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The Dynamics of Operations in Visual Memory: A Review and New Evidence for Oscillatory Priming

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Abstract. Evidence from neurophysiological studies indicates that the synchronization of distributed neuronal assemblies in the gamma frequency range is responsible for the integration of discrete stimulus components into coherent wholes (e.g., see Singer, 1999 for review). Psychophysical support for this hypothesis has been reported in experiments that demonstrate that the presentation of a synchronous-premask frame within a 40-Hz flickering premask matrix primes the subsequent detection of a target Kanizsa-type square by generation of a 40-Hz prime (Elliott & Müller, 1998). Psychopharmacological and electrophysiological evidence suggests that this priming mechanism is related to activity in interneuronal networks and relies on the combined function of prefrontal and posterior circuits. In addition, psychophysical experiments demonstrate the existence of a prime-specific visual short-term memory that oscillates at 40 Hz and remains functional for up to 300 ms post-stimulus offset, while, if an appropriate oscillatory mask is presented between premask-matrix offset and target display, onset priming appears to be weakened. These results are consistent with a view of the prime as a form of oscillatory mechanism, related to the persistence of visual information (Coltheart, 1980) and in the capacity guided by (prefrontal) top-down influences upon visual-cortical function.

Key words: , , ,

Introduction

A now substantial body of physiological evidence exists to suggest that correlated activity in distributed neuronal populations serves to relate separate visual features either rendering them as perceptual unities or providing the basis for the subsequent perception of coherence (an idea earlier enshrined in computational terms in the temporal correlation hypothesis of von der Malsburg, 1980; for more recent developments see Gray, 1999 and Singer, 1999 for reviews). Support for this hypothesis is derived in the main from physiological studies that report significant variations in the cross-correlation of firing between neurons responding to stimuli that group according to one or other Gestalt-grouping principles (Engel, Kreiter, König, & Singer, 1991; Gray, König, Engel, & Singer, 1989). The experiment reported by Gray and colleagues (Gray et al., 1989) may be considered generally representative of the effects of grouping stimuli upon (visual-cortical) neural activity. In their study, when the receptive fields of visuo-cortical cells in anaesthetized cats were stimulated by separate bars of light moving in opposite directions, oscillatory neural activity showed low cross-correlation. However, when bars were passed across the receptive fields in the same direction, a correlative relationship was observed between oscillatory activity within the 40–60 Hz range (considered and often referred to in terms of the EEG gamma-bandwidth

considered to centre on around 40 Hz). The strongest cross correlations were obtained when a single, connected bar stimulated the two neurons. On these grounds, the synchronization of oscillatory neuronal activity has been suggested as a mechanism in the service of perception and responsible for binding visual features that reflect global stimulus properties such as continuity, similarity, or orientation.

In broad agreement with these claims, Elliott and Müller (1998) have shown that the detectability of a Kanizsa-type target square (composed of four 90°-corner elements that formed an illusory square by virtue of collinearity grouping) presented within a matrix of nongrouping distracter elements (see Figure 1a) can be expedited if target presentation is preceded by the presentation of 4 synchronized and below threshold premask stimuli presented repeatedly for a short period of time in advance of and at the matrix location subsequently occupied by the target elements. Development of this premask paradigm was based on the assumption that feature-coding mechanisms are, in principle, entrainable by external stimulus modulation (e.g., Gur & Snodderly, 1997). On this assumption, a temporarily modulated premask comprising a flickering 3×3 matrix of crosses (see Figure 1a) was presented before the onset of the (static) target or nontarget matrix. This design permitted manipulation of the premask-presentation frequency independently of the task-relevant target display with the result that the effects of premask presentation upon target coding could be examined free from potential confounds arising from the effects of variations in spatial relative to temporal or temporal relative to spatial organizations of visual features or groupings. This consideration was based largely on the fact that a number of very similar paradigms employing direct perceptual report data have shown generally contradictory results, sometimes showing effects of temporal manipulations and sometimes not (i.e., Fahle, 1993; Fahle & Koch, 1995; Kiper, Gegenfurtner, & Movshon, 1996; Leonhards, Singer, & Fahle, 1997; Usher & Donnelly, 1998).

Although presented prior to target-matrix presentation, the premask- and target-matrices were related in one critical aspect, notably via presentation of a synchronous premask comprising four premask crosses in an identical phase of the global presentation frequency of premask-matrix presentation and presented in square arrangement at the matrix location subsequently occupied by the junction elements that came together to define a target. The synchronous premask contrasted with a random premask condition in which 4 elements were presented across the premask matrix in pseudo-random arrangement, while the elements presented at the locations of the target elements were presented across two or more
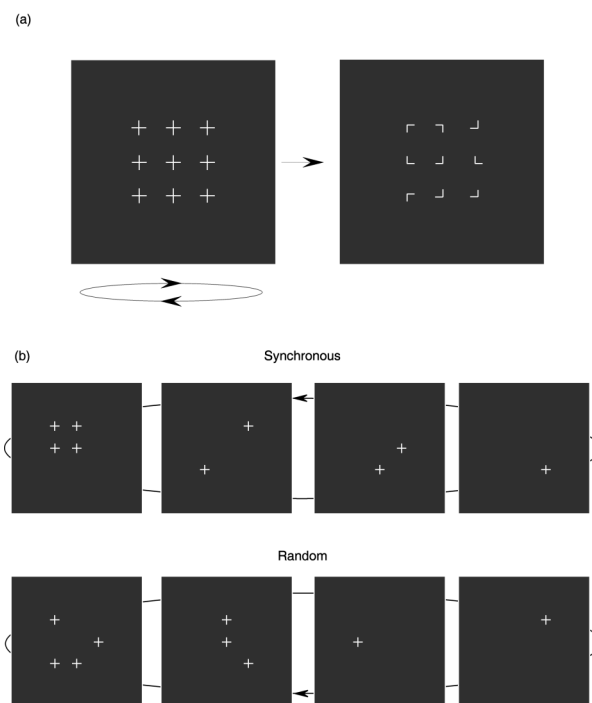

Figure 1. The stimulus presentation paradigm: In (a) the premask display presentation was followed by a target display of 90°-corner junctions to which observers had to make a speeded target (i.e., Kanizsa square) present or absent response. In (b) are shown example sequences of the four premask frames in both the synchronous (upper panels) and random (lower panels) conditions: In the former condition, one premask frame consists of four elements in square arrangement; see the upper far left panel.

premask frames (see Figure 1b). In the experiments described by Elliott and Müller (1998), the premask and target matrices comprised 9 elements in a 3×3 arrangement with premask elements presented across 4 frames. Consequently, in addition to the 4 synchronous or random premask elements there were 5 remaining premask-matrix locations at which premask elements were presented in pseudo-randomized arrangements within and across the 3 remaining premask-matrix frames (an example is given in Figure 1b).

In both premask conditions, the sequence of premask frames was repeatedly displayed in a fixed order for a given presentation time. The presentation frequency of the premask frames, and consequently that of the entire premask matrix, was determined by the repeat frequency of each frame, the duration of each frame, and the interval between successive frames. For 40-Hz premask display flicker, for example, each premask frame was repeated at 10 Hz, had a duration of 25 milliseconds (ms), and was followed by the next frame within less than 1 ms. Despite on-

set asynchronies of 100 ms for each individual frame (for 40-Hz flicker conditions), the premask display matrix had the appearance of a 3 × 3 matrix of seemingly static crosses, characterized by some variation in surface illumination of no clearly discernible spatiotemporal structure.

Following presentation of the premask display, all crosses were immediately reduced to 90° corner junctions that were presented on the display until the observer produced a speeded target-absent/present response. The target was defined as a Kanizsa-type target square of grouping 90° corner junctions, to be detected within a 3 × 3-element matrix of grouping target (if present) and nongrouping distracter junctions presented with pseudorandom orientation. The experiments were performed on the basis of the hypothesis that the presentation of the synchronous premask displays at entraining frequencies matching those of neural, stimulus-coding mechanisms should expedite target Kanizsa-type figure coding relative to premask-display presentation at other frequencies. Consistent with this, Elliott and Müller (1998, Experiment 1) reported that detection of the target was significantly faster in the synchronous relative to the random-premask condition only when the synchronous premask frame was presented within a matrix that flickered at a presentation frequency of 40 Hz. This frequency-specific synchrony effect was found to be target-conditional, that is, manifest only on trials that contained a Kanizsa-type figure in the target display and not on target-absent trials (and consequently, is hereafter referred to as a synchrony priming effect). In addition, investigations of the smallest priming duration showed a minimum of two full cycles of the four sequential premask frames (200 ms) to become manifest and did not vary as a function of premask-display duration from 200 ms onwards (see Müller & Elliott, 1999). Investigations of the prime-detectability furthermore demonstrated that synchrony priming was obtained despite observers being unable to detect the presence of a synchronous-premask frame (see Elliott & Müller, 1998, Experiment 2). Finally, it was observed in the absence of evidence that the synchronous-premask frame directs attention to its location (display quadrant) in the manner of an automatic spatial-attention cue (e.g., Posner & Petersen, 1990; see also Elliott & Müller, 1998, Experiment 3). This finding of a synchrony-enhancement (RT) effect was consequently interpreted in terms of target priming induced by the repeated presentation of the synchronous premask, with the synchronized neural response (generated by the premask) combining with the response generated by the presentation of the target Kanizsa-type figure. On this basis it was concluded that one important outcome of synchronous premask presentation was the presegmentation of the target quadrant, an idea

consistent with the claim made for neural synchronization in the computational theory originally given by von der Malsburg (1981).

Physiological Aspects of Premask–Induced Segmentation: How and where?

Combining Psychopharmacology with Synchrony Priming

Additional support for a figure-ground segmentation account of synchrony priming has been gathered in a study employing pharmacological methods. Administration of the benzodiazepine, lorazepam, which influences the temporal characteristics of inhibitory interneuronal function by fixation on the $GABA_A$ receptor, has been shown to selectively affect grouping and segmentation processes, enhancing segmentation performance while reducing performance in tasks involving detection of visual groupings (see Giersch, 1999 for review). Elliott, Becker, Boucart and Müller, (2000a) presented observers with enlarged 5 × 5 element premask-target matrices and found that RTs were increased relative to performance following administration of a placebo and of diazepam, a second benzodiazepine. This was taken to indicate a specific difficulty in target detection following lorazepam administration. However, Elliott and colleagues also found that priming effects were overall amplified by a factor of 1.33:1 following administration of lorazepam relative to both normal (unmedicated) and placebo performance. Given that lorazepam selectively enhances the efficiency of local inhibitory $GABA_A$ synapses, one outcome of which is the modification of neural transmission frequencies amongst efferent excitatory neurons (Whittington, Traub, Faulkner, Stanford & Jefferys, 1997), this evidence leads to speculation that $GABA_A$ergic activity might be responsible for the segmentation in phase of mechanisms responding to the presence of the synchronous premask relative to the phase of simultaneously active neural processors coding the repeated presentation of distracter elements. One consequence of this might be the formation of specific neural assemblies defined by their relative phase of activity: a hypothesis consistent with the temporal segmentation account of synchrony priming and testable by experimenting with observers administered with lorazepam. Thus, the increase in $GABA_A$-induced inhibition can be interpreted as an enhancement of stimulus-evoked synchronization related to perceptual segmentation and grouping, which may be directly related to the temporal dynamics of the response to synchronous premask-matrix presentation.

EEG Evidence Indicates a Role for Prefrontal Cortex in Prime Generation and Maintenance

Evidence that priming is related to activity in interneuronal networks causes some problems for determination of an adequate measure of priming in electroencephalographic (EEG) data. Problems arise because, while GABA$_A$ergic synchronization promotes synchronization amongst postsynaptic, excitatory neurons it does so by modulating the amplitude of the excitatory response with a reciprocal effect upon excitatory response frequency: Thus, increasing amplitudes are associated with decreasing frequencies, which appear to shift from around 40 Hz to between 10 and 30 Hz. Given that activity in interneuronal networks may not be easily distinguished from noise in the scalp recorded EEG the only option available using EEG to determine the physiological response to premask presentation seems to be to concentrate analysis on the excitatory activity recorded at the scalp, bearing in mind that it may be practically impossible to determine a-priori the precise frequency at which the oscillatory neuronal correlate with synchrony priming may be located. At least consistent with these conclusions, the 40-Hz response to (40-Hz) premask-matrix presentation recorded using psychophysical measures by Elliott and Müller, (2000, reviewed in later sections) was not evident in the EEG recorded concurrent with premask-matrix presentation by Elliott, Herrmann, Mecklinger and Müller, (2000b). At the time of testing, it was not yet known that the 40-Hz response to premask-matrix presentation (at 40 Hz) may reside in interneuronal mechanisms beyond the resolution of the EEG. Nevertheless, this outcome suggests that the primary method of time-frequency analysis used by Elliott et al. (2000b), in this instance analysis was carried out on Morlet wavelets convolved from the 40-Hz cross section of the EEG, may not be the optimal measure for exploring the temporal structure of the prime. Consequently and as detailed below, in a second EEG experiment the issue of the time-frequency response to premask related EEG activity was examined by using independent components analyses (ICA) as a means of distinguishing event-related perturbations in the EEG during premask matrix presentation. The time course of regularly occurring components were then subject to time frequency analysis in order to determine the major spectral constituents of a given component and thereby to approach an answer to the question of what effects synchronous premask presentation has upon the temporal characteristics of measurable brain activity.

Experiment

Participants

Data was collected from 12 right-handed participants (four male; mean age 24.1 years). All participants had normal or corrected-to-normal vision and received monetary payment for taking part in the experiment.

Design, Procedure, Apparatus, and Stimuli

Event timing, EEG trigger signals, data collection, and image frame generation were controlled by an IBM-PC compatible computer, which also controlled oscilloscopic image presentation through an Interactive Electronics point-plotter buffer with 8 MB frame store memory (Finlay, 1985). Stimuli were presented on a Tektronix 608 oscilloscope with very fast-decay P15 phosphor, which was set to plot the image frames with temporal control of 1 kHz. The EEG was recorded concurrent with participants performing the primed detection task of Elliott and Müller (1998, and illustrated in Figure 1). The particular stimulus paradigm employed in the experiment detailed here used an identical procedure and modifications to the stimulus paradigm as detailed in Elliott et al. (2000b). With respect to stimulus presentation, the premask matrices were increased to 150% of the size of those employed by Elliott and Müller (1998) in order to evoke a measurable EEG response to flickering premask-matrix presentation,. The physical specification of the target grouping was improved by specifying the continuances between premask and target elements by 40% and not 20% as in previous studies (thereby facilitating target detectability, see Figure 1), while the overall luminance of the stimuli was increased from 30 cd/m^{-2} to 120 cd/m^{-2}, representing an increase in contrast from 4:1 to 16:1 relative to measurements of background and ambient luminosity.

Electrophysiological Recording

The EEG was recorded from 19 Ag–AgCl electrodes at positions Fp1, Fp2, F7, F3, Fz, F4, F8, T3, C3, Cz, C4, T4, T5, P3, Pz, P4, T6, O1, O2, according to the international 10–20 system. The electrodes were mounted in an elastic cap and were referenced to Fz while the nose served as the ground electrode. Electrode impedance was maintained below 5 kOhm. Horizontal and vertical EOG was additionally registered with four electrodes. EEG activity was amplified by means of a NeuroScan apparatus. Data were

sampled at 500 Hz and analog-filtered with a 0.1 Hz high-pass and a 100 Hz low-pass filter. In addition, a 50 Hz notch filter was applied to remove artifacts related to the 50 Hz resonance frequency of the electricity supply. Averaging epochs lasted from 200 ms before premask presentation until 1200 ms. Baselines were computed in the $-200-0$ ms interval for each trial and subtracted prior to subsequent ERP analyses.

Analyses

Erroneous responses and RTs above or below 2.5 standard deviations (SD) from the mean of all correct observations were removed prior to data analysis proper. Both RT and EEG data paring procedures were combined such that the residual trials formed the basis for complementary data analysis. The corrected RT data were examined by means of a repeated measures analysis of variance (ANOVA) with the main terms of premask (synchronous, random) and target (present, absent). The time constant 300 ms with a low-pass filter at 70 Hz was used for the recording of EOG. The EOG channels were visually inspected for each trial, and trials with eye movement or blink artifact were rejected. Localized muscle artifacts (at electrodes T3 and T4) were identified and if present reconstructed by means of an extended independent component analysis (ICA) algorithm (Makeig et al., 1999). Following this phase of data preprocessing, an ICA approach was adopted by using the information maximization algorithm developed by Bell and Sejnowski (1995) and available in open source under http://www.cnl.salk.edu/~scott/. The ICA permitted time series in the form of component activations to be reconstructed from the averaged EEG (in this instance the event-related potential [ERP]) signals. Our ICA analysis was performed on the averaged ERP based upon the assumption that substantial variance in the ERP at given (but as yet unknown) intervals during premask-matrix presentation should relate to activity at some, as yet, unknown oscillatory response to repeated premask-frame presentation.

In order to identify component classifications, 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). Subsequently, classification 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 (cophenetic correlation coefficient $c =$ .81). The resulting clusters were considered if they included activations from more than 75% of subjects, with maxima within the period of priming display presentation.

Results and Discussion

Consistent with previous studies (e.g., Elliott & Müller, 1998, 2000), analyses of the RTs revealed significant main effects of target ($F[1, 11] = 49.49$, $p < 0.001$, $MSE = 741.97$; 583.91 vs. 528.59 ms for target absent vs. target present responses, respectively) and premask ($F[1, 11] = 9.87$, $p < 0.01$, $MSE = 44.81$; 548.51 vs. 563.99 ms for synchronous premask vs. random premask trials, respectively) and a significant interaction effect of premask * target ($F[1, 11] = 15.58$, $p < 0.01$, $MSE = 44.81$) indicating priming effects (i.e., faster RTs following synchronous relative to random premask presentation) to be specific to the target trials.

Analysis of the ERP by means of ICA revealed a single component that was particular to trials upon which a synchronous premask was presented. There were no corresponding patterns of effects (i.e., no clusterings that satisfied the earlier mentioned criteria) found upon the random-premask trials). The clustering of the synchronous premask ERPs comprised component maxima from 10 of the 12 experimental participants (clustering automatically excluded 2 subjects who showed no variance maxima with an appropriate latency or topography) with a mean maximum located at 341 ms post-premask matrix onset (standard deviation of the estimate was 29 ms, see Figure 2c). The average distribution of variance across the scalp at the mean time of maximum variance is represented in the head plot in Figure 2a: The averages were calculated from distributions on the scalp at the time of component maximum for each of the 10 independent components. 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. Figure 2b represents the averaged spectral power representation of the 10 component activations derived from separate Fourier transforms of the 10 component activations, in each case the sampling interval being from premask-matrix onset until the time of component maximum. Examination of variations in spectral power show peaks at 10, 35, and 62/66 Hz, but not at 40 Hz (the frequency of premask-matrix presentation). In Figure 2c the spectrogram represents the time-frequency decomposition of the average component activation: Notice at the intersection of horizontal traces of high fre-
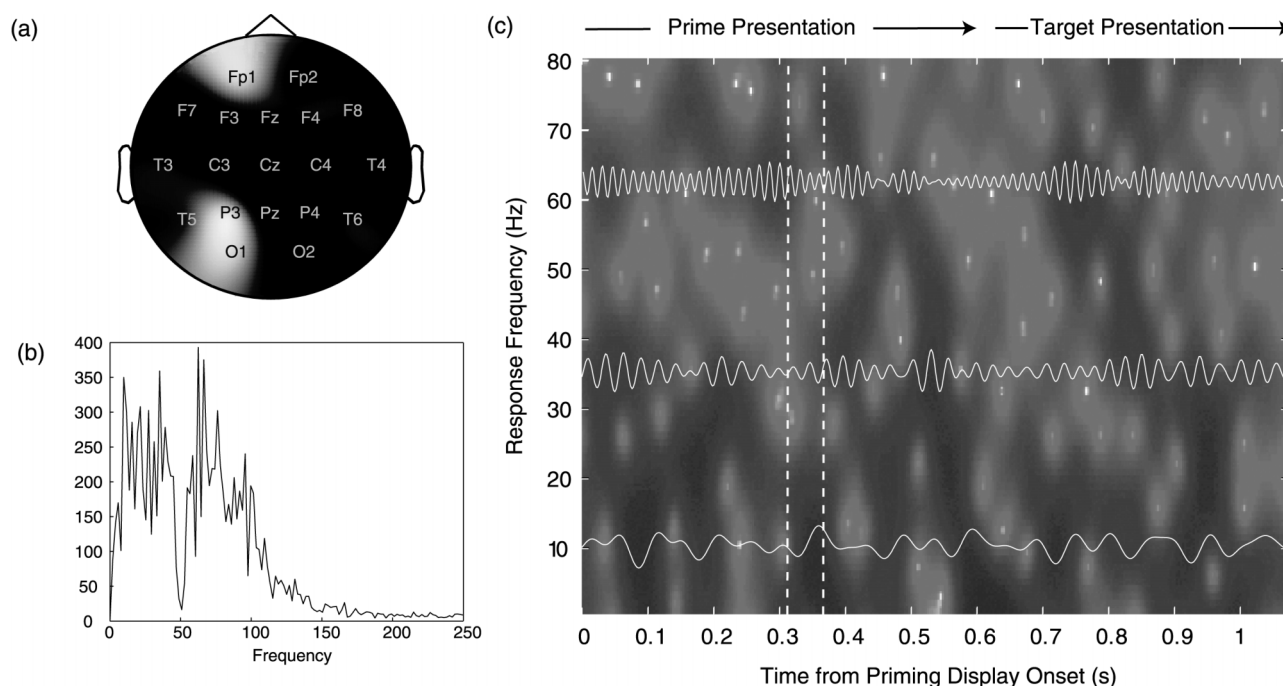
Figure 2. Prime-specific activation during synchronous-premask-matrix presentation: In (a) the head plot represents the distribution of variance across the scalp, averaged across observers, and at the mean time of maximum variance, which occurred at 341 ms post- premask-matrix onset (light–dark indicates 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 (the cluster algorithm 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. Fp1 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 (light–dark 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).

quency (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.

Two points emerge from the analysis presented here. The first is that the EEG response to synchronous-premask presentation relates to activity at a number of frequencies, although in the case of high frequency (> 10 Hz) activity, these frequencies are not predictable directly from the timing of either pre-mask-matrix or synchronous-premask presentation. It may be the case that the 10-Hz response represents

a delayed matching to sample response to synchronous premask-frame presentation (which repeats at 10 Hz) or, alternatively, the action of interneuronal networks encourages a downward shift in frequency which settles at around 10 Hz (notice in the spectrogram that activity appears to shift downwards in frequency with time). These patterns of premask-related EEG activity are suggestive of a dynamic structure which requires further experimental investigation.

The second point is that coactive prefrontal-posterior mechanisms appear to be involved in the formation of the prime response. One function of prefrontal cortex is a delayed matching to sample 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 poste-

rior assemblies coding the local spatio-temporal organization of the priming display. The prime may thus arise, in part, as a function of the development of a recurrent system that arises as a function of repeated premask matrix presentation. This issue is explored in some more detail in the following section.

Visual–Prime Persistence

Psychophysical Measures of Prime Duration and Structure

One dramatic and surprising effect reported by Elliott and Müller (1998) was the 40-Hz specificity of synchrony priming. In order to examine this effect further, subsequent experiments investigated the idea that the synchronous prime developed as a form of oscillatory, visual short-term memory that could maintain low level figure-ground segmentation for a brief period of time following premask-matrix termination (see Elliott & Müller, 2000). Consequently, the visual short-term memory under consideration was considered in terms of the persistence of prime-related neural activity (see Coltheart, 1980). Elliott and Müller (2000) conducted a series of experiments to investigate the efficiency of synchrony priming following introduction of an interstimulus interval (ISI) between premask-matrix offset and target-matrix onset. This examination of the temporal extent of synchronous-prime persistence revealed that the prime decayed monotonically between ISIs of 0 and 150–200 ms (see Figure 3). This is consistent with the idea of persistence as a decaying visual trace with duration of approximately 250–300 ms from prime-stimulus onset (taking into account that the final presentation of the synchronous-premask frame occurred 100 ms before premask-display offset, so that the duration of synchronous-prime persistence is calculated as 100 ms + 150 to 200 ms). This duration is equivalent to that of visible persistence (Coltheart, 1980) and corresponds well with other estimates of visual stimulus persistence (i.e., 240 ms; see Efron, 1970a, 1970b, 1970c). Although the prime exhibits duration consistent with the presentation of a visible stimulus, observers are unable to detect the presence of the synchronous premask frame within the premask display. However, a long persistence estimate is not inconsistent with the logic of the figure-ground segmentation account given by Elliott and Müller (1998), when it is considered that this account presupposes the synchronous prime to be coded within the context of the (visible) premask matrix. This might also entail that the synchronous prime inherits persistence properties from the premask matrix as a whole, extending persistence beyond durations usu-
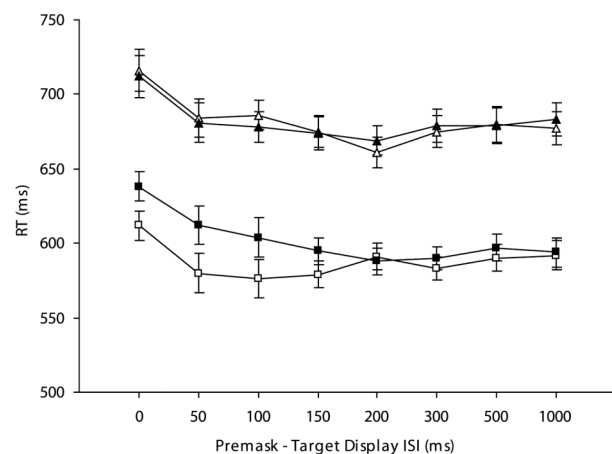

Figure 3. Mean correct target-present and target-absent RTs with standard error bars (in ms) for the synchronous and random-premask conditions as a function premask-target display ISI. The square and triangle symbols represent target-present and absent conditions, respectively, and the unfilled and filled symbols represent synchronous and random-premask presentation conditions, respectively.

ally consistent with nondetected stimuli (i.e., 80 ms, see Engel, 1970) to those of visible stimuli.

The conclusion drawn above, indicating that the persistence of the synchronous prime results from mechanisms that code the entire premask display leads to a second hypothesis, that the synchronous prime should also inherit the temporal (40-Hz) structure of the premask matrix. Specifically, this hypothesis relates to the basic assumption that synchronous-prime generation occurs through the entrainment of neural coding mechanisms at specific frequencies (i.e., 40 Hz). As we have noted earlier, the evidence suggests that a 40-Hz response might be better considered in terms of interneuronal function and not at the level of a large scale excitatory response to premask-matrix presentation. The EEG data presented in this paper suggests instead that a recurrent system develops, which is characterized by a 35-Hz response rather than a response at 40 Hz. However a response at 10 Hz was also evident in the EEG, and, on this basis, it cannot be entirely ruled out that any 40 Hz response may arise as a function of limited temporal resolution or when it is taken into account that most neurons are capable of maintaining high frequency responses in excess of 40 Hz due to the summing of responses within a cell or cells capable of responding to activity with a retinally specified receptive field of angular dimensions exceeding those of the premask matrix as a whole (i.e., with a receptive field > 8° of visual angle).

Irrespective of the precise nature of the carrier substrate and still consistent with the suggestions of

Elliott and Müller (2000), the temporal structure of the response to premask-matrix presentation might be considered in terms of a global response to the 40-Hz structure of the premask matrix, with separate representations of the synchronous (and random) premask frames and of the 3 additional premask frames within different phases of a general (or global) oscillation that develops at 40 Hz. In this way, the synchronous-prime response might be maintained concurrent with, but independent of, 40-Hz activity coding the remaining premask-matrix elements. One assumption of this model of the oscillatory response to prime generation is that the 40 Hz responses to synchronous and additional premask presentations would occur at a particular phase relative to premask-matrix presentation. The temporal conditions considered most effective for measuring the effects of synchrony priming were those under which targets would be presented at ISIs corresponding to a 0° phase angle relative to the 40-Hz rhythm of the premask matrix (i.e., in-phase with synchronous-premask presentation). In contrast, targets presented at ISIs out-of-phase (for example at 180°) might be expected to benefit from a weaker, if at all substantial, synchrony priming effect.

The following experiments all employed premask-target-matrix ISIs, with target presentation at 0°, 90°, or 180° to the presentation rhythm of the premask-display frames. These phase angles were defined with relation to the ISI duration mapped to a hypothetical stimulus-locked 40-Hz waveform. Accordingly, assuming a waveform duration of 25 ms with minima at 0 and 25 ms and a maximum at 12.5 ms, the ISIs for the 0° phase-angle condition were defined as 0, 25, and 50 ms, the ISIs for the 90° condition as 6, 18, and 31 ms, and the ISIs for the 180° condition as 12 and 37 ms. As evident in Figure 4, by alternating 0°-, 90°-, and 180°-phase angle shifts of ISIs within the 0–50 ms range, there was indeed a significant phase-angle effect. However, unlike the predictions described above, phase angle enhancements were greater for targets presented at ISIs corresponding to 180° compared to the 0° condition. In addition, this pattern of enhancements was also confirmed in a second experiment using larger ISI variations across the 0–137 ms range (see Elliott & Müller, 2000).

As can be seen from Figure 4, the observed modulatory pattern was confined only to synchronous-premask RTs, with no periodicity evident for the random-premask RTs. Thus, this pattern of results offers strong support for the hypothesis that the priming effects under investigation represent the formation of a figure-coding mechanism based on oscillatory characteristics that becomes engaged by synchronous-premask presentation, but are not related to ac-
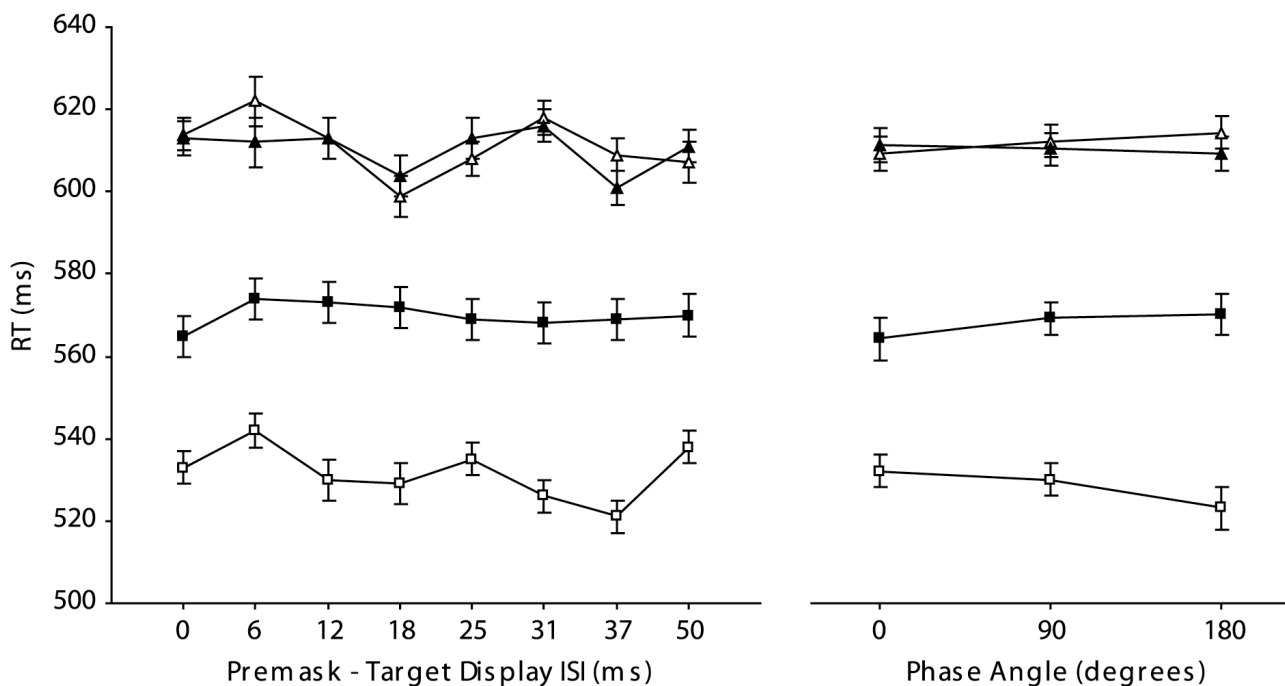

Figure 4. Mean correct target-present and absent RTs with standard error bars (in ms) for the synchronous and random conditions as a function of (a) premask-target ISI and (b) phase-angle. The square and triangle symbols represent target-present and absent conditions, respectively, and the unfilled and filled symbols represent synchronous and random-premask presentation conditions, respectively.
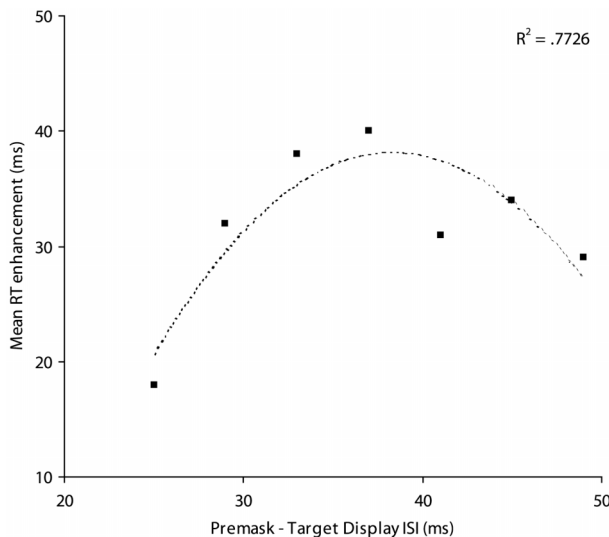
Figure 5. Mean target-present RT synchrony enhancements (i.e., random RTs minus synchronous RTs) as a function of ISI. Also illustrated is the quadratic function that best fitted the RT enhancements.

tivity of other, more general, mechanisms related to stimulus encoding or response generation. In an additional experiment, the aim was to replicate the maximum 180°-enhancement effects within a single cycle of the synchronous prime. ISIs were employed across the 25 ms (0°-phase angle) to 49 ms (≈0°) range, including an ISI of 37 ms (≈180°). Figure 5 presents the results of this experiment and shows consistencies with previous results. The synchrony enhancements were at maximum for the 37 ms ISI (≈180°), with a significant difference between the 37 ms (≈180°) and the 25 ms (0°) ISI. Furthermore, there were nonlinearly changing enhancement effects at intermediate ISIs, producing a quadratic enhancement/ISI function. Thus, additional support was obtained for the idea that the synchronous prime persistence was maintained within a 40-Hz oscillation, revealed by maximal RT enhancements to targets presented at 180° relative to the rhythm established by premask-display presentation.

However, phase-shifting of the 40-Hz prime activity on its own does not explain why there were significant RT enhancements for targets presented at 180° relative to premask-display frame onsets but not for targets presented at 0°. To explain this effect, how target-generated activity might integrate with the modulated 40-Hz response of the prime needs to be considered. One possible account is as follows: During the positive lobe of the 40-Hz response, when activity is near maximum, the intensity of a novel target stimulus presented in-phase with the 40-Hz structure of the prime might be low relative to the intensity of the prime; by contrast, the intensity of a target might be relatively high during the negative lobe. A high intensity of the target during the negative lobe of the prime would improve the saliency of the target, yielding faster RTs. This account would be consistent with the original idea that the phase angle of the prime is, at 0°, relative to the rhythm of premask-display presentation.

Recurrency Revisited: Putting Together the Pieces

The ideas advanced above to account for the evidence of premask persistence involve two apparently contradictory assumptions: While priming is assumed to occur in early mechanisms where the spatial specificity of stimulus information is preserved and where a 10-Hz response to premask-frame presentation might be expected to be propagated (Elliott and Müller, 1998, Experiment 3), the oscillatory structure of prime activity is assumed to be generated by some mechanism capable of coding relations across the entire premask display (at 40 Hz). However, this contradiction can be resolved by consideration of how synchrony might be transmitted within the brain.

It is reasonable to assume that the relative structure in the patterning of temporal-impulse responses to local premask-matrix elements is preserved with fidelity irrespective of the number of neural junctions through which this information passes. This has a precedent in the physiological literature: For example, Abeles and colleagues (Abeles, Vaadia, Bergman, Prut, Kaalman, & Slovin, 1993) reported repeatable patterns of precisely timed spike discharges in frontal cortex of behaving monkeys. Furthermore, many visual areas will be involved in premask-matrix coding, including relatively late areas, because premask-matrix presentation has a direct conscious-perceptual consequence. Thus, the phase of premask-matrix presentations may be preserved, at least in relative terms, within the entire system responsible for perception of the premask matrix. However, the particular (late) mechanism responsible for rendering the premask matrix into consciousness is apparently unable to resolve the temporal asynchronies existing between premask frames, even to the extent that the first and last frames in the four-frame sequence (which are separated by some 50 ms) are perceived at the same time. This cannot be attributed to certain fixed and relatively slow response frequencies of cells at later stages in the system. For example, infero-temporal (IT) and later prefrontal neurons with receptive fields greater than 20° of visual angle (i.e., a diameter approximately three times the size of the premask matrix) are known to be capable of maintaining firing at 40 Hz (see for example Figure 3 in

Chelazzi, Duncan, Miller, & Desimone, 1998). Instead, it might be assumed that, during the course of premask-matrix presentation at 40 Hz (globally), a later cell of this type does become active, responding to the rapid staccato of neural responses representing asynchronized premask frame presentations at 10 Hz. In this way, the 40-Hz structure of the premask matrix induces this neuron to oscillate at 40 Hz. However, because the individual premask frames follow each other effectively without lag, the response of this neuron to presentation of any particular frame might become integrated with identical responses to both preceding and subsequent frames. The neuron would, thus, maintain an average sustained response above the threshold for perception of the (whole) premask matrix, characterized by a relatively low-amplitude 40-Hz surface modulation that would never descend below the threshold and thereby permit the spatio-temporal structure of the premask display to be discerned.

As is suggested by neurophysiological evidence (Fries, Reynolds, Rorie, & Desimone, 2001) and supported by the previously discussed EEG evidence, a pattern of 40-Hz activity that comes to be coded as a function of a 10-Hz response to premask-frame presentations may feed back to earlier neurons inducing a local 40-Hz response amongst earlier neurons. Although it is not known precisely how, or with what modifications, information is relayed back to earlier stages, particularly given the presence of apparently unrelated frequencies such as 35 Hz and 62/66 Hz in the EEG response to premask-matrix presentation, one plausible possibility is that a recurrent 40-Hz code might come to interact with the bottom-up driven 10-Hz response via descending pathways that synapse on local interneuronal networks (see Whittington, Traub, Kopell, Ermentrout, & Buhl, 2000): If this were so, the neural response at 40 Hz might never become manifest in EEG recording, although it would be recordable using techniques sensitive to the timing of interneuronal activity. As a consequence of the interaction of 10- and 40-Hz activity, the timing of interneuronal mechanisms, considered to be a critical determinant of the timing of long-range excitatory projections, might become altered such that the time of arrival at the later neuron of locally mediated 10-Hz responses to premask-frame presentations becomes determined by the relationship between the regular timing of frame presentations and the developing temporal asynchronies at local interneuronal networks.

By this conjecture, the spatially and temporally distributed pattern of repeated interactions between the top-down induced 40-Hz rhythm with the stimulus-driven response to premask frame presentations at 10 Hz would lead to a series of shifts in the phase of each set of neurons responding locally to a given subset of premask elements. These shifts in phase would occur relative to activity across other neurons that also receive 40-Hz modulation, but code asynchronized subsets of premask elements. Thus, over time, highly dynamic and asynchronous patterns of 40-Hz activity develop across the entire set of lower-level neurons coding the premask matrix.

Consistent with the above ideas concerning the phase-specific segregation of prime activity, within the pattern of asynchronous 40-Hz activity across early, spatially-specific neurons, those neurons responding to the synchronous-premask elements would occupy the same phase angle of a 40-Hz rhythm, but a different phase angle to neurons responding to other, temporally asynchronous premask frame elements. In this way, a set of local and temporally precise coincidences in the early visuo-cortical activity would indeed result in the temporal segregation of activity, differentiating the prime from other premask-induced activity at 40 Hz.

Preliminary empirical evidence that supports the conception of such a recurrent network architecture for synchrony priming effects has been shown in an EEG experiment (see previous section and Elliott, Conci, & Müller, 2003) where a network between posterior and frontal areas evolved during prime presentation. While a loop may in this context operate at 35, 66 or 10 Hz in order to establish bottom-up and feedback driven connections, local nodes may well be oscillating at 40 Hz, relying on lateral connections that synchronize, but shift their phases at 40 Hz. Taken together, this hypothesis has gained some support, however, future research will be needed in order to establish the precise connection and relation between frequencies and their functional impact.

Effects of Phasic Masking on Prime Persistence

Priming by synchrony has been shown to operate on the basis of oscillatory persistence that remains active for up to 300 ms and is believed to be represented in the brain by the combined function of prefrontal and posterior mechanisms. In order to further posit a more specific locus of the synchronous prime in terms of central or peripheral activations (i.e., under the assumption that central may be best considered in terms of a metaphor for anterior while peripheral for posterior mechanisms), an additional set of experiments assessed the susceptibility of the prime to different forms of masking (Wendt, 2000). Because masking by visual noise and structure was found to reduce the effectiveness of synchrony priming equally and irrespective of the type of mask employed, the use of traditional masking stimuli offered

no answer to the question of at which loci masking is more effective.

In order to better address this question, a set of experiments was conducted using a novel masking by phase paradigm. In this paradigm, an oscillatory mask was presented at various ISIs between premask-matrix offset and target-matrix onset. The mask was figurally neutral in the sense that it appeared identical to the premask matrix but it included either synchronous or random mask frames factorially randomized relative to the presentation of synchronous and random premasks. The masking matrix was also varied in frequency appearing at 40 Hz (i.e., identical to the frequency of premask matrix presentation) and at 160 Hz, at which frequency the local mask elements repeated at 40 Hz, the hypothesized frequency of mechanisms coding the prime.

This modification to the paradigm of Elliott and colleagues assumed that local oscillatory persistence at 40 Hz is representative of activity in later processing stages while earlier processing stages might be characterized both by primes resonating at 40 Hz with modification by local 10-Hz responses to premask-frame presentations. Consequently, by varying the temporal-spatial patterning of mask relative to that of premask-matrix presentation masks might be expected to disrupt prime efficiency in early mechanisms if the temporal frequency of the mask frames were set to 10 Hz (i.e., mask matrices oscillated at a rate of 40 Hz). Conversely, with a local mask-frame frequency of 40 Hz (mask matrices oscillating at 160 Hz), local mechanisms might be relatively unaffected while later mechanisms, at which the prime would be maintained primarily at 40 Hz, may become disrupted by the novel spatio-temporal patterning in the mask matrix. On the basis of this logic, two conditions of mask-matrix presentation frequency (40 Hz and 160 Hz) were examined relative to a fixed premask-matrix presentation frequency of 40 Hz.

For the target-present trials (see Figure 6), masking at 160 Hz had fewer dramatic effects upon the RTs overall than at 40 Hz, and the presentation of a synchronous mask tended to expedite random premask RTs more than the presentation of a random mask disrupted the prime. For the 40-Hz masks, random premask RTs appeared to be slowed rather than expedited, as under 160-Hz masking conditions, while the prime was significantly disrupted when followed by a random mask. From these data, it could be concluded that random mask presentation is more effective, generally, at 40 than 160 Hz, while synchronous mask presentation is more effective on random-premask trials under 160-Hz rather than 40-Hz mask conditions. These results suggest that while the prime remains susceptible to disruption by an oscillating mask, networks that come to adopt a 40-Hz rhythm based upon premask are susceptible to desynchronization and resynchronization, only when
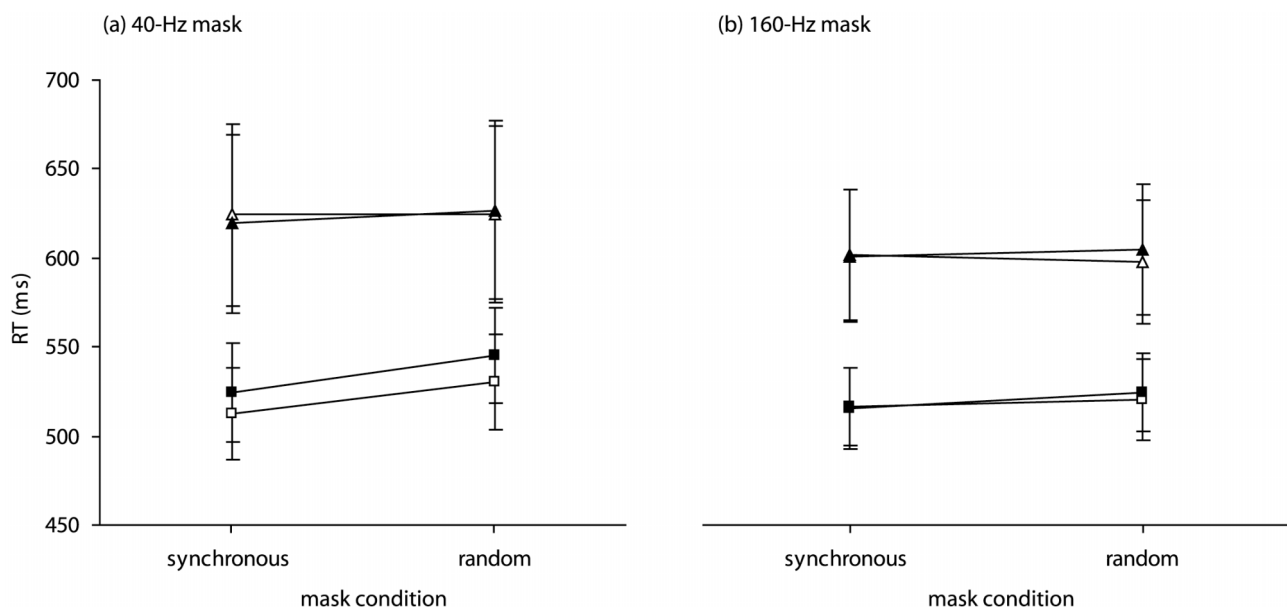

Figure 6. Mean correct target-present and target-absent RTs (± mean SE, in ms) for the synchronous and random premask conditions as a function of mask synchrony, separately for the 40 Hz condition (a) and the 160 Hz condition (b). For both mask conditions, the square and triangle symbols represent target-present and target-absent RTs, respectively, and the unfilled and filled symbols represent synchronous and random premask conditions, respectively.

local (mask) stimuli repeat at 40 Hz. Taken together, this can be taken as evidence in support of the idea that synchronization occurs primarily in early neural networks that oscillate at 40 Hz. In addition, the susceptibility of the prime to masking by phase suggests that figure-ground segmentation is essentially temporal in nature.

Summary and Conclusions

In summary, experimental work on the premask paradigm (Elliott & Müller 1998) presented in this contribution, offers support for an account of visual scene segmentation under specific conditions of external temporal modulation consistent with mechanisms of neuronal synchronization as proposed by von der Malsburg (1981). Investigations of the underlying physiological mechanisms of synchrony priming by employing pharmacological tools support the view that GABA$_A$ergic neuronal connections in interneuronal networks subserve the process of temporal grouping and segmentation (Elliott et al., 2000a). Complementary to these findings, an EEG study that employed independent component analysis (Elliott et al., 2003; see also Elliott et al., 2000b) revealed a prime-specific pattern of multiregional activation, including prefrontal and posterior recording sites, which depicted a spread in coherence across lower frequencies as a function of time and could be interpreted as the representation of an anticipatory segmentation mechanism that is exploited to guide the subsequent response to the target stimulus.

Psychophysical investigations of this recurrent system of synchrony priming revealed a prime-specific visual short term memory that remains functional for a persistence duration of 300 ms. In addition, the underlying persistence structure shows that the memory trace displays a clear (40-Hz) periodicity dependent upon the relationship of target onset to premask offset (Elliott & Müller, 2000). Finally, an estimation of the locus of prime activity established via a masking procedure (Wendt, 2000) showed no differential effects of form-based masking on the target detection rates. However, phasic masking procedures show some evidence in support for the hypothesis that synchronization occurs primarily in early networks that exhibit a specific temporal structure.

Taken together, the results presented in this review show that segmentation and grouping mechanisms can be manipulated by specific external temporal manipulations and may be expressed by temporal codes established in the neuronal system, while relying on a recurrent information processing architecture that may operate as a combined function of 40-Hz driven lateral connectivity and frontal-posterior loops that are functionally activated by a variety of frequencies. Whereas the findings summarised in this contribution offer support for an account of a visual short-term memory that operates in the order of up to 300 ms, showing recurrent 40-Hz codes interacting with bottom-up driven 10-Hz rhythms, other longer lasting memory mechanisms have reported comparable topographical distributions between frontal and posterior brain regions while retention might be accomplished by theta phase coherence between separate regions (see Sarntheim, Petsche, Rappelsberger, Shaw, & von Stein, 1998). Converging evidence also suggests that theta and upper alpha oscillations may reflect particular processes related to working memory performance (see Klimesch, Schack, & Sauseng, 2004). Taken together, both sets of findings seem to reflect similar processes based on highly specific temporal mechanisms of information processing but rely on different time scales of operation.

References

Abeles, M., Vaadia, E., Bergman, H., Prut, Y., Haalman, I., & Slovin, H. (1993). Dynamics of neuronal interactions in the frontal cortex of behaving monkeys. *Concepts in Neuroscience, 4,* 131–158.

Bell, A. J., & Sejnowski, T. J. (1995). An information-maximization approach to blind separation and blind deconvolution. *Neural Computation, 7(6),* 1129–1159.

Chelazzi, L., Duncan, J., Miller, E. K., & Desimone, R. (1998). Responses of neurons in inferior temporal cortex during memory-guided visual search. *Journal of Neurophysiology, 80,* 2918–2940.

Coltheart, M. (1980). Iconic memory and visual persistence. *Perception & Psychophysics, 27,* 183–228.

Efron, R. (1970a). The relationship between the duration of a stimulus and the duration of a perception. *Neuropsychologia, 8,* 37–55.

Efron, R. (1970b). The minimum duration of a perception. *Neuropsychologia, 8,* 57–63.

Efron, R. (1970c). Effects of stimulus duration on perceptual onset and offset latencies. *Perception & Psychophysics, 8,* 231–234.

Elliott, M. A., Becker, C., Boucart, M., & Müller, H. J. (2000a). Enhanced GABA$_A$ inhibition enhances synchrony coding in human perception. *Neuroreport, 11(15),* 3403–3407.

Elliott, M. A., Conci, M., & Müller, H. J. (2003). Prefrontal cortex and the generation of oscillatory visual persistence. *Behavioral and Brain Sciences* (invited commentary, forthcoming).

Elliott, M. A., Herrmann, C. S., Mecklinger, A., & Müller, H. J. (2000b). The loci of oscillatory visual-object priming: A combined electroencephalographic and reaction-time study. *International Journal of Psychophysiology, 8,* 225–241.

Elliott, M. A., & Müller, H. J. (1998). Synchronous information presented in 40–Hz flicker enhances visual feature binding. *Psychological Science, 9(4),* 277–283.

Elliott, M. A., & Müller, H. J. (2000). Evidence for a 40 Hz oscillatory short-term memory revealed by human reaction time measurements. *Journal of Experimental Psychology: Learning, memory and cognition, 26(3),* 703–718.

Elliott, M. A., & Müller, H. J. (2004). Towards quantitative and qualitative descriptions of the effects of stimulus synchrony upon perceptual organization. Manuscript submitted for publication.

Engel, A. K., Kreiter, A., König, P., & Singer, W. (1991). Synchronisation of oscillatory neuronal responses between striate and extrastriate visual cortical areas of the cat. *Proceedings of the National Academy of Science of the USA, 88,* 6048–6052.

Engel, G. R. (1970). An investigation of visual responses to brief stereoscopic stimuli. *Quarterly Journal of Experimental Psychology, 22,* 148–160.

Fahle, M. (1993). Figure-ground discrimination from temporal information. *Proceedings of the Royal Society of London B, 254,* 199–203.

Fahle, M., & Koch, C. (1995). Spatial displacement but not temporal asynchrony destroys figural binding. *Vision Research, 35,* 491–494.

Finlay, G. (1985). A high-speed point plotter for vision research. *Technical note. Vision research, 25,* 1993–1997.

Fries, P., Reynolds, J. H., Rorie, A. E., & Desimone, R. (2001). Modulation of oscillatory neuronal synchronisation by selective visual attention. *Science, 291,* 1560–1563.

Giersch, A. (1999). A new pharmacological tool to investigate integration processes. *Visual Cognitione, 6(3/4),* 267–297.

Gray, C. M. (1999). The temporal correlation hypothesis of visual feature integration: still alive and well. *Neuron, 24,* 111–124.

Gray, C. M., König, P., Engel, A. K., & Singer, W. (1989). Oscillatory responses in cat visual cortex exhibit inter-columnar synchronization which reflects global stimulus properties. *Nature, 338,* 334–337.

Gur, M., & Snodderly, D. M. (1997). A dissociation between brain activity and perception: Chromatically opponent cortical neurons signal chromatic flicker that is not perceived. *Vision Research, 37,* 377–382.

Homan, R. W., Herman, J., & Purdy, P. (1987). Cerebral location of international 10–20 system electrode placement. *Electroencephalography and Clinical Neurophysiology, 66,* 376–382.

Kiper, D. C., Gegenfurtner, K. R., & Movshon, J. A. (1996). Cortical oscillatory responses do not affect visual segmentation. *Vision Research, 36,* 539–544.

Klimesch, W., Schack, B., & Sauseng, P. (2004). The Functional significance of theta and upper alpha oscillations for working memory. *Experimental Psychology, 51(3),* ##–##.

Leonhards, U., Singer, W., & Fahle, M. (1997). The influence of temporal phase differences on texture segmentation. *Vision Research, 36,* 2689–2697.

Makeig, S., Westerfield, M., Jung, T. P., Covington, J., Townsend, J., Sejnowski, T. J., & Courchesne, E. (1999). Functionally independent components of the late positive event-related potential during visual spatial attention. *The Journal of Neuroscience, 19,* 2665–2680.

Müller, H. J., & Elliott, M. A. (1999). 40-Hz synchronicity priming of Kanizsa-figure detection demonstrated by a novel psychophysical paradigm. In G. Aschersleben, T. Bachmann, & J. Müsseler (Eds.), *Cognitive contributions to the perception of spatial and temporal events* (pp. 207–212). Amsterdam: Elsevier Science B. V.

Posner, M. I. & Petersen, S. E. (1990). The attentional system of the human brain. *Annual Review of Neuroscience, 13,* 25–42.

Sarntheim, J., Petsche, H., Rappelsberger, P., Shaw, G. L., & von Stein, A. (1998). Synchronization between frontal and posterior association cortex during human working memory. *Proceedings of the National Academy of Science of the USA, 95,* 7092–7096.

Singer, W. (1999). Neuronal synchrony: A versatile code for the definition of relations? *Neuron, 14,* 49–65.

Usher, M., & Donnelly, N. (1998). Visual synchrony affects binding and segmentation. *Nature, 349,* 179–182.

von der Malsburg, C. (1981). *The correlation theory of brain function* (Internal Report 81–2). Department of Neurobiology, Max-Planck-Institute for Biophysical Chemistry, 3400 Göttingen, Germany.

Wendt, J. (2000). *Masking the 40-Hz synchrony-priming effect by form and phase.* Unpublished diploma thesis, Institute for General Psychology, University of Leipzig, Germany.

Whittington, M. A., Traub, R. D., Faulkner, H. J., Stanford, I. M., & Jefferys, J. G. (1997). Recurrent excitatory postsynaptic potentials induced by synchronized fast cortical oscillations. *Proceedings of the National Academy of Science of the USA, 94,* 12198–12203.

Whittington, M. A., Traub, R. D., Kopell, N., Ermentrout, B., & Buhl, E. H. (2000). Inhibition-based rhythms: experimental and mathematical observations on network dynamics. *International Journal of Psychophysiology, 38,* 315–336.

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