Anticipatory Visual Cortical Dynamics of Temporal Expectation and Voluntary Temporal Attention

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Abstract

We can often anticipate the precise moment when a stimulus will be relevant for our behavioral goals. Directing voluntary temporal attention helps us see better at relevant times. How does the brain anticipate and select a relevant moment in a temporally precise manner? Here we used time-resolved steady-state visual evoked responses (SSVER) to investigate how temporal attention dynamically modulates visual activity when temporal expectation is controlled. We recorded MEG while observers directed temporal attention to one of two sequential grating targets with predictable timing. Meanwhile, we used a co-localized SSVER probe to continuously track visual cortical modulations leading up to the targets. We found both ramping and a low-frequency (~2 Hz) periodic modulation of the SSVER that anticipated the arrival of the targets, tied to temporal expectation. Furthermore, the low-frequency modulation shifted in phase according to which of two time points was attended. Thus, temporal attention flexibly coordinates visual cortical excitability to proactively prioritize sensory information at precise moments.

Keywords: temporal attention; temporal expectation; visual perception; steady-state visual evoked responses

Phenomena like the attentional blink (Raymond, Shapiro, & Arnell, 1992) and temporal crowding (Tkacz-Domb & Yeshurun, 2021) reveal limitations in processing stimuli that are hundreds of milliseconds apart. However, we can alleviate these constraints and improve perception by prioritizing certain moments. Voluntary temporal attention is the deliberate prioritization of a point in time that we know in advance will be relevant for our behavioral goals (Nobre & van Ede, 2018). There have been reports of fronto-parietal ramping (Breska & Ivry, 2020) and delta-band periodic modulations (Lakatos, Karmos, Mehta, Ulbert, & Schroeder, 2008) leading up to predictable and relevant time points. However, whether these anticipatory mechanisms are specific to voluntary temporal attention is unclear because previous neural studies (Miniussi, Wilding, Coull, & Nobre, 1999) have not isolated its influence from that of temporal expectation, which reflects timing predictability rather than relevance. Voluntary temporal attention has been shown to improve behavioral performance (Denison, Heeger, & Carrasco, 2017; Fernández, Denison, & Carrasco, 2019) and affect microsaccades (Denison, Yuval-Greenberg, & Carrasco, 2019; Palmieri, Fernández, & Carrasco, 2023), over and above the effects of temporal expectation, suggesting dissociable mechanisms.

Human observers (n = 10 x 2 sessions) performed a challenging orientation discrimination task while recording MEG (Figure 1A). A precue (75% validity) directed temporal attention to one of two brief,

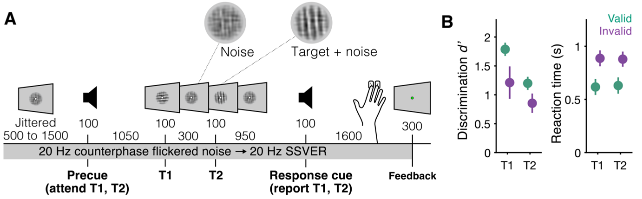

Figure 1: Temporal attentional cueing task. A) A precue directed temporal attention to one of two visual targets that were fully predictable in time. B) Temporal precueing improved orientation discrimination (*d'*) and reaction times. Error bars are ± 1 SEM.

sequential grating targets. On every trial, the timing of both targets was fully predictable following the precue, but the attended time point varied trial-to-trial according to the precue. A response cue after the targets instructed observers to report the tilt (clockwise or counterclockwise) of either the first (T1) or second (T2) target. Temporal attention improved orientation discrimination performance and speeded reaction times (Figure 1B), consistent with previous findings.

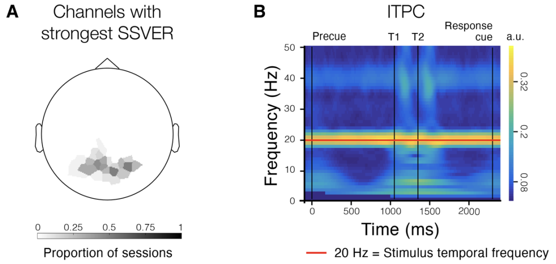

Figure 2: The SSVER was A) strongest in the back of the head and B) predominantly driven by phase coherence across trials (ITPC).

A 20 Hz noise probe flickered throughout the trial. The flicker generated a 20 Hz response in visual cortex (SSVER) by which we could continuously track visual cortical modulations. We identified the top five channels with the strongest SSVER power per session. As expected, the channels most strongly responsive to the visual stimulation were in the back of the head, consistent with occipital responses (Figure 2A). The SSVER was predominantly driven by phase coherence across trials (Figure 2B). We therefore tracked visual cortical modulations throughout the anticipatory period by measuring the 20 Hz intertrial phase coherence (ITPC) for these visually responsive channels.

Anticipatory ramping and periodicity of SSVER tied to temporal expectation

On every trial, a predictable interval of 1.05 s elapsed between the precue and T1, so observers could form an expectation about the timing of T1, regardless of whether it was attended. During this predictable interval (Figure 3A, gray bar), ITPC gradually ramped up and peaked around the time of the first target. The anticipatory ITPC also appeared to be periodically modulated. The slope of the ramp, quantified by a linear fit, was significantly above zero (Figure 3B), and the best-fitting frequency was close to 2 Hz (Figure 3A). The periodic component exceeded what would be expected from 1/f aperiodic activity. Therefore, temporal expectation elicits a ramping and delta-band periodic modulation of visual responses, time-locked to the precue.

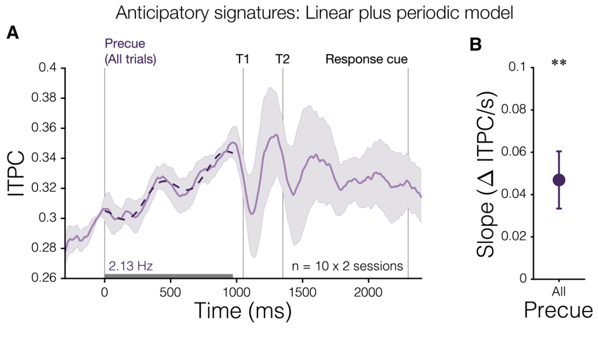

Figure 3: The ITPC time series exhibited A) periodic and B) ramping modulation in advance of the predictable onset of the targets.

Temporal attention phase-shifts the periodic modulation of SSVER

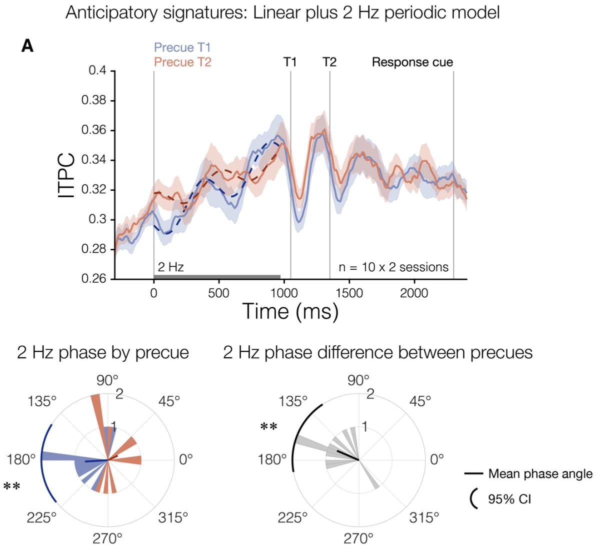

Figure 4: A) The anticipatory ITPC time series B) shifted approximately half a period in phase depending on the attended time point.

Next, we tested the effect of temporal attention on the ramping and periodic components of the anticipatory ITPC. We fit a linear plus 2 Hz periodic model to the ITPC time series for each precue condition (Figure 4A). We found a significant phase concentration on precue T1 trials and a significant difference between precue conditions in the fitted phase (Figure 4B). Interestingly, the 157° 2 Hz phase shift corresponds to 218 ms, which is similar to the stimulus onset asynchrony (SOA = 300 ms) between the two targets and the SOAs at which maximal attentional tradeoffs occur (Denison, Carrasco, & Heeger, 2021). One interpretation is that voluntary temporal attention coordinates slow oscillations modulating visual activity so that a more optimal phase for perceptual processing aligns with the anticipated task-relevant moment.

In summary, using time-resolved SSVER, we found: 1) a slow ramping plus periodic modulation of visual cortical responsiveness that anticipated predictable target times, reflecting temporal expectation and 2) a phase-shift of the periodic modulation according to the task-relevant moment, reflecting voluntary temporal attention.

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References

Breska, A., & Ivry, R. B. (2020). Context-specific control over the neural dynamics of temporal attention by the human cerebellum. *Science Advances*, *6*, eabb1141.

Denison, R. N., Carrasco, M., & Heeger, D. J. (2021). A dynamic normalization model of temporal attention. *Nature Human Behaviour*, 1–12.

Denison, R. N., Heeger, D. J., & Carrasco, M. (2017). Attention flexibly trades off across points in time. *Psychonomic Bulletin & Review*, *24*, 1142–1151.

Denison, R. N., Yuval-Greenberg, S., & Carrasco, M. (2019). Directing voluntary temporal attention increases fixational stability. *Journal of Neuroscience*, *39*, 353–363.

Fernández, A., Denison, R. N., & Carrasco, M. (2019). Temporal attention improves perception similarly at foveal and parafoveal locations. *Journal of Vision*, *19*, 12–12.

Lakatos, P., Karmos, G., Mehta, A. D., Ulbert, I., & Schroeder, C. E. (2008). Entrainment of neuronal oscillations as a mechanism of attentional selection. *Science*, *320*, 110–113.

Miniussi, C., Wilding, E. L., Coull, J. T., & Nobre, A. C. (1999). Orienting attention in time: Modulation of brain potentials. *Brain*, *122*, 1507–1518.

Nobre, A. C., & van Ede, F. (2018). Anticipated moments: temporal structure in attention. *Nature Reviews Neuroscience*, *19*, 34–48.

Palmieri, H., Fernández, A., & Carrasco, M. (2023). Microsaccades and temporal attention at different locations of the visual field. *Journal of Vision*, *20*, 1524.

Raymond, J. E., Shapiro, K. L., & Arnell, K. M. (1992). Temporary suppression of visual processing in an RSVP task: An attentional blink? *Journal of Experimental Psychology: Human Perception and Performance*, *18*, 849–860.

Tkacz-Domb, S., & Yeshurun, Y. (2021). Temporal crowding is a unique phenomenon reflecting impaired target encoding over large temporal intervals. *Psychonomic Bulletin & Review*, *28*, 1885–1893.