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Author(s)	Elliott, Mark
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Effects of stimulus synchrony on mechanisms of perceptual organization

Mark A. Elliott and Hermann J. Müller

Institut für Allgemeine Psychologie, Universität Leipzig, Germany

When neurons adopt a synchronized, oscillatory response to stimulus Gestalten, the phase of those oscillations almost always varies relative to stimulus activity. This has been taken to indicate that form-coding mechanisms are synchronized by internal timing mechanisms, and/or may be sensitive to stimulus activity only via motion detectors. This proposal is problematic for interpreting recent demonstrations of the effects of stimulus synchrony particularly when stimuli are stationary. Here we offer an account of stimulus-driven synchronization supported by evidence that segmentation by stimulus synchrony can be relatively insensitive to explicit motion signals. The argument is made that qualitative similarities between the effects of phase-independent and phase-locked oscillations in the EEG, the effects of phase synchronization at the cellular level and evidence for phase-enhanced stimulus grouping should be considered as functionally equivalent. This argument emphasizes the flexibility of temporal synchrony as a code for perceptual organization.

Visual objects or object groupings may be considered as composites of separable attributes or "features" describing the length, spatial frequency, orientation, colour, motion, etc. of their constituent elements. In order for an object to be perceived, its component features must be "bound" together to form a unified stimulus representation. A candidate process by which feature attributes may become bound is the phase synchronization of neural discharges across the separate mechanisms coding different attributes of the same visual stimulus (e.g., the "temporal-binding" hypothesis of Crick & Koch, 1990; see also

Eckhorn et al., 1988; Gray, König, Engel, & Singer, 1989). Evidence in support of this idea has been provided by physiological studies of phase synchronization in the primary visual cortex (areas 17 and 18) in anaesthetized cat and monkey (see Eckhorn et al., 1988; Engel, König, Kreiter, & Singer, 1991; Gray et al., 1989; Kreiter & Singer, 1992). When visuo-cortical cells with adjacent (but non-overlapping) receptive fields were stimulated by separate bars of light moving in opposite directions, oscillatory neural activity showed low cross-correlation. However, when the bars were passed across the receptive fields in the same direction, a correlative relationship was observed between oscillatory activity within the 20–80-Hz (approximately the gamma) bandwidth. The strongest cross-correlations were obtained when a single, connected, bar stimulated the cells. Thus, cross-correlated neuronal firing was manifest only when cells responded to separate elements of the same "Gestalt" (findings consistent with the temporal correlation hypothesis of von der Malsburg, 1981). These observations have given rise to the idea that oscillatory neural activity and the consequent synchronization of firing patterns represent one important neurophysiological correlate of the "binding" of stimulus feature elements. Occurrences of oscillatory synchronization are not regularly phase-locked to temporal stimulus modulation, that is, even though phase locking can occur, oscillatory synchronization may not be strictly dependent upon the timing of stimulus events. These findings have been taken as evidence for the internal generation of synchrony in primary visual cortex, possibly mediated by mechanisms in higher motion-sensitive areas (Singer, 1996; Singer & Gray, 1995).

These studies have raised a number of important issues concerning the relationship between neural synchronization and perceptual organization. One issue of particular importance is whether or not neural synchronization can be generalized to the coding of "stationary" groupings (i.e., groupings that are regularly presented at the *same place* in visual space). We will review evidence from experimental psychophysics and electroencephalographic (EEG) studies that support this generalization. Some studies have shown that the perceptual organization of stationary forms can be enhanced by rapid, repeated, and synchronized stimulus presentations (Elliott & Müller, 1998; Fahle, 1993; Usher & Donnelly, 1998). This raises the related issue of the extent to which neural synchrony in form-coding mechanisms is *dependent* upon support from motion-sensitive mechanisms coding rapid transient activity in the stimulus. More generally, should synchronization of form-coding mechanisms be considered exclusively in terms of third-party synchronization (e.g., modulated directly or indirectly by motion-sensitive mechanisms)? If not (and we shall argue against the exclusivity of this hypothesis), what assumptions are required in order to account for the various demonstrations of synchronization within a single explanatory framework?

THE EFFECTS OF SYNCHRONIZATION BY TEMPORALLY-MODULATED STATIONARY STIMULUS PRESENTATION

Experimental psychophysics has approached grouping by synchronization from the position that, when two or more stimulus events occur at the same time relative to other stimulus events (i.e., when they are specific to a single phase of multi-phase stimulus activity), the stimuli will be bound together due to common phase angle (Elliott & Müller, 1998; Fahle, 1993; Leonards, Singer, & Fahle, 1996; Usher & Donnelly, 1998) or temporal correlation (Alais, Blake, & Lee, 1998; Lee & Blake, 1999). Underlying this idea is the notion that, when phase-aligned stimuli group according to one or another Gestalt principle, the effects of phase alignment will modulate the temporal structure of neural mechanisms coding the group's elements, making them fire in synchrony. By this logic, the behavioural effects of stimulus synchronization (and its inferred effects upon neural synchronization) could range from the enhancement of groupings that would also be formed in the absence of temporal stimulus modulation, to the induction of groupings that would not be perceived otherwise (henceforth referred to as "enhanced" and "induced" groupings, respectively). Of course, if the individual stimulus events were clearly discernible, the effects of simultaneity would be trivial. Consequently, the to-be-grouped and non-grouping stimuli are presented at phase angles of a common presentation frequency, below the threshold for discriminating their temporal and/or spatial structure (Elliott & Müller, 1998; Parton, Donnelly, & Usher, this issue; Usher & Donnelly, 1998).

The paradigms of Elliott and Müller, Fahle, Leonards et al., and Usher and Donnelly have used stationary stimulus displays consisting of spatial configurations partly or entirely defined by temporal phase relative to background or distractor items. The various findings produced with these paradigms broadly support the idea that stimulus synchronization does influence grouping. The basic paradigm consists of displays composed of subsets of stimulus elements that differ in their presentation phase, with the result that, for certain temporal asynchronies and/or phase angles, either the perceptual saliency of a target subset was enhanced (Fahle; Leonards et al.) or a critical subset primed the detection of a subsequently presented target Gestalt (Elliott & Müller); or observers, presented with lattice displays of potentially bistable (row or column) organization, reported the organization supported by synchronized element presentation (Usher & Donnelly). Although all these studies appeal to synchronizing neural mechanisms to explain their results, the various accounts tend to diverge concerning the functional requirement for the grouping mechanism to respond *directly* to stimulus synchrony. Specifically, there is disagreement as to the extent to which the phase synchrony of repeated stimulus presentations is responsible for generating a matching pattern of phase synchrony in responding

neural mechanisms. The basis for disagreement lies in the findings mentioned earlier that, when neurons synchronize with an oscillatory pattern to stimulus activity, the phase of the oscillation varies relative to that of stimulus events.

One possibility examined by Leonards et al. (1996) was that the visual system may operate in different, but interacting modes when segmenting temporal and texture cues. In Leonards et al's study, the observers were presented with a matrix of 7×7 equally spaced line segments. This matrix contained vertically or horizontally oriented subsets of 3×5 or, respectively, 5×3 target line elements ("rectangle"), distinguished from the background elements by either textural or temporal cues or both. Observers had to discriminate the orientation of the target rectangle. There were five experimental conditions: (1) single target rectangle composed of elements that differed slightly in orientation from background elements (textural cues only); (2) single target rectangle with elements presented in frame alternating with frame of background elements (temporal cues only); (3) single target rectangle composed of elements that differed from background elements in both orientation and presentation frame (combined textural and temporal cues); (4) two "superimposed" rectangles, one defined by temporal offset and the other by orientation relative to the background elements; (5) target elements differing from background elements in orientation, but displayed in alternating frames each presenting random constellations of half the target and half the background elements. The results showed that the rectangle could be segregated from the background on the basis of temporal cues alone (given a temporal offset between the target and background elements >10 ms) and textural cues alone, but that figure–ground segregation was enhanced when both types of cue defined the target. When there was competition between the two types of cue, only the more salient figure was reported. Finally, the detection of a figure defined by textural cues was not affected by potentially conflicting temporal cues if these did not themselves define a figure.

Leonards et al. proposed that grouping may be based on two separate systems, the outputs of which might combine in a synergistic fashion[1] the motion-

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[1]It is not clear from the psychophysical (% correct) data of Leonards et al. (1996) exactly how the motion and form-based systems interact. Theoretically, both systems could determine the required orientation discrimination separately (assuming that the motion system has independent form representation capability), and there could be a parallel race between both systems to determine the discrimination, without any facultative ("synergistic") interaction between the two systems. Such a parallel race model could equally explain (a) why discrimination performance is superior when both temporal and textural cues are available (because the likelihood that at least one system produces the correct response within the limited exposure time available is increased), (b) why the more salient cues are dominating performance (because these permit orientation to be derived faster), and (c) why texturally-based discrimination is not interfered with by temporal cues that do not themselves define an oriented target form (because the motion-based response does then not conflict with the form-based discrimination). RT methodology designed to test the "race model inequality" (Miller, 1982) is more suited to distinguish between parallel-race and coactivation models.

sensitive system (system A) that processes temporal cues, and the form-based system (system B) that processes textural cues. System A "signal[s] with great precision on- and offset of stimuli, so that the timing of external events is precisely reflected by the time course of neuronal responses. This system could then exploit the synchronicity of responses to simultaneous visual events for binding". In contrast, system B "must allow texture cues to override conflicting temporal cues and should thus be rather insensitive to the temporal structure of stimuli. . . . [system B] responses . . . should be sufficiently sustained to bridge brief temporal interruptions of visual stimuli. . . . the responses to texturally related figure elements conveyed by system B [may] become synchronized and bound together by intracortical interactions and [. . .] *independently of the temporal structure of external stimuli*" (Leonards et al., 1996, p. 2696, emphasis added). Thus, critically, stimulus phase was argued to be neither necessary nor sufficient for neural synchronization to occur in form-based system B. That correlated spatiotemporal changes alone are effective for *motion-based* grouping has recently been demonstrated by Alais et al. (1998; see also Lee & Blake, 1999), who investigated the computation of global motion in a unique direction from local oscillating gratings viewed briefly through four discontinuous, non-overlapping, apertures (arranged in the form of a square). Global motion direction was most reliably derived when the contrast modulations of the four gratings changed in an identical fashion over time (i.e., when they were correlated). Alais et al. restated the "temporal correlation hypothesis" to explain their findings, specifically that "local visual features that vary together over time tend to be grouped together over space" (p. 162)—by synchronization of neural responses to those features, giving rise to the perception of global moving form based "solely" upon correlated (explicit) motion signals. However, as noted by Gegenfurtner (1998), "motion perception is—in the end—nothing but the determination of the spatiotemporal correlational structure of the stimulus. It should therefore not come as a surprise that synchronized contrast changes have a major effect on such correlations" (p. 98).

At issue however, is the extent to which explanations in terms of correlated motion signals might account for synchrony enhanced, or induced *stationary* figure grouping. Usher and Donnelly (1998, p. 179) questioned the idea that the motion-sensitive system is uniquely responsible for mediating the effects of stimulus synchrony. They argued that the orientation discrimination required in the task of Leonards et al. (1996) could be performed "on the basis of local gradients at texture boundaries . . . gradient computations at boundaries [may] generate a (possibly implicit) motion signal that partially mediates the effect". In their own study, Usher and Donnelly attempted to eliminate the potential influence of any such signals, to "demonstrate the existence of a grouping mechanism that is independent of the computation of motion (even if only implicit)" (p. 179). To achieve this, they presented a display matrix composed of identical and equally spaced elements, filled circles, with display frames of

alternate rows or, respectively, columns of elements presented successively and repeatedly. The use of identical elements removed the potential for synchrony to be conveyed by implicit motion signals generated at texture boundaries (by orientation displacements of a subset of display elements). In addition, the temporal asynchrony between successive display frames was subthreshold, giving rise to the perception of a "static" matrix with no noticeable motion or flicker. Nevertheless, repeated synchronized presentation of display elements within alternate rows or columns was found to bias observer's reports of the orientation of groupings within the matrix (as rows or columns), without the presentations being experienced in terms of motion. These results would appear to question the proposal of Leonards et al.: How can stimulus-related phase synchronization determine grouping if (1) the motion system (system A) is not engaged by stimulus presentation and (2) grouping within the form system (system B) is unrelated to the regular phase of oscillatory stimulus activity?

Despite the precautions taken by Usher and Donnelly, the possibility remains that their results may still be attributable to motion-sensitive mechanisms engaged by the repeated on- and offsets of the row or, respectively, column stimuli (Gegenfurtner, personal communication). Consistent with this, there is evidence for limited Gestalt representation by the motion system (e.g., Logothetis & Schall, 1989; Yantis, 1992), which, in Yantis' study, was based upon the finding that visual attention was preferentially deployed to sudden-onset stimuli if these formed regular polygons. This would suggest that the deployment of visual attention is important for form to be derived from motion cues (e.g., because visual attention is preferentially allocated in Gestalt configurations).

However, there are several qualifications to this line of argument. Elliott and Müller (1998) found no evidence that localized flickering stimuli summoned visual attention in their paradigm, arguing that the mechanisms involved in Yantis' paradigm are not invoked by all kinds of temporally modulated stimulation, in particular; not by the subthreshold phase modulation of stationary stimulus presentation used in the paradigms of Usher and Donnelly (1998) (and Elliott & Müller, 1998), which rendered the various asynchronized spatial structures within their display matrices non-detectable (i.e., all stimuli were always fully visible within the context of temporally contiguous display matrices). The flickering stimulation used in these paradigms probably generates multiple successive temporal-impulse responses. The partial integration of each response with preceding and subsequent responses would reduce the relative amplitude of any single response. As a result, no single stimulus presentation would generate a response with sufficient relative amplitude to uniquely signal its presence within the flickering display matrices. In other words, unlike

a single sudden stimulus onset, an individual stimulus onset within a train of repeated presentations would have insufficient strength to engage the visual attention system (see Elliott & Müller, 2000, for a more detailed development of this argument).

IS PRIMING BY STIMULUS SYNCHRONY
## DEPENDENT UPON LOCAL MOTION SIGNALS?

Considering all the evidence reviewed thus far, the necessity for facultative interactions between the motion and form systems during stimulus-driven synchrony generation is not generally supported. Instead, synchronized stimulus presentation influences perceptual organization in the absence of implicit or explicit motion cues, and without local transient signals acting in the same fashion as sudden-onset cues. However, these objections simply restate the fundamental question to be answered: How transient signals, although substantially weakened by the relative reduction in response amplitudes following rapid sequential stimulus presentation, become an effective means for synchronization in form coding mechanisms? We considered this question from two alternative perspectives: Either the motion system may not exclusively code stimulus synchrony, or stimulus synchrony is indeed coded as a result of responses within the motion system (despite an absence of implicit or explicit motion signals), though with little or no influence upon mechanisms responsible for the deployment of visual attention. Under these circumstances, the effects of neural synchronization for form coding may be a subtle outcome of coincident neural responses to repeated transient stimuli, which may become available for measurement only under very specific stimulus presentation conditions.

According to the proposals of Leonards et al. (1996), the form-coding system (B) is not capable of responding with the level of temporal precision, and at the temporal frequencies, required for temporal synchrony to be effective. However, this proposal may not be entirely accurate: The local presentation rates at which synchrony priming effects were obtained by Elliott and Müller (1998, 2000) are well within the temporal resolutions of form-coding mechanisms: Elliott and Müller presented premask display matrices (3 × 3 crosses) composed of four "local" asynchronized subset frames each presented at 10 Hz, for a given presentation time. In Elliott and Müller's paradigm the flickering premask display was followed by a static target display matrix (3 × 3 90°-corner junctions) that could contain an illusory (Kanizsa-type) target square

(a)
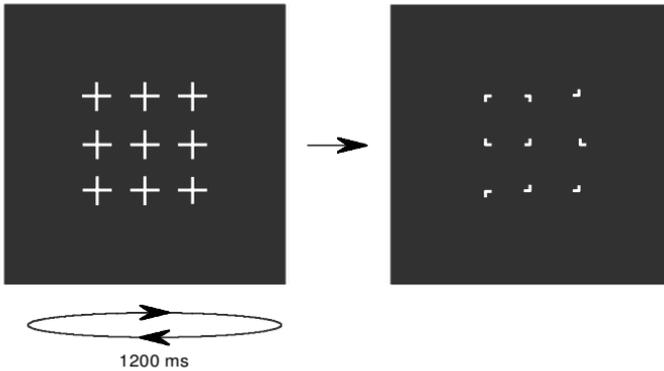
(b)
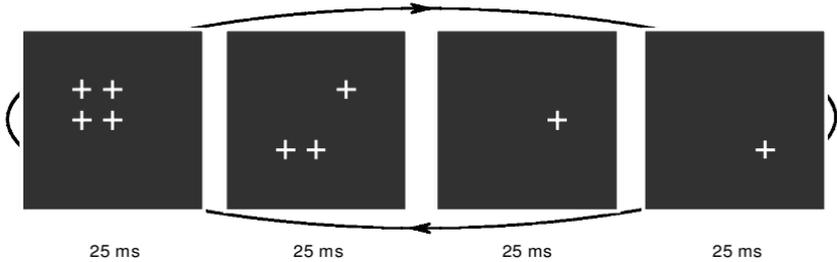
Figure 1. **(a)** Stimuli consisted of a flickering display of nine crosses illustrated on the left-hand side of the figure, followed by the presentation of a target display (right-hand illustration), to which the observers produced their target-present/absent RT response. This illustration shows premask-inducer and target-inducer specifications that are 60% and 20% respectively. In **(b)** an example sequence of the four separate premask-subset frames in the synchronous condition is illustrated (in which the first frame consists 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 1000 ms, with constant subset exposure duration of 25 ms and < 1ms inter-subset interval. In this way the premask sequence was continually "recycled" during premask presentation.

comprised of grouping corner junctions to be detected amongst the non-grouping distractor junctions (see Figure 1). In one condition, termed the "synchronous-premask" condition, the premask display contained a frame of four crosses in square arrangement presented at the location where the target figure appeared subsequently on target-present trials. This condition was compared to a "random-premask" condition in which the four premask crosses preceding the target figure were distributed across the four separate display frames. The basic finding was a "synchrony priming" effect, such that detection of a target square was expedited when it was presented at the same location as the four premask crosses in the synchronous-premask condition, relative to the random

condition.[2] By using a premask display comprised of four different frames each repeating at 10 Hz, Elliott and Müller (1998) found that synchrony priming was specific to conditions under which the *global* rate of premask presentations across the whole display matrix was set at 40 Hz. Elliott and Müller (2000) also found that the prime adopted a 40-Hz structure consistent with the global presentation frequency of the premask frame presentations. Elliott and Müller's proposal that the oscillating prime adopts the precise phase of stimulus presentation has received support from the examination of the matching frequency of neural activity in the EEG (Elliott, Herrmann, Mecklinger, & Müller, 2000). Using the basic paradigm of Elliott and Müller, Elliott et al. recorded a specific pattern of neural activity under priming conditions at the exact frequency and, importantly, locked to the phase of stimulus presentation only at electrodes overlying right posterior cortex (i.e., O2 and T6) which correlated well with more anterior cortical loci (i.e., P3 and T4).

Although little evidence was found by Elliott et al. (2000) to support the idea that priming is generated as a direct response to the local premask-frame repetitions at 10 Hz, generation of the 40-Hz prime is nevertheless related to the presentation of local 10 Hz signals, which could be coded within either magnocellular or parvocellular pathways or both (Lennie, Trevarthan, van Essen, & Wässle, 1990). This means that either, or both the motion and form-coding systems became induced locally by the temporal stimulus modulation. Elliott and Müller (2000) suggested that early mechanisms in the form system might be the principal location for the generation and maintenance of the "synchronous prime". However, there is no a priori reason to suppose that the motion system was not also involved, particularly given the stimulus-locked EEG responses at electrodes over motion sensitive areas (P3 and T6). This raises the question whether the prime becomes (also) active in motion-coding mechanisms. If so, it should be possible to isolate such motion-based effects by varying the structural integrity of the priming (premask) and target stimuli, with the aim of producing synergistic interactions between the form and motion-coding systems along the lines postulated by Leonards et al. (1996). This question was examined in a single experiment described next.

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[2]The effects of prime synchrony, expedited target detection reaction times (RTs) following synchronized premask presentation, were confined to target-present trials and obtained only when the global frequency of premask presentations was set to 40 Hz. The priming stimuli were non-detectable within the total premask display matrix. Furthermore, the priming effects were spatially specific: Target detection was expedited only when targets were presented in the same matrix location previously occupied by the synchronous premask (while there were neither benefits nor costs associated with synchronous premask presentation at other locations in the matrix relative to the target). This was taken to suggest that priming enhanced target coding in early mechanisms comprising neurons with highly spatially specific receptive fields (see Elliott & Müller, 1998, 2000).

EXPERIMENT

The experiment used a variant of Elliott and Müller's (1998, 2000) synchrony-priming paradigm. Reaction time (RT) measures were taken to the presence or absence of a target Kanizsa-type figures within a static target display matrix of 90°-corner junctions, which was preceded by a temporally modulated premask display matrix of crosses (synchronized and random conditions) (see Figure 1). In their previous studies, Elliott and Müller had used premask and target displays with identical dimensions and upon target display presentation, the premask crosses *reduced* to 90°-corner junctions by "removal" of redundant line segments (although the remaining line segments did not change in size). In the present experiment, the specification of the premask and target display stimuli was systematically varied by independently and factorially varying the length of the line segments making up the crosses (premask display) and corner junctions (target display). With regard to the target display, this effectively produced a variation of the "goodness" of the Kanizsa-type square target, which, according to Shipley and Kelman (1992), is a function of the ratio of the physically specified length of the collinear inducer (junction) segments to the total edge length of the Kanizsa-type square. The ratios introduced in the experiment were 20% ("poor" square), 40%, or 60% ("good" square) (with 20% being the ratio used in previous studies). The same ratios were used for the premask crosses, and premask-cross specification was manipulated independently of target-inducer specification. Thus, it was possible that the target inducers were specified at, say, 60%, whereas the preceding premask crosses were specified at 20%. In such cases of non-identical (i.e., non-covarying) specification, explicit motion cues were produced at target display presentation, for instance, with poorly specified premask crosses "expanding" along their axes into well-specified target inducers, or well-specified premask crosses "contracting" into poorly specified target inducers. In other words, at target display onset, more or less strong motions signals were generated that had the potential to influence target detection. Thus, by introducing these variations, the modified paradigm permitted figural cues (target goodness) to be manipulated independently of motion cues (temporal premask modulation plus any additional motion signals generated by inducer expansions or contractions at target display onset), so that possible interactions between the form and motion-coding systems could be examined.

The predictions were as follows. Target detection RTs, in both synchronous and random-premask conditions, were expected to decrease with increasing target-inducer specification, due to a general increase in target saliency. More important theoretically, based on the assumption of a facultative interaction between the motion and form systems (Leonards et al., 1996), it was also

predicted that, as targets became easier to detect with increasing figural specification, the accompanying effects of prime synchrony would decrease significantly in magnitude (i.e., the synchronous and random-condition RTs would converge). Such a pattern would be expected if synchrony priming is generated solely within the motion system, while figural target specification determines the speed of computations within the form system. As these (form-based) computations become faster with increasing target inducer specification, the influence of (motion-based) synchrony priming on detection performance would decrease concomitantly. Such a pattern could be taken to indicate the presence of the prime in motion-coding mechanisms at the time of interaction between the prime and the neural response to target presentation. Conversely, no such interactive pattern of effects is expected if synchrony priming is principally generated and maintained within the form-coding system, consistent with the Elliott and Müller (2000) account. (Since the latter account predicts the null-hypothesis of no interaction, 20 participants were used to increase the power of the experiment to reveal any interaction.)

If the effects of priming become principally active in early mechanisms, as proposed by Elliott and Müller (2000; see also Elliott et al., 2000), local transient stimulus activity might offer a further indication of the relative importance of motion-coding mechanisms for synchrony priming. In conditions in which the premask and target inducer specifications did not covary, there were multiple, sudden local expansions or contractions when the premask elements transformed into those comprising the target display. For each element, expansion or contraction would always occur in two orthogonal directions as the premask crosses simultaneously transformed into corner junctions by removal of two line segments and the increase or decrease in size of the remaining line segments along each element axis. The local expansions or contractions were necessarily correlated between target elements, as the direction of motion was always relative to the center of the Kanizsa-type square but the motion signals induced by local expansions or contractions around the distractor elements were uncorrelated (in contrast with the paradigm of Lee & Blake, 1999). These motion signals are likely to be coded by local neural mechanisms sensitive to direction-specific, transient activity within their receptive fields, leading to the additional hypothesis that matrix expansion or contraction would provide an additional, target-related motion signal. If the motion system was already primed by synchronized premask presentation, this additional signal might serve to increase overall signal-to-noise ratio across spatially localized (i.e., early) synchronized mechanisms, boosting activity across the prime and thereby supporting the interaction of target with prime activity. Conversely, enhanced priming would not be expected under conditions in which the premask and target-inducer specifications covaried.

Method

Observers.   Twenty observers (8 male; mean age 27.75 years; all with normal or corrected-to-normal vision), who were naive as to the purpose of the experiment, performed one block of practice trials immediately prior to each of three experimental sessions. Observers were paid at rate of 12.00 Deutschemarks per hour.

Apparatus and stimuli.   Event timing, data collection, and stimulus image frame generation were controlled by a PC-compatible computer, which also controlled oscilloscopic image presentation through an Interactive Electronics Systems point plotter buffer with 8 Mb frame store memory (Finley, 1985). Image frames were presented on a 6" Tektronix 608-oscilloscope monitor equipped with a very fast-decay P15 phosphor. The use of a P15 phosphor ensured that on-screen image persistence reduced to 10% of normal image intensity within 2.8 µs of image termination (Bell, 1970). The Interactive Electronic Systems point plotter buffer allowed pixels to be plotted at a rate of one pixel every microsecond. The presentation frequency of frames across the entire premask display was kept constant at 40 Hz, while the entire premask matrix, consisting of a sequence of four separate frames, was recycled at a rate of 10 repeats per second (i.e., each premask frame repeated at 10 Hz). Frames had a constant exposure duration of 25 ms and an inter-frame 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. Both the individual premask frames and the target display frames were presented semi-static at a fixed 1 kHz refresh frequency.

Observers viewed the monitor at a distance of 57 cm (maintained via a chin rest). The experiments were conducted under controlled lighting conditions (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. Display elements were arranged around the centre of the monitor screen (see Figure 1). Premask crosses (Figure 1b) subtended 51', 1°42', or 2°33' of visual angle and exhibited horizontal and vertical separations of 2°39', 1°48', or 57' for 20%, 40%, or 60% premask inducer specification conditions, respectively. The combination of these display dimensions produced premask displays in which the total 3 × 3 premask display matrix subtended 7°51' × 7°51', 8°42' × 8°42', or 9°33' × 9°33' of visual angle, respectively. For 20% inducer conditions, the premask crosses comprised 21 tightly spaced points, so that their segments appeared as uninterrupted lines, the number of pixels per cross was increased proportionate to the increased inducer specification for 40% and 60% inducer-specification conditions and relative to the 20% condition in order to equalize luminance across inducer-specification conditions. Premask frames could

consist of 1, 2, 3, or 4 crosses presented simultaneously (Figure 1b), so that the amount of pixels presented in a given frame for the 20% inducer-specification condition (for example) could be 21, 42, 63, or 84. This would also have resulted in the luminance of premask stimuli varying across frames, with frames comprising fewer elements appearing brighter than those with more elements. Thus in the case of the 20%, inducer-specification condition, an additional 979, 958, 937, and 916 pixels were plotted for one-, two-, three-, and four-element frames (respectively), to an invisible corner of the display (with X,Y coordinates 0,0). Comparable procedures were carried out for the 40% and 60% inducer-specification conditions thereby equalizing the amount of pixels plotted in a single frame and maintaining frame presentations at a constant background frequency of 1 kHz. These procedures ensured that each frame was equiluminant despite changes in the amount of (visible) stimulus information presented. Junction elements in the target display (Figure 1a) subtended 26', 51', and 1°17' of visual angle and were separated horizontally and vertically by between 2°39'–3°30', 1°48'–3°30', or 57'–3°30', for 20%, 40%, and 60% target-inducer specification conditions. These variations produced Kanizsa-type figures representing "square" figures with probabilities of .1, .45, and .71, respectively (see Shipley & Kelman, 1992). The target displays subtended between 6°59'–7°51' × 6°59'–7°51', 6°59'–8°42' × 6°59'–8°42', or 6°59'–9°33' × 6°59'–9°33', respectively. Each target display junction consisted of 11 tightly spaced points. The target display overall consisted of 99 pixels. According to an identical procedure to that used for the premask displays, additional 901 pixels were plotted to an invisible corner of the display (i.e., with 0,0,0, X,Y,Z coordinates).

A trial started with a brief (300 ms) 250 Hz computer-generated tone. Following a delay of 200 ms, observers were presented with the oscillating 3 × 3 matrix of premask crosses, which, after 1200 ms, reduced to simple 90° corner junctions by removal of redundant line segments (see Figure 1a). Observers were told to fixate the centre of the display and avoid eye movements during premask display presentation. Upon removal of the redundant line segments, observers were asked to produce a two-alternative forced-choice RT (keypress) response, as rapidly and accurately as possible, to the presence or absence of a target Kanizsa-type square within the matrix of 90° corner junctions, which remained in view until the response had been made. In the event of an erroneous response, feedback was provided through a (150 ms) 100 Hz computer-generated tone followed by a 500 ms delay.

Design and procedure.   Premask and target inducer specifications were varied independently and factorially. Each condition contributed to nine combinations of target-inducer specification (20%, 40%, and 60%) with premask-inducer specification (20%, 40%, and 60%), in addition to the variables target (absent vs. present) and synchrony (synchronous vs. random). Observers

performed 1920 trials over three sessions of 640 trials each. All factors were varied randomly within and across blocks.

Results

RT analysis.   RTs on trials on which a response error was made (2.6% of all trials) were removed from the data before removing outlier RTs more than 2.5 standard deviations above or below the mean for each observer and experimental condition (2.8% of all trials). Figure 2 presents the correct mean RTs (and associated 95% confidence intervals [CI]) as a function of target-inducer (Figure 2a) and premask-inducer specification (Figure 2b), separately for each target (present, absent) × premask synchrony (synchronous, random) condition.

The data were examined by means of a repeated-measures analysis of variance (ANOVA), with main terms for target (present, absent), synchrony (synchronous, random), premask-inducer specification (20%, 40%, 60%), and target-inducer specification (20%, 40%, 60%). Violations of the homogeneity of variance assumption were corrected by applying either Greenhouse–Geisser or Huynh–Feldt epsilon adjustments (Huynh & Feldt, 1976).

Target-absent RTs were slower than target-present RTs: 588 vs. 527 ms, $F(1,19) = 102.06$, $MS_e = 6675.55$, p .0001. Furthermore, the main effect of synchrony, $F(1, 19) = 29.5$, $MS_e = 483.94$, $p < .0001$, and the synchrony × target
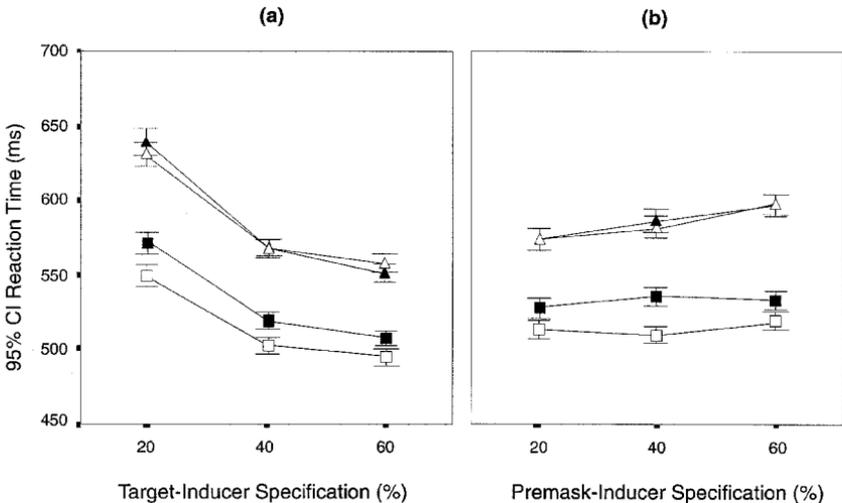
Figure 2.   Mean correct target-present and target-absent RTs (±95% confidence interval, in ms) for the synchronous and random conditions as a function of (a) the target-inducer specification and (b) the premask-inducer specification (in percentages). The square symbols represent target-present conditions, the triangle symbols target-absent conditions. The unfilled and filled symbols represent synchronous and random premask presentation conditions respectively.

interaction, $F(1, 19) = 41.126$, $MS_e = 258.36$, $p = .0001$, were significant. This pattern is consistent with previous findings (Elliott & Müller, 1998, 2000), and was due to expedited RTs for synchronous relative to random conditions on target-present trials: 518 vs. 535 ms, simple main effect, $F(1, 19) = 10.65$, $p < .005$; but not target-absent trials: 588 vs. 589 ms; $F(1, 19) = 0.058$, n.s.

As expected, increasing target-inducer specification expedited RT performance (target-inducer-specification main effect, $F(1.054, 20.022) = 47.172$, $MS_e = 13922.172$, $p < .0001$) (see Figure 2a). The main effect of premask-inducer specification was also significant, $F(2, 38) = 7.815$, $MS_e = 1454.227$, $p = .001$, due mainly to an RT increase with 60% premask-inducer specification on target-absent, but not target-present, trials (see Figure 2b): target × premask-inducer specification interaction, $F(1.594, 30.294) = 4.886$, $MS_e = 1201.067$, $p < .025$. This increase reflects a differential influence of premask-inducer specification on processes responsible for target detection as compared to processes responsible for verifying the absence of a target in the display, and, together with the RT decrease with increasing target-inducer specification, accounts for the significant premask-inducer specification × target-inducer specification interaction, $F(4,76) = 2.536$, $MS_e = 428.378$, $p = .047$.

Of greater theoretical importance, there were no significant effects of target-inducer and premask-inducer specification on synchrony priming (see Figures 2a and 2b): The target × synchrony × target-inducer specification, the synchrony × premask-inducer specification × target-inducer specification, and the target × synchrony × target-inducer specification × premask-inducer specification interactions were all non-significant, $F(1.598, 38) = 0.566$, n.s.; $F(3.242, 61.602) = 1.348$, n.s.; and $F(3.98, 75.62) = 2.026$, n.s., respectively. As can be seen from Figures 2a and 2b, the target-specific synchrony effects did not vary substantially with variations in either target-inducer or premask-inducer specification. That is, there is no statistical evidence in support of the (on the Leonards et al., 1996 account) expected interaction between form-based and temporal coding mechanisms.

The target specificity of the synchrony enhancements is consistent with the idea that synchronous-premask presentation primes the subsequent presentation of the target figure (a pattern of interaction that is consistently revealed with the premask paradigm; see Elliott & Müller, 1998, 2000). Consequently, in order to examine the effects of target-inducer expansion or contraction on prime efficiency, further analyses focused upon the pattern of effects revealed for target-present trials only. The target-present RTs were examined using an ANOVA with main terms for synchrony, premask-inducer specification, and target-inducer specification. (Note that no corresponding pattern of effects was revealed from an analogous ANOVA performed on the target-absent RTs.) As expected, the main effects for synchrony and target-inducer specification were significant, while that for premask-inducer specification was non-significant (see the lower two functions in Figure 2b), $F(1, 19) = 49.806$, $MS_e = 497.342$,

$p < .0001$; $F(1.112, 21.131) = 48.016$, $MS_e = 4498.272$, $p < .0001$; and $F(1.798, 34.17) = 2.109$, n.s.

The extent to which synchrony effects were influenced by target-inducer expansion or contraction is illustrated in Figure 3. For larger-range changes in inducer specification (i.e., 20–60% and vice versa), there was a tendency for synchrony effects to be slightly reduced relative to covarying premask-inducer and target-inducer specifications, whereas there was little effect with smaller-range expansions and contractions (20–40% and 40–60%, and vice versa). Statistically, the synchrony × premask-inducer specification and the synchrony × target-inducer specification × premask-inducer specification interactions were only borderline-significant, $F(1.552, 29.489) = 4.346$, $MS_e = 270.446$, $p < .05$; and $F(3.371, 70.898) = 2.891$, $MS_e = 293.938$, $p < .05$, which was mainly due to trend for expedited RTs on random premask trials with the result that the synchronous- and random-trial RTs show a tendency to converge with display expansions (see Figure 3). Further, the possibility that synchrony effects were maintained constant by a trade off between priming impaired by increased figural integrity but enhanced by display expansions or contractions can be ruled out on the basis of synchrony effects under conditions where premask and target specifications covaried. This finding also suggests against Leonards et al.'s (1996) suggestion of facultative interactions between form and motion coding as primarily responsible for mediating the effects of stimulus synchrony.

Error analysis.   An ANOVA of arcsine-transformed error data (with the same main terms as the RT data ANOVA) revealed the target miss rates to be slightly higher than the false alarm rates: main effect of target, $F(1, 19) = 8.109$,
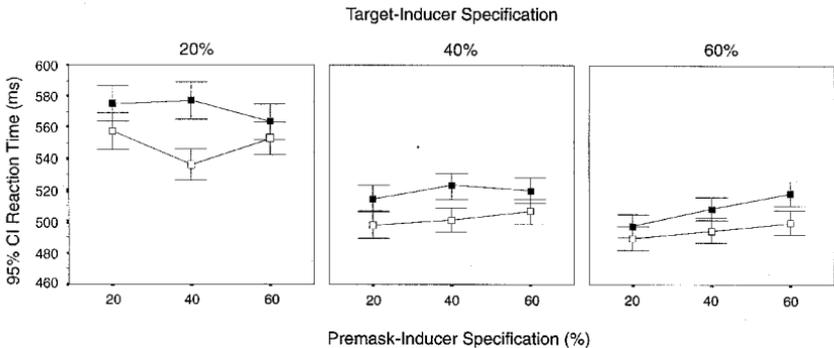
Figure 3.   Mean correct target-present and target-absent RTs (±95% confidence interval, in ms) for the synchronous and random conditions as a function of premask-inducer specifications seperately for each target inducer specification condition (inducer specification conditions given in percentages). The square symbols represent target-present conditions, the triangle symbols target-absent conditions. The unfilled and filled symbols represent synchronous and random premask presentation conditions respectively.

$MS_e = 0.008$, $p = .01$; 3.1% vs. 2.16%, respectively. Furthermore, trials on which a synchronous premask was presented were found to produce slightly less errors than random-premask trials: main effect of synchrony, $F(1, 19) = 17.428$, $MS_e = 0.02$, $p = .001$; 2.27% vs. 2.99%, respectively. Error rates decreased with increasing target-inducer specification, $F(1.185, 22.51) = 45.748$, $MS_e = 0.09$, $p < .0001$, due to the enhanced salience of the target figure in the 40% and 60% conditions relative to the 20% condition (2.1% and 1.22% vs. 4.58%). There were no effects involving premask-inducer specification, and no other interactions were significant. Thus, the error effects reinforce the RT results.

Discussion

Although target detection RTs did decrease with increasing target-inducer specification, indicating that figure coding was facilitated by a general increase in target saliency, the accompanying effects of prime synchrony remained constant (there was no statistical convergence of the synchronous and random RTs as a function of improving target specification). Consequently, the present results provide no support for the idea, proposed by Leonards et al. (1996), that form-based and temporal information interact facultatively. Instead, the data argue that figure-coding mechanisms are primed by appropriate temporal information, irrespective of variations in the target's figural integrity. Conceivably, the borderline-significant interactions between premask-inducer and target-inducer specification occur due to Gestalt coding across the premask being interrupted by the sudden element expansions or contractions, implying some facultative link between form-coding and motion-coding mechanisms. However, these effects were weak, did not abolish the synchrony effects and were mainly due to faster RTs to targets following random premask presentation. Thus, within the overall pattern of results, they offer little support for the idea that motion-coding mechanisms are the principle mechanisms mediating the generation of priming. Interestingly, one additional implication of these findings is that manipulation of the size of the premask-display crosses does not influence figure–ground segmentation and/or Gestalt coding. This seems somewhat counterintuitive considering other findings (i.e, Shipley & Kelman, 1992) that show the "goodness" of Kanizsa-types figures is largely due to the separation between inducer elements. It may be that, in this instance the collinear line segments do not encourage illusory contour formation (see, e.g., Gurnsey, Poirier, & Gascon, 1996) with the result that activity across the prime, although representing the square-arrangement of the synchronous premask elements, may not be considered in the same terms as the "subjective experience" of an illusory Kanizsa square (which is directly supported by perception of the illusory contours). This is plausible considering that observers do not detect the synchronous-premask frame, rendering tenuous an account of priming

according to stimulus properties more commonly associated with subjective experience. An alternative account (earlier stated) is that the prime may simply represent coincidence in the firing of neurons across the elements of the synchronous premask, implying that the effects of stimulus synchrony, although effective in promoting grouping may not be directly responsible for subjective experience of the grouping *per se*. This account would suggest that the neural synchronization responsible for signalling the spatio-temporal structure of the premask display should not be considered directly equivalent to the "perception", or "subjective experience" of grouping or segmentation. Again, this account seems plausible given that the priming stimulus is not detected by observers. Nevertheless, both accounts remain putative, with much more work required to examine these and other possible explanations for this particular pattern of effects.

GENERAL DISCUSSION

Although both parvocellular and magnocellular pathways may respond with zero-phase lag at the frequency of premask presentation, the present results revealed no pattern suggestive of facultative interaction between form and motion-coding systems as a function of the goodness of the target Gestalten. The interaction revealed in the study of Leonards et al. (1996), if they can indeed be interpreted in terms of a facultative interaction (see footnote 1), may be due to the presence of implicit motion signals in their displays (as suggested by Usher & Donnelly, 1998).

These present results, together with those of Usher and Donnelly (1998), suggest an interpretation in terms of the external, stimulus-locked synchronization of form-coding mechanisms independently of the motion system (which does not rule out that effects of synchronizing either system may result in qualitatively similar effects at the level of Gestalt organization). The present results also indicate that the synchronous prime is relatively insensitive to form-based characteristics of either the target stimuli (priming was not significantly influenced by the goodness of the target stimuli) or the premask stimuli (priming was equally effective whatever the premask-cross specification). Consistent with the latter, Müller and Elliott (1999) observed that the grouping effects of stimulus synchrony persisted even when premask circles were displayed instead of cross stimuli (with only the latter, but not the former, sharing figural elements with the subsequently presented target inducers; see also Usher & Donnelly, 1998). These findings support the idea that stimulus-driven synchrony may represent no more than coincidence in the firing pattern of a subset of neurons, although they also suggest that the neural coincidence has the potential to directly influence figure–ground segregation and/or Gestalt coding (see Elliott & Müller, 1998).

Taking previous studies of synchrony priming into consideration, the synchrony effects produced by this priming paradigm appear to differ from physiological recordings of synchronous neural activity in one critical respect: The pattern of synchrony across the prime matches the frequency of premask presentations with zero phase lag (Elliott & Müller, 2000; Elliott et al., 2000). Recall that physiological recordings are usually of synchronization that is not regularly phase locked to stimulus activity. These findings contributed to Leonards et al.'s (1996) suggestion that the external synchronization of form-coding mechanisms could only result from third-party synchronization via motion-coding mechanisms responding to stimulus flicker. However, as will be outlined later, the interpretation of the role of phase-jittered synchronization has been questioned by the results of recent EEG studies that suggest that synchronization between neural assemblies as it relates to coding spatial aspects of the stimulus may be much more sensitive to the timing of stimulus events than previously thought.

Are stimulus-locked and internally timed oscillations functionally similar?

There are two classes of oscillation that are of particular significance for functional accounts of synchronization (for the complete taxonomy of brain rhythms from which these examples are taken, see Başar-Eroglu, Strüber, Schürmann, Stadler, & Başar, 1996, and Galambos, 1992). Stimulus-phase-locked oscillations are generally referred to as "evoked" (i.e., generated directly by the stimulus), and are recorded from human scalp during stimulation with simple stimuli such as auditory clicks or light flashes (see Başar, 1980, and Galambos, 1992, for reviews). Oscillations that show no specific phase locking to stimulus activity are referred to as "induced" and are considered an index of the "cognitive" response to a stimulus (Tallon-Baudry & Bertrand, 1999). For the most part, multi-unit single cell recordings of oscillatory synchronization may be considered as a form of induced activity. Induced oscillations are also revealed in local-field potential (EEG) recordings following presentation of Gestalt groupings (Tallon, Bertrand, Bouchet, & Pernier, 1995; Tallon-Baudry, Bertrand, Delpeuch, & Pernier, 1996, 1997). The stimulus-specific characteristics of induced oscillations contrast with those of evoked activity, recorded in the same EEG, which are relatively insensitive to the type of stimulus presented (Karakaş & Başar, 1998; Tallon et al., 1995; Tallon-Baudry et al., 1997).

Arguably, the effects of stimulus synchrony observed in psychophysical studies with stationary forms should be attributable to evoked, rather than induced, oscillatory synchronization, even though evoked oscillatory activity does not appear to directly influence perceptual organization. However, the claim that induced oscillations are exclusively responsible for

stimulus-specific perceptual processing has been challenged by Pulvermüller, Keil, and Elbert (1999), who argue that induced oscillations in the gamma band may be more related to stimulus classification and related memory processes. In addition, recent EEG and magnetoencephalographic (MEG) studies of the neural response to figure presentation have shown that the evoked gamma-band response varies with variations in the spatial configurations of the stimulus (see, Herrmann, Mecklinger, & Pfeifer, 1999; Herrmann & Mecklinger, 2000, this issue). Herrmann et al. replicated the basic paradigm of Tallon et al. (1995) by presenting Kanizsa figures that either grouped or did not group according to the local orientations of inducer pie slices. Contrary to the results of Tallon et al., Herrmann and colleagues reliably observed stimulus-specific variations in oscillatory activity in the evoked, but not the induced, oscillations. Further, employing the same analytical procedure (see Herrmann, Mecklinger, & Pfeifer, 1999, for details), Herrmann, Elliott, Mecklinger, and Müller (1999) first reported that repeated presentation of the premask stimuli of Elliott and Müller (1998) evoked a stimulus phase-locked 40 Hz response over posterior-cortical electrodes (see also Elliott et al., 2000). This response was specific to the synchronous-premask-target condition and might be interpreted as a specific patterning in the EEG that encoded the precise spatial and temporal structure of the priming stimulus. Given the earlier arguments that perceptual effects can arise through variations in spatio-temporal stimulus structure, which may not be specifically attributable to the response of motion-coding mechanisms, these results offer further evidence that the oscillatory neural response to synchronized-stimulus presentation can adopt the phase of stimulus activity with consequent effects on stimulus grouping and segmentation.

Summary and conclusions

We have reviewed investigations of the extent to which external synchrony can encourage or enhance the perception of figural stimuli and presented data, with the aim of resolving some of the issues that have prevented consideration of these effects in similar terms to those of physiological recordings of neural synchrony, with which they are presumed to relate. The principle issue concerns whether or not synchronization could conceivably follow presentation of stationary stimuli. Several studies and paradigms were reviewed in support of this idea, although a further issue arose from their findings: Whether internally generated synchronization, held to be responsible for neural synchronization observed in physiological studies, could be mediated by motion-coding mechanisms responding to rapid repeating stimulus presentation. Experimental evidence was presented consistent with the idea that motion-based responses do not necessarily influence synchrony during form coding. Given the evidence that repeated presentation of synchronized stimuli results in a phase-locked oscillatory response, the distinction between evoked and induced neural

oscillations was introduced and their functional correlates in the EEG were reviewed. It was concluded that there is some evidence to consider the effects of evoked oscillatory activity in similar terms to those of induced activity; that is, repeated synchronized stimulus presentations may generate an equivalent, phase-locked pattern of activity in the brain. These considerations might provide the ground for more detailed studies of the timing parameters under which stimulus-evoked synchrony, stimulus-induced synchrony, and the timing of perceptual organization processes, operate.

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