Role of synchrony in contour binding: some transient doubts sustained

Steven C. Dakin and Peter J. Bex

Institute of Ophthalmology, University College London, 11-43 Bath Street, London EC1V 9EL, UK

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The temporal correlation hypothesis proposes that neurons signal mutual inclusion in complex features, such as extended contours, by phase-locking their firing [C. M. Gray and W. Singer, Proc. Natl. Acad. Sci. USA **86**, 1698 (1989)]. Although this hypothesis remains controversial, a number of recent psychophysical studies have suggested that temporal correlation among features can indeed promote perceptual grouping. In particular, subjects are better at detecting extended visual contours embedded within a field of distractor elements when a small delay is present between a cycling presentation of the contour and the background [Nature **394**, 179 (1988)]. We have replicated this finding and examined three potentially confounding factors. First, we controlled local density and used more curved contours composed of bandpass elements to confirm that the effect was associated with contour integration and not with the operation of coarse-scale spatial filters. Second, we minimized the effects of saccadic eye movements (which could combine with the flicker of the asynchronous display to introduce motion cues at the contour location) both by using a fixation marker that was visible only when observers made a saccade (allowing them to reject these trials) and by retinally stabilizing the stimulus. We report that eye movements contribute to the effect. Third, we asked if either visible persistence or transients at the onset and the offset of the asynchronous stimuli might contribute to the effect. We report that the effect is largely abolished by the inclusion of prestimulus and poststimulus masks and is entirely abolished by ramping the contrast of the stimulus on and off. Neither ramping, masking, nor stabilization should specifically disrupt a contour-binding scheme based on temporal synchrony, and we conclude that it is the transient component at the onset and the offset of these stimuli that is responsible for the reported advantage for asynchronous presentation. © 2002 Optical Society of America

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1. INTRODUCTION

The temporal correlation hypothesis proposes that widespread patterns of oscillatory discharge (of approximately 30–60 Hz) observed in the visual cortex[1] arise from neurons synchronizing their firing to signal mutual inclusion in spatially extensive features such as contours.[2–4] This idea remains controversial: It has also been argued that such oscillations neither are stimulus dependent[5] nor could form the basis of a useful code given the noise constraints of cortical architecture.[6] Unfortunately, pertinent psychophysical evidence is equivocal. Segmentation of randomly oriented bandpass elements, with carriers moving at random speeds and directions, is possible based solely on the synchrony of direction change within the field.[7] Recently, however, it has been suggested that simple low-pass temporal filtering mechanisms may reveal the presence of such structure without recourse to mechanisms involving synchrony.[8] Leonards *et al.*[9] reported that detection of an orientation-defined texture patch is facilitated if the patch and the background are presented asynchronously, i.e., as alternate frames of a movie sequence, compared with the case when patch and background are presented synchronously, i.e., simultaneously within a frame. These authors also show that if the asynchronous sequence is inconsistent with spatial cues to the location of the patch, then performance returns to the lower level associated with synchronous presentation but does not collapse. This, they reason, suggests that there are two grouping systems operating in a complementary and facultative manner: the first resistant to temporal fluctuations, operating in a sustained manner; the second a transient system exploiting synchronization of afferent signals directly. However, others using a similar methodology have not found any facilitatory effect of asynchronous presentation at all.[10]

Usher and Donnelly[11] combined the synchronous versus asynchronous comparison[12,13] with a contour integration paradigm[14] where subjects are required to locate contours, composed of a series of oriented features, embedded within a field of randomly oriented distractor elements. Contour stimuli were presented as movie sequences: In the synchronous condition [Fig. 1(c)], contour and distractors appeared together (interlaced with blank frames), and in the asynchronous condition [Figs. 1(a) and 1(b)], the movie alternated between the contour in isolation and the distractor elements. Note that the examples shown in Fig. 1 are the same type of stimuli as that used by Usher and Donnelly, but their contours were composed of lines and were near straight. Movies were presented at 60 frames per second, ensuring that the duration of each frame was "... below the integration time of the visual system" (Ref. 11, p. 179). Although, on informal inspection, the two conditions appear identical, detection of the contours was systematically better in the asynchronous condition at a variety of exposure times (i.e., movie lengths), supporting the idea that it is the temporal coincidence of contour elements that is promoting their mutual association.

We have identified three problems with this paradigm. The first is that, judging from their figures, Usher and

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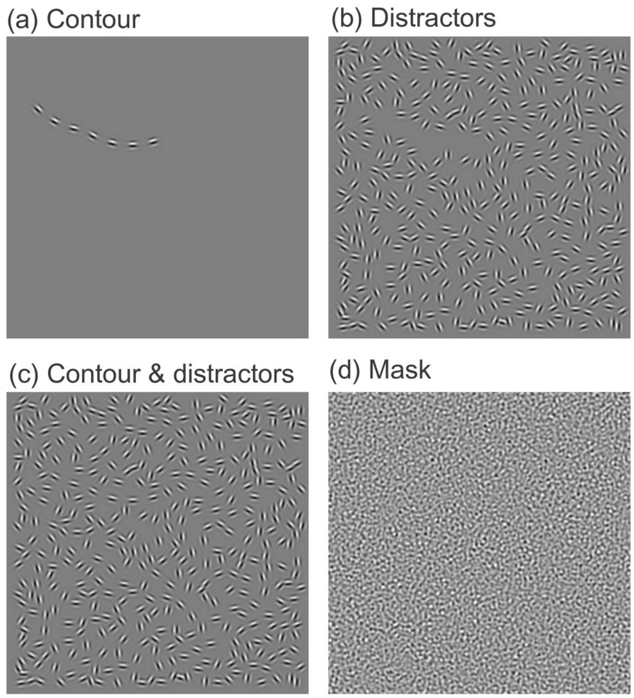

Fig. 1. Examples of the stimuli. Subjects were required to identify which quadrant of a movie display contained an embedded contour. In the asynchronous condition frames alternated between (a) an image containing a contour and (b) a set of distractor elements. (c) In the synchronous condition the contour and the distractor were presented simultaneously, and this frame alternated with a blank field. (d) To limit the effects of visible persistence, a mask preceded and followed the stimulus in certain conditions. This was a phase-randomized version of a typical contour stimulus.

Donnelly[11] did not carefully control local stimulus density at the contour location and used near-straight contours composed of lines. It is known that explicit contour linking processes are not required to detect near-straight stimuli but rather that the output of a coarse-scale filtering mechanism will suffice.[15] This problem is compounded by the use of spatially broadband stimuli (composed of short line elements) and/or by any small density cues. It is therefore possible that the reported advantage for asynchronous presentation is simply linked to the operation of such coarse-scale mechanisms, which are believed to operate very quickly.[16] To test this possibility, we used curved contours (the orientation of neighboring elements along our contours differed by 15°) composed of narrow-band Gabor elements, and we carefully controlled local density so that the presence of the contour was not revealed by chance overlaps between distractor and contour elements.

The second problem is more fundamental to psychophysical paradigms using flicker to investigate synchrony. It is that eye movements made during stimulus presentation shift the retinal location of elements and that this may combine with the appearance and the disappearance of elements to induce a local motion cue at the location of the contour. With extended viewing of the asynchronous stimuli, this cue may be manifested as a “wobbling” of the contour. Clearly, such motion cues are useless in the synchronous condition because both distractor and contour elements move together. Indeed, this problem may have been compounded in the original experiment, where no fixation marker was used. We devised a novel method, illustrated in Fig. 2, to minimize the effect of saccadic eye movements on this experiment. Our fixation marker, presented in the center of the stimuli, consisted of “cross hairs” superimposed on a radial Gabor patch that was counterphase flickering at a rate of 60 Hz [Fig. 2(b) and 2(c); the marker has been enlarged, but in the experiment the carrier grating was matched to that of the Gabor elements used to construct the stimuli]. Because the bull’s-eye component is being presented beyond the flicker fusion limit, the grating should be invisible if the subject keeps both eyes steady, but involuntary eye movements will produce the instantaneous appearance of the Bessel patch. When subjects signaled such an event, it initiated a repeat of the trial using a new stimulus. Because this is only an indirect method for controlling eye movements, we also conducted a further experiment involving the retinal stabilization of the stimulus to investigate further the role of eye movements in this task.

The final problem with the methodology as given is that contours are presented in isolation only within the asynchronous movie sequence. Therefore either visible persistence may confer an advantage if the contour falls at the end of the movie sequence or the observer may use transient structure that occurs at either the onset or the offset of the stimulus. We therefore modified the original procedure either by presenting visual masks [phase-scrambled versions of the stimuli; Fig. 1(d)] for 250 ms immediately before and after each stimulus or by smoothly ramping on the contrast of the stimuli. Both such manipulations minimize transient/persistent cues but would not be expected to selectively target a grouping mechanism relying on synchrony.

2. METHODS

A. Apparatus

Stimuli were generated with a Macintosh system running MatLab (MathWorks Ltd.) using code from the PsychToolbox[17] and the VideoToolbox.[18] The screen was a La Cie 22-in. Electron Blue monitor fitted with a video attenuator. The attenuated signal was amplified and copied, with the use of a line splitter, to the three guns of the monitor to generate a monochrome image. The display was linearized by using look-up tables (to give pseudo-12-bit contrast accuracy) and had a resolution of 832×624 pixels (24 pixels per centimeter) and a vertical blanking rate of 120 Hz. The screen was viewed binocularly (apart from the stabilization experiment) at a distance of 115 cm and had a mean background luminance of 50 cd/m^2.

For the retinal stabilization experiment, the same computer and display were used in conjunction with an eye-tracking/stabilization setup manufactured by Fourward Optical Technologies. This had a resolution $<$1 arc min, a range of $\pm$10°, a bandwidth of 400 Hz, and an input/output delay of 1 ms. Subjects viewed the stimuli monocularly through an optical system consisting of four lenses and four silver mirrors, so that the system produced a total attenuation on the order of 30%. In this

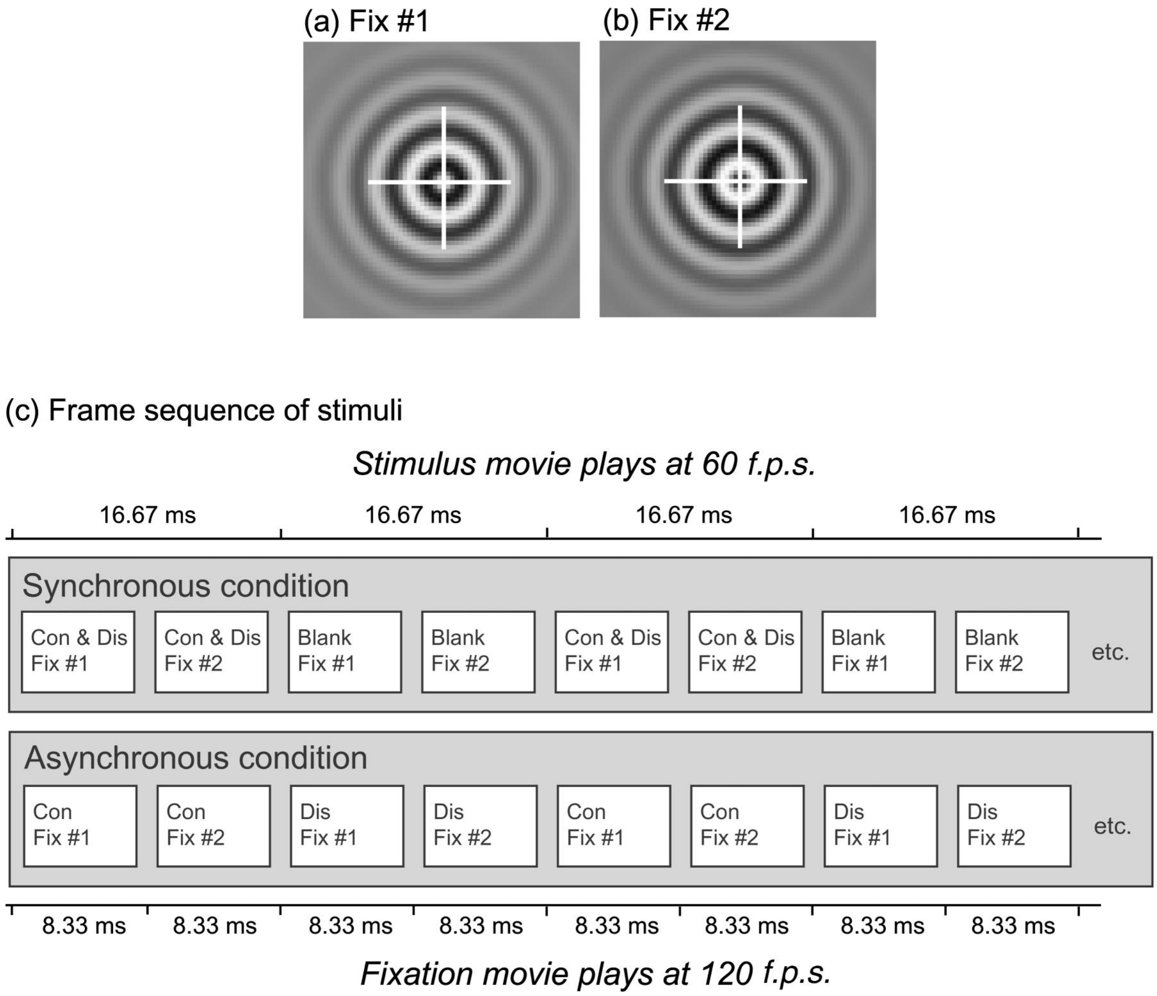

Fig. 2. (a), (b) The fixation marker consisted of a movie sequence alternating, at 60 reversals per second, between the two images shown. Thus involuntary eye movements were revealed by the appearance of the bull's-eye grating, which was otherwise invisible below the cross hairs. (c) Frame sequence of stimuli (Con = contour presented alone, Dis = distractors presented alone, Con & Dis=contour embedded in distractors, Fix = fixation marker). All stimuli movies were played at 120 frames per second (f.p.s.), but stimulus frames were doubled up to give an effective frame rate of 60 f.p.s. Both conditions consisted of two interleaved sequences. In the asynchronous condition, contour and distractor elements were interleaved. In the synchronous condition, contour and distractor appeared together within a frame and were interleaved with blanks. Qualitatively, conditions cannot be distinguished from one another.

condition, subjects' head movements were restricted by means of a bite bar and a chin rest.

B. Stimuli

Stimuli were fields of Gabor patches (a circular Gaussian with a σ of 4 arc min, windowing a sine-wave grating with a spatial frequency of 7.5 cycles per degree) with each of the 400 elements positioned within a 20×20 grid of cells, notionally divided into four quadrants. Background elements were randomly oriented. Target/contour elements had positions and orientations arranged to be consistent with an underlying contour.[14] Unless stated otherwise, adjacent contour elements differed in orientation by $\pm 15°$. Mean element separation was 32 arc min, and the total size of the display subtended 7.5°. The central element of each contour was constrained to be at a grid position within ± 2 cells of the center of each quadrant to avoid contours falling on or near quadrant boundaries. Stimuli were presented at 100% contrast, so that, with frame interleaving, their effective contrast was 50%. Stimulus movies were played at frame rates (120 f.p.s.), but frames of the stimulus were repeated in pairs to give an effective presentation rate of 60 f.p.s., which was similar to the rate used by Usher and Donnelly.[11] A cross-hair fixation marker was presented in the center of the display, superimposed on a low-frequency Bessel patch that was counterphase flickering at 60 Hz (i.e., 60 reversals per second). Observers attempted to maintain steady fixation and used the keyboard either to indicate in which quadrant they thought the contour appeared or to signal that they had seen the flickering patch appear behind the cross hairs (indicating an involuntary eye movement; this technique was inspired by Dennis Pelli's "SaccadeDemo.m" demonstration from the PsychToolbox.[17] In the latter case the trial was repeated with a fresh stimulus. Auditory feedback was provided following incorrect trials. Masks were phase-scrambled versions of the stimuli, generated by computing the fast Fourier transform of a stimulus, setting the phase values to random values in the interval 0–2π while maintaining Hermitian symmetry, then backtransforming to produce a real image. In the contrast-ramped condition we used a raised cosinusoidal temporal envelope, so that stimuli were smoothly elevated from 0 to maximum contrast in 150 ms.

Further details of the stimulus presentation are given in Fig. 2.

C. Observers

The authors (SCD, PJB) and three naïve observers (TM, IE, SBG) participated in the first set of experiments. All wore optical correction as necessary. PJB and SCD are very experienced in contour detection tasks. Naive subjects performed practice trials (typically lasting approximately 30 min) to familiarize themselves with the task. Only the authors participated in the stabilization experiments, which were conducted with monocular viewing.

3. EXPERIMENT 1: EFFECT OF SYNCHRONY ON DETECTION OF CURVED, BANDPASS CONTOURS

Performances of the five observers on the contour detection task are plotted in Fig. 3, with circle and upward-pointing triangle symbols showing data from the synchronous and asynchronous conditions, respectively. Error bars show 95% confidence intervals derived by using a binomial statistic; thus nonoverlapping error bars indicate a statistically significant difference between conditions. The results are qualitatively consistent with those of Usher and Donnelly[11] in that there is a sizable and generally statistically significant advantage for asynchronous presentation, for all subjects at a range of stimulus presentation times. We show a larger trend than the average advantage of approximately 16% reported by those authors. Given that we had tighter control on density and element bandwidth, it seems that the advantage as reported is associated with contour integration and not the operation of coarse-scale spatial filters.

Figures 3(a) and 3(b) also show the results from two control conditions. Square symbols show data from a synchronous condition where the stimulus contrast was reduced by 50% and stimuli were displayed continuously rather than being interleaved with blanks. This was done to test if the observed effect is attributable to a *reduction in performance* for synchronous presentation in

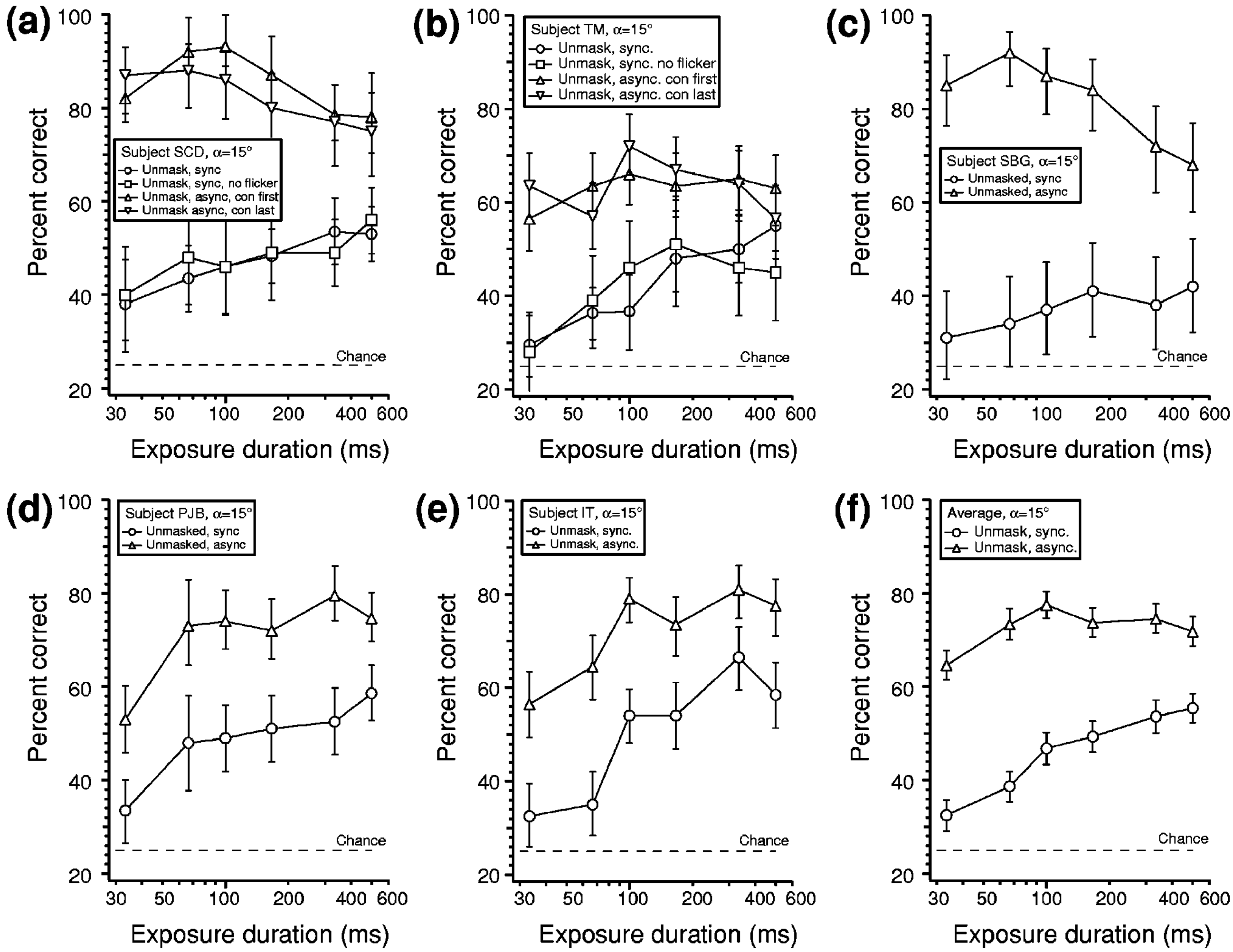

Fig. 3. Results from experiment 1: probability of detecting a contour as a function of stimulus exposure duration. Results from the five subjects are given in (a)–(e), and (f) gives the average performance. The contour was presented either synchronously (circles) or asynchronously (upward-pointing triangles) with the background/distractor elements. Results indicate a sizable and generally statistically significant advantage for asynchronous presentation. The first two plots include data from two additional control conditions examining the effect of reversing the order of asynchronous presentation (upward-pointing triangles) and reducing the visible flicker within the synchronous condition (squares). Neither manipulation alters performance significantly from the respective conditions.

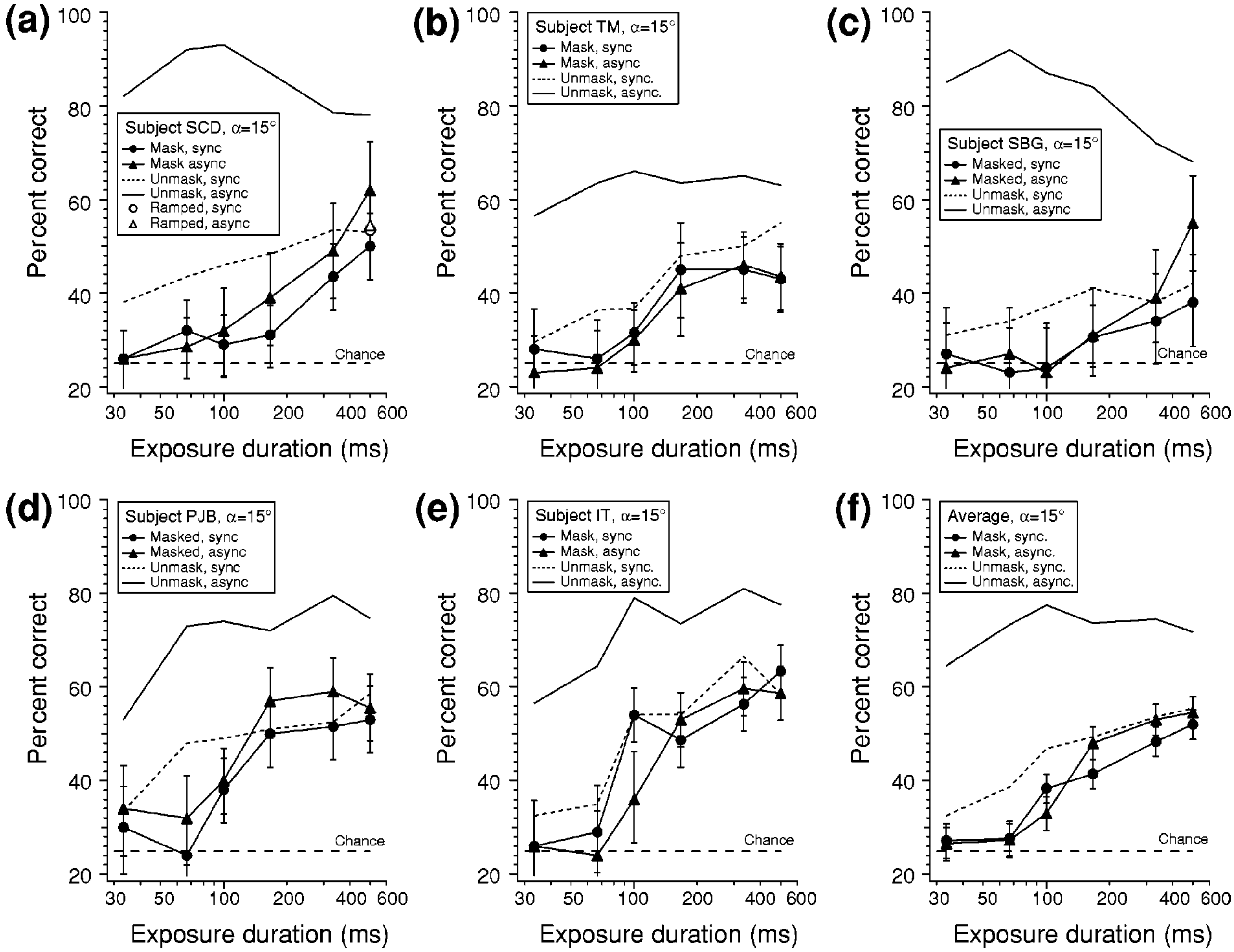

Fig. 4. Results from experiment 2: contour detection as a function of the exposure duration (stimulus movie length) for stimuli that have been premasked and postmasked with filtered noise. Comparing masked with unmasked conditions (closed symbols versus solid and dashed lines), one can clearly see that there is a moderate reduction in performance for synchronous presentation, particularly at shorter exposure times, but that there is an enormous reduction in performance for asynchronous presentation across all exposure times. With masking, the asynchronous advantage is no longer statistically significant for any subject at any exposure time.

the presence of full-screen flicker. The results are clearly comparable with those for normal synchronous presentation, disconfirming this hypothesis. A second control condition asked if the asynchronous advantage was due to the content of the first or last frame in the sequence and simply reversed the order of asynchronously presented contour presentation from contour–background... contour–background to background–contour... background–contour. Data from this condition (downward-pointing triangles) indicate similar performance in both asynchronous conditions, irrespective of frame order, showing that the effect is not wholly attributable to the first or last frame.

Note that we show a very large asynchronous advantage at our shortest exposure duration of 33 ms when stimuli consisted of only one cycle of contour–background. This finding refutes any notion that the asynchronous advantage results from some form of phase locking between a neural response and the extended temporal characteristics of the stimulus. This cannot be happening between cycles but must be happening within one cycle and, specifically, within one frame of one cycle (16.7 ms). Note that this result cannot rule out the possibility that the visual system employs an internal code based on synchronous firing; i.e., contour structure within a single frame could initiate neural phase locking. Indeed, it seems difficult to envisage a psychophysical paradigm using external synchrony (synchronous temporal structure in the stimulus) that can rigorously address this question; it is currently unclear, for example, how poststimulus masking noise affects signal-induced phase locking. Here we make a smaller point: that stimulus oscillations, although popular in psychophysical paradigms probing synchrony, are not necessary to promote grouping.

Average performance [Fig. 3(f)] highlights a second feature of the results. Performance improves at longer exposure durations with synchronous presentation but peaks or plateaus at shorter exposure durations (approximately 80 ms) for asynchronous presentation. Longer exposure times do not improve the task under asynchronous viewing conditions and for 2/5 of the subjects actually makes it harder. We return to this point in Section 6 (Discussion).

4. EXPERIMENT 2: EFFECT OF PRESTIMULUS AND POSTSTIMULUS MASKING

To investigate further the role of transients at the onset or the offset of the stimuli, we performed the same experiment but introduced 250-ms prestimulus and poststimulus masks. Masks not only disrupt onset and offset transients but also minimize visible persistence. Masks were matched to the global spatial frequency and orientation structure of stimuli and were phase-scrambled versions of contours embedded in distractors [Fig. 1(d); note that we did not use the obvious masking stimulus, a field of randomly oriented Gabors, because such patterns introduce irrelevant motion cues at the location of stimulus elements that might disrupt performance independently of any masking]. Mask contrast was maximized, and masks were presented continuously (i.e., without flicker) before and after each stimulus movie. The results, shown in Fig. 4, are unequivocal. Masking selectively demolishes performance in the asynchronous condition; no subject shows a statistically significant advantage for masked asynchronous presentation at any exposure duration. On average [Fig. 4(f)] the reduction in performance in the synchronous condition is much more modest. Again, it is hard to see, in the context of the temporal correlation hypothesis, why masking should selectively target a grouping mechanism based on synchrony. Instead, we are again driven to the more parsimonious explanation based on detection of transients at the onset and the offset of the stimulus.

Based on the data shown in Figs. 3 and 4, we are confident that the effects described so far are due to information at the onset and the offset of the stimulus. However, it is evident from Fig. 4(f) that there is a small (but statistically nonsignificant) advantage for asynchronous presentation at the longer exposure durations. Our final experiment asks if small eye movements could be contributing to the task and, by inference, to this residual advantage.

5. EXPERIMENT 3: CONTRIBUTION OF EYE MOVEMENTS

Throughout the course of the experiments described, we employed the flickering-fixation marker technique, described in Section 2 (Methods), to give subjects a self-monitored means of rejecting trials where they made involuntary eye movements. Ultimately, such a technique is limited by subjects' reliability at reporting the grating visibility and is, at best, an indirect means of controlling the influence of saccades. To get direct control over movement of the stimulus on the retina, and minimize any motion cues interacting from saccadic eye movements and stimulus flicker, we performed a final experiment. We stabilized the stimuli on the retinas of two subjects (the authors) and compared the effects of asynchronous versus synchronous presentation, with stimuli that did or did not contain onset/offset transients. In this experiment we also minimized transient structure by contrast-ramping the stimulus on and off over the course of the first 150 ms of the stimulus presentation. We then compared results from the four conditions (stabilized/unstabilized × ramped/abrupt) with results from an unstabilized condition, where subjects viewed stimuli through the same optical apparatus and used the same dental restraint but with the stabilization system switched off. The experiment was conducted with the use of a 500-ms presentation. We used this, the longest exposure duration from our previous experiments, for three reasons. First, it gives a residual advantage under masked conditions, and we are interested to see if eye movements are contributing to this effect. Second, we would expect the contribution of eye movements to increase with exposure duration by increasing the probability of detecting the motion artifact. Third, it is long enough that the ramping can occur over 150 ms and still leave a clear 200 ms where there is no change in contrast. This duration is sufficient to give large asynchronous advantages in unmasked conditions [Figs. 3(a) and 3(d)], so any reduction in performance under asynchronous, ramped conditions cannot be attributable to a reduction in the effective exposure duration of the stimulus.

Data from the stabilization experiment are plotted in Fig. 5. Consider the unstabilized results first (leftmost set of four bars) for each subject. Under abrupt onset/offset there is a substantial and statistically significant advantage for asynchronous presentation (light versus dark bars), but this is absent when the contrasts are

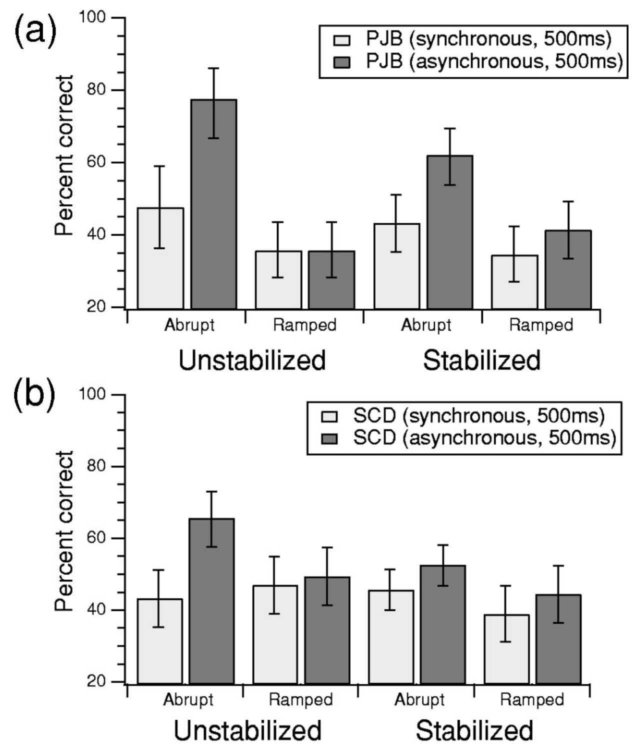

Fig. 5. Contour detection performance measured with two subjects for synchronous (light bars) and asynchronous (dark bars) presentation. Stimuli were viewed monocularly through the optical apparatus of an image stabilizer and either were presented abruptly or were smoothly contrast ramped to remove transient structure at the onset and the offset. The left-hand and right-hand sets of four bars show data with and without image stabilization, respectively. The asynchronous advantage is present for unstabilized monocular viewing but is abolished by contrast ramping and diminished by retinal stabilization.

ramped. Compare this pattern of results with those shown under stabilized conditions. Now the size of the advantage for asynchronous presentation is diminished for both observers, still being significant for PJB but no longer for SCD. This is due to a selective reduction of performance with asynchronous presentation; compare the dark bars in abrupt/unstabilized conditions with the dark bars in abrupt/stabilized conditions. Ramping still produces no significant asynchronous advantage. We conclude that eye movements can and do contribute to this effect, although to a lesser extent than do onset and offset transients.

6. DISCUSSION

To summarize, we have described four novel findings associated with the advantage for asynchronously presented contour and distractors:

1. The advantage for asynchronous presentation peaks or becomes asymptotic at approximately 100 ms.
2. There is still an asynchronous advantage with only one stimulus cycle, indicating that the cyclic structure of stimuli is not a requirement for the phenomenon.
3. The asynchronous advantage is largely abolished with either prestimulus and poststimulus masking or contrast ramping, implicating the use of onset and offset transients.
4. The advantage is reduced under retinal stabilization, indicating a contribution from eye movements under free viewing conditions.

The finding that performance peaks or becomes asymptotic in the asynchronous condition at approximately 100 ms and that the asynchronous advantage is present even with stimuli containing only one stimulus cycle would seem to be problematic for an account of contour binding based on synchrony. If the cycling temporal structure of the stimuli encourages neural synchronization, one would not expect that a single stimulus cycle could support phase locking between stimulus and a grouping mechanism relying on temporal correlation. Furthermore, one might expect that longer exposure durations will *encourage* such phase locking, which runs contrary to the plateau in performance that we observe with asynchronous presentations of 100 ms and beyond. An alternative proposal is that phase locking is independent of the temporal repetition of the stimulus, and therefore a one-cycle condition is equally as informative as a multiple-cycle condition. Under this view, however, perceptual facilitation simply arises from the temporal delay between targets and distractors. Putting this finding another way—"detecting a target within distractors is easier if they are presented in separate frames"—reduces it to a somewhat modest (and intuitive) assertion. If this is the case, then the impact of these findings seems to have been based on a fundamental misunderstanding of the experiment, and the use of cycling stimuli may have encouraged this confusion; why is the duration of a cycling stimulus of interest if it bears no relation to internal synchronization?

These flickering movie sequences are rich in transient structure, and our data are consistent with subjects selectively exploiting this structure in the asynchronous conditions. However, we do not find that all transients are treated equally; experiments 2 and 3 offer evidence that subjects rely heavily on structure at the onset and the offset of the stimulus. "Contour-only" frames at the beginning and the end of the movie sequence in the asynchronous condition are unique in that they are not immediately preceded and followed by an image exclusively containing distractor elements. However, it is not the case that *any structure presented in isolation* within these sequences is equally detectable. Usher and Donnelly[11] performed an interesting control experiment (which we have replicated with our stimuli) showing that subjects cannot detect asynchronously presented contours that are composed of randomly oriented elements. In the context of our findings, this result suggests that detection of onset/offset transients may be enhanced with collinear contour elements. However, here we briefly consider a simple alternative explanation; that it is not contour structure *per se* but merely the presence of high orientation uniformity (i.e., narrow orientation bandwidth) within the near-straight contour stimuli that facilitates transient detection. This effect might be expected if, for example, one were monitoring the output of a simple orientationally bandpass filter, with transient sensitivity, operating over some portion of the stimulus. We conducted an experiment to examine this possibility. Subjects were required to detect a contour ($\alpha = 15°$, 100-ms presentation) whose elements were rotated by some amount (the orientation offset) from the local contour direction (i.e., the orientation expected if the element were aligned with the underlying contour structure). In this way we could manipulate collinearity while minimizing orientation bandwidth differences between conditions.

Figure 6 plots results from this experiment, demonstrating that the asynchronous advantage is greatest when local elements are coaligned with contour direction (parallel local orientation). Although this would seem to demonstrate that the asynchronous effect is associated with local collinearity and not orientation bandwidth, manipulation of the orientation offset in this manner does not maintain constant orientation bandwidth, since paths composed of elements with collinear elements still have a lower orientation bandwidth [full width at half-height (FWHH) of approximately 57°][19] compared with the case when elements are oriented perpendicular to contour direction (FWHH of approximately 43°). The only way to truly equate orientation bandwidth of stimuli is to alter the aspect ratio of the contour components. By reducing the 1:1 aspect ratio of the Gaussian envelope component of the Gabors to 0.63, one can construct 0° orientation-offset contour stimuli whose orientation bandwidths are equated to the 90° orientation-offset condition, where the asynchronous advantage is minimal. The inset image in Fig. 6 labeled 0° and attached to a dashed line shows an example of a contour constructed from "shortened" micropatterns, and filled symbols show performance with such stimuli. This manipulation of element aspect ratio has no discernible effect on detection of contours that are presented synchronously, which is consistent with local element bandwidth having only a limited impact on the detection of contours composed of spatially band-limited

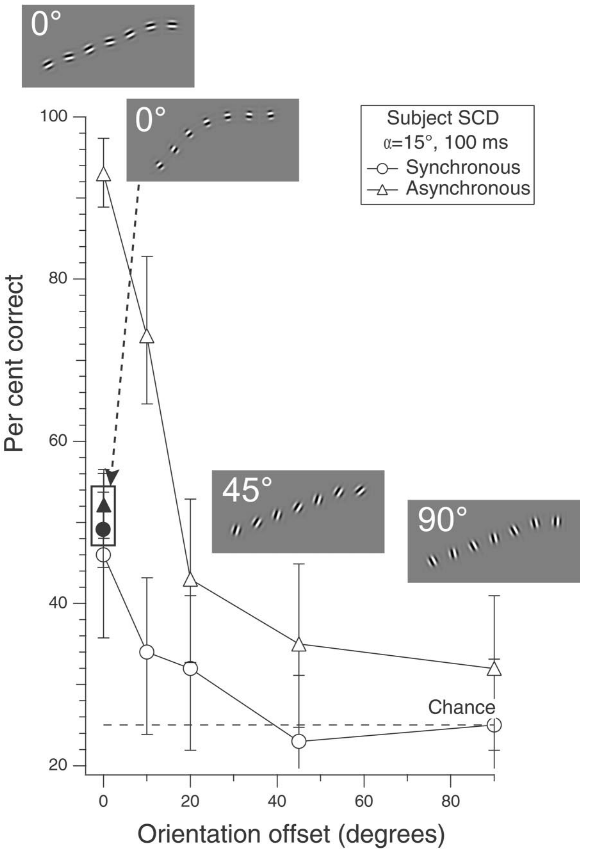

Fig. 6. Open symbols show contour detection measured as a function of the orientation difference between the components of the contour and the local contour direction. Embedded images show examples of the (isolated) contour with various orientation offsets. Note that the advantage for asynchronous presentation is particularly pronounced when elements are coaligned. However, this may be due not to coalignment but to the effect of orientation bandwidth, which covaries with orientation offset. Filled symbols show detection performance for a coaligned contour where the elements have been "shortened" so that the global orientation bandwidth is now matched to the 90° orientation offset condition. The asynchronous advantage is now abolished.

features.[20,21] Interestingly, reducing the aspect ratio does abolish the asynchronous advantage, even though elements are still coaligned. We found the same effect with a second subject and also verified that the abolition of the effect was due to a reduction in orientation bandwidth and not a reduction in rms contrast by confirming that the asynchronous advantage was present when patches were *lengthened* (i.e., the area of the envelope was reduced by the same extent but now was lengthened so that it had an aspect ratio of 1:0.63). Although by no means conclusive (arguably, changing element aspect ratio also changes element spacing, etc.), these results suggest that the global orientation bandwidth of these stimuli is of importance in determining the degree to which asynchronous presentation affects the detectability of contour targets. The texture segmentation study of Leonards *et al.*,[9] which showed strong effects of synchrony, used texture elements that were near collinear and were positioned on a regular grid, while a similar study that reported no effect of synchrony at all[10] used elements that were less collinear and whose positions fell on a jittered grid. Since stimuli from the latter study have a higher orientation bandwidth than those from the former, it is tempting to speculate that this difference could explain the failure of Kiper *et al.*[10] to find a facilitative effect of synchrony. In summary, a failure of subjects to detect contours composed of randomly oriented elements may not be an adequate control for subjects using single frames from the movie stimuli. Instead, this adds to the findings reported above in suggesting that subjects simply exploit onset and offset transients in asynchronously presented contour stimuli. This in turn calls into question whether this psychophysical paradigm can bear on the proposition that visual contour integration is subserved by mechanisms exploiting external synchrony (i.e., within the stimulus). As to whether the visual system uses *internal* synchrony to encode properties such as contour collinearity, we consider this hypothesis open but untestable with the use of existing psychophysical paradigms.

Note added in proof: Since we submitted this paper, Beaudot[22] has arrived at conclusions similar to our own, although his advantage for asynchronous presentation was contingent largely on stimuli ending with an isolated contour.

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Corresponding author Steven C. Dakin's e-mail address is s.dakin@ucl.ac.uk.

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