

BRIEF REPORT

Temporal integration depends on increased prestimulus beta band power

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Abstract

Temporal integration was examined using a missing element task, in which task performance depends on the ability to integrate brief successive stimulus displays. Previous studies have suggested that temporal integration is under endogenous control and that integration is more likely when stimuli match the observer's temporal expectancies. Beta oscillations have previously been related to such cognitive (and attentional) control, as well as to audiovisual integration. We thus hypothesized that prestimulus power in the beta frequency band might reflect "integration readiness" and distinguish trials in which stimuli were successfully integrated from unsuccessful ones. The results showed increased upper beta power (21–30 Hz) prior to successful integration over central and parietal electrodes. This finding supported the idea that increased prestimulus beta power might reflect general control processes that can facilitate integration.

Descriptors: Temporal integration, EEG, Beta frequency band, Prestimulus activity

The ability to perceive events in time allows us to maintain coherence in an ever-changing stream of perceptual input and enables appropriate actions. Event perception relies heavily on temporal integration: When visual stimuli appear in rapid succession within ± 200 ms, the brain tends to treat them as a single, integrated event (Eriksen & Collins, 1967). Temporal integration has been observed with various types of stimuli, such as letters that form a word (Forget, Buiatti, & Dehaene, 2010), two halves of faces (Cheung, Richler, Phillips, & Gauthier, 2011), and dot matrices (Hogben & Di Lollo, 1974).

Temporal integration is not entirely automatic, however. Several factors influence whether integration will occur. Stimulus characteristics such as duration and luminance affect integration frequency (Di Lollo, 1977, 1980; Hogben & Di Lollo, 1974; Long & Beaton, 1982). Endogenous factors that reflect the state of the observer's cognitive and perceptual system, such as the expected presentation speed (Akyürek, Toffanin, & Hommel, 2008) and the availability of (transient) attention, also affect integration (Visser & Enns, 2001; Yeshurun & Levy, 2003). Electrophysiological studies on temporal integration have shown resultant modulations of the N1, N2, P3, and N2pc components of the event-related potential (ERP), each of which might indeed relate to endogenous factors (Akyürek & Meijerink, 2012; Akyürek, Schubö, & Hommel, 2010).

However, ERPs do not allow for examination of prestimulus effects, which could be important if the state of the perceptual

system—even before stimulus onset—indeed affects temporal integration. Prestimulus effects on temporal integration may be detected by examining electroencephalogram (EEG) oscillatory power, in particular in the beta frequency band, which has been related to cognitive control as well as audiovisual integration (Engel & Fries, 2010; Keil, Müller, Ihssen, & Weisz, 2012). Both pre- and poststimulus beta oscillations are also linked to attention (Deiber et al., 2007; Gross et al., 2004; Kranczioch, Debener, Maye, & Engel, 2007; Wróbel, 2000). A common theme in these studies is that beta power (and/or synchrony) and task performance increase when the perceptual system is optimally set up to process the current or the upcoming stimulus, the latter due to successful prediction or because the previous stimuli were similar. Importantly, when controlling temporal integration is concerned, this optimal state could be related closely to the currently preferred duration of event timing.

To determine whether prestimulus differences in oscillatory power might affect temporal integration, data presented in Akyürek et al. (2010) were presently reanalyzed. In this experiment, participants performed a missing element task (MET), in which two successive stimulus displays (S1 and S2) were presented with a 10-ms interstimulus interval (ISI). Each display contained 12 out of 25 possible squares in a 5 × 5 matrix. One matrix position remained empty, and participants were instructed to localize that missing element. When the two displays are perceived separately, this is very hard to accomplish in a limited amount of time (here 1800 ms). However, when the two displays are temporally integrated into one percept, the missing element is easy to spot. When S1 was presented for 70 ms and S2 for 10 ms, participants responded correctly in about half of the trials. This allowed a

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comparison of the trials in which temporal integration occurred with trials in which it did not. On the basis of the literature described above, we expected increased prestimulus beta power on trials in which temporal integration eventually succeeded.

Methods

Participants

Twenty-one students (18 female, 3 male) with normal or corrected-to-normal vision and a mean age of 23 years (range 19–30 years) participated in the study. This study presents a new analysis of the EEG data collected in Experiment 4 of Akyürek et al. (2010). Further details with regard to its design and execution are reported there.

Stimuli and Task

Participants searched for the missing element in a MET, consisting of two successive display frames, each containing a random selection of 12 out of 25 possible squares (without overlap), so that only one square was not drawn in either display. In the condition exclusively analyzed here, S1 was presented for 70 ms, followed by a 10-ms blank, and followed by S2 for another 10 ms. Participants responded to a prompt showing all matrix positions, which appeared 600 ms after stimulus offset and which remained on screen until a response was registered or 1200 ms had elapsed. After a blank screen with a (random) duration of 600–800 ms, the next trial started.

Electrophysiological Recording and Data Analysis

EEG was recorded with 64 Ag-AgCl electrodes laid out according to the extended international 10–20 system. The electrodes were referenced to Cz and re-referenced off-line to the average of both mastoids. Horizontal and vertical eye movements were recorded from the outer canthi of the eyes and above and below the left eye, respectively. Electrode impedance was kept below 5 k Ω . Data were recorded with a 500-Hz sample rate and a 125-Hz low-pass filter and a 0.1-Hz high-pass filter. Off-line, the data were filtered with a 100-Hz low-pass filter and a 0.16-Hz highpass filter (both 48 dB/oct). Subsequently, the data were segmented into 2500-ms segments, starting 1000 ms prior to the onset of S1 and ending 1500 ms afterward. Ocular artifacts (blinks and eye movements) were corrected using the Gratton–Coles procedure (Gratton, Coles, & Donchin, 1983). Trials with voltage steps exceeding 50 mV/ms were excluded from analysis.

The analysis compared trials with unsuccessful temporal integration to trials with successful integration, as evidenced by the participants' response accuracy (excluding missing responses). Time–frequency analyses were performed with the Matlab-based FieldTrip toolbox (Oostenveld, Fries, Maris, & Schoffelen, 2011) using Morlet wavelets. This analysis produced an estimate of oscillatory raw power for each time sample between 600 ms prestimulus and 600 ms poststimulus (in 10-ms steps) and for each frequency between 8 and 60 Hz (in 0.5-Hz steps). The Morlet wavelets contained a fixed number of cycles of sinusoidal oscillations for each frequency band (8–12 Hz, 6 cycles; 13–20 Hz, 7 cycles; 21–30 Hz, 8 cycles; 31–60 Hz, 9 cycles). Subsequently, following Grandchamp and Delorme (2011), a relative baseline correction was applied in which the power on each time point and frequency was divided by the average power of that frequency in the entire epoch

(–600 ms to 600 ms) for each channel separately. This procedure reduces the effect of artifactual trials with high power estimates.

A nonparametric cluster-based randomization technique was used to identify whether the power was different for correct and incorrect trials (Maris & Oostenveld, 2007). This method deals with the multiple comparisons problem while accounting for the dependency of the data by clustering neighboring samples that show the same effect. The analysis was performed separately for the average power in each of four frequency bands, alpha (8–12 Hz), lower beta (13–20 Hz), upper beta (21–30 Hz), and gamma (31–60 Hz). Independent sample *t* tests (correct vs. incorrect trials) were performed on all channels and time points. Samples in which this *t* value exceeded an uncorrected threshold of $p < .05$ were subsequently clustered. The sum of the *t* values within a cluster was used as the cluster-level statistic. By randomizing the data across the two conditions and recalculating the test statistic 2,000 times, a reference distribution of maximum cluster *t* values was generated to evaluate the statistic of the actual data.

Results

As reported previously by Akyürek et al. (2010), temporal integration was achieved in approximately half the trials (mean correct = 52.1%, $SEM = 3.1\%$). The cluster-based randomization technique revealed that power in the upper beta band (21–30 Hz) between 280 and 180 ms before stimulus onset (see Figure 1) was significantly higher in successful integration than in unsuccessful integration trials ($p = .02$). Tests in the alpha ($p = .94$), lower beta ($p = 1$), and gamma bands ($p = .57$) did not show significant results, either pre- or poststimulus. The upper beta effect was mainly present over parietal and central electrodes.

Discussion

Consistent with our expectations, prestimulus oscillatory power was related to temporal integration. Specifically, prestimulus upper beta power (21–30 Hz) over parietal and central electrodes was significantly higher in trials with stimulus integration compared to trials without. Together with previous evidence that temporal integration is under endogenous control, the present findings are compatible with one hypothesized role of beta band oscillations in the maintenance of the status quo of the perceptual system (Akyürek et al., 2008; Engel & Fries, 2010). The data thus suggested that integration is most likely to succeed when the perceptual system is optimally tuned for the upcoming task, which likely requires adopting a relatively long integration window, able to encompass the two successive stimuli. This may be one way in which beta activity is related to temporal (onset) expectations (Cravo, Rohenkohl, Wyart, & Nobre, 2011), which may eventually also subservise motor planning (Alegre et al., 2003).

Such optimization of the state of the perceptual system may be related to the availability of attention. Indeed the current results provide support for the idea that attention facilitates temporal integration (Visser & Enns, 2001; Yeshurun & Levy, 2003). Several studies have related beta synchrony and beta power to attention. Increased beta power has been related to higher performance in vigilance tasks (Belyavin & Wright, 1987) and was found to increase during stimulus expectancy periods (Basile et al., 2007). Beta synchrony has furthermore been found to predict the perception of briefly presented visual stimuli (Hanslmayr et al., 2007), the perception of the second target in attentional blink tasks (Gross et al., 2004; Kranczioch et al., 2007), and the application of top-down

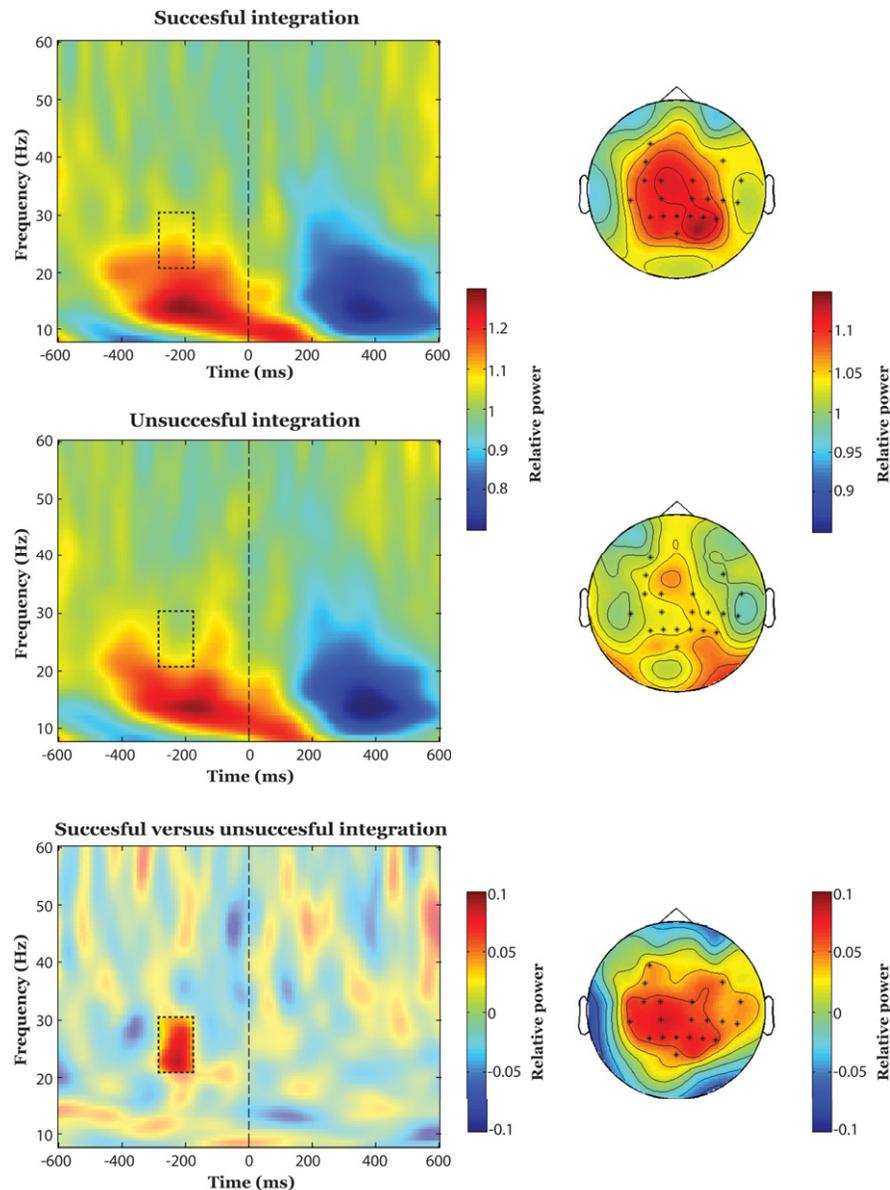


Figure 1. Time–frequency plots for successful integration trials, unsuccessful integration trials, and the difference between successful and unsuccessful integration trials. The plots show relative power (dB) averaged over the five electrodes showing the strongest differences between these conditions (P1, P2, P3, CP1, and CP3). The dashed square indicates where successful and unsuccessful integration trials were significantly different. The scalp maps represent relative power distributions (calculated over the upper beta average) over the scalp at 230 ms before stimulus onset. The stars indicate electrodes that belong to the cluster that shows a significant difference between the trial types.

attentional control (Buschman & Miller, 2007). The present increase in beta power before stimulus onset fits well with the idea that (anticipatory) attention may facilitate temporal integration. Behaviorally, this may also transpire in longer perceived durations of attended stimuli (e.g., Enns, Brehaut, & Shore, 1999). Whether these effects reflect spontaneous waxing and waning of attention over trials or active preparation for upcoming stimuli remains to be determined.

The perceptual state reflected by the prestimulus beta activity cannot only reflect an increased ability to discern stimuli; in the present task this could lead to the arguably more accurate perception of two successive stimuli, rather than one integrated percept.

Thus, the present beta activity must also reflect an increased tendency to integrate sensory input. In one previous study, increased prestimulus beta power was related to auditory–visual integration (Keil et al., 2012), in which beamformer source analysis pointed to a network of left superior temporal gyrus, precuneus, and right middle frontal gyrus. In another study by Hipp, Engel, and Siegel (2011) beta band synchronization in a similar fronto-parietal-occipital network also predicted integration of visual and auditory information. The current results may be related to these findings by assuming that prestimulus beta power might reflect processes that facilitate integration in general, both between modalities as well as in the temporal domain.

References

- Akyürek, E. G., & Meijerink, S. K. (2012). The deployment of visual attention during temporal integration: An electrophysiological investigation. *Psychophysiology*, *49*, 885–898. doi:10.1111/j.1469-8986.2012.01380.x
- Akyürek, E. G., Schubö, A., & Hommel, B. (2010). Fast temporal event integration in the visual domain demonstrated by event-related potentials. *Psychophysiology*, *47*, 512–522. doi:10.1111/j.1469-8986.2010.00962.x
- Akyürek, E. G., Toffanin, P., & Hommel, B. (2008). Adaptive control of event integration. *Journal of Experimental Psychology: Human Perception and Performance*, *34*, 569–577. doi:10.1037/0096-1523.34.3.569
- Alegre, M., Gurtubay, I. G., Labarga, A., Iriarte, J., Malanda, A., & Artieda, J. (2003). Alpha and beta oscillatory changes during stimulus-induced movement paradigms: Effect of stimulus predictability. *NeuroReport*, *14*, 381–385. doi:10.1097/01.wnr.0000059624.96928.c0
- Basile, L. F. H., Anghinah, R., Ribeiro, P., Ramos, R. T., Piedade, R., Ballester, G., & Brunetti, E. P. (2007). Interindividual variability in EEG correlates of attention and limits of functional mapping. *International Journal of Psychophysiology*, *65*, 238–251. doi:10.1016/j.ijpsycho.2007.05.001
- Belyavin, A., & Wright, N. A. (1987). Changes in electrical activity of the brain with vigilance. *Electroencephalography and Clinical Neurophysiology*, *66*, 137–144. doi:10.1016/0013-4694(87)90183-0
- Buschman, T. J., & Miller, E. K. (2007). Top-down versus bottom-up control of attention in the prefrontal and posterior parietal cortices. *Science*, *315*, 1860–1864. doi:10.1126/science.1138071
- Cheung, O. S., Richler, J. J., Phillips, W. S., & Gauthier, I. (2011). Does temporal integration of face parts reflect holistic processing? *Psychonomic Bulletin & Review*, *18*, 476–483. doi:10.3758/s13423-011-0051-7
- Cravo, A. M., Rohenkohl, G., Wyart, V., & Nobre, A. C. (2011). Endogenous modulation of low frequency oscillations by temporal expectations. *Journal of Neurophysiology*, *106*, 2964–2972. doi:10.1152/jn.00157.2011
- Deiber, M., Missonnier, P., Bertrand, O., Gold, G., Fazio-Costa, L., Ibañez, V., & Giannakopoulos, P. (2007). Distinction between perceptual and attentional processing in working memory tasks: A study of phase-locked and induced oscillatory brain dynamics. *Journal of Cognitive Neuroscience*, *19*, 158–172. doi:10.1162/jocn.2007.19.1.158
- Di Lollo, V. (1977). Temporal characteristics of iconic memory. *Nature*, *267*, 241–243. doi:10.1038/267241a0
- Di Lollo, V. (1980). Temporal integration in visual memory. *Journal of Experimental Psychology: General*, *109*, 75–97. doi:10.1037/0096-3445.109.1.75
- Engel, A. K., & Fries, P. (2010). Beta-band oscillations—Signalling the status quo? *Current Opinion in Neurobiology*, *20*, 156–165. doi:10.1016/j.conb.2010.02.015
- Enns, J. T., Brehaut, J. C., & Shore, D. I. (1999). The duration of a brief event in the mind's eye. *Journal of General Psychology*, *126*, 355–372. doi:10.1080/00221309909595371
- Eriksen, C. W., & Collins, J. F. (1967). Some temporal characteristics of visual pattern perception. *Journal of Experimental Psychology*, *74*, 476–484. doi:10.1037/h0024765
- Forget, J., Buiatti, M., & Dehaene, S. (2010). Temporal integration in visual word recognition. *Journal of Cognitive Neuroscience*, *22*, 1054–1068. doi:10.1162/jocn.2009.21300
- Grandchamp, R., & Delorme, A. (2011). Single-trial normalization for event-related spectral decomposition reduces sensitivity to noisy trials. *Frontiers in Psychology*, *2*, 236. doi:10.3389/fpsyg.2011.00236
- Gratton, G., Coles, M. G. H., & Donchin, E. (1983). A new method for off-line removal of ocular artifact. *Electroencephalography and Clinical Neurophysiology*, *55*, 468–484. doi:10.1016/0013-4694(83)90135-9
- Gross, J., Schmitz, F., Schnitzler, I., Kessler, K., Shapiro, K., Hommel, B., & Schnitzler, A. (2004). Modulation of long-range neural synchrony reflects temporal limitations of visual attention in humans. *Proceedings of the National Academy of Sciences, USA*, *101*, 13050–13055. doi:10.1073/pnas.0404944101
- Hanslmayr, S., Aslan, A., Staudigl, T., Klimesch, W., Herrmann, C. S., & Bäuml, K. (2007). Prestimulus oscillations predict visual perception performance between and within subjects. *NeuroImage*, *37*, 1465–1473. doi:10.1016/j.neuroimage.2007.07.011
- Hipp, J. F., Engel, A. K., & Siegel, M. (2011). Oscillatory synchronization in large-scale cortical networks predicts perception. *Neuron*, *69*, 387–396. doi:10.1016/j.neuron.2010.12.027
- Hogben, J. H., & Di Lollo, V. (1974). Perceptual integration and perceptual segregation of brief visual stimuli. *Vision Research*, *14*, 1059–1069. doi:10.1016/0042-6989(74)90202-8
- Keil, J., Müller, N., Ihssen, N., & Weisz, N. (2012). On the variability of the McGurk effect: Audiovisual integration depends on prestimulus brain states. *Cerebral Cortex*, *22*, 221–231. doi:10.1093/cercor/bhr125
- Kranczioch, C., Debener, S., Maye, A., & Engel, A. K. (2007). Temporal dynamics of access to consciousness in the attentional blink. *NeuroImage*, *37*, 947–955. doi:10.1016/j.neuroimage.2007.05.044
- Long, G. M., & Beaton, R. J. (1982). The case for peripheral persistence: Effects of target and background luminance on a partial-report task. *Journal of Experimental Psychology: Human Perception and Performance*, *8*, 383–391. doi:10.1037/0096-1523.8.3.383
- Maris, E., & Oostenveld, R. (2007). Nonparametric statistical testing of EEG- and MEG-data. *Journal of Neuroscience Methods*, *164*, 177–190. doi:10.1016/j.jneumeth.2007.03.024
- Oostenveld, R., Fries, P., Maris, E., & Schoffelen, J. (2011). FieldTrip: Open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. *Computational Intelligence and Neuroscience*, *2011*, Article ID 156869. doi:10.1155/2011/156869
- Visser, T. A. W., & Enns, J. T. (2001). The role of attention in temporal integration. *Perception*, *30*, 135–145. doi:10.1068/p3089
- Wróbel, A. (2000). Beta activity: A carrier for visual attention. *Acta Neurobiologiae Experimentalis*, *60*, 247–260.
- Yeshurun, Y., & Levy, L. (2003). Transient spatial attention degrades temporal resolution. *Psychological Science*, *14*, 225–231. doi:10.1111/1467-9280.02436

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