter or

longer than that of the first. In the orientation task (right), two Gabor patches were presented

sequentially. Participants judged whether the orientation of the second stimulus was rotated

clockwise or counterclockwise compared to the first. A response was required in every trial during

the response period, indicated by a red fixation point.

Target localization for tSMS

We employed a tSMS, a cylindrical neodymium magnet, with a diameter of 60 mm and a

thickness of 30 mm (MAG 60 r+, Neurek SL., Toledo, Spain). The magnetic field strength was

0.511 T at the surface of the magnet. The right IPL (MNI coordinates x, y, z = 66, -34, 34) and

SMA (x, y, z = 2, 0, 70) were selected as the stimulation sites based on preceding fMRI studies

[8,11]. To determine the individual's positions of the stimulation sites, we collected T1-weighted

images for each participant with a magnetization-prepared rapid acquisition with a gradient echo

(MPRAGE) sequence using a 3T MRI scanner (Siemens Inc., Erlangen, Germany),

MAGNETOM Prisma (0.9 mm isotropic resolution, TR = 2700 ms, and TE = 3.68 ms) or

MAGNETOM Prisma Fit (0.8 mm isotropic resolution, TR = 2500 ms, and TE = 2.18 ms). For

each participant, we localized the right IPL and SMA by converting the MNI coordinates into

positions within that individual's structural T1-weighted image. Using statistical parametric

mapping (SPM12) software implemented in MATLAB, we calculated an affine transformation

matrix to align the individual's T1-weighted image with the standard brain (MNI template).

Subsequently, we used the inverse of the transformation on the neuronavigation system

(Brainsight, Rogue Research Inc., Montreal, Quebec, Canada) to determine the positions of the

right IPL and SMA within the participant's structural image.

Experimental Procedure

We conducted two sessions of experiments on different days: one targeting the IPL and the

other targeting the SMA. Before each session, we aligned the MR images with the participant's

head and marked the scalp position for placing the magnet using the Brainsight navigation system.

Participants completed 10 practice trials for both the duration and orientation discrimination tasks.

Experiments consisted of baseline and test blocks, with each block lasting approximately 20

min. In these blocks, participants performed duration and orientation discrimination tasks two

times each (Fig. 2A). Following baseline threshold measurements, which were taken without

applying tSMS, we fixed the magnet over the targeted region using a custom-assembled clamp

with a sliding arm (Slick Co., Ltd., Tokyo, Japan), ensuring that the center of the magnet's bottom

surface aligned with the marked position on the scalp. A chin rest was used to stabilize the

participant's head position. Based on a previous report showing suppression of cortical excitability

following administration of tSMS for 30 min [24] we positioned tSMS over the IPL or SMA for

30 min prior to the test block and maintained the position throughout the test block (Fig. 2B).

Participants were randomly assigned to one of two groups: one group received tSMS over the

IPL in the first session and over the SMA in the second, while the other group was tested in the

opposite order. The task order for the baseline and test blocks was counterbalanced within each

group, with half of the participants performing the duration task followed by the orientation task,

and the other half performing the tasks in reverse order. For each participant, the task order

remained consistent across both sessions.

Fig. 2. Experimental procedure. (A) Timeline of the experiment. During both the baseline and

test blocks, participants performed duration and orientation tasks, each repeated two times. tSMS

was applied for approximately 50 min, beginning 30 min before and continuing throughout the

20-min test block. (B) Target regions. We identified the target regions, right IPL and SMA, based

on MNI coordinates from previous studies. The figure illustrates the target regions on coronal

(left) and sagittal (right) views of a standard brain image.

Data Analysis

To determine the discrimination thresholds with the staircase procedure, we averaged the last

six reversal points from the collected data [25]. The threshold values were then averaged between

two measurements to establish an individual's discrimination threshold. If the number of reversal

points in one of the two measurements was less than eight, we excluded the data and used the

threshold from the other measurement as the participant's discrimination threshold.

To assess any potential changes in the baseline threshold across sessions, we compared the

average baseline threshold values between the first and second sessions using two-tailed paired t-

tests ($\alpha = 0.05$), with adjustments for multiple comparisons using the Bonferroni correction. Also,

to evaluate the stability of individual differences in baseline discrimination thresholds, we

calculated Pearson correlation coefficients between the baseline thresholds obtained in the first

and second sessions. To investigate the changes in discrimination thresholds induced by tSMS,

we performed two-tailed one-sample t-tests ($\alpha = 0.05$) on the difference between the test and

baseline thresholds, applying the Bonferroni correction for multiple comparisons across two

target brain regions.

Finally, we examined whether the magnitude of the tSMS effects depends on the distance

between the targeted cortical area and the magnet. We calculated the Pearson correlation

coefficient between the distance from the scalp to the stimulation site (either the IPL or SMA)

and the change in discrimination threshold between the test and baseline blocks. The distance was

measured using the ruler tool in the Brainsight navigation system. We tested the significance of

correlations (two-tailed, $\alpha = 0.05$). Differences in correlation coefficients between tasks were also

tested by bootstrap resampling (10,000 samples) using the Robust Correlation Toolbox

implemented in MATLAB [26].

All statistical analyses, except for the bootstrap resampling, were performed using JASP

(https://jasp-stats.org/).

Results

Reliability of the baseline threshold

Among the collected data from the 48 participants, threshold data from eleven measurements in the IPL sessions (four baseline and three test threshold measurements for the duration task, and one baseline and three test thresholds measurements for the orientation task) and six measurements in the SMA sessions (three baseline and two test thresholds measurements for the duration task and one test threshold measurements for the orientation task) were disregarded due to the insufficient number of reversal points. For these blocks, the individual's baseline or test threshold was determined based on the threshold value obtained in the other measurement (see *Data analysis* section in the Material and methods).

Preceding to our main analyses, we examined whether the baseline thresholds differed between the first and second sessions. As expected, a paired t-test revealed that the baseline thresholds for duration discrimination were not statistically different ($t(47) = 0.258$, $p = 0.798$, Cohen's $d = 0.037$) (Fig. 3A, left). In contrast, baseline thresholds for orientation discrimination were significantly lower in the second session compared to the first session ($t(47) = 4.244$, $p < 0.001$, Cohen's $d = 0.613$) (Fig. 3B, left). This result suggests that, while baseline thresholds were maintained in the duration task, the threshold for the orientation task was improved as the experiment progressed.

We also tested whether the individual differences in baseline thresholds were maintained across sessions. Our correlation analyses revealed that individual differences between the first and the second baseline thresholds were correlated in both duration ($r = 0.437$, $p = 0.002$) (Fig. 3A, right) and orientation tasks ($r = 0.656$, $p < 0.001$) (Fig. 3B, right). These results indicate that,

although the threshold was improved in the second session in the orientation task, individual

differences in the baseline thresholds were maintained across sessions in both tasks.

Fig. 3. Baseline thresholds. Baseline thresholds for the first (Day 1) and second sessions (Day

2) for the duration task (A, left) and for the orientation task (B, left). Each bar represents the

average discrimination thresholds, with error bars indicating the standard error. The gray lines

indicate the change in individual thresholds between Day 1 and Day 2. Correlations between

thresholds for Day 1 and Day 2 for the duration task (A, right) and the orientation task (B, right).

The black circles represent individual data. The gray solid line represents the regression line. The

black dashed line represents the diagonal line. ** p < 0.01, *** p < 0.001, corrected for multiple

comparisons.

Effect of tSMS on task performances

Next, we examined whether tSMS over the IPL and SMA altered discrimination thresholds in

duration and orientation tasks. A one-sample t-test for the duration discrimination threshold

revealed no significant difference from the baseline, both in the IPL and SMA conditions (IPL: t

(47) = -0.716, p = 0.477, Cohen's d = -0.103; SMA: t (47) = 0.381, p = 0.705, Cohen's d = 0.055;

Fig. 4A). In contrast, the orientation discrimination threshold significantly decreased when tSMS

was applied over the IPL (t (47) = -2.464, p = 0.017, Cohen's d = -0.356; Fig. 4B). No such

reduction in the orientation discrimination threshold was observed in either task when tSMS was

applied over the SMA (t (47) = -0.393, p = 0.696, Cohen's d = -0.057; Fig. 4B).

Fig. 4. Modulation of discrimination thresholds by tSMS. Differences in the discrimination

threshold between baseline and test phases (Test – Baseline) in the duration (**A**) and the orientation

tasks (**B**) when tSMS was applied over the IPL (magenta bars) and SMA (blue bars). The gray

circles indicate individual data. Each bar depicts the mean threshold difference, with error bars

indicating the standard error. * p < 0.05, corrected for multiple comparisons.

Effect of magnetic field strength on performance improvement

Since the effective magnetic field strength of tSMS depends on the distance between the

magnet and target, we wondered whether the variability in the effect size of tSMS across

participants is explained by the scalp-to-target distance. First, we examined whether the mean

scalp-to-target distance differed between the two target regions. A paired t-test revealed that the

scalp-to-target distance for the IPL (16.1 ± 0.2 mm) was significantly closer than for the SMA

(24.0 ± 0.2 mm) (t (47) = -25.467, p < 0.001, Cohen's d = -3.676; Fig. 5), indicating that magnetic

field strength in the IPL was greater and probably more effective than that in the SMA.

Fig. 5. Distance from the scalp to the target. The average distance from the scalp to the IPL and the SMA across participants. The magenta bar represents the mean distance to the IPL, while the blue bar represents the mean distance to the SMA. Error bars indicate the standard error. Gray lines represent individual data. *** p < 0.001

Next, we tested whether individual differences in the scalp-to-target distance explain the effect size of tSMS. Our correlation analyses revealed that individual differences in the scalp-to-IPL distance were positively correlated with the change in orientation discrimination thresholds (r = 0.304, p = 0.036; Fig. 6B), whereas such a correlation was absent for the duration task (r = -0.029, p = 0.846; Fig. 6A). A bootstrap analysis further confirmed that the degree of correlations significantly differed between the two tasks (95% confidence interval (CI) = -0.607−-0.006, p = 0.046; Fig. 6C). For the SMA, individual differences in the scalp-to-SMA distance were not correlated with the degree of threshold modulation in either the duration (r = 0.022, p = 0.883; Fig. 6D) or orientation task (r = 0.016, p = 0.917; Fig. 6E). Our bootstrap analysis confirmed that the correlations not significantly differed between these two tasks (95% CI = -0.396–0.456, p = 0.941; Fig. 6F). These findings together suggest that the scalp-to-target distance in the IPL, which was shorter than that in the SMA, was predictive of the degree of improvement in behavioral performances, specifically for the orientation task.

Fig. 6. Correlation between the scalp-to-target distance and the behavioral effect of tSMS.

Correlation between the scalp-to-target distance (**A and B** for IPL**, D and E** for SMA**)** and the

change in discrimination thresholds (**A and D** for duration task, **B and E** for orientation task).

Gray lines indicate regression lines and circles indicate individual data. Distribution of differences

in correlation coefficients between tasks (i.e., duration – orientation task) for IPL (C) and SMA

(F), estimated by the bootstrap method. The solid line represents the 95% confidence interval, and

the dashed line indicates the value of differences in correlation coefficients between tasks. * p <

0.05

Discussion

This study investigated whether the local activities in the IPL and SMA are causally involved

in temporal and spatial processing by comparing duration and orientation discrimination

thresholds before and during the application of tSMS. Our within-subject experiments, which

included a relatively large sample size (n = 48), showed no significant changes in duration

discrimination thresholds, irrespective of the target regions. Unexpectedly, however, we found

that orientation discrimination thresholds significantly improved when tSMS was applied over

the IPL (but not SMA). Additionally, the degree of improvement in the orientation task correlated

with individual differences in the scalp-to-target distance of the IPL.

Lack of tSMS effect on duration task

In our experiment, performance in the duration task was not significantly altered by the tSMS

applied over the IPL or SMA. This result may seem surprising given that numerous neuroimaging

studies have reported the involvement of these regions in temporal processing [8,9,11,27,28]. The

absence of a tSMS effect in our study might be related to the distributed nature of temporal

representations in the brain. A lack of disorders associated with a selective impairment in timing

abilities suggests that time representations might be distributed across various regions [29].

Supporting this idea, previous neuroimaging studies have consistently shown that timing

information is spread across cortical areas, forming a timing network [10,11,19,30,31]. Therefore,

we speculate that disrupting one region of this timing network may not significantly affect timing

performance because the brain can flexibly utilize other reliable sources of timing information

within the network to maintain behavioral performance.

Although our study found no evidence of tSMS effect on time discrimination, previous studies

have reported impairments in timing performance when TMS was applied over the IPL [12,14,15].

This discrepancy may be explained by the combination of the distributed timing network idea

described above and the difference in the degree of focality between tSMS and TMS methods.

TMS is known to influence neuronal activity not only in the targeted areas but also in anatomically

connected regions, which is referred to as the remote effect [32–35] In contrast, tSMS is believed

to have a more focal effect due to its mechanism of working through the deformation of lipids in

the cell membrane [22,23]. Therefore, the varying degrees of focality between TMS and tSMS

may account for different behavioral outcomes. Specifically, while TMS can disrupt timing

performance through broader interference within the timing network, more localized disruption

by tSMS might be compensated for by utilizing timing information from intact areas.

The lack of tSMS effect on the SMA could be explained by the significant distance between

the SMA and the scalp. As demonstrated in the orientation discrimination task (Fig. 6B), the

impact of tSMS on behavioral performance is influenced by the scalp-to-target distance. The

targeted SMA was located on the medial wall of the brain, which may have rendered the magnetic

field too weak to effectively disrupt cortical activity. This notion is consistent with previous TMS

studies that reported no significant effect on time perception when TMS was administered over

the SMA [36–38]. Our findings suggest a need for future studies to employ neuromodulation

techniques that can effectively stimulate deeper areas (e.g., transcranial focused ultrasound

stimulation) to better clarify the role of the SMA in duration discrimination tasks.

tSMS over the right IPL improved orientation discrimination performance

In contrast to the duration discrimination task, orientation discrimination performance was

improved when tSMS was applied over the right IPL. This finding aligns with previous studies

showing that TMS over the right IPL significantly increased reaction times for detecting target

orientations [32,39], suggesting that the IPL plays a crucial role in orientation discrimination.

The paradoxical enhancement in performance due to the inhibitory effects of tSMS can be

attributed to increased lateral inhibition mechanisms of orientation-tuned neural populations in

the IPL. In the visual cortex, higher GABA concentration levels have been linked to better

orientation thresholds [40], likely due to the enhanced lateral inhibition in orientation-tuned

neurons [41–43]. Notably, a recent fMRI adaptation study highlighted the existence of spatiotopic

receptive fields for orientations in the IPL [44]. Given that another study reported that tSMS

enhances inhibitory signal mediated by GABA receptors [45], we speculate that our tSMS

application might have increased GABA concentration or sensitivity of GABA receptors

associated with orientation channels in the IPL. Consequently, this rise in GABA levels could

have enhanced orientation selectivity, leading to improved orientation discrimination

performance.

Additionally, we found that participants with shorter scalp-to-target distances showed greater

improvements in their orientation discrimination performance. This finding suggests that scalp-

to-target distance could be a useful metric for evaluating the effectiveness of tSMS. For other

neuromodulation techniques, such as TMS, simulating induced electric field in the target region

has been common [46]. Our findings imply that such simulations may also be beneficial in

predicting the effectiveness of tSMS. An important avenue for future research with tSMS might

be to control the dosage across participants based on these simulations, allowing for an optimal

selection of magnetic strength that standardizes the dose or effectiveness of tSMS across different

participants and target regions.

Limitations

A limitation of the current study is that our experimental design, which employed the staircase

method, only assessed the modulation of threshold. Consequently, it remains unclear whether

tSMS impacted perceived duration and/or orientation (i.e., bias). Previous studies have suggested

that the right IPL is associated with the subjective experience of time [8,14,15], highlighting the

necessity of measuring biases in perceived duration. This can be clarified by using discrimination

tasks that involve a stable reference unaffected by tSMS, such as a bisection task with an internal

reference.

Second, since tSMS was applied continuously during the discrimination tasks, the specific

processes being modulated (e.g., stimulus encoding, maintenance, comparison) in the orientation

task remain unclear. This lack of temporal specificity may not be easily addressed due to the

nature of tSMS, necessitating the use of more temporally specific stimulation methods, such as

focused ultrasound stimulation.

Conclusions

The current study aimed to identify the brain regions causally associated with temporal and

spatial perception using tSMS. The task-specific improvements provided by tSMS suggest a

potential dissociation between temporal and spatial processing in the right IPL. Furthermore, we

demonstrated that individual differences in the distance from the scalp to the right IPL correlated

with the effectiveness of tSMS, underscoring the importance of considering anatomical

differences when predicting and evaluating the efficacy of tSMS.

CRediT authorship contribution statement

Masakazu Sugimoto: Methodology, Software, Validation, Formal analysis, Investigation, Data Curation, Writing- Original draft preparation, Visualization. **Ikko Kimura:** Methodology, Writing- Reviewing and Editing. **Masamichi J. Hayashi:** Conceptualization, Methodology, Software, Writing- Reviewing and Editing, Supervision, Project administration, Funding acquisition

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Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work, the authors used ChatGPT, Grammarly, and DeepL in order to improve the readability and language of the manuscript. After using these tools, the authors reviewed and edited the content as needed and took full responsibility for the content of the published article.

References

1. Magyari L, De Ruiter JP, Levinson SC. Temporal preparation for speaking in question-answer sequences. Front Psychol. 2017;8. doi:10.3389/fpsyg.2017.00211

2. Magyari L, Bastiaansen MCM, de Ruiter JP, Levinson SC. Early anticipation lies behind the speed of response in conversation. J Cogn Neurosci. 2014;26: 2530–2539. doi:10.1162/jocn_a_00673

3. Ross JM, Iversen JR, Balasubramaniam R. Motor simulation theories of musical beat perception. Neurocase. Routledge; 2016. pp. 558–565. doi:10.1080/13554794.2016.1242756

4. Teki S, Grube M, Kumar S, Griffiths TD. Distinct neural substrates of duration-based and beat-based auditory timing. Journal of Neuroscience. 2011;31: 3805–3812. doi:10.1523/JNEUROSCI.5561-10.2011

5. Wiener M, Turkeltaub P, Coslett HB. The image of time: A voxel-wise meta-analysis. Neuroimage. 2010;49: 1728–1740. doi:10.1016/j.neuroimage.2009.09.064

6. Naghibi N, Jahangiri N, Khosrowabadi R, Eickhoff CR, Eickhoff SB, Coull JT, et al. Embodying Time in the Brain: A Multi-Dimensional Neuroimaging Meta-Analysis of 95 Duration Processing Studies. Neuropsychology Review. Springer; 2023. doi:10.1007/s11065-023-09588-1

7. Coull JT, Droit-Volet S. Explicit Understanding of Duration Develops Implicitly through Action. Trends in Cognitive Sciences. Elsevier Ltd; 2018. pp. 923–937. doi:10.1016/j.tics.2018.07.011

8. Hayashi MJ, Ivry RB. Duration selectivity in right parietal cortex reflects the subjective experience of time. Journal of Neuroscience. 2020;40: 7749–7758. doi:10.1523/JNEUROSCI.0078-20.2020

9. Protopapa F, Hayashi MJ, Kulashekhar S, Van Der Zwaag W, Battistella G, Murray MM, et al. Research article chronotopic maps in human supplementary motor area. PLoS Biol. 2019;17. doi:10.1371/journal.pbio.3000026

10. Harvey BM, Dumoulin SO, Fracasso A, Paul JM. A Network of Topographic Maps in Human Association Cortex Hierarchically Transforms Visual Timing-Selective Responses. Current Biology. 2020;30: 1424-1434.e6. doi:10.1016/j.cub.2020.01.090

11. Hayashi MJ, van der Zwaag W, Bueti D, Kanai R. Representations of time in human frontoparietal cortex. Commun Biol. 2018;1: 1–10. doi:10.1038/s42003-018-0243-z

12.   Bueti D, Bahrami B, Walsh V. Sensory and association cortex in time perception. J Cogn
Neurosci. 2008;20: 1054–1062. doi:10.1162/jocn.2008.20060

13.   Riemer M, Rhodes D, Wolbers T. Systematic underreproduction of time is independent of
judgment certainty. Neural Plast. 2016;2016. doi:10.1155/2016/6890674

14.   Wiener M, Kliot D, Turkeltaub PE, Hamilton RH, Wolk DA, Coslett HB. Parietal
influence on temporal encoding indexed by simultaneous transcranial magnetic
stimulation and electroencephalography. Journal of Neuroscience. 2012;32: 12258–12267.
doi:10.1523/JNEUROSCI.2511-12.2012

15.   Wiener M, Hamilton R, Turkeltaub P, Matell MS, Coslett HB. Fast forward:
Supramarginal gyrus stimulation alters time measurement. J Cogn Neurosci. 2010;22: 23–
31. doi:10.1162/jocn.2009.21191

16.   Wang JB, Hassan U, Bruss JE, Oya H, Uitermarkt BD, Trapp NT, et al. Effects of
transcranial magnetic stimulation on the human brain recorded with intracranial
electrocorticography. Mol Psychiatry. 2024;29: 1228–1240. doi:10.1038/s41380-024-
02405-y

17.   Bergmann TO, Varatheeswaran R, Hanlon CA, Madsen KH, Thielscher A, Siebner HR.
Concurrent TMS-fMRI for causal network perturbation and proof of target engagement.
Neuroimage. 2021;237. doi:10.1016/j.neuroimage.2021.118093

18.   Rafique SA, Solomon-Harris LM, Steeves JKE. TMS to object cortex affects both object
and scene remote networks while TMS to scene cortex only affects scene networks.
Neuropsychologia. 2015;79: 86–96. doi:10.1016/j.neuropsychologia.2015.10.027

19.   Protopapa F, Kulashekhar S, Hayashi MJ, Kanai R, Bueti D. Effective connectivity in a
duration selective cortico-cerebellar network. Sci Rep. 2023;13. doi:10.1038/s41598-023-
47954-4

20.   Oliviero A, Mordillo-Mateos L, Arias P, Panyavin I, Foffani G, Aguilar J. Transcranial
static magnetic field stimulation of the human motor cortex. Journal of Physiology.
2011;589: 4949–4958. doi:10.1113/jphysiol.2011.211953

21.   Sinha A saran, Shibata S, Takamatsu Y, Akita T, Fukuda A, Mima T. Static magnetic field
stimulation enhances shunting inhibition via a SLC26 family Cl − channel, inducing
intrinsic plasticity . The Journal of Neuroscience. 2024; e1324222024.
doi:10.1523/jneurosci.1324-22.2024

22.   Arthur D. Rosen. Mechanism of Action of Moderate-Intensity StaticMagnetic Fields on
Biological Systems. Cell Biochem Biophys. 2003;39: 163–173.

doi:10.1385/CBB:39:2:163

23.   Hernando A, Galvez F, García MA, Soto-León V, Alonso-Bonilla C, Aguilar J, et al.
Effects of Moderate Static Magnetic Field on Neural Systems Is a Non-invasive
Mechanical Stimulation of the Brain Possible Theoretically? Front Neurosci. 2020;14: 1–
9. doi:10.3389/fnins.2020.00419

24.   Takamatsu Y, Koganemaru S, Watanabe T, Shibata S, Yukawa Y, Minakuchi M, et al.
Transcranial static magnetic stimulation over the motor cortex can facilitate the
contralateral cortical excitability in human. Sci Rep. 2021;11: 5370. doi:10.1038/s41598-
021-84823-4

25.   Hayashi MJ, Kantele M, Walsh V, Carlson S, Kanai R. Dissociable Neuroanatomical
Correlates of Subsecond and Suprasecond Time Perception. J Cogn Neurosci. 2014;26:
1685–1693. doi:10.1162/jocn_a_00580

26.   Pernet CR, Wilcox R, Rousselet GA. Robust correlation analyses: False positive and
power validation using a new open source matlab toolbox. Front Psychol. 2013;3.
doi:10.3389/fpsyg.2012.00606

27.   Hayashi MJ, Ditye T, Harada T, Hashiguchi M, Sadato N, Carlson S, et al. Time Adaptation
Shows Duration Selectivity in the Human Parietal Cortex. PLoS Biol. 2015;13.
doi:10.1371/journal.pbio.1002262

28.   Coull JT, Charras P, Donadieu M, Droit-Volet S, Vidal F. SMA selectively codes the active
accumulation of temporal, not spatial, magnitude. J Cogn Neurosci. 2015;27: 2281–2298.
doi:10.1162/jocn_a_00854

29.   Wiener M, Matell MS, Coslett HB. Multiple mechanisms for temporal processing. Front
Integr Neurosci. 2011;5. doi:10.3389/fnint.2011.00031

30.   Cona G, Wiener M, Scarpazza C. From ATOM to GradiATOM: Cortical gradients support
time and space processing as revealed by a meta-analysis of neuroimaging studies.
Neuroimage. 2021;224. doi:10.1016/j.neuroimage.2020.117407

31.   Cona G, Wiener M, Allegrini F, Scarpazza C. Gradient Organization of Space, Time, and
Numbers in the Brain: A Meta-analysis of Neuroimaging Studies. Neuropsychology
Review. Springer; 2023. doi:10.1007/s11065-023-09609-z

32.   Sack AT, Kohler A, Bestmann S, Linden DEJ, Dechent P, Goebel R, et al. Imaging the
brain activity changes underlying impaired visuospatial judgments: Simultaneous fMRI,
TMS, and behavioral studies. Cerebral Cortex. 2007;17: 2841–2852.
doi:10.1093/cercor/bhm013

501 33. Watanabe T, Hanajima R, Shirota Y, Tsutsumi R, Shimizu T, Hayashi T, et al. Effects of
502   rTMS of pre-supplementary motor area on fronto basal ganglia network activity during
503   stop-signal task. Journal of Neuroscience. 2015;35: 4813–4823.
504   doi:10.1523/JNEUROSCI.3761-14.2015

505 34. Siebner HR, Funke K, Aberra AS, Antal A, Bestmann S, Chen R, et al. Transcranial
506   magnetic stimulation of the brain: What is stimulated? – A consensus and critical position
507   paper. Clinical Neurophysiology. Elsevier Ireland Ltd; 2022. pp. 59–97.
508   doi:10.1016/j.clinph.2022.04.022

509 35. Hirose M, Mochizuki H, Groiss SJ, Tanji Y, Nakamura K, Nakatani-Enomoto S, et al. On-
510   line effects of quadripulse transcranial magnetic stimulation (QPS) on the contralateral
511   hemisphere studied with somatosensory evoked potentials and near infrared spectroscopy.
512   Exp Brain Res. 2011;214: 577–586. doi:10.1007/s00221-011-2855-0

513 36. Del Olmo MF, Cheeran B, Koch G, Rothwell JC. Role of the cerebellum in externally
514   paced rhythmic finger movements. J Neurophysiol. 2007;98: 145–152.
515   doi:10.1152/jn.01088.2006

516 37. Giovannelli F, Innocenti I, Rossi S, Borgheresi A, Ragazzoni A, Zaccara G, et al. Role of
517   the dorsal premotor cortex in rhythmic auditory-motor entrainment: A perturbational
518   approach by rTMS. Cerebral Cortex. 2014;24: 1009–1016. doi:10.1093/cercor/bhs386

519 38. Méndez JC, Rocchi L, Jahanshahi M, Rothwell J, Merchant H. Probing the timing
520   network: A continuous theta burst stimulation study of temporal categorization.
521   Neuroscience. 2017;356: 167–175. doi:10.1016/j.neuroscience.2017.05.023

522 39. Sack AT. Parietal cortex and spatial cognition. Behavioural Brain Research. 2009. pp. 153–
523   161. doi:10.1016/j.bbr.2009.03.012

524 40. Edden RAE, Muthukumaraswamy SD, Freeman TCA, Singh KD. Orientation
525   discrimination performance is predicted by GABA concentration and gamma oscillation
526   frequency in human primary visual cortex. Journal of Neuroscience. 2009;29: 15721–
527   15726. doi:10.1523/JNEUROSCI.4426-09.2009

528 41. Brouwer GJ, Heeger DJ. Cross-orientation suppression in human visual cortex. J
529   Neurophysiol. 2011;106: 2108–2119. doi:10.1152/jn.00540.2011.-Cross-orientation

530 42. Rosario J Del, Coletta S, Kim SH, Mobille Z, Peelman K, Williams B, et al. Lateral
531   inhibition in V1 controls neural & perceptual contrast sensitivity. bioRxiv. 2023.
532   doi:10.1101/2023.11.10.566605

533 43. Li G, Yang Y, Liang Z, Xia J, Yang Y, Zhou Y. GABA-mediated inhibition correlates with

orientation selectivity in primary visual cortex of cat. Neuroscience. 2008;155: 914–922.

doi:10.1016/j.neuroscience.2008.06.032

44.   Dunkley BT, Baltaretu B, Crawford JD. Trans-saccadic interactions in human parietal and

occipital cortex during the retention and comparison of object orientation. Cortex.

2016;82: 263–276. doi:10.1016/j.cortex.2016.06.012

45.   Nojima I, Koganemaru S, Fukuyama H, Mima T. Static magnetic field can transiently alter

the human intracortical inhibitory system. Clinical Neurophysiology. 2015;126: 2314–

2319. doi:10.1016/j.clinph.2015.01.030

46.   Axel Thielscher, Andre Antunes, Guilherme B Saturnino. Field modeling for transcranial

magnetic stimulation: A useful tool to understand the physiological effects of TMS? 2015

37th Annual International Conference of the IEEE Engineering in Medicine and Biology

Society (EMBC). 2015; 222–225. doi:10.1109/EMBC.2015.7318340.