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Commentary on "Working Memory Retention Systems: A State of Activated Long-Term Memory" by Daniel S. Ruchkin, Jordan Grafman, Katherine Cameron, and Rita S. Berndt

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Prefrontal cortex and the generation of oscillatory visual persistence

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Abstract

In this contribution, the formation of 'pre-iconic' visual-prime persistence is described in the context of prime-specific, independent-component activation at prefrontal and posterior EEG-recording sites. While this activity subserves near identical neural systems to those described by Ruchkin and colleagues, we consider priming to be a dynamic process, identified with patterns of coherence and temporal structure of very high precision.

Neural oscillations in electrophysiological investigations are found throughout the cortex at a wide range of frequencies and at every level of resolution. The extent to which the brain appears to employ oscillations and the complexity of the physiologically observed phenomena challenge any precise description of their functional role. If we are to consider the timing of neural activity as an organic instantiate of (inner) psychophysical processes at work, with a physical structure that allows correspondences to be made between these levels of analysis, then 'precise description' may be considered to refer to the specification of which characteristics of neural timing relate with which characteristic of the psychophysical process under examination. Good temporal frequency resolution in the EEG provides a means of resolving this problem by permitting correspondences to be made between the timing of neural events and observations on behavior. Considered from the psychophysical perspective, perhaps the optimal conditions to address this question are those in which perception becomes influenced by variations in the temporal characteristics of stimulus events. However, the majority of psychophysical methods employed are conceptually static in nature, while the questions addressed here, namely the relation of memory storage with the binding of activity across neural mechanisms, explicitly aim at dynamic aspects of psychophysical structure.

Is there evidence for dynamic psychophysical structure related to temporal binding? One line of evidence relates to the subthreshold, oscillatory-priming effects reported by Elliott and colleagues (Elliott & Müller, 1998, 2000; Kompass & Elliott, 2001). Prime responses exhibit a number of particular temporal characteristics: Primes persist for duration shorter than that of iconic memory but consistent with the persistence of a visible stimulus (i.e. <= 300 ms, see Coltheart, 1980), and are periodic, characterized by the frequency of priming-display presentations (the prime reaction time (RT) x premask-target ISI functions were periodic with a frequency of around 40 Hz, see Elliott & Müller, 2000). That prime persistence comes to be characterized by the frequency of prime- display presentation (the priming stimulus comprises one of four repeatedly presented but asynchronized image frames each presented at 10 Hz) has been taken as an indication that the prime is generated by mechanisms capable of coding global stimulus properties in interaction with relatively early visual-coding mechanisms. A second line of evidence, which supports this view, draws from the observation of Kompass and Elliott that the prime response temporally precedes regular, priming-stimulus presentation, and (given presentation at an identical phase relative to the rhythm of priming display presentation) target-display presentation by some tens of milliseconds. In this case the prime is understood to involve an anticipatory response in higher cortical mechanisms which serves to 'preactivate' lower level prime- and target-coding mechanisms.
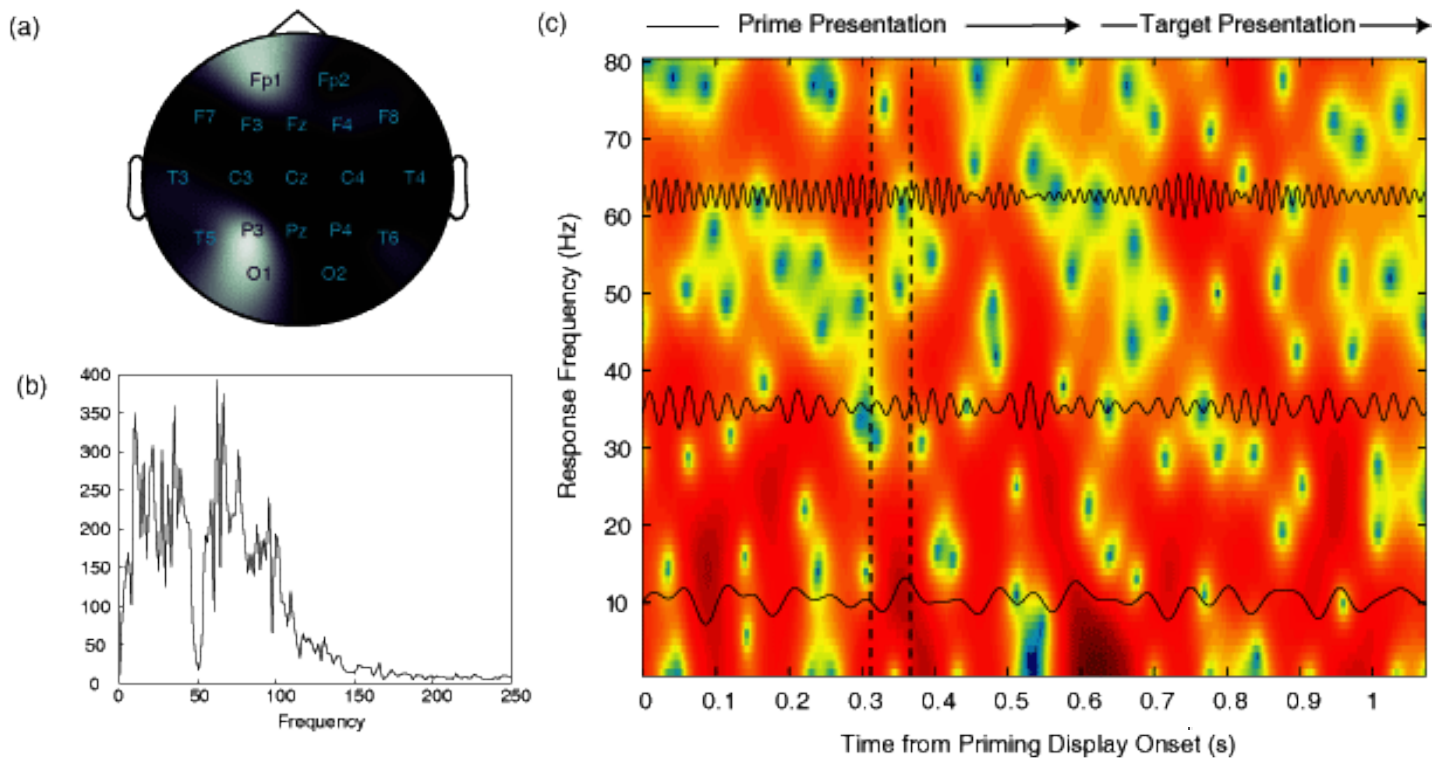
Figure 1: Prime-specific activation during priming-display presentation. In (a) the head plot represents the average distribution of variance across the scalp at the mean time of maximum variance, which occurred at 341 milliseconds (ms) post- priming display onset (light - dark indicates maximum - minimum absolute variance). Averages were calculated from separate components from 10 subjects derived from a series of independent-components reconstructions of the averaged event-related potentials (ERPs) for each of 12 subjects. Clustering automatically excluded 2 subjects who showed no variance maxima with an appropriate latency or topography. Prominent are maxima under posterior electrodes O1 and P3 and electrode Fp1, which lies approximately over the superior frontal gyrus (Homan, Herman & Purdy, 1987) and is associated with dorsolateral prefrontal activation. In (b) is shown the averaged spectral power representation of the 10 component activations. Peaks are evident at 10, 35, and 62/66 Hz. In (c) the spectrogram represents the time-frequency decomposition of the average component activation (blue - red indicates minimum - maximum log variance). The vertical dashed lines illustrate the time range over which variance maxima were clustered (the mean time, +- 1 standard deviation was 341 +- 29 ms). Horizontal traces represent (in ascending order) the averaged representation of oscillatory activity at 10, 35 and 62 Hz. Times of priming-display and target-display presentation are indicated at the top of panel (c).

Evidence for multiregional prime activity, with particular temporal characteristics may also be drawn from examination of the EEG[1] accompanying priming-stimulus presentation. Component activations reconstructed from the EEG provide evidence for prime development as the combined function of occipito-parietal and prefrontal cortical activation. This is shown in Figure 1. Here component activity consists of coactive neural assemblies located under electrodes Fp1 and O1/P3. One function of prefrontal cortex is a delayed sample to matching response and it seems likely that the coactivation necessary for coding repeated prime presentation, in terms of the global frequency of priming-stimulus presentation, might be carried out by assemblies under

Fp1 responding to a staccato of 10-Hz signals from posterior assemblies coding the local spatio-temporal organization of the priming display. Of particular interest is the timing of the oscillatory response to priming-display presentation. Notice in Figure 1 (c), at the intersection of horizontal traces of high frequency (35 and 62- Hz) activity within the time period of maximum variation lie on, or just after a brief loss of coherence and prior to a subsequent burst of coherent oscillatory activity. From ontogenesis > 66 Hz at 400 ms, coherence spreads across lower frequencies as a function of time. Related activity occurs in the 35-40-Hz region at around 530-540 ms with corresponding activity at around 10 Hz at 590 ms, almost immediately prior to target-display presentation at 600 ms. The pattern of coactivation between neural assemblies under Fp1 and O2/P3 thus offers itself as a strong candidate for generation of the anticipatory response reported by Kompass and Elliott.

Two points emerge from the analyses presented here. The first is that prefrontal-posterior synchronization appears to be involved in the formation of stimulus-related persistence, which has been shown to possess a duration sufficiently short to suggest coactive neural assemblies may remain functional for as little as 200 - 300 ms post-stimulus offset (Elliott & Müller, 2000). The second is that at least one characteristic of the prime response, the temporal precession of prime activity relative to target display presentation, may emerge as a function of cascading fluctuations in coherence between various frequency responses to prime stimulus presentation. An identification of particular dynamic states, which appear to be related to particular psychophysical performance refocuses attention towards the requirement for description of active cognitive states in terms of the dynamic states upon which they may depend.

Footnotes

1. For 12 subjects (4 male, mean age 24.1 years) the EEG was recorded from 19 Ag-AgCl electrodes (electrode positions are shown in Figure 1 (a)) according to the international 10-20 system. Subjects performed a variant of the primed target detection task described in Elliott and Müller (1998). The experiment described here employed a priming-display presentation frequency of 40 Hz while priming displays were presented for 600 ms and followed immediately by target-display presentation. The electrodes were mounted in an elastic cap, were referenced to Fz while the nose served as the ground electrode. Electrode impedance was maintained below 5 kOhm. Horizontal and vertical electroocculargram (EOG) was additionally registered with four electrodes. EEG activity was amplified by means of NeuroScan amplifiers, digitized on-line with a sampling rate of 500 Hz and analog-filtered with a 0.1-Hz high-pass and a 100-Hz low-pass filter. A 50-Hz notch filter was applied to remove artifacts related to the mains electricity supply. For the recording of EOG, the time constant 300 ms with a low pass filter at 70 Hz was used. The EOG-channel was visually inspected for each trial, and trials with eye movement or blink artifact were rejected. Localized muscle artefacts (at electrodes T3 and T4) were identified and if present reconstructed by means of an extended independent components analysis (ICA) algorithm (see, Makeig, Westerfield, Jung, Covington, Townsend, Sejnowski & Courchesne, 1999). Averaging epochs lasted from termination of an alerting tone 200 ms before, until 1200 ms after priming-display presentation. Baselines were computed in the –200-0 ms interval for each trial and subtracted prior to subsequent

analyses. Analyses were carried out on the averaged event-related potential (ERP) for each subject. In a first step a series of component activations were recovered from each averaged signal by means of ICA using information maximization (infomax) techniques described by Bell and Sejnowski (1995) with variants of the ICA Matlab package (v.3.52) available under http://www.cnl.salk.edu/~scott/. In order to classify components and identify particular groups of clusters that appeared during premask-matrix presentation components were defined in terms of the latency and topographical distribution of variance maxima (in this case topographical projections were standardized by substituting raw activation at each electrode with the corresponding z-value computed relative to all projected activations at the time of maximal activation). Classification then proceeded by means of cluster analysis, calculating Euclidean distance between objects and computing linkages in a hierarchical cluster tree based upon the average distances between groups of objects and a threshold of 19 clusters (cophonetic correlation coefficient $c = 0.81$). The resulting clusters were considered for further analysis if (i) they included activations from more than 75% of subjects (i.e. 9 or more of 12 activations), (ii) they were specific to priming-stimulus presentation (iii) maxima fell within the period of priming-display presentation and (iv) if following examination of the frequency component of each component activation by means of a 256-point fast-Fourier transform (FFT), strong peaks were evident at, or close to the priming-display presentation frequency of 40 Hz. On these criteria a single component cluster was identified, which is described in Figure 1 and the main body of text.

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