Title	Synchronization and stimulus timing: Implications for temporal models of visual information processing.
Author(s)	Elliott, Mark
Publication Date	2004
Publication Information	Elliott, M. A. & Müller, H, J. (2004). Synchronization and stimulus timing: Implications for temporal models of visual information processing. In C. Kaernbach, E. Schröger, & H. Müller (Eds.). Psychophysics beyond Sensation. Mahwah, NJ: Lawrence Erlbaum and Associates (pp. 137-156).
Publisher	Lawrence Erlbaum and Associates / Psychology Press (Taylor & Francis)
Link to publisher's version	http://www.booktopia.com.au/psychophysics-beyond-sensation/prod9780805842500.html
Item record	http://hdl.handle.net/10379/1555

7

Synchronization and Stimulus Timing: Implications for Temporal Models of Visual Information Processing

Mark A. Elliott and Hermann J. Müller
Ludwig-Maximilians-Universität München, Germany

THE NATURE OF PERCEPTUAL ORGANIZATION AS A TEMPORAL PROCESS

In the visual system, objects and object groupings may be initially coded in terms of physically separable attributes or features, representing differential spatial frequencies, orientations, colors, directions of motion, and so on, which in combination come to define wholistic perceptual representations. Although it has been known for some time that visuocortical neurons can display quite specific response preferences for particular features, it is only recently that evidence has been gathered concerning the mechanisms by which these specific neural representations might become combined or "bound" to form a unified representation.

In a series of electrophysiological studies, Gray, König, Engel, and Singer (1989; see also Eckhorn et al., 1988) reported that, when the receptive fields of visuocortical cells in anesthetized cats were stimulated by separate bars of light moving in opposite directions (i.e., when the light bars were not apparently related), neural responses were unrelated. However, when bars were passed across the receptive fields in the same direction, a correlative relationship was observed

between emergent oscillations within the 20- to 80-Hz frequency range. The strongest cross-correlations were obtained when a single, connected bar stimulated two separate neurons. Thus, the emergent oscillations and associated cross-correlations between neuronal firing patterns were only obtained for different cells when those cells responded to the parallel trajectories of the separate bar stimuli. Thus, the oscillatory and "synchronized" neuronal activity may be considered one important neurophysiological correlate with the processes by which independent stimulus activities may come to be bound within a unitary perceptual framework. By generalization, this idea has been extended to the perception of visual groupings, giving rise to the hypothesis that the perception of a Gestalt derives from the binding of separate feature-attributes by means of similar, if not identical, patterns of oscillatory neuronal synchronization.

The empirical support for this hypothesis of binding by synchronization by oscillation rests mainly on physiological experiments with anesthetized animals. However, convergent evidence has been provided by psychophysical experiments, which showed that detection of multielement target groupings (configurations) presented within a matrix of homogeneous distractor elements may be enhanced by the prior presentation of a temporally synchronized (target figure-neutral) priming stimulus (see Elliott & Müller, 1998, Experiments 1 and 3). Specifically, detection reaction times (RTs) to a display matrix containing a target Kanizsa-type square (an illusory square consisting of grouping 90° corner junctions) were expedited when the target was preceded by the presentation of four temporally synchronized crosses within a flickering matrix comprising multiple, asynchronized premask crosses (see Fig. 7.1).

The effects of the synchronized-cross (hereafter "synchronous premask") presentation were measured relative to a random-premask condition, in which one frame comprised four crosses that were pseudorandomly arranged in a nonsquare configuration; see Fig. 7.1(b).[1] In an examination of the difference between synchronous and random-condition RTs as a function of premask-presentation frequency (see Fig. 7.2), RTs were found to be expedited for synchronous relative to random premask presentation only when targets followed premask matrices presented at 40 Hz. Furthermore, these RT enhancements occurred only when the synchronous premask was presented across the locations in the premask matrix subsequently occupied by the target figure (Elliott & Müller, 1998, Experiment 3). That the RT enhancements were confined to target-present conditions (target specificity) in which the synchronous premask and target elements shared the same display locations (spatial specificity) was interpreted as evidence for the

---

[1]Additional findings of priming even when the premask matrix contained no local target-relevant inducer edges (i.e., when the edge-aligned premask crosses were replaced by circles; see Müller & Elliott, 1999) suggest a more precise, segregative function for neuronal synchronization. By this account, early synchronization might serve as a code by which activity representing the elements belonging to the figure can be easily differentiated from those across figurally unrelated, distractor elements (see von der Malsburg, 1981).

(a)

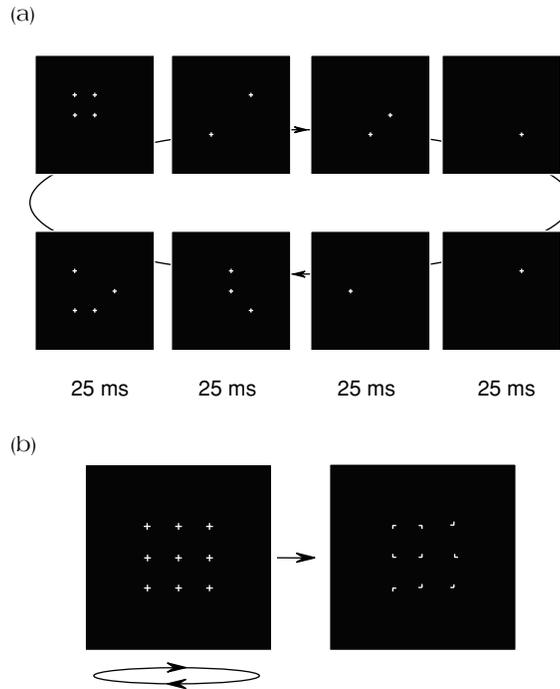25 ms   25 ms   25 ms   25 ms

(b)

FIG. 7.1. (a) Example sequence of the four separate premask frames in the synchronous and random-premask conditions. Elliott and Müller (1998) used these seven premask-presentation frequencies: 25, 29, 33, 40, 50, 67, and 100 Hz. For the 40-Hz premask-presentation condition, frequency was defined as the frequency of occurrence of premask subsets per second; that is, the entire premask matrix was presented as 10 times the four premask frames per 1,000 ms, with a constant subset exposure duration of 25 ms and an interframe interval of <1 ms. (b) The premask sequence was continually recycled for a period of time, after which the premask-matrix elements reduced to simple corner junctions. (In Elliott and Müller, 1998, priming effects were consistent across presentation times between 300 and 4,800 ms; in subsequent studies, presentation times were kept constant at either 600 or 1,200 ms.)

idea that synchronous premask presentation "primes" target coding by virtue of the organization of activity across the premask matrix in phases of the premask-matrix presentation rhythm. By this account, mechanisms responding to elements of the synchronous premask frame would become synchronized within a single phase, but they would be asynchronized relative to the mechanisms responding to other, nongrouping, distractor premask crosses, which would themselves become
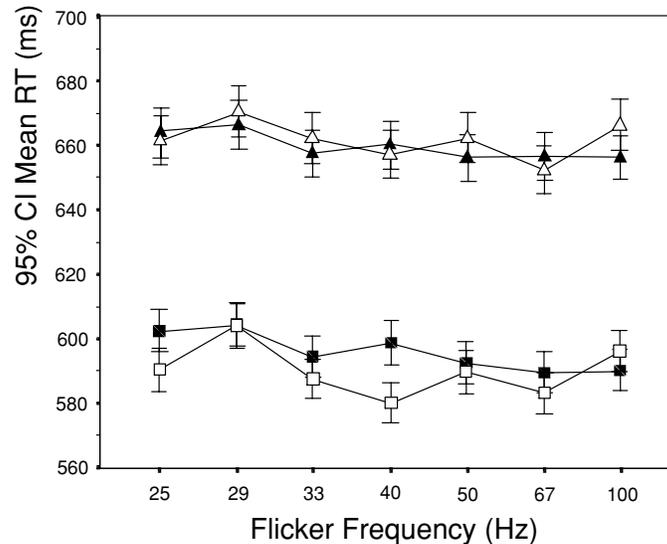
FIG. 7.2. Mean target-present RT synchronicity enhancements (random RTs minus synchronous RTs) as a function of premask-presentation frequency for frequencies across the 25- to 100-Hz range. The squares and triangles represent target-present and target-absent conditions, respectively, and the unfilled and filled symbols represent synchronous and random-premask presentation conditions, respectively. The target-present RTs reveal that significant priming occurred only for premask-matrix presentation at 40 Hz. CI = confidence interval.

synchronized across different spatial arrangements (when more than one cross is presented in a given distractor frame).

The spatial specificity of the priming effects provides some indication of the possible locus of prime activity. In particular, priming might arise as a result of the synchronization of mechanisms located in early visual areas, consisting of neurons with relatively small receptive fields. That synchronization occurs at a late stage of visual coding would appear to be precluded by observations that, in brain areas such as the temporal cortex, the receptive fields of single neurons are sufficiently large for the neurons to respond to stimuli anywhere within the premask matrix. If synchronization occurred late, then some effects of priming might be expected purely on the basis of synchronous premask presentation alone, irrespective of its precise location. A further argument against a late locus of prime formation derives from the finding that observers were unable to discern the composition of individual frames within the 40-Hz premask matrix (mean signal detection sensitivity parameter $A_z = 0.528$, $SD = 0.058$; chance level = 0.500; see Elliott & Müller, 1998, Experiment 2).

Implicit in the notion of stimulus-induced synchronization is the idea that the priming effects are likely to arise directly from transient properties of the stimuli. One possibility is that highly dynamic stimuli engage motion-coding mechanisms, which, it has been argued, could provide one account for demonstrations of temporally induced perceptual grouping with correlated stimulus motion (e.g., Alais, Blake & Lee, 1998). Temporally induced perceptual grouping would thus be explicable in terms of the spatiotemporal correlations ordinarily computed within motion-sensitive mechanisms (Gegenfurtner, 1998). However, inconsistent with this suggestion, Elliott and Müller (in press) found that the effects of priming by means of premask-matrix presentation were little influenced by possible motion signals induced by premask-matrix flicker or during the instantaneous transformation of the premask into the target matrix. Another possibility is that the development of an oscillatory structure to nonmoving dynamic stimulus presentations will closely follow the time course of local stimulus events. This possibility relates directly to the implicit notion of priming by means of the phase of premask presentation and, in the case of premask presentation, raises the question as to which stimulus frequency best explains the tendency for prime formation at 40 Hz: In particular, it has been noted (Müller, 1999) that the four-frame premask matrix used by Elliott and Müller (1998) results in local element repetitions at 10, rather than 40 Hz; see Fig. 7.1(b). This raises the question whether the temporal characteristics of the prime should be considered in terms of local 10-Hz (steady-state) responses in the neural substrate, rather than a 40-Hz response to the premask matrix as a whole.

A number of theoretical considerations (outlined in subsequent paragraphs) have offered support to the idea that when premask matrices flicker at 40 Hz, the resulting code that develops around the synchronous premask matches (in phase) the global frequency of the premask presentation. Nevertheless, for this idea to be examined more specifically, subsequent studies were designed to examine the temporal characteristics of prime activity (its oscillatory structure) by measuring priming effects at various interstimulus intervals (ISIs) between the premask-matrix offset and the target-matrix onset (e.g., Elliott & Müller, 2000). A prerequisite for these studies, which also offered an important indication of the type of mechanism at work during prime coding, was an examination of the duration of prime "persistence" in the absence of an inducing stimulus. As is illustrated in Fig. 7.3, the prime was reduced in efficiency between ISIs of 0 and 150–200 ms, which is consistent with the idea of persistence as a decaying visual trace with a duration of approximately 240–300 ms from prime-stimulus onset (taking into account that the onset of the final priming, i.e., synchronous premask, frame occurred 100 ms before the premask-matrix offset, so that the duration of synchronous prime persistence should be calculated as 100 ms + 150–200 ms). In a follow-up study (Wendt, 2000), the premask-presentation duration was set at 625 ms (rather than 600 ms, as in Elliott & Müller, 2000), permitting a more reliable estimate of the duration of prime persistence from the onset of the final (synchronous premask) frame
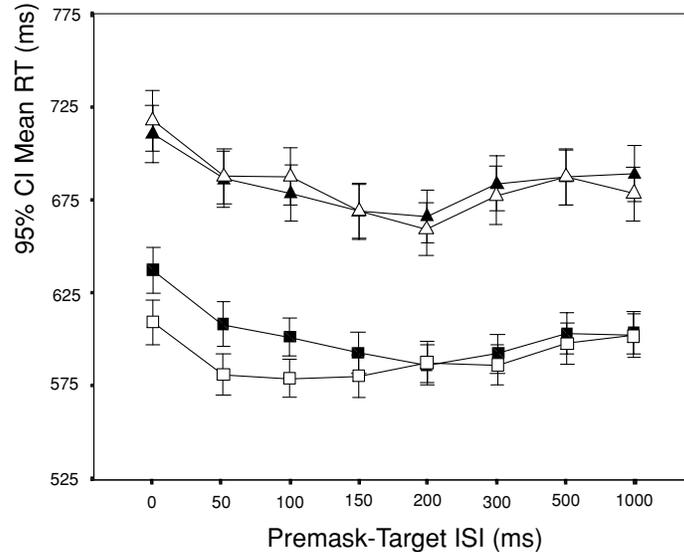
FIG. 7.3. Mean target-present and target-absent RTs (squares and triangles) for the synchronous and random-premask conditions (filled and unfilled symbols), as a function of premask-target ISI. The convergence of the lower functions at between 150 and 200 ms confirms that prime activity persists for up to 150 ms following premask-matrix termination. CI = confidence interval.

in the premask-presentation sequence (i.e., when the onset of the final synchronous premask frame occurred 25 ms before the premask-matrix offset). Consistent with the persistence estimate of Elliott and Müller (2000), that is, 250–300 ms, Wendt found evidence of prime persistence following premask-target ISIs of 300 ms, but not with ISIs of 400 ms and longer.

These estimates of approximately 300 ms correspond well with estimates of visual-stimulus persistence (i.e., 240 ms; see Efron, 1970a, 1970b, 1970c), which are described in terms of stimuli that are fully perceived by the observer (Coltheart, 1980). Thus, it may be concluded that the synchronous prime possesses a persistence duration consistent with that of visible stimuli, despite the fact that observers are unable to detect the presence of the synchronous premask frame within the premask matrix. A possible resolution to this apparent inconsistency is based on the idea that the synchronous prime is generated within the spatiotemporal context of the entire premask matrix (including the elements of the synchronous premask), which is, of course, fully visible. This entails that the synchronous prime inherits persistence properties from the premask matrix as a whole, which would account for why persistence extends beyond durations evoked by undetected stimuli (i.e., 80 ms; see Engel, 1970).

Concerning the presumed oscillatory structure of the synchronous prime, it remained an empirical issue whether the phase of any such code is better described in terms of a local 10-Hz rhythm or a global 40-Hz rhythm. Although visual mechanisms are commonly assumed to respond to local periodicities in the stimulus, there are several findings that cast doubt on this assumption with regard to the present paradigm. In particular, the absence of effects related to variations in local premask-feature specification and, indeed, the apparent redundancy of edge-aligned premask elements for generation of the priming effects[1] (see Elliott & Müller, in press; Müller & Elliott, 1999), suggest that priming works by means of the segregation of the synchronous premask frame from distractor frames (rather than element–element, i.e., feature–conjunction, binding). Given that segregation here refers to segregation in time (no spatial segregation is actually perceived), it is unlikely that segregated temporal codes develop independently across the local premask-matrix presentation frames (in the form of multiple local 10-Hz oscillations). Rather, more plausibly, if the synchronous prime is generated within the spatiotemporal context of the premask matrix as a whole, it follows that segregation of the synchronous premask must occur within the context of the global 40-Hz rhythm of premask presentation for which a common reference frequency is available for local phase adjustments.

In this respect it is important to note that, by this temporal-segregation account, entrainment would be expected to occur for all premask-matrix elements (irrespective of the Gestalt properties of a given premask frame). Under these circumstances, the pattern of activity across the premask matrix would come to take the form of multiple, separately oscillating neural clusters, each maintaining an internally synchronized and thereby specific pattern of activity across appropriate premask-matrix elements. In this way, the synchronous prime would develop and become maintained separately in time relative to other clusters of oscillatory neural activity. It is important that the notion of segmentation in time, or more specifically in phases, of the global premask-matrix presentation frequency makes quite clear the notion that the temporal characteristics of mechanisms coding local premask frames should be considered in terms of a 40-Hz response, with representations of the synchronous prime and of the three distractor frames located uniquely within different phases of this globally induced rhythm. Although this idea is consistent with computationally derived theories of information storage within different phases of a general processing rhythm (see, e.g., Lisman & Idiart, 1995), the empirical question remains as to whether or not, when premask matrices flicker globally at 40 Hz, the prime comes to possess a matching oscillatory structure.

To answer to this question, Elliott and Müller (2000) conducted a series of experiments with target presentation following at ISIs approximating a 0°, 90°, or 180° phase-angle extension to the global presentation rhythm of the premask-matrix frames. That is, phase angles were defined in terms of ISI duration relative to a hypothetical stimulus-locked 40-Hz rhythm. Thus, with the assumption of a
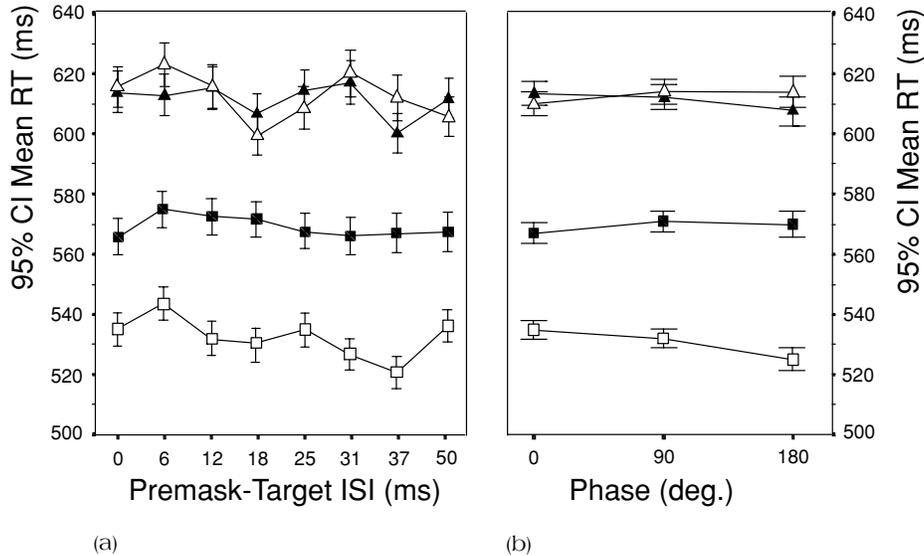
FIG. 7.4. Mean target-present and target-absent RTs (squares and triangles) for the synchronous and random-premask conditions (filled and unfilled symbols), as a function of (a) premask-target ISI and (b) phase angle. In (a), RTs are characterized by a modulatory (40-Hz) pattern across ISIs. In (b), priming effects are revealed to be maximal when target presentation followed ISIs corresponding to a 180° phase shift in the rhythm of the premask-matrix presentation.

periodic (temporal-impulse response) function of 25-ms duration with minima at 0 and 25 ms and maximum at 12.5 ms, the ISIs (within the range 0–50 ms) were 0, 25, and 50 ms for the 0° phase-angle condition, 6, 18, and 31 ms for the 90° condition, and 12 and 37 ms for the 180° condition. As shown in Fig. 7.4, by alternating 0°, 90°, and 180° phase-angle ISIs within the range 0–50 ms, there was indeed a significant phase-angle effect, which greater priming for targets presented at 180° phase-angle ISIs compared with 0° ISIs. This pattern was confirmed in another experiment using ISIs across the range 0–137 ms, and, as shown in Fig. 7.5, an experiment examining ISIs, in 4-ms steps, across the range from 25 (0° phase angle) to 49 ms (∼0°). In the latter experiment, priming was strongest for the 37-ms ISI (∼180°), with a significant difference between the 37-ms (∼180°) ISI and the 25-ms (0°) ISI. The nonlinearly changing priming effects at intermediate ISIs produced a quadratic enhancement–ISI function, providing strong support for the idea that synchronous prime persistence was maintained within a 40-Hz oscillation, with maximal RT enhancements to targets presented at a 180° phase angle relative to the rhythm established by premask-matrix presentation.
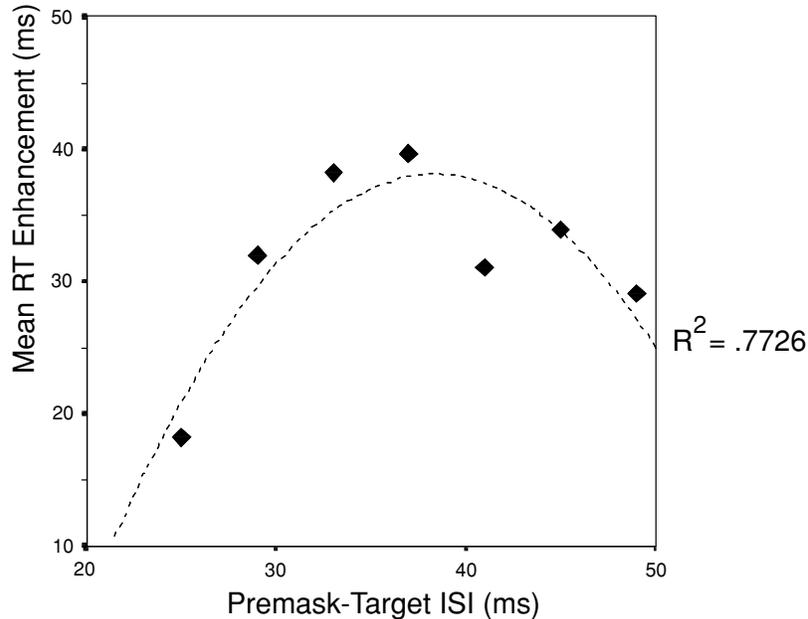
FIG. 7.5. Mean target-present RT synchronicity enhancements (random RTs minus the synchronous RTs) as a function of ISI. Also illustrated is the quadratic function that best fitted the RT priming effects, reaching its maximum at 37-ms ISIs, which corresponds to a phase angle of $\sim 180°$ relative to the projected rhythm of premask-matrix presentation.

It is important that the modulatory pattern obtained in these experiments was confined to the synchronous premask (target-present) RTs, with no general pattern of periodicity evident for the target-absent or random-premask RTs. This pattern of results strongly supports the idea that the observed priming effects reflect the operation of an oscillatory segregative mechanism that becomes engaged by synchronous premask presentation, rather than the activity of other, more general, mechanisms related to stimulus encoding or response generation.[2]

---

[2]An analysis of the RT distributions from a number of experiments provides evidence of periodicities present in the RT data. Autocorrellograms derived from the RT distributions of individual observers indeed show peaks at between 3 and 4 ms and at 24 ms. These peak periods are invariant relative to changes in stimulus conditions, the type of response (target present or absent), the observer's handedness, and the phase of target presentation relative to the 40-Hz rhythm of premask-matrix presentation, and they are also invariant across subjects. Although this invariance is interesting in its own respect, in the present context it precludes a simple account of the 40-Hz modulation of synchronous target RTs in terms of a tendency for response preparation or generation to occur in phase with a stimulus-driven 40-Hz rhythm.

A RECURRENT MODEL
OF SYNCHRONOUS PRIME GENERATION

The ideas advanced herein to account for the evidence of premask persistence involve two apparently contradictory assumptions: Whereas priming is assumed to occur in early mechanisms where the spatial specificity of stimulus information is preserved, the oscillatory structure of prime activity is assumed to be generated by some mechanism capable of coding relations across the entire premask display. However, this contradiction can be resolved by consideration of how synchrony might be propagated 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. 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, inferotemporal (IT) cells, 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. Instead, one could assume 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. 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 spatiotemporal structure of the premask display to be discerned.

As is suggested by anatomical evidence and supported by recent findings of Fries, Reynolds, Rorie and Desimone (2001), the pattern of 40-Hz activity generated by an IT neuron is fed back to earlier neurons that comprise the receptive field of that IT neuron, inducing them to oscillate at 40 Hz. In the present context, it is reasonable to assume that the response characteristics of earlier neurons would come to be determined by both recurrent 40-Hz activity and the repeated presentations of

(local) premask elements at 10 Hz. Although it is not known precisely how, or with what modifications, information is relayed back to earlier stages, two possibilities emerge that might explain the phase shifting of local neurons within the context of a global 40-Hz rhythm. On one hand, on the basis of electroencephalogram evidence, it seems plausible to consider that there may be a mismatch in the amplitudes of the recurrent 40-Hz rhythm with local 10-Hz, stimulus-evoked, steady-state responses, such that the integration of the 10-Hz response with the induced 40-Hz code modifies the amplitude of the 40-Hz response, resulting in maxima of that response that become slightly amplified and at the same time temporally "shunted" relative to the 40-Hz rhythm universally fed back by the later neuron. On the other hand, the recurrent 40-Hz code might interact with the 10-Hz response via descending pathways that synapse on local interneural networks (see Whittington, Traub, Kopell, Ermentrout, & Buhl, 2000). As a consequence, the timing of interneural mechanisms, considered a critical determinant of the timing of long-range excitatory projections, might become altered such that the time of arrival at the IT 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 interneural networks.

By either of these conjectures, 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, there develop highly dynamic and asynchronous patterns of 40-Hz activity across the entire set of lower-level neurons coding the premask matrix.

Consistent with these 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 visuocortical activity would indeed result in the temporal segregation of activity, differentiating the prime from other premask-induced activity at 40 Hz.[3]

TIMING AND ITS RELATION TO STIMULUS-INDUCED SYNCHRONIZATION

Thus far, the effects of prime generation have been considered for just one frequency, 40 Hz. In fact, in initial experiments (Fig. 7.2), 40 Hz emerged as the

[3]See the chapter by Kompass (chap. 20, this volume) for a more detailed consideration of these issues.

only frequency at which priming effects were observed (priming was not found with other premask-matrix presentation frequencies, both higher and lower than 40 Hz), suggesting that priming at 40 Hz represents a special case of stimulus frequency-induced effects. This immediately led to the question of why, within an architecture of recurrent neural transmission between later and early visual processing mechanisms, primes should become generated at 40 Hz, but not at other premask-presentation frequencies. However, for the question to be posed properly, it became necessary to examine whether performance exhibits inherent regularities as a function of linear separations in frequency. In addition, analysis in the frequency domain promised to help separate true priming effects from the impact of other factors, such as conduction latencies or synaptic "gating" mechanisms that are known to influence the frequency characteristics of long-range, excitatory neuronal activity (e.g., Traub, Whittington, Buhl, Jefferys, & Faulkner, 1999; Whittington, Traub, & Jefferys, 1995).

Figures 7.6(a) and 7.6(b) present of the results of two experiments (briefly reported in Elliott & Müller, 1999) that examined the frequency dependence of priming effects (with premask-target matrix ISI = 0 ms). Consistent with the original findings of Elliott and Müller (1998), Fig. 7.6(a) reveals a priming effect in a narrow frequency range near 39–40 Hz, pointing to some degree of priming specificity centered on 39.5 Hz. However, Fig. 7.6(b) indicates that the notion of frequency-specific priming requires modification: Although the pattern of effects in the vicinity of 40 Hz (38–40 Hz) was similar to that represented in Fig. 7.6(a), further priming effects were revealed at 33 Hz and between 46 and 47 Hz, at local minima in the absolute RT-by-frequency functions (for all target-by-synchrony conditions). It is important that these frequencies are separated, across the 28- to 51-Hz bandwidth, by an interval of ∼6.75 Hz, a fine-grained patterning hitherto unknown from the literature on visual perception.

On the basis of the finding of priming at 40 Hz and the corresponding 40-Hz modulation of the synchronous target RT by premask-target ISI function, it might be assumed that, for each frequency at which priming occurs, a corresponding pattern of prime activity develops with a characteristic modulatory pattern matching the frequency of premask-matrix presentation. It follows that an analysis of the RT by frequency relationships should proceed from the logically necessary relationship between ISI-dependent RT characteristics on one hand and frequency-dependent characteristics on the other. This implies that the family of possible empirical RT-by-ISI functions with frequency as a parameter represents the same data as the family of RT-by-frequency functions with ISI as a parameter. Another empirically based assumption is that priming as a function of ISI is characterized by a 180° phase shift such that priming is most efficient for ISIs that are out of phase with the projected rhythm of premask-matrix presentation (see Figs. 7.4 and 7.5) and that this "phase-angle rule" holds in general for any critical frequency.

Apart from the existence of more than one priming frequency, the graphs of Fig. 7.6(b) diverge in a second important respect from earlier expectations
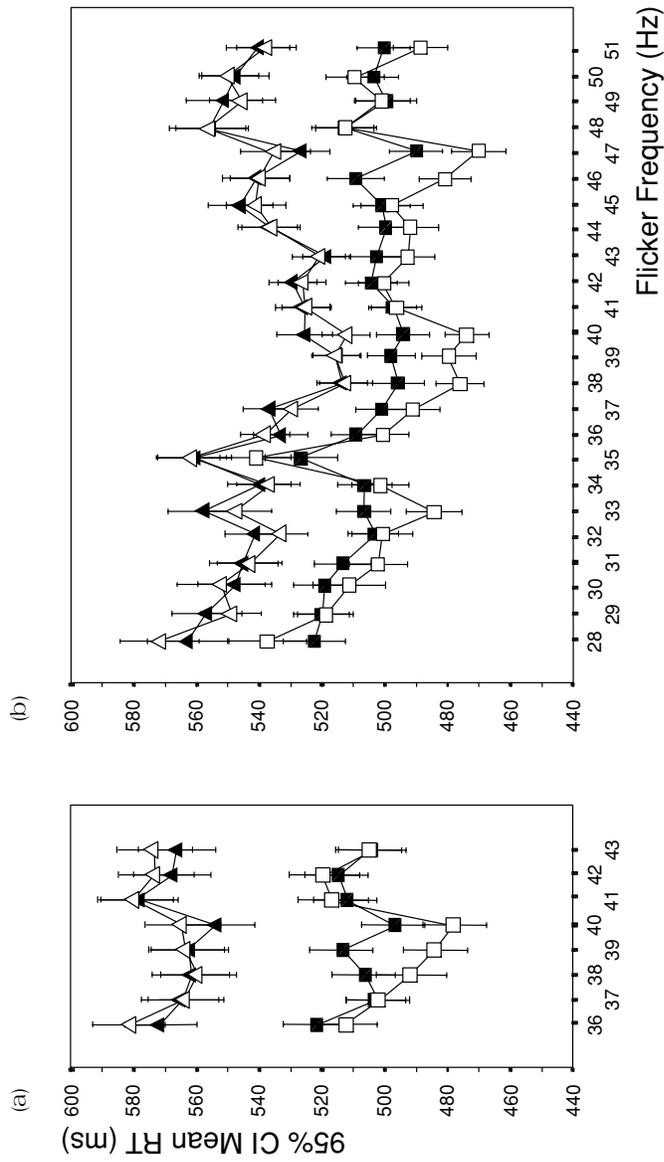
FIG. 7.6.   (a) Mean target-present and target-absent RTs (squares and triangles) for the synchronous and random-premask presentation conditions (unfilled and filled symbols), as a function of premask-presentation frequency in the 36- to 42-Hz range. The target-present RTs revealed priming to be evident only between 38 and 40 Hz. (b) Mean target-present and target-absent RTs as a function of premask-presentation frequency in the 28- to 51-Hz range. Here, priming effects were revealed to be specific to frequencies of 33 Hz, 39–40 Hz, and 46–47 Hz. CI = confidence interval.
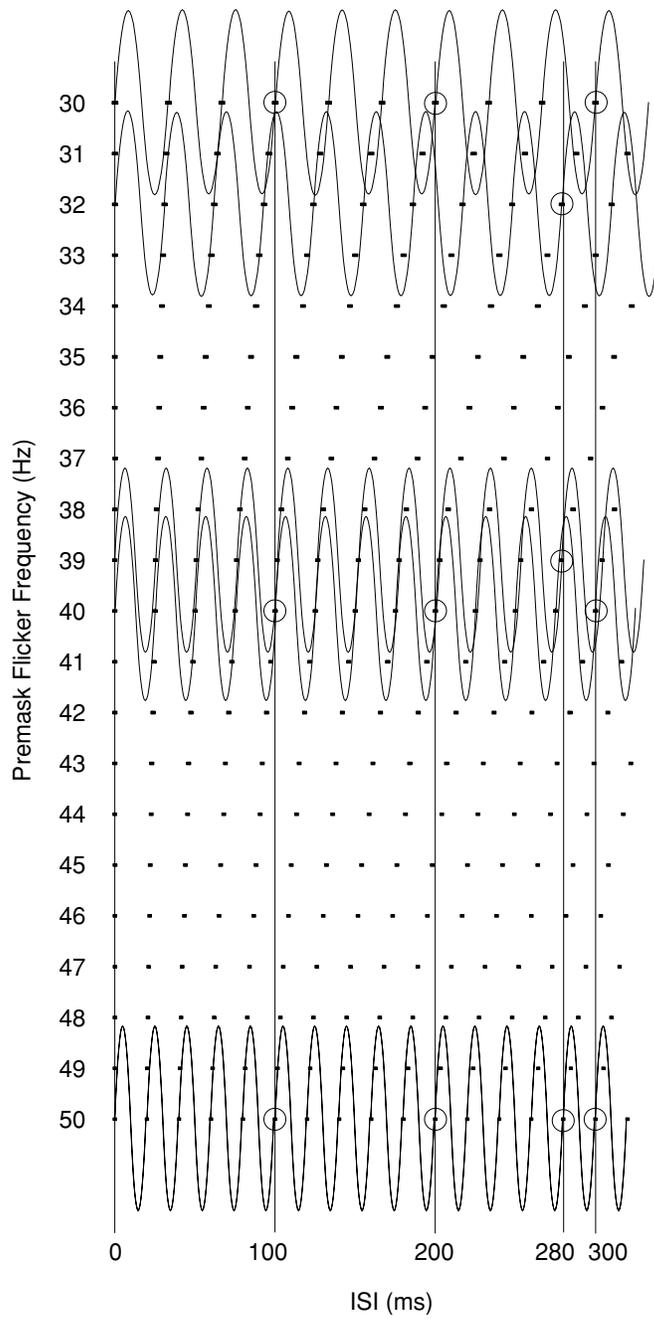
149

FIG. 7.7. The projected ISIs for which priming is predicted on the basis of the RT-by-frequency functions presented in Fig. 6(b). For each frequency, circles indicate the points in time of common

Au: Pls. provide Fig. callout 7.7.

concerning the priming effect: There is a strong similarity of trends among all four of the depicted functions. In fact, the differences between maximum and minimum RTs within the basic trend of the target-present synchronous premask condition are up to three times larger than the maximum priming effect observed. Most strikingly, the trends of the target-present RTs for the synchronous premask and random-premask conditions show virtually the same maxima and minima (allowing for a constant upward shift and a shrinking by a constant scaling factor for the random-premask relative to the synchronous premask RTs) and are statistically indistinguishable; (synchronous, random) RT rank-order correlation $r_s = .791$). This strongly suggests that random premasks exert the same influence as synchronous premasks. The observation that priming occurs only at the minima of the basic trend suggests that priming is in some way dependent on this underlying trend.

Proceeding from these data-inherent regularities, we can address the first of the main issues raised herein concerning the consistency of the phase-angle rule with the observed (general) frequency trends. This issue can be resolved by assuming that the relevant time axis does not coincide with ISI itself, but represents an internal processing time differing from ISI in its zero point. The corresponding constant delay can be estimated from the data. Specifically, we assume the following generalized phase-angle hypothesis (GPAH) that, for a given priming frequency f and corresponding period duration $\tau = 1/f$, facilitation reoccurs at every time point

$$J(\tau) = \left(n\tau + \frac{1}{2}\right)\tau - T,$$

where $n\tau$ is a frequency-specific integer multiplier and T denotes a constant quantal time delay. The term $+ \frac{1}{2}$ accounts for the observation that, for $f = 40$ Hz, maximal facilitation occurred at phase angles of $180°$ relative to the rhythm of premask-matrix presentation.

A fit with the observed minima is obtained for $T = 138 \pm 2$ ms, where T and multiples of T correspond to those points in time at which the phases of all frequencies located at the minima of the RT-by-frequency function coincide. If this constant is conceived of as a time barrier, RTs may be assumed to reflect (on average) some delay in time proportional to the absolute deviation of the most

---

(*Continued*) phase angle, and the black squares indicate the times equivalent to a phase angle of 0°. For illustrative purposes, the projected rhythms of the premask matrix are illustrated as sinusoidal. On the assumption that the projected rhythm of premask-matrix presentation originates at the 0-ms ISI, the pattern of RT-by-frequency functions presented in Fig. 6(b) should be obtained by means of phase-angle interactions at ISIs of 100, 200, 280, and 300 ms for premask-matrix presentation frequencies of 30–32 Hz, 39–40 Hz, and 50 Hz. These frequencies approximate those shown to be effective empirically.
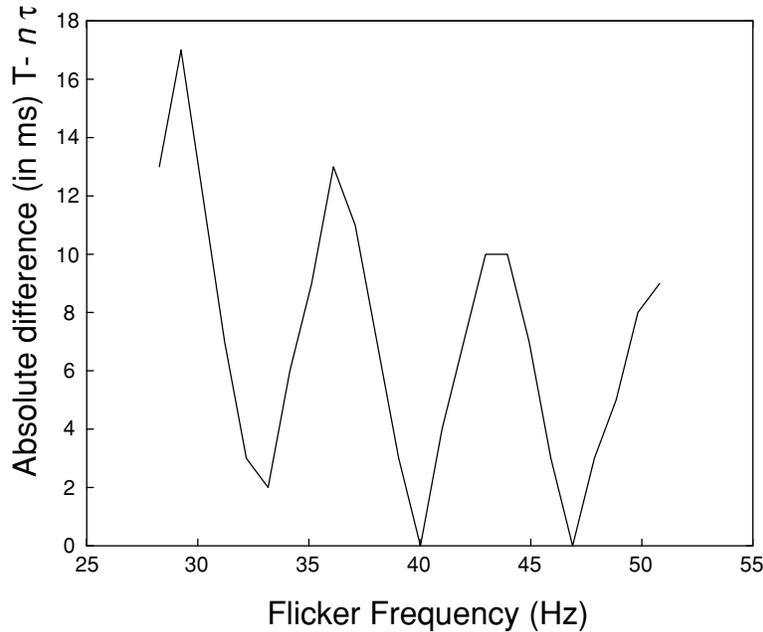
FIG. 7.8.   Model data predicted on the assumption that RT minima
and maxima reflect the absolute difference between the negative
lobe of a hypothetical stimulus-induced frequency that matches a
premask-matrix presentation frequency and a quantal timing pa-
rameter of 138 ± 2 ms. The predicted function describes both the
patterning of minima and maxima and the overall trend for maxi-
mal amplitudes to decrease with increasing frequency.

proximal estimate of (the frequency-specific integer multiplier) $n\tau$ from the time
window around this barrier.

IMPLICATIONS AND SPECULATIONS
RELATED TO PHASE-SPECIFIC
PROCESS TIMING

The analysis just given simultaneously refers to two directly observable aspects
of premask-induced RT variation, namely the $180°$ phase shift of prime activity
relative to the projected rhythm of premask-matrix presentation and the regular
separations of priming frequencies across the range from 28 to 51 Hz. It is im-
portant that, by means of this analysis, a unified account can be presented for
both. Moreover, stricter criteria are provided for relating the data presented to

other known facts. One pertinent issue in this context concerns the open question of how frequency in the experiments should be considered. Against the 40-Hz range assumption, it has been objected that premask stimuli repeat locally with a frequency of 10 Hz. This objection could be resolved by the finding that the synchronous target RTs by premask-target ISI functions are indeed modulated at 40 Hz (Elliott & Müller, 2000). However, this evidence pertains only to 10 and, respectively, 40 Hz. The presence of additional priming frequencies, which, by virtue of adopting the phase shift characteristic of 40 Hz, share common interactions in time, strengthens our theoretically and empirically driven hypothesis: One fundamental consequence of repeating premask-matrix presentation is the generation of an identical rhythm in the brain, which, under certain specific temporal conditions, carries information of particular relevance for subsequent target detection.

On the assumption of stimulus-induced brain rhythms that carry target-relevant information at 40 Hz, these data suggest a strong relationship to induced 40-Hz oscillations revealed in physiological binding research, while also presenting a challenge to physiologically inspired theories of temporal coding. Most striking in this respect is the occurrence of several fine-tuned minima in the RT-by-frequency characteristics, which are strongly consistent across observers. The fact that frequency-dependent modulation is also observed under random-premask conditions suggests that even weak agreement with certain sharp frequencies is effective and, thus, that these frequencies should also be "preferred" under natural processing conditions.

To substantiate such a general proposal, the aforementioned analysis supports tentative conclusions as to the nature of the observed enhancement effects, which are consistent with notions of perceptual organization by means of frequency-specific synchronization. The target-absent characteristics and one of the target-present (random-premask) characteristics exhibit near-identical shapes, pointing to a premask-frequency effect that remains constant irrespective of target presence. [The Target × Frequency interaction was nonsignificant in an omnibus analysis of variance of the data in Fig. 7.6; F (7,100) = 1.78, Ms_e = 1949, p = .17; Huynh–Feldt epsilon correction applied]. This argues against the possibility that the observed frequency-specific priming effects arise in the decision or response-generating stages of the entire process; instead it suggests, as previously hypothesized, that they originate within processes responsible for perceptual organization. However, the similarity of RT-by-frequency trends for random-target and synchronous target conditions challenges the previous proposal that frequency specificity is developed only under synchronous premask conditions when targets are actually presented (see Fig. 7.4). Rather, this similarity strongly suggests that the frequency-dependent modulation of target detection revealed for synchronous premask target-present conditions is only one instance of some frequency-related, general-purpose mechanism that is active in all other conditions.

IMPLICATIONS AND SPECULATIONS
CONCERNING PRIMING BY SYNCHRONY

Thus, the account set out in the previous section provides a challenge to the notion of frequency-specific priming proposed to account for the 40-Hz specificity of the synchronicity enhancement effects (Elliott & Müller, 1998). Instead, the GPAH is more consistent with the idea that there is no specific resonance at any of the observed minima of the RT-by-frequency function. Rather, irrespective of which of the priming frequencies is concerned, priming will develop through generation of either a structurally homogeneous oscillation (which, on the basis of the RT-by-ISI functions described herein, is likely to be 40 Hz) or an oscillation with a structure matching the particular presentation frequency of the premask display. If, as assumed in the GPAH, all premask-presentation frequencies will engender neural resonance at a matching frequency (i.e., there is no specific priming frequency), the question naturally arises as to why certain frequencies prime (i.e., are functionally equivalent), whereas others do not. In this respect, the GPAH deviates from the idea that consideration of neural resonance alone may resolve the question of priming specificity. Instead, according to the GPAH, particular frequencies will come to prime by virtue of the phase angle of the induced oscillation after a defined time of internal transmission, that is, the phase angle of the presentation frequency relative to some constant time delay of the order of $T = 138$ ms, or, more tentatively, the relationship between the phase angle of the induced oscillation and the phase angle of a slower rhythm [i.e., ~7.3 Hz (1,000 ms/138 ms)].

Given that a slower frequency is indeed involved in prime generation, the range of premask-induced oscillations may not be confined to the precise frequency of premask-matrix presentation. To illustrate, if the premask-induced oscillation at 40 Hz comes to prime because of phase coherence with a slower rhythm, the phase of the slower rhythm should also be determined by some temporal aspect of premask presentation (that is, e.g., the premask-presentation frequency itself or the time of premask-display onset). Otherwise, if one takes into consideration the relatively small time window specified by the GPAH within which successful phase interaction would have to take place (i.e., with an error of ~2 ms relative to the critical phase of the slower frequency), priming would most certainly occur with a high degree of inconsistency, making it very difficult for reliable differences between the synchronous target and random-target detection RTs to be observed.[4]

The account presented herein suggests that priming occurs by virtue of the relationship between a stimulus-induced rhythm, adopting the frequency of premask presentation and carrying information related to the spatial composition of the

---

[4]If priming occurs by virtue of the phase angle of the induced oscillation after a defined time of internal transmission, then, by the same logic, the induced oscillation and time of transmission must ultimately relate to the same temporal reference. If this were not the case, the induced oscillation would appear to be unlikely to arrive at its critical phase angle at certain points in processing time with a sufficient degree of accuracy for prime generation to occur with any reliability.

individual premask frames, which is coordinated very precisely with a frequency-related general-purpose processing mechanism. This general-purpose mechanism is in some way responsible for the facilitation of information transmission at certain points in processing time.

Evidence in support of a frequency-related, general-purpose processing mechanism may also be taken from the additional assumption that the neural process by which the synchronous prime and target Kanizsa-type figure become integrated represents the only specific difference to the remaining conditions, while the effects continuously follow the same laws of transmission and processing. This leaves the difficult task of explaining why, for the target-present synchronous premask condition, the RT trend deviates from this regularity, that is, of providing a full and detailed explanation of "how" stimulus synchrony engenders a facilitatory effect on target trials. This question is the subject of current research.

RELATIONS TO OTHER TEMPORAL FACTORS

One additional consideration concerns the quantal delay parameter T and its relationship to other known quantal time constants. The value of $T = 138$ ms agrees nearly exactly with the upper bound of the smallest range of quantal time values in perception and cognition proposed by the taxonomic quantum model (Geissler, 1987). Specifically, for an assumed ideal value of the absolutely smallest quantal time unit of $T_0 = 4.57$ ms, the upper bound is predicted at $TM = 30 \times T_0 = 137$ ms. This value accounts for the empirical minima by 4.5/0.137 s = 32.9 Hz, 5.5/0.137 s = 40.2 Hz, and 6.5/0.137 s = 47.4 Hz (less marked minima are expected at 7.5/0.137 s = 53.4 Hz, 8.5/0.137 s = 62.0 Hz, and so on). This account gains some plausibility within the context of other results (based on item recognition tasks) that show a preference of 30 times a quantal period (e.g., 30×9 quantal periods; see Petzold & Edeler, 1996; Petzold, Edeler, & Geissler, 1999). Of course, the hypothetical relation given here is still to be regarded as "indirect" with reference to an assumed basic period of 4.57 ms. However, the existence of such a relation would imply that, although the common upper reference is a multiple of T_0, the critical period durations for each of the priming frequencies may show integer relations but need not be multiples of T_0. This, in turn, implies the emergence of nonlinearities by means of second-order relations to T_0, which, if substantive, extend the series of observed relations beyond the current framework of taxonomic quantum model predictions.

CONCLUSIONS

This chapter has been devoted to the examination, by means of psychophysical methods, of a physiological hypothesis concerning the organization of perceptual information. Thus, to conclude, it seems appropriate to refer back to physiol-

ogy to assess the putative validity of our conclusions, in particular the idea that priming occurs by means of interactions between neural resonance that matches premask-presentation frequency and a constant time delay that may be related to the operation of much finer-scale timing of the order of 4.57 ms. Although the numerical relation between the priming frequencies, a constant delay of 138 ms, and the smallest hypothesized quantal timing unit of 4.57 ms can be assumed, and although very similar ideas of temporal interactivity have been used to successfully simulate certain, well-determined cognitive processing limitations (e.g., see the short-term memory storage model of Lisman & Idiart, 1995), to our knowledge, no concrete physiological evidence exists to specify perceptuocognitive operations as a function of the phase of an ongoing gamma-bandwidth oscillation relative to fixed points in process time. Consequently, the drawing of analogies between the psychophysical structures described here and the defining structures of neural resonance is not ultimately permissible. However, some indication of how best to approach the physiological questions that arise from the GPAH may be gathered from a combination of evidence relating to the temporal characteristics of visuocortical mechanisms and experimental evidence pointing to a possible link between activity within these mechanisms and the coding of stimulus synchrony within 40-Hz premask-matrix flicker.

With respect to neural timing, it is known that the timing of activity across interneural gap junctions occurs within a temporal range very close to 4.5 ms (specifically, ∼5 ms peak–peak intervals in the neocortex, equivalent to a frequency of activity varying in the range 200–250 Hz; X. W. Singer, personal communication, 17th March, 2000), and that this delay is critical for the rapid synchronization of inhibitory interneuron activity. Applied to the present paradigm, that inhibitory interneuron activity may be precisely related to priming is suggested by the finding of enhanced priming effects following treatment with the benzodiazepine lorazepam (Elliott, Becker, Boucart, & Müller, 2000). Lorazepam is known to enhance γ-aminobutyric acid-induced inhibition uniquely at receptors located at interneuron synapses, which in turn stabilize and reduce the frequency of postsynaptic, excitatory activity by synchronizing their own discharges at around 40 Hz. In the context of the recurrent model of prime activity outlined herein, this set of findings supports the idea that feedback projections would influence lower-level activity by means of interneural mechanisms. When both the frequency of interneural activity and the timing of activity at the interneuron synapse are taken into consideration, this idea allows for the further speculation that the coding of stimulus synchrony is indirectly but fundamentally determined by synaptic gating at times approximately equivalent to T_0 and multiples thereof.

Currently, these related speculations receive no direct empirical support. However, the careful modeling of the times and locations of temporal variability within recurrent networks, coupled with examination of the extent to which the RT-by-frequency and RT-by-ISI functions vary between γ-aminobutyric acid enhanced and control conditions, could provide results that are interpretable in terms of

variability directly related to the behavior of internal timing parameters with firmly established neurophysiological correlates. This constitutes a promising proposal for corroborating the temporal patterning described here in terms of patterns of temporal activity in the brain.

ACKNOWLEDGMENTS

REFERENCES

Alais, D., Blake, R., & Lee, S. H. (1998). Visual features that vary together over time group together over space. *Nature Neuroscience, 1*, 160–164.

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

Eckhorn, R., Bauer, R., Jordan, W., Brosch, M., Kruse, W., Munk, M., & Reitboeck, H. J. (1988). Coherent oscillations: A mechanism for feature linking in the visual cortex. *Biological Cybernetics, 60*, 121–130.

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

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

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

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

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

Elliott, M. A., & Müller, H. J. (1999). On the role of 40-Hz, and evidence of faster-frequency oscillations during visual-object perception. In P. R Killeen & W. R. Uttal (Eds.), *Fechner Day 99. The end of 20th century psychophysics. Proceedings of the 15th annual meeting of the International Society of Psychophysics* (pp. 13–18). Tempe, AZ: The International Society for Psychophysics.

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

Elliott, M. A., & Müller, H. J. (in press). Effects of stimulus synchrony on mechanisms of perceptual organization. *Visual Cognition*.

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

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

Gegenfurtner, K. (1998). Visual psychophysics: Synchrony in motion. *Nature Neuroscience, 1*, 96–98.

Geissler, H.-G. (1987). The temporal architecture of central information processing: Evidence for a tentative time-quantum model. *Psychological Research, 49*, 99–106.

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.

Lisman, J. E., & Idiart, M. A. P. (1995). Storage of 7 ± 2 short-term memories in oscillatory subcycles. *Science, 267*, 1512–1515.

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. 323–340). Amsterdam: Elsevier.

Müller, K. (1999). Is 40-Hz-synchronicity priming demonstrated by a novel psychophysical paradigm indeed a 40-Hz phenomenon? Commentary on H. Müller & Elliott. In G. Aschersleben, T. Bachmann, & J. Müsseler (Eds.), *Cognitive contributions to the perception of spatial and temporal events* (pp. 341–343). Amsterdam: Elsevier.

Petzold, P., & Edeler, B. (1996). Organization of person memory and retrieval processes in recognition. *European Journal of Social Psychology, 25*, 249–267.

Petzold, P., Edeler, B., & Geissler, H.-G. (1999). Discrete clusters of processing time in a verbal item-recognition task. In P. R Killeen & W. R. Uttal (Eds.), *Fechner Day 99. The end of 20th century psychophysics. Proceedings of the 15th annual meeting of the International Society of Psychophysics* (pp. 25–30). Tempe, AZ: The International Society for Psychophysics.

Traub, R. D., Whittington, M. A., Buhl, E. H., Jefferys, J. G. R., & Faulkner, H. J. (1999). On the mechanisms of the $\gamma > \beta$ frequency shift in neuronal oscillations induced in rat hippocampal slices by tetanic stimulation. *Journal of Neuroscience, 19*, 1088–1105.

von der Malsburg, C. (1981). *The correlation theory of function* (Internal Rep. No. 81–2). Göttingen, Germany: Max-Planck-Institute for Biophysical Chemistry, Department of Neurobiology.

Wendt, J. (2000). *Masking the 40-Hz synchrony-priming effect by form and phase*. Unpublished master's thesis, Universität Leipzig, Germany.

Whittington, M. A., Traub, R. D., & Jefferys, J. G. R. (1995). Synchronized oscillations in interneuron networks driven by metabotropic glutamate activation. *Nature, 373*, 612–615.

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.