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Evidence for 40-Hz Oscillatory Short-Term Visual Memory Revealed by Human Reaction-Time Measurements

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Four experiments show that presentation of a synchronous premask frame within a 40-Hz, flickering premask matrix primes subsequent detection of a Kanizsa-type square by generation of a 40-Hz prime. Reaction time (RT) priming effects indicated a 150–200-ms prime duration following premask display. RTs were also found to be sensitive to the phase relationship between offset of the premask display relative to the onset time of the target: Priming effects were maximal when the target was presented out of phase with premask presentation (i.e., at interstimulus intervals displaced by 180° relative to the 40-Hz rhythm of premask-frame presentation). Taken together, these results demonstrate the existence of a very short-term visual memory that oscillates at 40 Hz. The findings are discussed in the context of complementary psychological and neurophysiological findings related to visual-object coding and the role of gamma-band activity in the brain.

In order to represent the organization of separable feature elements as a single perceptual entity, the elements must be independently coded and then recombined or “bound” into a composite object representation. Neurophysiological studies have demonstrated that separate features of a stimulus object are coded by functionally specialized neurons, optimally tuned to particular stimulus attributes such as length, spatial frequency, spectral density, and orientation (e.g., Hubel & Wiesel, 1959; Livingstone & Hubel, 1988). In addition, recent single-cell recording studies have demonstrated that, although features belonging to the same object are coded by separate neurons, these neurons adjust their firing patterns to fire in synchrony. These findings have led to the hypothesis that synchronization of patterns of activity among feature-coding neurons is the most likely neurophysiological correlate of psychophysical “feature binding” (e.g., Gray, König, Engel, & Singer, 1989).

The electrophysiological recordings of synchronized neuronal activity have typically been obtained from a series of

spatially separate cortical neurons with adjacent receptive fields in anesthetized cats (e.g., Gray et al., 1989) or monkeys (e.g., Eckhorn, Fien, Bauer, Woelbern, & Kehr, 1993; Fien, Eckhorn, Bauer, Woelbern, & Kehr, 1994; Kreiter & Singer, 1992). Gray et al. (1989), and subsequently Freiwald, Kreiter, and Singer (1995), recorded from neurons in area 17 of the cat visual cortex. They found that, when the neurons’ receptive fields were stimulated by separate bars of light moving in opposite directions, related neural activity showed low cross-correlation. However, when bars traversed the receptive field in the same direction (i.e., when their motion was coherent), a correlative relationship was observed between neural firing within the 30- to 70-Hz frequency range. The cross-correlation was strongest when the motion of a single (connected) bar stimulated the relevant cortical neurons. Gray et al. concluded that neural synchrony was an important factor for binding stimuli that group according to Gestalt principles such as stimulus continuity, as well as proximity and common fate motion (e.g., Engel, König, Kreiter, & Singer, 1991; Gray et al., 1989). Furthermore, synchronous neural activity has frequently been observed to take the form of coherent oscillatory activity between neurons responding to the same visual object. This has given rise to the idea that coherent oscillations are a means by which synchronous firing may be achieved (see Singer, 1996).

Complementary to this work, Elliott and Müller (1998) have recently presented evidence that human reaction times (RTs) to detect a Kanizsa-type configuration (of four 90°-junction elements that grouped to form an illusory square) within a matrix of (nongrouping) distractor elements may be enhanced by “synchronicity priming.” The paradigm of Elliott and Müller was designed to examine the psychophysical basis for temporal binding, guided by the idea that visual coding mechanisms could be entrained by the temporal characteristics of a stimulus display (e.g., Gur & Snodderly, 1997). Thus, prior to target display onset, observers were presented with an entraining premask display matrix of 3 ×

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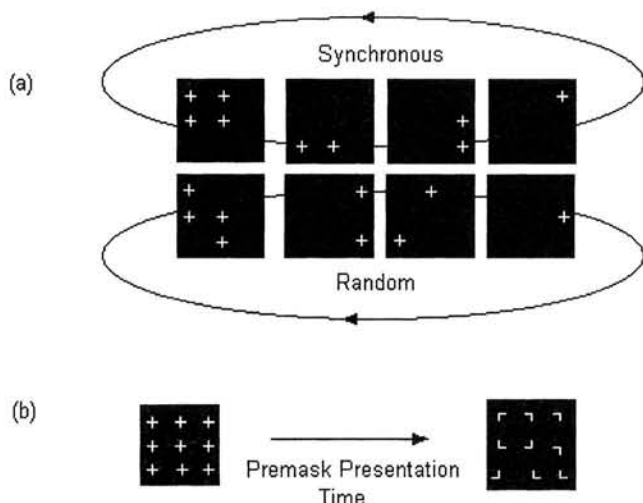


Figure 1. (a) An example sequence of the four separate premask subset frames in the synchronous condition (in which one frame consisted of four elements in square arrangement). The 40-Hz premask presentation frequency was defined as the frequency of occurrence of premask subsets per second. In other words, the entire premask matrix was presented as 10 times the 4 premask subsets per 1,000 ms, with a constant subset exposure duration of 25 ms and < 1 ms intersubset interval. In this way, the premask sequence was continually recycled during premask presentation. This produced the effect of a flickering display of nine crosses illustrated on the left-hand side of Figure 1(b). In Experiments 1 to 4, a short interstimulus interval followed premask presentation, during which time no stimulus was presented on the monitor screen. As illustrated in (b), this period was followed by target-display presentation, to which the observers produced their target-present or target-absent reaction time response.

3 flickering crosses (see Figure 1), which contained target figure-relevant information. The premask display involved the repeated presentation of four asynchronized image frames, each consisting of between one and four crosses that were repeatedly presented at a fixed location within the 3×3 element matrix. Accordingly, the premask display flickered by virtue of the asynchronized presentation of crosses across the four different display frames (Figure 1a) and as a function of the presentation frequency of the individual frames.

There were two premask conditions, the synchronous and random conditions (illustrated in Figure 1a). In the synchronous condition, one premask frame consisted of four crosses presented at the display location subsequently occupied, on target-present trials, by corner junctions defining a target Kanizsa-type square (i.e., an illusory square figure defined by the collinear arrangement of 90° corner junctions). In the random condition, there was also one frame comprising four crosses, which were presented in pseudorandom arrangement that did not correspond to a square.

In both conditions, each 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 display was deter-

mined by the oscillation frequency of each frame, the duration of each frame, and the interval between successive frames. For the 40-Hz premask display flicker, for example, each premask frame oscillated at 10 Hz, had a duration of 25 ms, and was followed by the next frame within less than 1 ms. Despite onset 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 stochastically flickering crosses, with no discernible spatio-temporal structure.

Following premask display presentation, all nine crosses were immediately replaced by a (target) display of 90° -corner junctions that remained in view until observers produced a target-present or target-absent RT response. The target was a Kanizsa-type square of grouping 90° -corner junctions, to be detected within a 3×3 element matrix of grouping target (if present) and nongrouping distractor junctions. The choice of Kanizsa-type target figures was based on psychophysical studies that had shown Kanizsa figure detection to operate in parallel across the visual display, that is, at the preattentive stage of figure-ground segmentation (e.g., Davis & Driver, 1996; Donnelly, Humphreys, & Riddoch, 1991). This is consistent with an idea originally proposed by von der Malsburg (1981) that one important visual function subserved by synchronized neural activity was low-level, preattentive figure-ground segmentation.

Accordingly, it was expected that, in the synchronous premask condition, presentation of premask displays at (entraining) frequencies that matched 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) observed that target detection 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 40 Hz.¹ First, this 40-Hz synchronicity enhancement effect was target conditional, that is, it was manifest only on trials containing a Kanizsa-type figure in the target display, not on target-absent trials. Second, it took 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 onward. This finding suggests that the generation of the prime occurs at some time between 100 and 200 ms from premask display onset (see Elliott, 1998; Elliott & Müller, 1998). Third, this effect was obtained even though observers were unable to discern whether the

¹ Elliott and Müller (1998) examined flicker frequencies between 25 and 100 Hz and also reported a borderline significant RT synchronicity enhancement when premask display presentation was set at 25 Hz. However, an interpretation of this effect in terms of synchronicity priming was brought into question by evidence that observers experienced some phenomenal awareness of premask structure at 25 Hz (Elliott & Müller, 1998, Experiment 2), which could provide the basis for the deployment of strategic processing resources (i.e., spatial-attentional deployment; see Elliott & Müller, 1998, for details).

sequence of premask frames contained a synchronous or a random premask (see Elliott & Müller, 1998, Experiment 2).² Fourth, it was observed in the absence of evidence that the synchronous-premask frame summons 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). Elliott and Müller have interpreted the synchronicity-enhancement (RT) effects in terms of target priming induced by the repeated presentation of the synchronous premask, with the synchronized neural response generated by the synchronous premask (henceforth referred to as the *synchronous prime*) combining with the response generated by the presentation of the target Kanizsa figure. By this account, the synchronous prime facilitates the segregation of target figure from background activity (Singer, 1996; von der Malsburg, 1981).

Persistence Properties of the Synchronous Prime: Duration and Structure

The principal aim of the present study was to demonstrate the psychophysical validity of the concept of feature-object binding through the activity of an oscillatory mechanism, as derived from electrophysiological studies, by investigating the duration and structure of the synchronous prime. The guiding idea was that the prime acts as an oscillatory visual short-term memory (VSTM) that maintains information about the figure-ground organization of the visual field for a brief period of time. The duration of the prime will be referred to in terms of the persistence of prime activity, with implied reference to the persistence of neural activity that accompanies premask display or synchronous premask frame presentation, or both. To develop psychophysically testable hypotheses concerning synchronous prime duration and structure, it is useful to review previous research into VSTM and relate it to the notion of synchronicity priming proposed by Elliott and Müller (1998).

Duration

Three findings or considerations are of particular relevance concerning the likely persistence of the synchronous prime. First, priming effects are generated following premask display durations of between 100 and 200 ms (i.e., two presentations of the complete premask display) or longer. Second, observers are unable to detect the presence of a synchronous premask frame within the premask display (even when the premask display is presented for up to 2,400 ms; see Elliott & Müller, 1998, Experiment 2), whereas the flickering premask display matrix, within which the synchronous premask is embedded, is fully perceived by the observers. Third, synchronicity priming entails that the response to the target interacts with the existing response to the prime, thereby expediting target figure coding and detection RTs (Elliott & Müller, 1998, 1999). Furthermore, the premask paradigm resembles other paradigms designed to study VSTM, which have involved the successive presentation of two related stimuli, with a brief interstimulus interval (ISI), so as to permit an assessment of the residual

perceptual or persistence properties of the first stimulus according to its influence on the perception of the second. Following this logic, in the present study, we examined the duration and structure of the synchronous prime by introducing variable ISIs between the offset of the oscillating premask display and the onset of the target display, during which prime activity received no reinforcement by premask frame presentation.

From studies of visual memory for complex patterned stimuli, the shortest duration of stimulus retention has been estimated in the order of 4 s for a "visualized" representation of the to-be-remembered stimulus (Phillips, 1974). Given that participants had been instructed to match the component structure of two presented patterns, Phillips's estimate is likely to be much longer than the duration of persistence associated with synchronous premask presentation, which is not detected by observers and might be difficult (if not impossible) to render in terms of a visualized representation. Instead, of more particular relevance to synchronous prime persistence are estimates for VSTM duration of around 300 ms, which has often been reported as the maximum period for which stimuli may be maintained during perceptual coding. For example, Sperling (1960) found that partial reports of the identity of letters embedded in multiletter displays reduced to an asymptotic limit as the duration between array offset and the onset of an indicator to the to-be-reported letter row was increased to around 300 ms. A similar duration has also been estimated by Eriksen and Collins (1967, 1968), who found that identification of nonsense syllables formed by the superposition of one random-dot image upon another decreased with increasing ISI between the two images, reaching asymptote within the range of 100 to 300 ms. Further examinations of the relationship between stimulus duration and persistence have produced evidence that persistence is the inverse of stimulus duration up to a maximum overall duration of 300 ms or less. This inverse duration effect was first demonstrated by Efron (1970a, 1970b, 1970c), who proposed that a fixed perceptual duration of 240 ms was composed of a minimum perceptual onset latency of 130 ms plus persistence, which was fixed at 110 ms for stimuli with a duration of 130 ms or less and inversely related to stimulus durations greater than 130 ms. Subsequently, Coltheart (1980) extended the duration of persistence to be an inverse function of stimulus duration of up to 300 ms.

Coltheart (1980) defined persistence in terms of a visual memory that decays asymptotically, is characteristically visible, and therefore is central or late cortical in origin. This definition raises two questions concerning the likely persistence of the synchronous prime. The first is whether or not the nondetectability of the synchronous premask frame (Elliott & Müller, 1998, Experiment 2) precludes consideration of synchronous prime persistence in similar terms to that of visible stimuli (i.e., in terms of visible persistence).

² $A_z = 0.52$; A_z is a measure of signal detection sensitivity equivalent to the area under the receiver operating characteristic curve, ranging between 0.5, chance performance, and 1.0, perfect performance (for further details, see Dorfmann & Alf, 1969).

The second question concerns the relationship between premask display duration and synchronous prime persistence.

Concerning the first question, the persistence estimates of 240 to 300 ms were all obtained from studies in which stimuli were detected by observers (i.e., stimuli were at least partially "visible" as distinct perceptual items), whereas the synchronous premask was not at all discernible within the context of 40-Hz premask display flicker (see earlier description), although the premask display was fully visible to observers. Thus, making the assumption that the 240- to 300-ms persistence duration extends to the synchronous prime entails that prime persistence is generated by virtue of its relationship with a visible stimulus, that is, the premask display as a whole. This assumption is plausible when it is considered that the 40-Hz synchronicity enhancement effect reflects the segmentation of the synchronous premask quadrant from the remainder of the premask display, in other words, the coding of the synchronous premask within the context of the premask display as a whole. Accordingly, it could be hypothesized that activity across the synchronous prime exhibits persistence consistent with the persistence of the entire premask display, that is, persistence equivalent to that of a visible stimulus.

Concerning the second issue raised earlier, namely, the inverse relationship between (premask) display duration and (synchronous prime) persistence, the preceding persistence-duration hypothesis would seem to entail that there should be little or no synchronicity priming effect for premask display presentations of 300 ms and over, which is at variance with the findings of Elliott (1998) and Elliott and Müller (1998). To avoid this difficulty, an alternative estimate of synchronous prime persistence could be made by measuring from the onset of the final synchronous premask frame during premask display presentation, as this is the last occasion on which internal synchronous prime activity can be reinforced by the entraining stimulus. Thus, if premask display presentation terminates after presentation of the final frame in the sequence, the measurable persistence of the synchronous prime might be expected to be equivalent to the duration of persistence (300 ms) minus the duration of the synchronous premask frame (25 ms) and minus the period of time during which other three premask frames are presented (75 ms). Accordingly, synchronous prime persistence could be hypothesized to be within 200 ms from premask display offset.

Structure

The preceding duration hypothesis assumes that premask display persistence is approximately equivalent across the premask elements (irrespective of the temporal display composition), although synchronous prime persistence becomes in some way distinct from persistence across the remaining elements. This raises the question of how the synchronous prime may be generated and maintained independently of the remaining premask display elements, without the synchronous premask frame becoming discernible to observers (even after extended viewing of the entire premask display) and without it operating as a spatial-

attention cue to the likely target location (e.g., Elliott & Müller, 1998, Experiment 3).

A hypothesis may be derived from the following set of ideas. A fundamental assumption made by Elliott and Müller (1998) was that synchronous prime generation occurs through entrainment of neural-coding mechanisms at 40 Hz. Entrainment would occur for all premask display elements (irrespective of the Gestalt properties of a given premask frame), so that the pattern of activity across the premask display may be conceptualized in terms of clusters of oscillating neural mechanisms. Each cluster maintains a specific pattern of activity across appropriate premask display elements, with one of the clusters maintaining the pattern of activity across the synchronous prime. The most plausible hypothesis is that the synchronous prime is maintained separately in time relative to other premask coding activity, according to some property of the oscillatory code established by premask display presentation.

This idea gains support from a number of empirical and theoretical studies that have explored temporal stimulus coding or dynamic binding, or both, as a medium for information storage. For example, Dehaene (1993) and Geissler, Schebera, and Kompass (1999) have argued that visuo-perceptual processing is characteristically temporal, and by the latter account, may be described in terms of "time quanta" providing the structure for various types of stimulus coding operations and their temporal coupling. Furthermore, recent computational modeling studies of dynamic binding (e.g., Hummel & Holyoak, 1997; Lisman & Idiart, 1995; Shastri & Ajanagadde, 1993) have demonstrated that separate attributes of a stimulus may be maintained within different phases of a global processing rhythm. This work lends support to the idea that the entire premask display is encoded within a single oscillation at 40 Hz, with representations of the synchronous prime and of the three distractor frames located uniquely within different phases or subcycles of the 40-Hz oscillation. In this way, activity across the prime may be maintained concurrently with, but independently of, related patterns of 40-Hz activity coding the remaining premask display elements. This hypothetical account of the structure of the synchronous prime leads to the question of what phase relationship would become adopted by the synchronous prime, relative to the 40-Hz rhythm of the premask display.

According to electroencephalographic (EEG) studies of visual-object coding, presentation of a visual stimulus is accompanied by an evoked, that is, stimulus-locked, 40-Hz response within the first 100 ms of stimulus onset, which occurs irrespective of whether the stimulus exhibits good Gestalt organization (e.g., Schürmann, Başar-Eroglu, & Başar, 1997; Tallon-Baudry, Bertrand, Delpeuch, & Pernier, 1996, 1997; Tallon, Bertrand, Bouchet, & Pernier, 1995). If it does, the early response is followed by an induced, that is, not stimulus-locked, 40-Hz response some 250 to 300 ms after stimulus onset (e.g., Tallon-Baudry et al., 1996, 1997; Tallon et al., 1995).

As noted earlier, synchronicity enhancement effects become manifest after one repeat of the 40-Hz premask display, that is, between 100 and 200 ms of premask display

presentation. This short latency suggests that the neurons coding the various premask frame elements will be evoked by the rhythm of the premask display to respond at 40 Hz in a stimulus-locked manner (40-Hz entrainment). Accordingly, the conditions most conducive to producing synchronicity priming should be those under which target Kanizsa figures are presented at ISIs corresponding to a stimulus-locked or 0° phase angle relative to the 40-Hz rhythm of the premask (i.e., in phase with synchronous premask presentation), whereas targets presented at, say, 180° (i.e., out of phase) ISIs would be expected to reveal a weaker, if any, synchronicity priming relative to in-phase targets.

Summary of the Experiments

Experiment 1 was designed to map the duration of the 40-Hz synchronicity enhancement effect by varying the ISIs between premask display offset and target display onset within the range of 0 to 1 s. As expected, the activity of the synchronous prime outlasted premask display presentation for a short period, more precisely, for up to 150 to 200 ms. Consequently, Experiment 2 focused on ISIs shorter than 150 ms, to examine the dynamic structure of synchronous prime persistence. This was achieved by varying the phase angle of target display onset relative to the 40-Hz periodicity of premask frame onsets: Target displays were presented following ISIs that terminated either in phase (i.e., at a phase angle of 0°) or out of phase (i.e., at 180°) relative to premask frame (i.e., synchronous premask) onsets. To illustrate, a target display presented at an ISI of 12 ms was considered to be presented at $\approx 180^\circ$ (i.e., offset by $\approx 25/2$ ms) relative to the regular 40-Hz rhythm of premask frame onsets, whereas a target display presented at an ISI of 25 ms would be at 0° (i.e., offset by 0 ms) relative to the rhythm of premask frame onsets. Experiment 2 indeed revealed the synchronicity-enhancement effect (i.e., the synchronous premask condition RTs) to be sensitive to the phase angle of target display onset relative to the 40-Hz periodicity of premask frame onsets, consistent with a 40-Hz oscillatory structure of the synchronous prime. However, maximum enhancement was observed when the target was presented at 180° (out of phase) ISIs, rather than 0° (in phase) ISIs. Experiment 3 was designed to replicate this advantage for out-of-phase ISIs, by focusing on a single cycle of the 40-Hz prime (ISIs varying between 25 and 49 ms). The pattern of effects was consistent with that in Experiment 2: The enhancement was significantly greater for targets presented at the 180° ISI (37 ms) relative to targets presented at 0° ISIs (25 and 49 ms). However, unlike Experiment 2, some (nonsignificant) modulation of target-present RTs was also evident under random premask conditions, weakening the argument that target coding is expedited only when the target figure is preceded by a figurally relevant (i.e., synchronous) frame in the premask display. Consequently, Experiment 4 examined whether the modulation of target-present RTs, with maximum enhancement at 180° ISIs, was confined to synchronous premask conditions or whether variations in the random premask condition RTs were contributing to the modulation. The pattern of effects replicated those of

Experiments 2 and 3: RT enhancements were maximal for targets presented at 180° phase angles, with the periodic pattern of RT enhancements confined to RTs under synchronous premask conditions.

Experiment 1

Experiment 1 set out to investigate the hypothesis that the synchronous prime persists for a brief period of time following premask display offset. Accordingly, the premask paradigm described earlier was modified by introducing an ISI between premask-display offset and target-display onset (see Figure 1b). ISIs were varied across the range 0 to 1,000 ms.

Method

Observers. Twenty observers, all with normal or corrected-to-normal vision, participated in Experiment 1 (8 males; mean age 26.2 years). Observers performed one block of practice trials immediately before the experiment proper, and they were naive as to the precise experimental conditions presented in the experiment. Observers were paid at a rate of 12.00 Deutsche Marks per hour. (Practice and payment were the same in the subsequent experiments.)

Apparatus and stimuli. Event timing, data collection, and stimulus-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 (Finley, 1985). Stimuli were presented on a Tektronix 608 oscilloscope with a very fast-decay P15 phosphor, which was capable of plotting image frames with temporal control greater than 1 kHz. The P15 phosphor ensured that on-screen image persistence was reduced to 10% of normal image intensity within 2.8 μ s of image termination (Bell, 1970). Observers viewed the displays at a distance of 57 cm, maintained via a chin rest. Experiments were conducted in a dimly lit room (mean screen surround luminance 0.078 cd/m²), with stimulus luminance maintained at 0.3 cd/m² upon a background field of 0.075 cd/m². The 3 \times 3 matrix of premask elements (Figure 1b), presented at the center of the screen, subtended 7°51' \times 7°51' of visual angle. Premask elements were crosses of size 51' and were separated from their nearest horizontal and vertical neighbors by 2°39'. Premask crosses consisted of 19 tightly spaced points, so that their segments appeared as uninterrupted lines. Premask frames could consist of 1, 2, 3, or 4 crosses presented simultaneously (Figure 1a), so that the number of pixels presented in a given frame were 21, 42, 63, or 84. In order to ensure that all frames were equiluminant, an additional 979, 958, 937, or 916 pixels, respectively, were plotted to an invisible corner of the display (with x, y coordinates 0,0), equalizing the number of pixels plotted in a single frame. Junction elements in the target display subtended 26' of visual angle and were separated horizontally and vertically by between 2°39' and 3°30'. Each target display junction consisted of 11 tightly spaced points, and the target display overall consisted of 99 pixels. According to an identical procedure to that used for the premask displays, an additional 901 pixels were plotted to an invisible corner of the display. The size and separation of the inducer elements produced a Kanizsa-type square, which, according to recent formulations (Shipley & Kellman, 1992), represents a "good square" with a probability of less than 0.1.

Design and procedure. Following a brief computer-generated tone, observers were presented with an oscillating 3 \times 3 matrix of

premask crosses. After a fixed presentation time, the premask crosses reduced to simple 90° corner junctions by removal of superfluous line segments. Observers then had to discern the presence of a Kanizsa-type square (target) within this matrix of corner junctions and produce a target-present or target-absent RT response. Premask crosses comprised four separate frames the elements of which were presented simultaneously, but asynchronously relative to the elements of other frames. This permitted two premask conditions to be defined, the synchronous and random premask conditions. In the synchronous condition, one subset of premask elements consisted of four crosses presented at the display location subsequently occupied, on target-present trials, by corner junctions defining the target Kanizsa-type square. In the random condition, there was also one subset comprising four elements, which were presented in a pseudorandom arrangement that did not correspond to a square.

Premask displays were presented for 600 ms,³ with the presentation frequency of frames across the entire premask display maintained at 40 Hz. That is, the entire premask matrix, consisting of a sequence of four separate frames, was recycled six times (i.e., each premask frame oscillated at 10 Hz), with a constant frame exposure duration of 25 ms and an interframe interval of less than 1 ms. The continual recycling of the premask frame sequence produced the phenomenal experience of a flickering display of nine crosses, within which observers were unable to discern the structure of a given frame. Target displays did not oscillate but were presented at a fixed 1-kHz refresh frequency until the keypress response was made.

To investigate the duration of synchronicity priming, premask presentation was followed by a variable ISI between the offset of the premask display and the onset of the target display. No stimuli were presented on the oscilloscope screen during the ISI period. ISIs were set at 0 (i.e., no interval), 50, 100, 150, 200, 300, 500, or 1,000 ms.

In summary, Experiment 1 used a within-subject design, with the factors synchronicity (synchronous, random premask), target (present, absent), and ISI (in the range 0–1,000 ms). All factors were varied randomly within 64-trial blocks. Observers performed a total of 1,280 trials over two 640-trial sessions.

Results and Discussion

Extreme RTs (< 150 ms and > 1,500 ms) and RTs on trials in which a response error was made (2.9% of all trials) were removed from the data, prior to removal of RTs above or below 2.5 standard deviations from the means of correct responses. Erroneous responses, collapsed across synchronicity and ISI conditions, revealed no speed-accuracy trade-offs; and an omnibus analysis of variance (ANOVA) of the arcsine-transformed error data revealed no significant effects. Figure 2 presents the correct mean RTs (and their associated standard errors [SE mean]) as a function of premask target display ISI, separately for each target (present, absent) × synchronicity (synchronous, random premask) condition.

The RT data were examined by means of an ANOVA with main terms of synchronicity (synchronous, random premask), target (present, absent), and ISI (0, 50, 100, 150, 200, 300, 500, 1,000 ms). Target-absent RTs were slower than target-present RTs (688 vs. 599 ms), $F(1, 19) = 49.93$, $MSE = 25,440.21$, $p < .05$, consistent with the task involving a component of visual search. More importantly, in agreement with Elliott and Müller (1998, Experiments 1

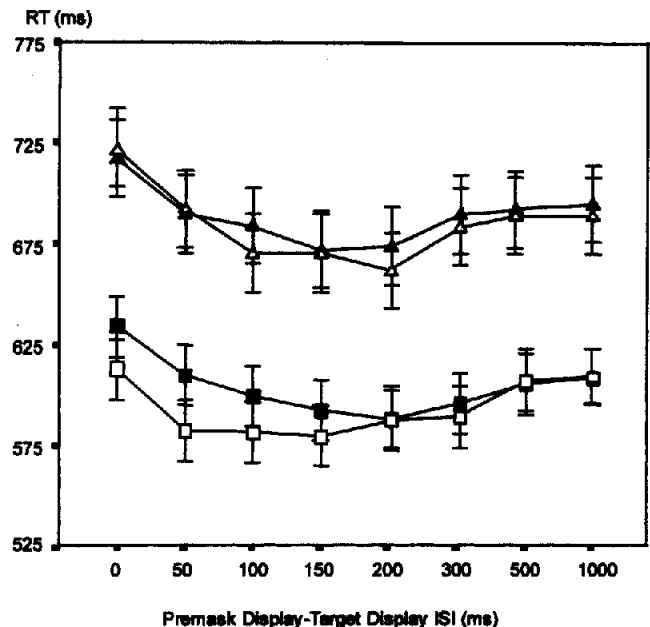


Figure 2. Mean correct target-present and target-absent reaction times (RTs) with standard-errors bars (in ms) for the synchronous and random premask conditions as a function of premask target interstimulus interval (ISI) in Experiment 1. The square and triangle symbols represent target-present and absent conditions, respectively, and the unfilled and filled symbols represent synchronous and random premask presentation conditions, respectively.

and 3), there was a significant synchronicity enhancement effect confined to target-present trials (mean enhancement [SE mean] of 12 [3] ms for target-present trials as compared to 2 [2] ms for target-absent trials), Synchronicity × Target interaction, $F(1, 19) = 7.63$, $MSE = 542.05$, $p < .025$. Furthermore, as expected, the target-present synchronicity effect was confined to short ISIs, significant Synchronicity × Target × ISI interaction, $F(7, 133) = 2.10$, $MSE = 598.92$, $p < .05$. This was confirmed by follow-up ANOVAs conducted separately for target-present and target-absent RTs, which revealed a significant Synchronicity × ISI interaction only for target-present RTs, $F(7, 133) = 2.61$, $MSE = 400.06$, $p < .025$; for target-absent RTs, $F(7, 133) = .51$, ns . A series of simple main effect analyses revealed the synchronous target-present RTs to be significantly faster than the random RTs at ISIs of 0, 50, and 100 ms, $F(1, 133) = 18.95$, 16.02, and 7.4, respectively, $p < .001$, with a marginally significant effect at 150 ms, $F(1, 133) = 3.06$, $p < .1$. No synchronicity enhancements were evident at ISIs longer than 150 ms. The magnitude of the enhancement decreased with increasing ISI from 28 (0-ms ISI) to 11 ms (150-ms ISI), with essentially a null effect at the 200-ms ISI (1-ms enhancement). Thus, the results of Experiment 1 are

³ The fixed premask presentation time of 600 ms was decided upon on the basis of previous studies (see Elliott, 1998, Experiment 6; Elliott & Müller, 1998, Experiments 1 & 3), in which premask presentation times in the range of 200 to 4,800 ms were not found to significantly influence synchronicity effects.

consistent with the expectation that the 40-Hz synchronous prime persists, in the absence of direct stimulus reinforcement, for a short period of time (< 200 ms) following premask display offset.

Experiment 2

Experiment 2 was designed to examine the hypothesis that the synchronous prime possesses a periodic structure that matches the 40-Hz periodicity of premask presentation and that is differentiable from activity across the remainder of the premask display by virtue of being maintained within a different phase angle of the 40-Hz rhythm induced by premask display presentation. Experiment 2 employed ISIs within the 150–200-ms period of prime persistence established in Experiment 1. To examine the periodic structure of the synchronous prime during this period, the phase angle of target-display presentation relative to the 40-Hz periodic structure of premask display presentation was systematically varied: Target displays were presented at ISIs that terminated either in phase (i.e., at 0°) or out of phase (i.e., at 180°) relative to premask display offset. Given that the prime acts as a 40-Hz oscillatory VSTM, the synchronicity enhancement effect was expected to show evidence of a 40-Hz periodicity, with more marked enhancement for in-phase (i.e., 0° phase angle) relative to out-of-phase (180°) ISIs. (Given that Experiment 1 had revealed no significant synchronicity effects for ISIs of 150 to 200 ms and longer, too few sampling points were available for an assessment of a 10-Hz periodicity of the prime.)

Method

Observers. Twelve observers, with normal or corrected-to-normal vision, participated in Experiment 2 (3 males; mean age 26 years).

Design and procedure. The design and procedure were as in Experiment 1, with the following exceptions: The maximum ISI was set at 137 ms, that is, at just below the ISI value (150 ms) at which the synchronicity effect was no longer significant in Experiment 1. Furthermore, ISIs were divided into two conditions: in-phase ISIs, with a 0° phase angle between premask offset and target onset (i.e., ISIs of 0, 25, 50, and 100 ms), and out-of-phase ISIs, with a 180° premask target phase angle (i.e., ISIs of 12, 37, 87, and 137 ms). Experiment 1 had used in-phase ISIs only.

In summary, Experiment 2 used a within-subjects design, with the factors synchronicity (synchronous, random premask), target (present, absent), and ISI (0, 12, 25, 37, 50, 87, 100, 137 ms). All factors were varied randomly within 64-trial blocks. Observers performed 1,280 trials over two 640-trial sessions.

Results and Discussion

Extreme RTs (< 150 ms and $> 1,500$ ms) and RTs on trials in which a response error was made (3% of all trials) were removed from the data, prior to removal of RTs according to the 2.5 standard deviation criterion. Erroneous responses, collapsed across synchronicity and ISI conditions, revealed no speed-accuracy trade-offs, and an ANOVA of the arcsine-transformed error data revealed no significant effects. Figure 3 presents the correct mean RTs (and asso-

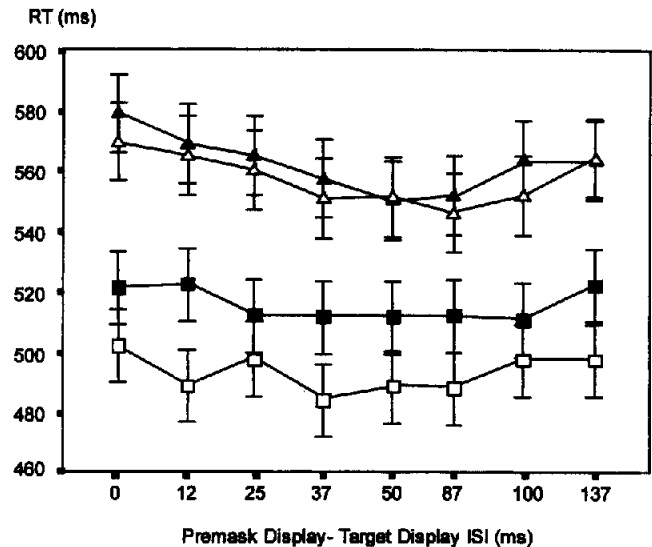


Figure 3. Mean correct target-present and target-absent reaction times (RTs), with standard-errors bars (in ms) for the synchronous and random conditions as a function of premask target interstimulus interval (ISI) in Experiment 2. The square and triangle symbols represent target-present and target-absent conditions, respectively, and the unfilled and filled symbols represent synchronous and random premask presentation conditions, respectively.

ciated SE mean) as a function of premask target display ISI, separately for each Target (present, absent) \times Synchronicity (synchronous, random premask) condition.

The RT data were collapsed across ISIs into their respective phase-angle conditions (0° : 0-, 25-, 50-, and 100-ms ISIs; 180° : 12-, 37-, 87- and 137-ms ISIs) and examined by an ANOVA with main terms of synchronicity (synchronous, random premask), target (present, absent), and phase angle (0° , 180°). Target-present RTs were faster than target-absent RTs, $F(1, 11) = 40.73$, $MSE = 1,766.36$, $p < .0001$, and RTs were expedited overall following synchronous relative to random premasks, $F(1, 11) = 29.04$, $MSE = 152.23$, $p < .005$. However, consistent with Experiment 1 and previous work (Elliott & Müller, 1998), synchronous premasks gave rise to significantly faster RTs than random premasks only on target-present trials (mean enhancements [and SE mean] of 23 [4] ms for target-present trials, as compared with 5 [2] ms for target-absent trials), Synchronicity \times Target interaction, $F(1, 11) = 13.5$, $MSE = 142.26$, $p < .005$.

The most important finding was a significant Synchronicity \times Target \times Phase-Angle interaction, $F(1, 11) = 6.98$, $MSE = 35.64$, $p < .025$, which was due to a significant Synchronicity \times Phase-Angle interaction for target-present RTs, $F(1, 11) = 8.78$, $MSE = 48$, $p < .025$, but not target-absent RTs, $F(1, 11) = .06$, *ns*. For target-present RTs, the synchronicity effect was larger for 180° phase angles than for 0° phase angles (28 vs. 17 ms; in both cases, the enhancement was significantly greater than zero). This 40-Hz modulation effect was consistent across the range of ISIs tested (see Figure 3). For shorter ISIs, the synchronicity effect increased from 0- to 12-ms ISIs, decreased from 12- to

25-ms ISI, increased from 25- to 37-ms ISIs, and decreased from 37 to 50 ms. A similar modulatory pattern was also evident for transitions between longer in-phase and out-of-phase ISIs (i.e., 50 to 87 ms, 87 to 100 ms, and 100 to 137 ms). This is particularly interesting, as the set of longer ISIs sampled did not form a regular series of successive 180° phase shifts of the expected 40-Hz duty cycle of the synchronous prime, although neighboring ISI samples always involved a change from in phase to out of phase or vice versa. This pattern indicates that phase-related differences in the synchronicity effect may be obtained at any sample point during the lifetime of the ISI-based synchronicity effect.

A different view of this interaction may be gained by examining the 0° to 180° phase-angle RT differences separately for each synchronicity condition (simple main effects analysis). With synchronous premasks, target-present RTs were revealed to be significantly slower for 0° than for 180° premask-target phase angles, $F(1, 11) = 7.24$, $p < .025$; in contrast, with random premasks, RTs showed no reliable difference between 0° and 180° phase angles, $F(1, 11) = 2.25$, $p > .10$. This pattern of effects suggests that the phase-dependent modulation of the synchronicity effect (out of phase > in phase) was due to phase-dependent modulation of the synchronous premask RTs. These differential phase effects are of particular importance as they provide direct evidence that the synchronous prime is an oscillatory structure with a 40-Hz periodicity. However, the results also suggest that the prime activity is offset by a phase angle of 180° relative to the optimal presentation time of the target (180° enhancement > in-phase enhancement), which is at variance with the original expectation.

Experiment 3

Experiment 2 revealed that synchronicity enhancement effects do exhibit a periodic structure consistent with the 40-Hz rhythm of premask display presentation. Unexpectedly, however, greater enhancements were obtained when the target was presented out of phase with premask display offset. Experiment 2 used ISIs that represented either 0° or 180° phase angles of target display onset relative to premask display offset (but no intermediate ISIs corresponding to intermediate phase angles). This leaves open the question of whether the maxima and minima of the RT enhancement were located at the particular phase angles examined. Experiment 3 was designed to address this question by employing ISIs corresponding to successive phase shifts of 60° relative to premask display offset across one full cycle of the synchronous prime (i.e., ISIs at regular 4-ms [$\approx 25/6$ ms] intervals across the range of 25–49 ms). Experiment 3 was expected to replicate the finding of maximum synchronicity enhancements at the ISI corresponding to the 180° phase angle, with other ISIs displaying a graded enhancement relative to both the 0° and 180° phase-angle conditions.

Method

Observers. Fourteen observers, with normal or corrected-to-normal vision, participated in Experiment 3 (5 males, mean age 30.8 years).

Design and procedure. The design and procedure were as in Experiment 1, except that ISIs were varied within the range of 25 to 49 ms in 4-ms steps to examine the pattern of synchronicity enhancement effects within a single 40-Hz cycle of the oscillatory prime (i.e., from a phase angle of 0° at the 25-ms ISI through 180° at the 37-ms ISI to $\approx 0^\circ$ at the 49-ms ISI).

In summary, Experiment 3 used a within-subjects design with the factors synchronicity (synchronous, random premask), target (present, absent), and ISI (25, 29, 33, 37, 41, 45, 49 ms). Given the short durations of the ISIs tested, ISI was kept constant within each 40-trial block, while the synchronicity and target factors were presented randomly within each block. Observers performed 1,120 trials over two separate sessions of 560 trials each.

Results and Discussion

RT analysis. Extreme RTs (< 150 ms and > 1,500 ms) and RTs on trials in which a response error was made (2.5% of all trials) were removed from the data, prior to filtering RTs according to the 2.5 standard deviation criterion. Figure 4 presents the correct mean RTs (and associated SE mean) as a function of premask-target display ISI, separately for each Target (present, absent) \times Synchronicity (synchronous, random-premask) condition.

The RT data were examined by means of an ANOVA with main terms of synchronicity (synchronous, random premask), target (present, absent), and ISI (25, 29, 33, 37, 41,

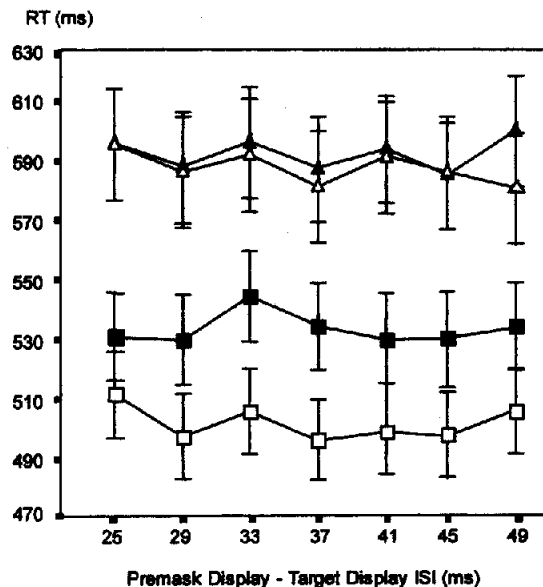


Figure 4. Mean correct target-present and target-absent reaction times (RTs) with standard-errors bars (in ms) for the synchronous and random conditions as a function of premask target interstimulus interval (ISI) in Experiment 3. The square and triangle symbols represent target-present and target-absent conditions, respectively, and the unfilled and filled symbols represent synchronous and random premask presentation conditions, respectively.

45, 49 ms). Target-present RTs were significantly faster than target-absent RTs (518 vs. 591 ms), $F(1, 13) = 35.31$, $MSE = 14,638.16$, $p < .0001$. RTs were overall faster on trials on which target displays were preceded by a synchronous rather than a random premask, $F(1, 13) = 20.15$, $MSE = 1,714.77$, $p < .001$, although enhancements were evident only for target-present trials (mean enhancement [SE mean]: 32 [5] ms on target-present trials as compared with 5 [6] ms on target-absent trials), Synchronicity \times Target interaction, $F(1, 13) = 26.38$, $MSE = 621.82$, $p < .001$. Importantly, as with Experiments 1 and 2, the target-conditional synchronicity enhancement effects outlived the duration of premask presentation.

To further examine these effects, the target-present data were subjected to a second ANOVA with the factors synchronicity and ISI. In addition to a significant synchronicity main effect, $F(1, 13) = 47.81$, $MSE = 1,030.87$, $p < .0001$, synchronicity was revealed to interact significantly with ISI, $F(6, 78) = 2.24$, $MSE = 155.55$, $p < .05$. This interaction is illustrated in Figure 5, which presents the mean RT enhancement (random RT minus synchronous RT) as a function of ISI. As expected from Experiment 2, the enhancement effects were largest at the 37-ms ISI, when the target was presented at a phase angle of 180° relative to premask display offset (mean enhancement [SE mean]: 40 [6] ms), and smallest at the 0° ISIs of 25 and 49 ms (18 [7] and 29 [5] ms, respectively). Pairwise comparisons of the enhancement effects using a least-significant-difference test (with $\alpha = 2.5\%$) revealed the difference between the 25- and 37-ms ISIs to be significant (whereas the effect at the 37-ms ISI was numerically greater than that at the 49-ms

ISI). Furthermore, as can be seen from Figure 5, the enhancement effects at the intermediate ISIs were graded in magnitude, with the enhancement/ISI function best described by a quadratic relationship, $F(4) = 6.8$, $p = .052$, $r^2 = .77$.

Although the expected 40-Hz phase modulation of the RT enhancement effect (i.e., maximal enhancements for the 180° conditions relative to the 0° conditions) was only significant on synchronous premask (target-present) trials, some additional modulatory influence appeared to be present on the random premask trials, specifically, at ISIs between 25 and 37 ms (see Figure 4). Based on the hypothesis of a global 40-Hz mechanism, periodic RT performance on both synchronous and random premask trials might be expected. Such results would reflect a more general phenomenon, such as the priming of motor-response mechanisms responsible for generation of the speeded target-present response (see Dehaene, 1993; Pöppel, 1968). However, the finding of a 40-Hz modulation on both types of trial would be inconsistent with the idea of Elliott and Müller (1998) that target coding is sensitive to the 40-Hz structure of activity across the premask coding mechanisms only when they contain a synchronous prime.

Error analysis. An omnibus ANOVA of the arcsine-transformed error data, with main terms of synchronicity, target, and ISI, revealed the synchronicity main effect, $F(1, 13) = 13.15$, $MSE = 0.02$, $p < .005$, and Synchronicity \times Target interaction, $F(1, 13) = 19.84$, $MSE = 0.05$, $p < .001$, to be significant. Synchronous-premask trials produced slightly less errors than random premask trials due to a reduced target miss rate for synchronous relative to

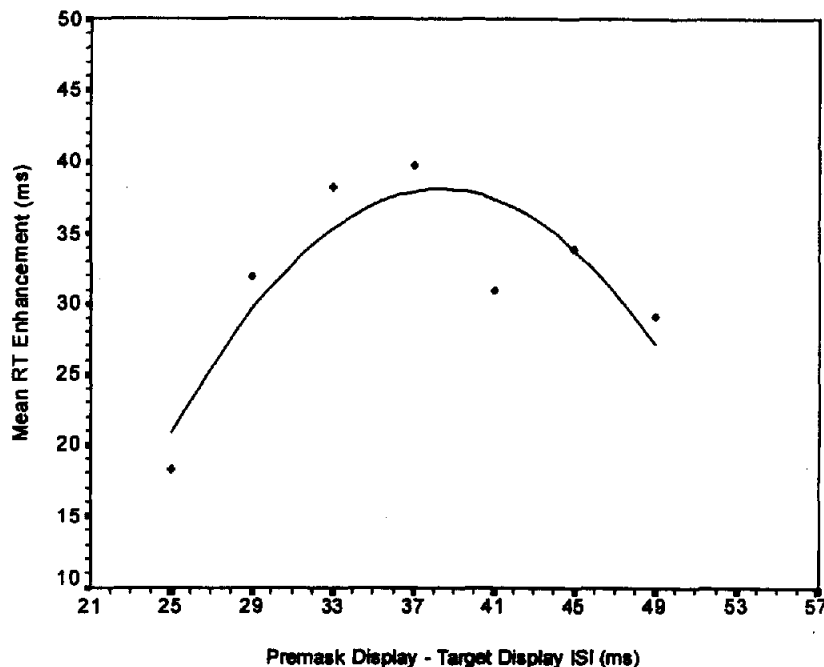


Figure 5. Mean target-present reaction time (RT) synchronicity enhancements (i.e., random RTs minus synchronous RTs) as a function of interstimulus interval (ISI) in Experiment 3. Also illustrated is the quadratic function that best fitted the RT enhancements.

random trials (3.9% vs. 1.6%), simple main effect, $F(1, 13) = 3.271$, $p < .1$, with no significant difference in false-alarm rates (2.6% vs. 1.9%), $F(1, 13) = .275$, *ns*. Taken together, the error data argue against the RT synchronicity effects obtained in Experiment 3 being confounded by speed-accuracy trade-offs.

In summary, in agreement with the results of Experiment 2, Experiment 3 demonstrated a periodic influence on the target-present synchronicity enhancements, which favored targets presented under 180°, relative to 0°, phase-angle conditions. However, the results of Experiment 3 also raise the question of the extent to which RT enhancements may be influenced by modulation of the random premask RTs. This issue was explored in Experiment 4.

Experiment 4

Both Experiments 2 and 3 showed that synchronicity enhancement effects were at maximum when targets were presented out of phase with the presentation frequency of the premask display, specifically, at an ISI corresponding to a phase angle of 180° relative to premask display offset. Furthermore, in Experiment 3, some additional periodic modulation of target-present RTs was also evident on random premask trials. This modulation is inconsistent with the idea that target RTs are sensitive to the 40-Hz structure of activity across the premask coding mechanism only when it contains a figurally relevant prime, and it would leave the possibility that the RT periodicity reflects some process other than the coding of the synchronous prime (e.g., motor-response preparation to the target). Accordingly, Experiment 4 was conducted to both replicate the main finding of maximum RT enhancement at 180° ISIs and provide an assessment of the extent to which this enhancement was due to periodic modulation of either the synchronous or both the synchronous and random premask RTs. Given that the modulatory pattern of random premask RTs in Experiment 3 appeared both weak (i.e., nonsignificant) and unrelated to the 180° phase position of the synchronous prime, it was expected that significant periodic RT effects would be confined to the synchronous premask RTs.

In Experiment 4, periodic effects were examined by varying premask target display ISI across the range 0 to 50 ms, in steps of 6 ms (or 2×6 ms). The resulting ISI values constituted three phase-angle conditions: 0° or in phase (0-, 25-, 50-ms ISIs), 90° or quarter phase (6-, 18-, 31-ms ISIs), and 180° or out of phase (12-, 37-ms ISIs).

Method

Observers. Fourteen observers, with normal or corrected-to-normal vision, participated in Experiment 4 (2 males, mean age 22.1 years).

Design and procedure. The design and procedure were as in Experiment 1, except that ISI was varied across the range of 0 to 50 ms (ISIs of 0, 6, 12, 18, 25, 31, 37, and 50 ms) to confirm the 40-Hz modulation of the RT enhancement effects revealed in Experiments 2 and 3.

In summary, Experiment 4 used a within-subjects design, with the factors synchronicity (synchronous, random), target (present,

absent), and ISI (0, 6, 12, 18, 25, 31, 37, 50 ms). ISI was kept constant within each 40-trial block, while the synchronicity and target factors were presented randomly within each block. Observers performed a total of 1,280 trials over two separate sessions of 640 trials each.

Results and Discussion

RT analysis. Extreme RTs (< 150 ms and > 1,500 ms) and RTs on trials on which a response error was made (1.9% of all trials) were removed from the data, prior to removal of RTs according to the 2.5 standard deviations criterion. Figure 6 presents the correct mean RTs (and associated SE mean) as a function of premask target display ISI, separately for each Target (present, absent) \times Synchronicity (synchronous, random premask) condition.

The RT data were collapsed across ISIs into their respective phase-angle conditions (0° condition: 0-, 25-, 50-ms ISIs; 90° condition: 6-, 18-, 31-ms ISIs; and 180° condition: 12-, 37-ms ISIs) and examined by means of an ANOVA with main terms of target (present, absent), synchronicity (synchronous, random premask), and phase angle (0°, 90°, 180°). Target-present RTs were significantly faster than target-absent RTs, $F(1, 13) = 23.88$, $MSE = 6,343.468$, $p < .0001$; mean RTs: 548 vs. 608 ms. Furthermore, RTs were overall faster on trials on which target displays were preceded by a synchronous rather than a random premask, $F(1, 13) = 86.18$, $MSE = 136.091$, $p < .0001$, although enhancements were evident only for target-present trials (mean enhancement [SE mean]: 34 [4] ms on target-present trials as compared with -1 [2] ms on target-absent trials), Synchronicity \times Target interaction, $F(1, 13) = 67.87$, $MSE = 208.01$, $p < .0001$. This pattern of target-conditional synchronicity enhancements is consistent with the previous experiments.

Importantly, the Target \times Synchronicity \times Phase Angle interaction was also significant, $F(2, 26) = 3.9$, $MSE = 88.223$, $p < .05$, providing evidence for phase-related differences in the magnitude of the synchronicity enhancement effects on target-present RTs. Follow-up analyses performed on target-present RTs only revealed that, although the synchronicity enhancements were significantly greater than zero at all ISIs (see Figure 6), they differed in magnitude according to the phase angle of target onset relative to premask display offset: They were largest at 180° phase-angle ISIs (mean enhancement [and SE mean]: 40 [4] ms), simple main effect, $F(1, 13) = 128.55$, $p < .0001$; intermediate with 90° ISIs (35 [5] ms), $F(1, 13) = 97.81$, $p < .0001$; and smallest with 0° ISIs (30 [5] ms), $F(1, 13) = 70.33$, $p < .0001$. This pattern is consistent with Experiments 2 and 3.

A further series of simple main effects (based on the error term of the significant three-way interaction) were calculated to examine whether these phase-angle-related differences in synchronicity enhancements were solely attributable to the synchronous premask RTs, rather than being attributable to both the synchronous and random premask RTs (as in Experiment 3). A significant difference was revealed between the synchronous 0° versus 180° phase-angle RTs, $F(1, 13) = 6.85$, $p < .025$, whereas there were no

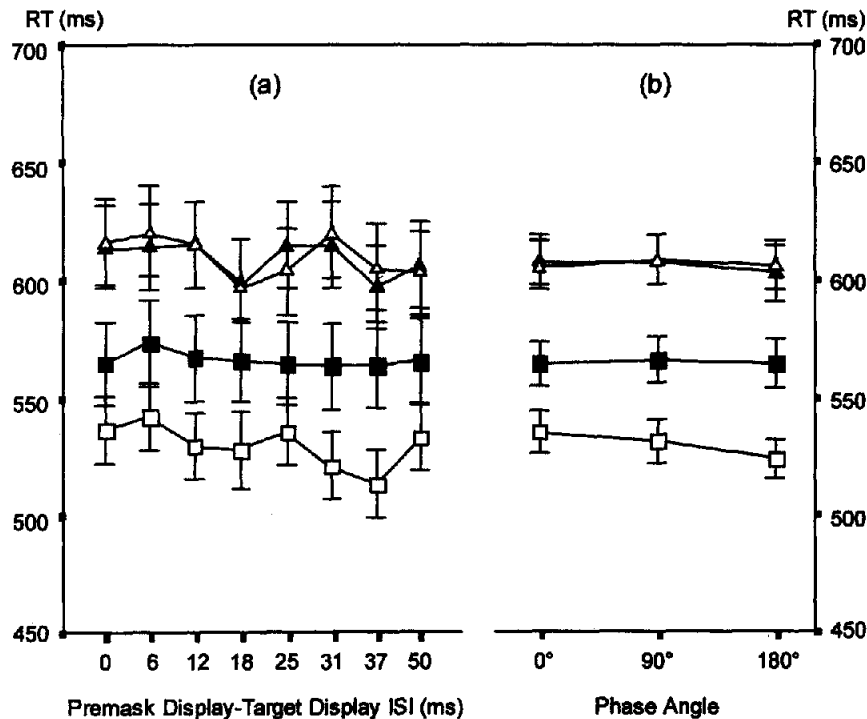


Figure 6. Mean correct target-present and target-absent reaction times (RTs), with standard-errors bars (in ms) for the synchronous and random conditions as a function of (a) premask-target interstimulus interval (ISI) and (b) phase angle in Experiment 6. The square and triangle symbols represent target-present and target-absent conditions, respectively, and the unfilled and filled symbols represent synchronous and random premask presentation conditions, respectively.

significant differences between the synchronous 0° versus 90° RTs and the synchronous 90° versus 180° RTs, $F(1, 13) = 0.36$ and $F(1, 13) = 0.391$, respectively. In contrast, no significant differences were obtained for any of the random trial comparisons, $F(1, 13) = 0.812$, 0.111 , and 0.322 , for the 0° versus 90° , 0° versus 180° , and 90° versus 180° phase-angle comparisons, respectively. Thus, the principal findings were of increased enhancements for targets presented under 180° phase-angle conditions relative to targets presented under 0° (and 90°) conditions, which were attributable to significantly faster RTs under synchronous, not random, premask conditions.

Error analysis. An omnibus ANOVA to the arcsine-transformed error data, with main terms of synchronicity, target, and ISI, revealed a significant synchronicity main effect, $F(1, 13) = 5.78$, $MSE = 0.02$, $p < .05$. The synchronicity main effect was due to a slight increase in error responses for random relative to synchronous trials (1.5% vs. 2.3% for synchronous and random trials, respectively). As with the previous experiments, the patterns of error data argue against the RT synchronicity effects obtained in Experiment 4 being confounded by speed-accuracy trade-offs.

General Discussion

Based on the idea that the prime acts as an oscillatory short-term memory that maintains information about the

figure-ground organization of the visual field for a brief period of time, Experiments 1 to 4 introduced ISIs between premask display and target display presentation in order to examine the duration and structure of the synchronous prime. Experiment 1 produced evidence that the synchronous prime decayed monotonically between ISIs of 0 and 150 to 200 ms. This is consistent with the idea of persistence as a decaying visual trace with a duration of approximately 240 to 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 $100 \text{ ms} + 150 \text{ to } 200 \text{ ms}$). Thus, the duration of the synchronous prime is equivalent to that of visible persistence (Coltheart, 1980), despite the fact that observers are unable to detect the presence of the synchronous premask frame within the premask display.

This long persistence estimate is consistent with Elliott and Müller's (1998) figure-ground segmentation account for synchronicity priming, according to which the synchronous prime is coded within the context of the (visible) premask display as a whole. However, it raised the question of how the synchronous prime becomes independent of persistence across the remaining premask display elements. One possibility, considered in the introduction, was that the synchronous prime becomes temporally segmented from activity across the remaining premask display elements. Experi-

ments 2 to 4 were designed to examine two hypotheses related to the notion that the pattern of synchronous prime activity would become uniquely coded within a specific phase of the 40-Hz activity generated by premask display presentation. The first hypothesis was that the synchronous prime possessed an oscillatory structure matching that of the 40-Hz premask display. This hypothesis was based on the idea that if the synchronous prime inherited persistence properties from the premask display as a whole, it should also adopt the (40-Hz) temporal structure of the premask display. Based on theoretical accounts of oscillatory memory formation, the magnitude of synchronicity enhancements was expected to be differentially influenced by ISIs that corresponded to a particular phase angle of the 40-Hz premask display rhythm. Further, based on the phase characteristics of the 40-Hz response revealed within the EEG, it was expected that RT enhancements would be at maximum with ISIs corresponding to a 0° phase angle of target display presentation relative to the rhythm of premask display presentation. Experiment 2 employed alternating 0° and 180° phase angle ISIs within the 0- to 137-ms range. Although the results revealed RT enhancements for all (0° and 180° phase angle) ISIs, there was indeed a significant phase-angle effect. However, unexpectedly, enhancements were greater for targets presented at ISIs corresponding to a phase angle of 180° compared to 0° ISIs.

Experiment 3 sought to replicate the maximum 180° enhancement effect of Experiment 2 within a single cycle of the synchronous prime, employing ISIs across the range 25 ms (0° phase angle) to 49 ms (\approx 0°), including an ISI of 37 ms (\approx 180°). Consistent with the results of Experiment 2, synchronicity enhancement effects were at maximum for the 37-ms ISI (180°), relative to all other ISIs, 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, Experiment 3 provided additional support for the idea that the synchronous prime persistence was maintained within an oscillatory structure that was shifted by 180° relative to the rhythm established by premask display presentation. However, Experiment 3 also suggested some evidence for periodicities within the random premask RTs, which introduced the possibility that the periodic RTs measured in Experiments 2 and 3 may have represented a more general oscillatory phenomenon (e.g., priming of motor mechanisms or decision processes responsible for generation of the target-present RT response). As a result, Experiment 4 reexamined whether the periodic RT enhancements were solely due to modulation of the synchronous premask RTs or to combined modulation of both the synchronous and the random premask RTs. Consistent with both Experiments 2 and 3, Experiment 4 revealed synchronicity effects at all ISIs, with significant enhancements for ISIs corresponding to phase angles of 180° relative to 0° ISIs. Importantly, the modulatory pattern obtained in Experiment 4 was confined to the synchronous premask RTs, with no periodicity evident for the random premask RTs. Thus, the results of Experiment 4 offer strong support for the hypothesis that the priming effects under investigation

represent the operation of an oscillatory figure-coding mechanism that becomes engaged by synchronous premask presentation, but that these effects are not due to activity across other more general mechanisms related to stimulus encoding or response generation.

Taken together, the results of Experiments 1 to 4 demonstrate two related properties of the synchronous prime: The prime inherits both persistence consistent with that of the premask display as a whole and, importantly, a 40-Hz structure consistent with the overall frequency of premask frame presentations. Nevertheless, observers do not detect the synchronous premask that generates the prime, although the premask display is fully visible. In addition, priming effects exhibit spatial specificity, that is, they are confined to targets presented at the location of the synchronous premask (Elliott & Müller, 1998, Experiments 2 and 3), suggesting that the synchronous prime becomes segmented from activity across the remaining premask frames. This pattern of results raises a number of issues concerning the generation and structure of the synchronous prime, which will be addressed in the subsequent sections. One question concerns the likely (cortical) mechanisms involved in the generation and subsequent maintenance of the 40-Hz prime. A second, related question concerns how priming effects become phase shifted relative to the regular rhythm of premask frame presentation. Issues related to these questions, which are also addressed later, include the spatial specificity of the priming effects and the mechanism by which 40-Hz prime arises with the repeat cycle of the synchronous premask set at 10 Hz.

Premask Display Coding and Synchronous Prime Persistence

Although observers were unable to detect the presence of the synchronous premask frame, the duration of 40-Hz synchronous prime persistence corresponds well with the upper boundary for visible persistence (Experiment 1). This finding is not surprising, given that each frame is fully visible in the context of the display as a whole. However, the duration of prime persistence implies that there is a common mechanism involved both in generating the synchronous prime and in producing explicit perception of the premask display as a whole. This raises the question as to the locus of the mechanism that is capable of rendering visible the premask display, while simultaneously generating a nondetectable synchronous prime.

Given that stimuli that can persist for 240 to 300 ms are characteristically visible, their persistence has been regarded as a central, or cortical, phenomenon (see Coltheart, 1980). Because early visual cortex (V1) is not considered to directly generate the visual experience of a stimulus (e.g., Crick & Koch, 1995, 1998; He, Cavanagh, & Intriligator, 1996), visible persistence is likely generated in areas later than V1. Applied to the present stimuli, this implies that the premask display is coded at some stage later than V1, in extrastriate or higher visuocortical areas, or both. Possible candidate areas include V4 and IT (inferotemporal) cortex. Both V4 and IT are in the ventral-processing stream

responsible for object coding and recognition (Ungerleider & Mishkin, 1982). Furthermore, neurons in V4 and IT have receptive fields wide enough to code across the maximum angular separations between adjacent premask display elements (i.e., $2^{\circ}39'$; see Moran & Desimone, 1985), so that the response of a single neuron in V4 or IT would be minimally sufficient to account for the presence of two or more elements within a given premask frame. At the most oblique angles, a given premask display frame might also include elements at separations of up to $8^{\circ}42'$. An 8° to 9° angular separation is beyond the spatial resolution of V4 neurons, but not of neurons in IT. Thus, the entire premask display may be coded across the receptive field of a single neuron (or a set of neurons) located in IT. Given that IT neurons are capable of firing frequencies in excess of 40 Hz (e.g., Chelazzi, Miller, Duncan, & Desimone, 1993; Fuster & Jervey, 1982), it is unlikely that the nondetectability of the individual premask display frames is due to a loss of temporal resolution during the coding of the entire display.

There remain two other possible (and mutually compatible) accounts for the loss of temporal resolution during premask display coding. According to the first, detection of the individual premask frames is precluded by a loss of temporal resolution within the mechanisms that enter into "consciousness" the premask display information coded in IT. This account is based on evidence that the mechanisms rendering conscious experience do so periodically, or following delays of between 100 and 200 ms, or both, from stimulus onset (e.g., consistent with the claims of Efron, 1970a; see also Harter, 1967; Velmans, 1991, for reviews). Thus, even at the best temporal resolution of such a system, all four premask frames would be integrated into a single composite perception of the whole premask display matrix by the time conscious experience of the premask display becomes available.

According to the second account, the 40-Hz structure of the premask display induces the IT neuron to oscillate at 40 Hz. However, because the individual premask frames follow each other at delays of ≈ 0 ms, the response of the IT neuron to any particular frame would become integrated with its response to both preceding and subsequent frames. In this way, the IT neuron would maintain an average response above the threshold for detection of the premask display (the average would reflect the contrast between the premask frames and the background field), with the average sustained response characterized by a relatively low amplitude 40-Hz modulation. Although the 40-Hz modulation of the IT neuron is maintained by premask display presentation, the minima of this modulation would never descend below the sensory threshold and thereby permit the spatiotemporal structure of the premask display to be detected. In fact, the phenomenological effects of this modulation would be the perception of a stochastic surface flicker on an otherwise static display of nine crosses, which is precisely what observers report. Whichever account is appropriate, the mechanisms concerned are not top-down penetrable. This finding is supported by Elliott and Müller's (1998) Experiment 2 in which observers were aware that the synchronous premask frame might appear on any given trial, but they

were still unable to detect it with greater than chance accuracy.

The Structure of the Synchronous Prime

According to the account of premask display coding outlined earlier, the synchronous prime is unlikely to be generated and then maintained as undetectable later than in areas such as IT. Nevertheless, both the persistence properties (revealed in Experiment 1) and temporal structure of the synchronous prime are inherited from the activation of neuron(s) capable of coding the premask display as a whole. In other words, the long persistence and the 40-Hz activity of the synchronous prime may be supported by the same mechanism responsible for coding the whole premask display, without observers ever becoming aware of the existence of the synchronous premask.

However, a problem with this account arises when it is considered that synchronicity priming effects were only obtained when the target was presented at the same location as the synchronous premask frame, but not when the target was "mislocated" relative to the synchronous premask frame within the 3×3 display matrix. This spatial specificity of synchronicity priming argues against an exclusive account of priming in IT. Although IT neurons are involved in object-based priming (e.g., Chelazzi et al., 1993), the effects observed in IT do not depend on a precise spatial matching of prime to target presentation locations. Instead, the spatial specificity of synchronicity priming suggests that the synchronous prime becomes principally active across contributive neurons in earlier stages of visual processing, such as V1 or V4, or both, where neurons, due to their receptive field dimensions, code only the smaller regions of visual space occupied by premask frame subsets, but not the entire premask display.

This raises the question of how earlier premask coding processes adopt the persistence and 40-Hz code generated by a later structure and how they then develop specific patterns of spatiotemporal activity. A plausible solution is that the activation and 40-Hz code generated by premask display presentation must be backpropagated from the IT neuron concerned to contributive neurons in earlier stages such as V1 or V4, or both. Backpropagation would modulate, at 40 Hz, the firing patterns of visuocortical neurons responding to the local 10-Hz presentation of premask display frames, which would then signal the combination of 10- and 40-Hz activity back to the IT neuron. In this way, a network of activity would develop characterized (in part) by a 40-Hz rhythm established in IT. However, by itself, the backpropagation of a 40-Hz response does not explain how the local patterns of 40-Hz activity become phase independent of one another. This requirement is important, because, if all local patterns of activity (representing the four premask frames) were in phase with one another, completely equivalent RTs should be obtained for target presentation anywhere in the display matrix, irrespective of the location, or presence, of the synchronous premask.

Instead, local asynchronies in the phase structure of the global 40-Hz response could arise from the convergence of

the backpropagated 40-Hz activity with the subsequent, local responses to 10-Hz premask frame presentations in early visual processing areas such as V1 or V4. This may be achieved if the internal network of cycling 40-Hz activity is shunted by the arrival of local bottom-up 10-Hz signals that are both spatially specific and delivered with different latencies to different sets of local mechanisms. The idea of shunting may be conceived as a modulation of the timing of the 40-Hz activity, arising due to differences in the amplitude or the overall form of the 10-Hz response relative to that at 40 Hz. The outcome of a series of integrations of this type would be successive shifts in the latency of the periods within each local 40-Hz rhythm relative to those within other localized 40-Hz rhythms. In this way, the relative phases of the local 40-Hz activity become continually adjusted by the 10-Hz rhythm of premask frame presentation.

The idea that the 10-Hz bottom-up modulation has a shunting effect on the local pattern of 40-Hz prime activity, rather than amplifying it, is supported by the pattern of results obtained in Experiment 2. In Experiment 2, no particular pattern of RT enhancements was obtained for those ISIs corresponding to the onset time of the synchronous premask in the premask display sequence (i.e., at the 0- and 100-ms ISIs) relative to ISIs corresponding to the onset times of other (nonsynchronous) frames in the premask display. In addition, in Experiment 4, a 40-Hz RT modulation was also obtained for ISIs that corresponded to regular repeats of nonsynchronous-premask frames, demonstrating that the repeat cycle of the synchronous premask frame is not critical for generating the modulation. Such effects would not have been expected if the bottom-up 10-Hz activity simply amplified the induced 40-Hz activity at regular intervals, in a fashion akin to Lisman and Idiart's (1995) idea of component 40-Hz oscillations that become nested within a slower 10-Hz oscillation. Nevertheless, the extent to which the phase patterning of the 40-Hz activity depends upon the 10-Hz repeat of the premask frames is a matter of speculation. It seems likely, though, that in a system with continuous feed-forward and feed-back, this pattern would arise as a result of complex and temporally evolving interactions between the global (IT-level) and spatially specific (lower level) patterns of activity. These issues remain topics for further research.

The idea that the different premask display subsets become coded at different phases of the global 40-Hz rhythm is entirely consistent with an earlier mentioned proposal, that different attributes of a single object may be encoded within different phases of a single oscillation (e.g., Hummel & Biederman, 1992; Hummel & Holyoak, 1997; Shastri & Ajjanagadde, 1993). In the present case, the single object would be the premask display as a whole, and the pattern of correspondence between the different elements of a single premask-display subset would be within a given phase, but with an absence of phase correspondence between the elements of different subsets. However, on its own, phase shifting of the 40-Hz prime activity does not explain why the RT enhancements were significantly greater for targets presented at 180° relative to premask display

frame onsets than for targets presented at 0°. To explain this effect, one would need to consider how target-generated activity might integrate with the 40-Hz modulated response of the prime. 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; conversely, the intensity of a target might be relatively high during the negative lobe. The relatively high intensity of the target during the negative lobe of the prime would improve the saliency of the target, yielding faster RTs. This is entirely consistent with the results of Experiments 2 to 4 (Vincent DiLollo, personal communication, March 15, 1999) and also consistent with the original hypothesis, that the phase angle of the prime is at 0° relative to the rhythm of premask display presentation.

Conclusion

In summary, the results of Experiments 1–4 are consistent with previously reported findings (Elliott & Müller, 1998) but present a new perspective on synchronicity priming. According to this perspective, the synchronous prime represents a pattern of 40-Hz activity that extends across cortical regions: The prime is generated relatively late in the visual processing stream, but becomes active within earlier mechanisms through backpropagation of a global pattern of 40-Hz activity. It is suggested that the 40-Hz activity develops through integration of a cascade of 10-Hz signals by neurons with receptive-field dimensions such as those of cells within IT. These ideas are supported by the present finding that repeated premask presentation leads to the formation of short-term visual persistence that outlasts synchronous-premask presentation by up to 240 to 300 ms, a period of time consistent with a visible stimulus, despite the fact that the synchronous premask is not detected by observers.

The prime exhibits a phase specificity, which could arise through the backpropagation of induced 40-Hz activity, converging at an earlier stage of visual coding (i.e., V1 or V4, or both) with the bottom-up generated response to the repeat of the premask frames at 10 Hz. The precise relationship between the 40-Hz code across the prime and the 10-Hz structure of the premask frames remains an issue for further study. One particular question to be investigated concerns whether premask frame presentation at 10-Hz is critical for generating and maintaining a stimulus-specific 40-Hz coding mechanism. Importantly, though, the proposed phase specificity of the prime supports previous theoretical work, which has suggested that one mechanism for short-term (and long-term) memory storage is within separate phases across a global processing rhythm.

Taken together, the findings support the idea that 40-Hz priming enhances the detection of a subsequent Kanizsa-type square through figure-ground segmentation according to the Gestalt organization of the visual field (Engel et al., 1991; Gray et al., 1989; von der Malsburg, 1981) and that figure-ground information is maintained as a very brief visual memory that persists in the form of an oscillatory

pattern of neural activity. Finally, these findings were revealed in human observers by means of RT measurements, which confirms that specific gamma-band coding mechanisms are directly available for psychophysical examination.

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