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## Role of onset asynchrony in contour integration <sup>☆</sup>

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### Abstract

Evidence that visual grouping is facilitated when elements comprising a foreground figure are presented simultaneously, and are temporally separated from elements comprising the background, has suggested cortical synchronous oscillations as a possible neural substrate. Supporting this theory, Usher and Donnelly (Nature 394 (1998) 179) showed in one of their experiments that contour integration is facilitated when path and background elements alternate with an asynchrony below the integration time of the visual system, suggesting that these flickering stimuli interact with this hypothetical binding mechanism. I replicated this experiment and report that the effect depends in fact on the order of asynchrony between path and background elements in the first cycle of stimuli presented for more than 100 ms: facilitation in visual grouping only occurs when path elements are presented before background elements. A second experiment, exploring the effect of onset delays between path and background elements, demonstrates a strong priming effect of path elements. I conclude that Usher and Donnelly's result is likely due to the high sensitivity of the visual system to stimulus onset, and that simple flickering stimuli are inadequate for revealing the neural code for binding in figure-ground segregation without controlling for the effect of stimulus onset. © 2002 Elsevier Science Ltd. All rights reserved.

*Keywords:* Contour integration; Onset asynchrony; Dynamics; Figure-ground segregation

### 1. Introduction

The question of which mechanisms support perceptual grouping is of major topical interest, not only because it is still very controversial but because it is a key issue in understanding visual processing. In particular it has been suggested that selective synchronization in the firing pattern of individual cortical cells could be the substrate for solving the binding problem in perceptual grouping (see Gray, 1999 for a recent review). Numerous studies have tried to assess this temporal correlation hypothesis, mainly within the context of figure-ground segregation (Alais, Blake, & Lee, 1998; Blake & Yang, 1997; Fahle, 1993; Fahle & Koch, 1995; Hess, Beaudot, & Mullen, 2001; Keele, Cohen, Ivry, Liotti, & Yee, 1988; Kiper, Gegenfurtner, & Movshon, 1996; Lamme & Spekreijse, 1998; Lee & Blake, 1999; Leonards & Singer, 1998; Leonards, Singer, & Fahle, 1996; Usher & Donnelly, 1998; Ziebell & Nothdurft, 1999), by synchro-

nously or asynchronously modulating the figure from its background. As a partial support for this temporal theory of binding, some of these results have shown that temporal asynchrony between figure and ground improves segregation (Fahle, 1993; Usher & Donnelly, 1998; Ziebell & Nothdurft, 1999), while others have shown that large temporal asynchrony has no significant effect on figural binding, compared to, for example, small spatial displacement which can destroy it (Fahle & Koch, 1995; Keele et al., 1988).

The relevance of the temporal theory of binding to contour integration was unknown until Yen and Finkel (1998) proposed a cortical-based model accounting for the perceptual salience of contours embedded in noisy background based on the level of synchronized neural activity. The suggestion that contour integration could be based on the temporal correlation hypothesis was strengthened by Usher and Donnelly (1998) (see their second experiment illustrated by Fig. 2, p. 181): using a contour integration paradigm (Field, Hayes, & Hess, 1993; Kovacs & Julesz, 1993) in which contour and background line elements were flashed cyclically in anti-phase, they demonstrated that grouping is facilitated for a temporal asynchrony (13 ms, equivalent to a flickering frequency of 38 Hz) between contour and background

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elements below the integration time of the visual system (Colheart, 1980). This latter result is particularly puzzling since square-wave flickers at a frequency of 38 Hz should be perceived as steady for most observers, being above the fusion limit for these stimuli. How can the visual system still gain access to such small asynchrony between figure and background?

In this paper I test whether the order of the stimuli sequence affects the results reported by Usher and Donnelly (1998). I first replicate Usher and Donnelly's second experiment using Gabor elements and a temporal 2AFC method similar to previous works on contour integration (Field et al., 1993; Hess et al., 2001; Mullen, Beaudot, & McIlhagga, 2000), and I find that the stimuli order in the first cycle of the flickering presentation affects significantly performance in contour detection. My conclusion is supported by a second experiment in which I investigate the effect of various onset delays between path and background elements in a steady rather than flickering presentation in a way similar to Ziebell and Nothdurft's experiment on the dynamics of orientation pop-out (Ziebell & Nothdurft, 1999).

## 2. Methods

Stimuli, apparatus and calibrations were described previously (Hess et al., 2001). Paths with a curvature of  $20^\circ$  [curvature threshold for contour integration, see Mullen et al. (2000)] and Gabor elements with contrast of 50% were used in all experimental conditions. Examples of stimuli are shown in Fig. 1.

### 2.1. Protocol

A temporal 2AFC paradigm was used in the two experiments to measure the subject's ability to detect the path, in which the choice was between a path stimulus and a no-path stimulus (Fig. 1). Each trial consisted of this pair of stimuli presented sequentially for the same duration. Presentations were abrupt with a 0.5 s inter-stimulus interval. The inter-stimulus interval was spatially homogeneous with the same mean luminance than stimuli presented during test intervals. After each trial the subject indicated the interval perceived as containing a path by pressing the appropriate mouse button. The number of trials per session for each experiment was 50 for each subject, and several sessions (3–5) were performed per duration and asynchrony condition. Feedback was given. A small fixation mark appeared in the center of the display during the whole session. Stimuli were generated on-line, and a new stimulus was generated for each presentation.

In the first group of experiments, path and background elements were flashed cyclically according to a square-wave modulation function (38 Hz, half cycle of 13 ms) similarly to Usher and Donnelly's experiment. Three conditions have been considered; path and background elements could be presented synchronously, asynchronously with a 13 ms advance for the path elements (path-first), or asynchronously with a 13 ms advance for the background elements (background-first) (Fig. 2A). Path detection was measured over a range of duration (26, 52, 105, 158 and 210 ms corresponding to 1, 2, 4, 6 and 8 cycles of presentation).

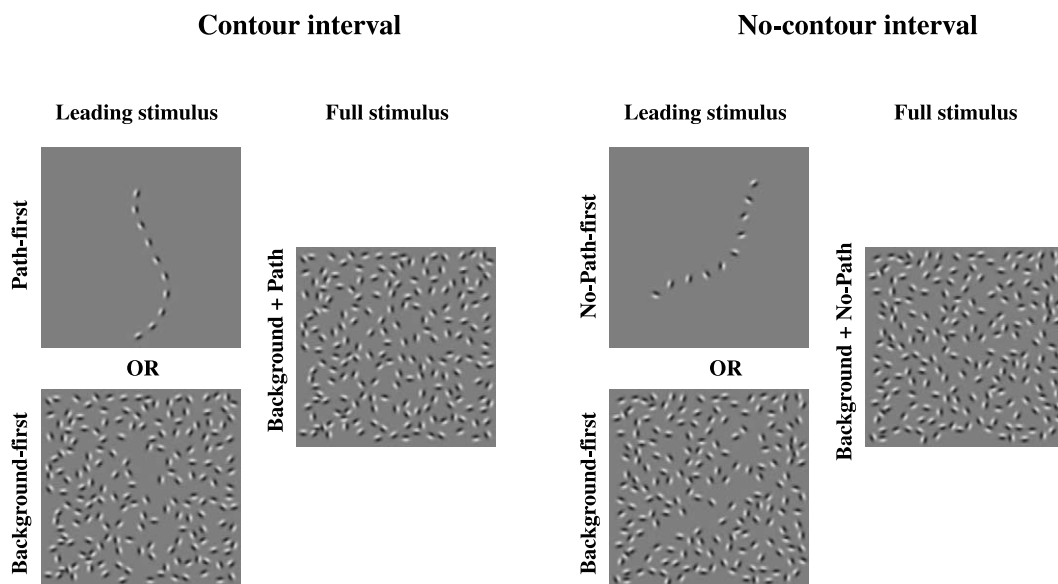


Fig. 1. Example of stimuli for the contour and no-contour intervals. Only leading stimuli are used in experiment 1 where they are presented in alternation and cyclically. Both leading and full test stimuli are used in experiment 2 where they are presented in sequential order.

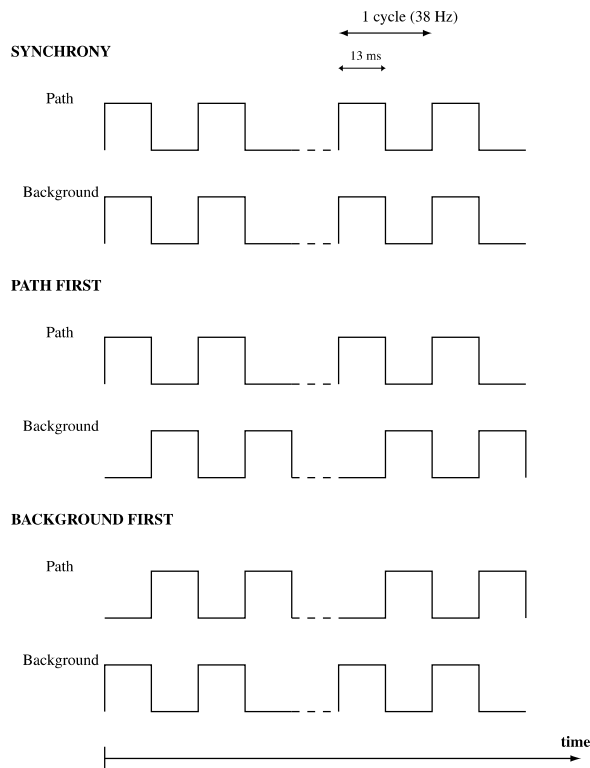
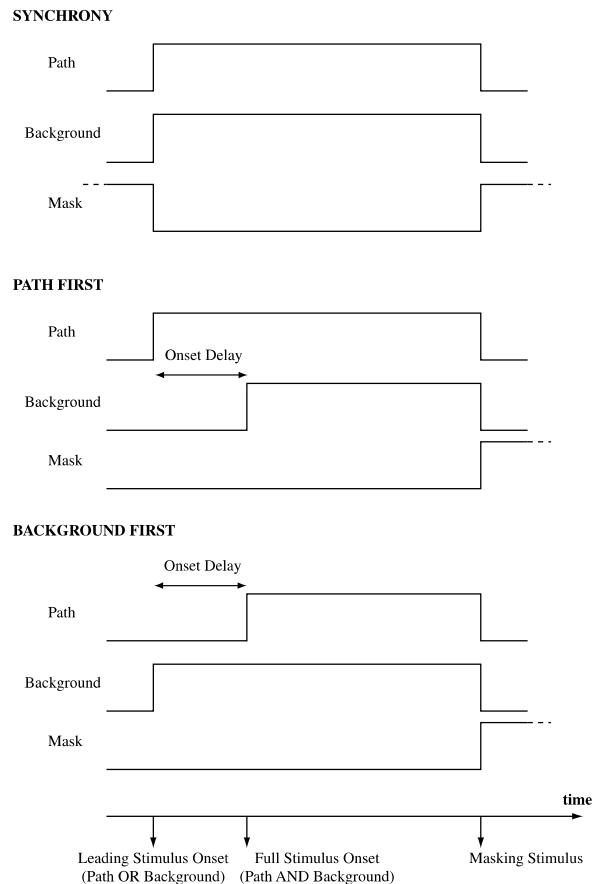
**A. Experiment 1****B. Experiment 2**

Fig. 2. (A) Stimuli sequence in experiment 1 and (B) stimuli sequence in experiment 2. In both experiments, the order of the stimuli sequence (path vs background elements) determines the asynchronous condition.

In the second group of experiments, I looked at the effect of various onset asynchronies between path and background elements of contour stimuli, in a steady rather than flickering presentation. Following on from the argument by Ziebell and Nothdurft (1999), one should expect that contour detection would be improved if the binding processes among path or background elements are already established when the full stimulus (path and background elements together) is switched on. To test this prediction, path and background elements were presented at different onset delays, in order to determine whether a preceding presentation of path or background elements enhances contour detection. I considered three conditions (Fig. 2B): (1) a synchronous condition in which the full stimulus (containing a path or not, see Fig. 1) was embedded between a 500 ms forward and backward masking stimulus, (2) an asynchronous condition in which path elements were presented first (path-first or no-path-first, see Fig. 1), and joined by the background elements after a short duration to form the full stimulus, and (3) another asynchronous condition in which the background elements were presented first (background-

first, see Fig. 1), and joined by the path elements after a short duration to form the full stimulus. Two onset delays were used, 13 and 26 ms. In both asynchronous conditions, the full stimulus was followed by a 500 ms masking stimulus. In the no-path interval, the leading stimulus could be a no-path or a background stimulus depending on the asynchronous condition. The no-path stimulus is a path made of randomly oriented elements (no-path-first in Fig. 1). I verified that the resulting full stimulus (no-path stimulus + background stimulus) does not contain any positional cues allowing the detection of a  $20^\circ$  contour defined by randomly oriented elements. Path detection was measured over a range of duration of the full stimulus (13–250 ms). In the three conditions, the masking stimulus consisted of arrays of Gabor elements placed identically to those of the full stimulus with a random change in their orientations in the range  $\pm 45$ – $135^\circ$ . A path could not be detected any more once the mask is switched on. This masking stimulus was designed to prevent path integration continuing beyond the presentation of the test stimulus (see Hess et al., 2001).

### Effect of 180 deg phase shift between figure and ground

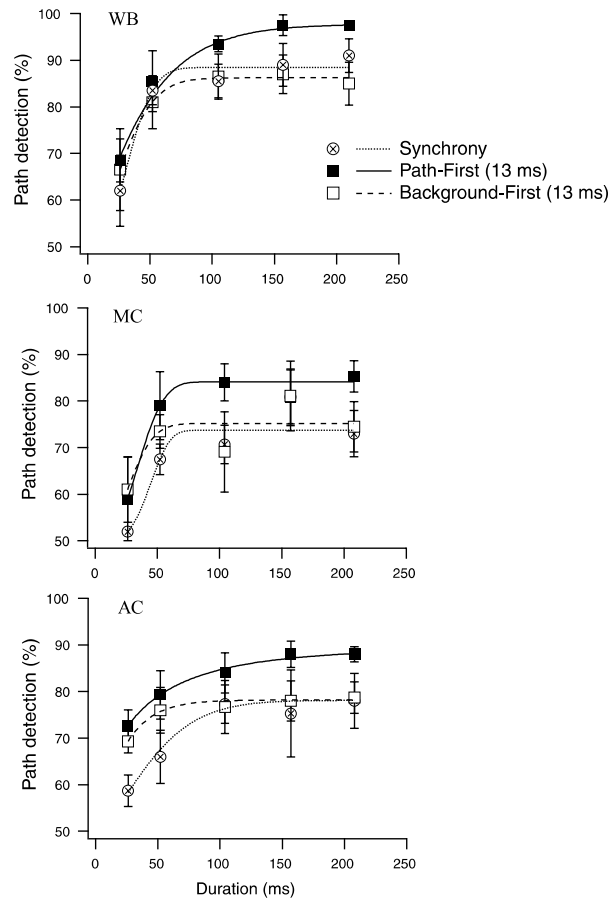


Fig. 3. Effect on path detection of the stimuli order between path and background elements in the cyclically flickering presentation as a function of stimulus duration. Data are shown for the three subjects. Each subject performed 3–5 sessions of 50 trials per data point. Crossed circle and square symbols represent performance measurement (% correct) in synchronous and asynchronous conditions, respectively. Filled and open square symbols denote path-first and background-first conditions, respectively. Solid, dashed and dotted lines denote fits of a Weibull function to data of each condition (see footnote 1). Error bars denote standard deviations.  $Q$  values for each fit were calculated and are as follows (see footnote 2): WB, path-first 0.82, background-first 0.95, synchronous 0.55; AC, path-first 0.93, background-first 0.96, synchronous 0.89; MC, path-first 0.81, background-first 0.57, synchronous 0.35.

#### 2.2. Observers

The observers were one author (WB) and two naïve subjects (MC & AC). All have normal, or refracted to normal (luminance) vision. All experiments were done under binocular conditions.

### 3. Results

#### 3.1. Effect of asynchrony in repetitive presentation

The first experiment replicated Usher and Donnelly's path experiment. Results are shown for the three subjects in Fig. 3 by data points, and the curves denote fits

for the asynchronous and synchronous conditions as described below. Each curve represents performance on path detection as a function of duration.

Data show that in all conditions performance rises smoothly with the increase of the stimulus duration until reaching an asymptotic performance level. Both asynchronous conditions seem to show a slight advantage compared to the synchronous condition below 100 ms. However, performance for the path-first condition starts to be significantly higher than for the background-first condition only above 100 ms, while performances for background-first and synchronous conditions saturate at about the same level. To quantify these differences, I fitted the data of Fig. 3 (performance as a function of duration) with a Weibull function corrected to take the differing asymptotic performance levels into

Table 1

Weibull parameters (mean and standard deviation) for the first experiment estimated by the fitting procedure for each subject and each condition (PF: Path-first, BF: Background-first, SYN: Synchronous conditions)

	PF	BF	SYN
<i>Asymptotic performance (%)</i>			
WB	97.74 ± 1.10	86.24 ± 2.63	88.43 ± 2.23
MC	84.15 ± 2.38	75.18 ± 3.91	73.76 ± 2.78
AC	89.34 ± 5.58	78.21 ± 2.54	78.13 ± 4.94
Mean across subjects	90.41 ± 5.60	79.87 ± 4.67	80.11 ± 6.15
<i>Critical duration (ms)</i>			
WB	46.59 ± 7.52	35.04 ± 10.60	38.79 ± 6.21
MC	40.80 ± 10.20	33.31 ± 11.20	48.32 ± 5.21
AC	32.68 ± 15.50	22.71 ± 7.33	52.72 ± 21.20
Mean across subjects	40.02 ± 5.70	30.35 ± 5.45	46.61 ± 5.81
<i>Slope</i>			
WB	1.13 ± 0.27	1.68 ± 1.35	2.46 ± 1.20
MC	2.63 ± 2.01	2.24 ± 1.89	3.92 ± 0.60
AC	0.68 ± 0.47	1.07 ± 1.26	1.49 ± 0.81
Mean across subjects	1.48 ± 0.83	1.66 ± 0.48	2.62 ± 1.00

account.<sup>1</sup> The least-squares weighted fits (Levenberg–Marquardt algorithm) to the data are shown by the solid, dashed and dotted lines in Fig. 3. The associated  $Q$  values for each fit are given in the figure legend, and all  $Q$  values indicate a statistically acceptable fit.<sup>2</sup> All fits were weighted with the inverse of the standard deviation measured experimentally, and the fitting procedure produced an estimation of the asymptotic performance with its estimated standard deviation. Asymptotic performance levels, critical duration and slope extracted from this fitting procedure are summarized in Table 1 for each condition and each subject. Means and standard deviations across subjects are also included in Table 1. I focused my analysis on asymptotic performance since this parameter shows the lowest coefficient of variation for all subjects.<sup>3</sup> I applied a one-way repeated measures ANOVA to analyze the differences in

asymptotic performance across conditions. A significant main effect of condition was found ( $F_{(2,4)} = 107.235$ ,  $p = 0.0003$ ). Differences among conditions were further explored using a Turkey–Kramer post-hoc analysis with a 5% significance level which showed that: (1) asymptotic performance is significantly higher for the path-first condition compared to the background-first and synchronous conditions (by about 10.5%), and (2) there is no significant difference in asymptotic performance between the background-first and synchronous conditions.

The main result of this experiment is that contour detection is significantly facilitated (for asymptotic performances) when the path elements are presented before the background elements in the first cycle of the stimuli sequence, and not at all when the background elements precede the path elements. This result demonstrates that the effect reported by Usher and Donnelly may primarily depend on the order of stimulus sequence rather than on temporal asynchrony per se. However, the estimation of critical durations (Table 1, subjects AC and MC) also suggests that performance for the synchronous condition may rise slightly slowly compared to both asynchronous conditions, which could result in the early facilitation found for both asynchronous conditions (below 100 ms). This difference in dynamics may indicate that the effect of temporal asynchrony depends less on stimuli order for short presentation, and may reflect the activation of a transient mechanism rather than a synchrony-binding mechanism relying on many cycles of presentation (see discussion).

### 3.2. Effect of onset delay in continuous presentation

In the second experiment, I changed from using a flickering presentation to a steady presentation and

<sup>1</sup> The Weibull function used to fit performance as a function of duration is given by:

$$PC(x) = pc_{\max} - (pc_{\max} - 50) \times e^{-(x/T)^\beta}$$

where PC is percent correct,  $pc_{\max}$  is the asymptotic performance level,  $T$  is the critical duration (corresponding to a relative increase of  $(1 - 1/e)\%$ )  $\beta$  is the slope, and  $x$  is duration.

<sup>2</sup>  $Q$  is a  $\chi^2$  distribution function which gives the probability that the minimum  $\chi^2$  is as large as it is purely by chance. For small  $Q$  values, the deviation from the model is unlikely to be due to chance and the model may be incorrect. For larger  $Q$  values, the deviation from the model is likely to arise by chance suggesting the model is an adequate description of the data. A  $Q \geq 0.1$  suggests an acceptable model fit (Press, Teukolsky, Vetterling, & Flannery, 1992).

<sup>3</sup> The coefficient of variation measures the relative variability of the parameters estimation and is defined by “standard deviation/mean”. Averaged across subjects, the coefficient of variation is  $3.8 \pm 1.7\%$  for the asymptotic performance,  $28.0 \pm 11.4\%$  for the critical duration ( $T$ ), and  $63.4 \pm 30.0\%$  for the slope ( $\beta$ ). Large variations in the estimation of  $T$  and  $\beta$  have little impact on the estimation of asymptotic performances.

### Effect of onset asynchronies between figure and ground

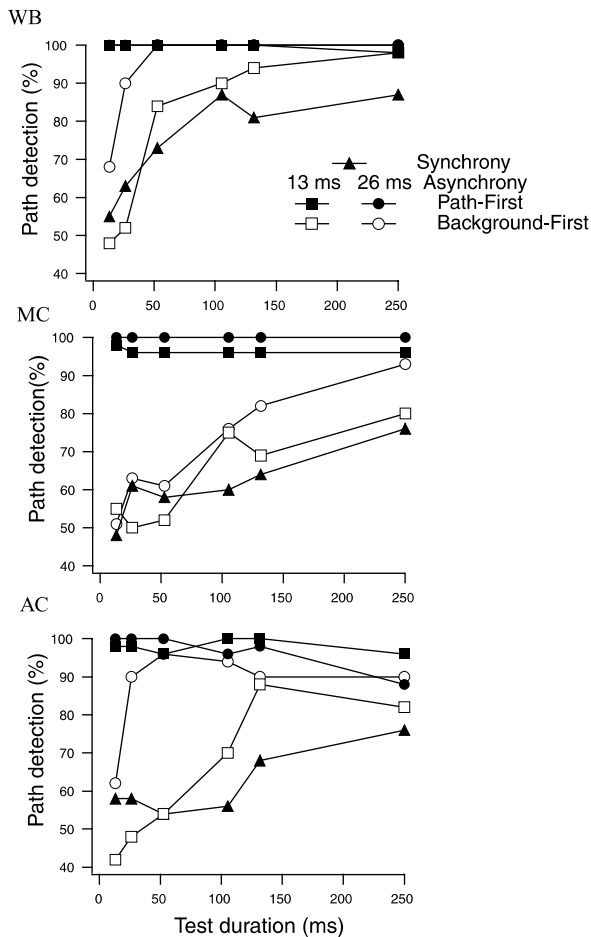


Fig. 4. Effect on path detection of onset asynchrony between leading stimuli (path or background elements) and full stimulus as a function of duration of the full stimulus. Data are shown for the three subjects. Each subject performed 3–5 sessions of 50 trials per data point.  $\Delta$ ,  $\square$  and  $\circ$  symbols represent performance measurement (% correct) for the synchronous condition and for an onset delay of 13 and 26 ms, respectively. For these two asynchronous conditions, filled and open symbols denote path-first and background-first conditions, respectively.

systematically varied the onset delays (or stimulus onset asynchronies, SOA) between figure/ground (see Figs. 1 and 2B). Results are shown for the three subjects in Fig. 4 by data points representing performance on path detection as a function of duration of the full stimulus (path + background elements).

Data for all subjects show that performance is already optimal for the shortest duration in the path-first condition (filled square and circle symbols), while performance rises smoothly with stimulus duration in the background-first and synchronous conditions (open symbols and filled triangle symbols). When the path elements are presented first, regardless of the onset asynchrony, contour integration is greatly facilitated, no such effects are seen when the background elements are

presented first. The shortest delay I used (13 ms) is as effective as the longest one in the path-first condition, while increasing the delay boosts the performance in the background-first condition. Performances in the synchronous condition are generally lower than for the background-first condition, and rise even more slowly. Despite the fact that the path was presented 13 or 26 ms longer in the path-first condition compared to the synchronous condition, data shown in Fig. 4 demonstrate the specific effect of this asynchrony: performance for the synchronous condition at the same total duration cannot compensate for the gain in performance of the path-first condition.

This experiment demonstrates that the visual system is highly sensitive to short onset asynchronies between path and background elements, and that the underlying transient mechanism retains the orientation of stimulus elements to prime contour integration in the subsequent test stimulus.

## 4. Discussion

### 4.1. Priming effect instead of synchrony-binding mechanism

I presented two sets of consistent data demonstrating that it is the order of presentation not the asynchrony per se, which results in facilitation in contour integration. The first experiment is in agreement with Usher and Donnelly's experiment to the extent that it replicates their findings that an asynchrony between path and background elements below the visual integration time can facilitate path detection. However I also demonstrate the asymmetry of this effect for durations above 100 ms; facilitation occurring only when path elements are presented first in the stimuli sequence. Thus, despite the limitations of drawing a conclusion from a blocked design and only three subjects, the present results suggest a potential flaw in the interpretation of Usher and Donnelly's findings, namely the facilitatory effect on path detection is likely mediated by the stimuli order in the first cycle, and not by the asynchrony between figure and background in the remaining cycles of the stimulus. Thus contrary to Usher and Donnelly (1998), I conclude that this experiment does not demonstrate that a synchrony-based binding mechanism is involved in visual grouping. The second experiment clearly demonstrates the priming effect of the onset asynchrony between figure and ground: asymptotic performance is reached for the smallest delay when path elements precede background elements, while performance increases smoothly with stimulus duration when background elements precede path elements, the speed of the rise increasing with the delay.

#### 4.2. Comparison with other studies

My experiments differ from those of Usher and Donnelly (1998) and Ziebell and Nothdurft (1999) in two main aspects: the stimuli and the type of task. Both used luminance line segments, while I used Gabor elements which one would argue are better signals to activate specific sets of cortical visual neurons. In their contour integration paradigm, Usher and Donnelly aligned these segments along paths of low curvature (about  $10^\circ$ ), which are more salient and more rapidly detected than paths of higher curvature (Beaudot & Mullen, 2001; Hess et al., 2001). Their experimental condition may not require any binding mechanism since paths of low curvature may be detected by a single, spatially tuned unit with an elongated receptive field (Hess & Dakin, 1997). Contour integration is also very different from Ziebell and Nothdurft's experiments in which it is the binding of the background elements (with similar orientation) that forms a homogeneous region, from which an orthogonal line perceptually stands out. In this case the 'texture' pop-out results from a feature contrast between the target and a feature-homogeneous background, and it is difficult to discern the contribution of local and global feature contrasts in such figure-ground segmentation. Again contrary to contour integration, this task does not necessarily require a binding mechanism. Both experiments also used a simultaneous 4AFC experiment, while I used a temporal 2AFC task resulting possibly in a smaller difference in performance between the conditions (25–100% vs 50–100%). Moreover the simultaneous 4AFC requires that the subjects fixate a central locus surrounded by the four quadrant stimuli presented more peripherally. During one trial these four stimuli are flickering in the periphery of the visual field, an ideal condition (Allen & Hess, 1992) for optimal detection of the temporal transient identified by the present experiments. This type of display is then likely to favor peripheral detection of temporal changes, and may result in better performances for detecting a path in the asynchronous conditions. On the contrary a temporal 2AFC favors the involvement of the central visual field, and provides a better control of the locus of the focal attention by ensuring it is the same during the whole experiment. Finally and more importantly, Usher and Donnelly did not control for the order of path and background elements in the first stimulus cycle, and it is possible that the target (path elements) in their asynchronous condition was always presented before the background in the first cycle of the stimulus presentation.

#### 4.3. Comparison of experiments 1 and 2

Although the two experiments presented in this paper support the same conclusion with regard to the priming

effect of the path elements, they also show some quantitative differences. In particular, there is a striking difference in performance between experiments 1 and 2 for the smaller durations (below 50 ms) of the path-first condition: performance is as low as 60% in the first experiment while performance has already reached a ceiling of 100% in the second experiment. I can see three factors that could have contributed to this effect: a difference in perceived contrast, a difference in the perceived temporal modulation, and a masking effect.

The perceived contrast is different between the two experiments because the first is based on a flickering presentation, while the second is based on a steady presentation, placing a strong constraint on contrast integration. Clearly, the perceived contrast for the former follows a Talbot–Plateau law (25%, that is half of the physical contrast), and the perceived contrast for the latter is identical to the physical contrast (50%). However for both experiments the perceived contrast is well above the detection threshold for contour integration (Mullen et al., 2000), and it should not much affect the performance. Besides the difference in perceived contrast, the subjects also perceive differently the temporal modulations applied in each experiment. While all subjects are unaware of the condition (synchronous, path-first or background first) and do not report any perceived asynchrony or flicker in the first experiment (the stimulus is perceived as steady), they clearly detect a temporal change related to the onset asynchrony between path and background elements in the second experiment. This difference in the perception of the temporal changes is likely to affect significantly the performance for path detection if the subjects rely on the temporal segregation of the elements to detect a path. Once path and background elements are segregated on the basis on their temporal asynchrony, path detection is not limited by the noise elements (background). This may be the main source of the difference in performance between the two experiments. Another reason based on a masking effect (see Macknik & Livingstone (1998) for a recent hypothesis according to which it is the transient responses in V1 that render a stimulus visible), which could have induced the perceived differences in temporal modulation, may explain more directly why a transient mechanism can retain the target information in experiment 2 and not in experiment 1 for the shortest presentation (26 ms). In experiment 1, the presentations of path and background elements are mutually exclusive, and the background elements could act as a forward or backward mask towards the path elements depending on the order in the first cycle, reducing the visibility of the latter, and thus requiring a longer stimulation to be effective. In experiment 2, the presentations of path and background elements are not mutually exclusive, but rather additive, which could enhance, rather than reduce, the visibility of the path elements after 13 ms.

The second experiment differs in another way from the first experiment: its synchronous condition shows a lower performance with a slower increase compared to the background-first condition, while these two conditions show no significant difference in the first experiment (at least above 100 ms). This apparent discrepancy might be solved for the same above reason. Since there is a clear difference in awareness of the temporal changes between the two experiments, path detection for the background-first condition may be accomplished through the temporal segregation of the elements in experiment 2 (high signal-to-noise ratio) while contour integration may be required in experiment 1 (low signal-to-noise ratio). This seems particularly true for the two naive subjects (MC & AC) who show a very shallow increase of performance for the synchronous condition in experiment 2 (see Fig. 4). They may favor path detection based on the temporal segregation between path and background elements rather than on the orientation continuity. Subject WB, on the other hand, shows a much steeper increase in performance that may reflect his better training in path detection.

It is also noteworthy that the performance advantage of the path-first condition in the first experiment remains almost constant over time despite it originates from the first cycle of the stimulus presentation. In Usher and Donnelly (1998), this advantage is still present at 500 ms. This suggests that the asynchrony in the initial cycle of the presentation, even if unnoticed by the subjects, could have a long-term effect on the subsequent visual processing. A possible explanation compatible with experiments 1 and 2 is that the initial onset asynchrony between path and background elements could tag the location of the path elements, facilitating their detection or their participation in contour integration afterwards. The longer visual persistence for short stimulus duration (Bowen, Pola, & Matin, 1974; Breitmeyer, 1984; Colheart, 1980) and illusory contours (Meyer & Ming, 1988) may account partially for this effect. This could also be related to the feature inheritance and shine-through effects recently reported by Herzog et al. (Herzog, Fahle, & Koch, 2001; Herzog & Koch, 2001; Herzog, Koch, & Fahle, 2001).

## 5. Conclusion

My findings do not preclude that synchronous neural activation is important in figure-ground segregation (e.g., based or not on the onset delay). However they suggest that, if this hypothesis is correct, flickering stimuli do not interact with a neural binding mechanism that uses oscillatory temporal synchronization as an underlying mechanism. Hence, I argue that Usher and Donnelly's result is likely due to the high sensitivity of the visual system to stimulus onset, and that simple

flickering stimuli may be inadequate for revealing the neural code for binding in figure-ground segregation without controlling for the effect of stimulus onset. The importance of transient activation in contour integration is also supported by another recent study (Dakin & Bex, 2001, in press) although it fails to report an effect of stimulus order.

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