Pop-out from abrupt visual onsets

P. J. B. Hancock & W. A. Phillips

Centre for Cognitive and Computational Neuroscience,

Department of Psychology,

University of Stirling

FK9 4LA

The authors contributed equally to this work

To appear in Vision Research

ABSTRACT

We report a novel psychophysical paradigm that distinguishes the information present in abrupt stimulus onset from that in the following display. The task is to pick the one odd item from a set added to a pre-existing background of similar items. When all new items are added simultaneously, observers are impaired even at distinguishing one red item amongst several green ones. An asynchrony of about 40ms between target and distracter items restores performance, with evidence that it is cortical, rather than stimulus timing difference that is significant. The results are consistent with a role for neural synchrony in dynamic grouping.

Keywords: Abrupt visual onsets; Dynamic grouping**;** Pop-out; Synchronization; Transient signals

Introduction

Abrupt visual onsets are highly salient, and, though they have been often studied, much remains to be discovered concerning the perceptual organization of multiple onsets. Here we study the perceptual organization of multiple onsets that occur at or near the same time, in particular, we ask whether basic processes of figure-ground organization apply. This requires a paradigm that distinguishes the processing of information in the onset from that in the sustained input following onset. Previous studies have shown that when this is done multiple onsets can be seen as a whole in that their overall form can be identified (Wilson 1981). Those studies did not require figure to be distinguished from ground within the set of onsets, however, as all of the onsets were part of the form to be identified. When multiple abrupt onsets occur at or around the same time it is likely that they relate to a common event, so it is useful to perceive them as a whole, as suggested by the Gestalt principle of 'common fate'. Some ability to segregate synchronous events into figure and ground may also be useful, however, because different things can happen at the same time. Empirical studies are therefore needed to determine the extent to which the well-established principles of Gestalt organization apply also to the processing of abrupt onsets.

One simple initial hypothesis is that pre-attentive grouping applies to both abrupt onsets and sustained inputs, but post-attentive grouping applies only to sustained inputs. This is suggested by evidence that pre-attentive processes operate rapidly, whereas post-attentive processes may operate too slowly to be able to affect the brief transient burst of activity that signals onset. For example, there is evidence that figure-ground effects apply to both the transient and the sustained components of the activity of cells in visual cortex, whereas other effects, such as some of those involving attention, apply only to the sustained components of neural response (Lamme & Roelfsema, 2000). Here we focus on pre-attentive organization, which according to this hypothesis should apply to the perception of abrupt onsets as well as to sustained inputs.

The pre-attentive process studied here is that reflected by the phenomenon known as ‘pop-out’. It is well established that elements that contrast with a homogeneous background of other elements on features such as colour or orientation automatically attract both attention and eye-movements and can be detected on close to 100% of trials in visual search tasks. Such elements are therefore said to 'pop-out' (Nothdurft 1991). Rapid detection within a large array of surrounding elements is evidence that this figure-ground segregation occurs pre-attentively (Bergen & Julesz, 1983; Nothdurft, 1992). As pop-out effects are strong and well established we designed our experiments to ask whether they apply specifically to the perception of a set of abrupt onsets containing one element that contrasts with all the other new elements.

Prior studies of pop-out do not tell us this because most have used tasks that can be performed by processing information in the sustained input that follows onset. When a stimulus array appears against a blank background then the information in the sustained input is the same as that in the onsets. This confounding has been removed in previous studies of the perception of single events by first presenting a background of homogeneous elements and then adding or deleting one element at a randomly selected location. This element differs from the others only in being changed, so can be detected only by processing information about change, and cannot be detected by processing the information in the input that continues after the onset or offset (e.g. Phillips & Singer 1974). Here we generalize this design so as to study the perception of multiple onsets. The logic of this design could also be used to study the perception of multiple offsets.

Fig. 1 gives an example of the display sequence used. First, a random background of line elements is shown, then a set of new elements of the same kind appears at random locations within this background. Subjects are told to ignore the background and attend only to the new elements. This enables us to study how various patterns of onset are perceived when new elements are distinguished from the background only in being new. In Fig.1 b the background elements can be distinguished from the new elements as they are of lower contrast. Experiment 1 studies such conditions together with that in which new and background elements are of equal contrast. This latter condition is used in all following experiments.

Fig. 1 about here

Abrupt visual onsets rapidly produce brief transient bursts of neural activity that rise above the sustained neural response to sustained input (Colby & Goldberg, 1999; Irwin, Colcombe, Kramer, & Hahn, 2000; Gawne & Martin, 2000). These transient neural responses occur with short latency, and last for less than 100 ms. As they are closely time-locked to external events, studies of the perception of abrupt visual onsets can be used to provide psychophysical evidence on the role of the timing of neural activity in signalling figural organization. In particular, it has been suggested that the synchronization of neural responses may be a signal for grouping, so our experiments were designed to provide evidence on this issue. The synchronization hypothesis has been supported by physiological studies in visual (Gray, 1999; Singer, 1999; Castelo-Branco et al., 2000), auditory (DeCharms & Merzenic, 1996; Patel & Balaban, 2000), somatosensory (Steinmetz et al., 2000) and sensorimotor domains (Roelfsema et al., 1997), and by computational arguments (e.g. von der Malsburg, 1999). Some physiological findings have been thought to disprove this hypothesis, however (e.g. Shadlen & Movshon, 1999). For example, it has been found that neurons in V1 responding to texture elements are not more likely to synchronize when those elements are seen as part of the same figure (Lamme & Spekreijse, 1998). This evidence is not conclusive, however, as the relevant synchronization may have occurred in other visual areas.

Psychophysical paradigms based on controlling stimulus timing cannot provide direct evidence that the timing of neural activity is a signal for grouping when it is free to be set by internal criteria. However, if timing is not a dominant cue for grouping when it is determined by the input, then it is unlikely to be so when set by internal criteria.

Previous studies have limited the time available for pop-out by adding other items to the display after the background and target have been presented (e.g. Olds, Cowan and Jolicoeur, 2000; Nothdurft, 2000). If these masking items appear too quickly, then pop-out is prevented. In our study, the background items effectively form the mask, preventing pop-out once the transient signal from the new items has faded.

Experiment 1 studies performance when the onset of all new elements occurs synchronously, but one of them contrasts with the others in colour, luminance and orientation. We find that when no pre-existing background is visible then performance is close to 100%, for displays of both 50 and 300msec. When the pre-existing background elements have the same luminance as the new elements, however, performance is much lower. Experiment 2 studies performance when background and new elements have the same luminance, and one onset occurs at a different time from all the others but differs in no other way. Performance is then found to be close to 100% when the stimulus onset asynchrony (SOA) between target and other onsets is greater than about 40 ms. Experiments 3-5 study the asynchrony required for pop-out when combined with contrasts on other dimensions. We again find that an SOA greater than about 40 ms is required for reliable pop-out. By using elements that produce cortical responses with different latencies in Experiment 4 we find evidence that segregation depends upon the relative timing of cortical rather than of stimulus events.

General methods

Stimuli

Displays were composed using two square arrays, one on each side of the fixation point, each containing a total of about 80 distinct elements (Fig. 1). The elements were short line segments, placed in randomly chosen positions within the 10x10 square array. New random displays were computed on each trial. All experiments involved three groups of onsets within each trial. First, a background of about 70 elements per array (Fig. 1a) is displayed. A group of from 9 to 13 new elements is then added to each array. One of these is a single target element, added, to one array only, after 1s. The remainder are several contrasting non-target elements, added, together, at various Stimulus Onset Asynchronies (SOAs) as measured by their temporal relation to the onset of the target element. When target and non-target elements are added simultaneously this SOA is 0. In these trials there are then only two distinct displays: the background lasting for 1s (Fig. 1a); then a display lasting, in most experiments, 0.3 s in which target and non-target elements are both added to the background (Fig 1b). When target onset precedes that of non-targets the SOA is coded as positive, and asynchronies of 20, 40 and 100 ms were studied. In these trials there are therefore three distinct displays: the background, the background plus target, and finally the background plus both target and non-target elements. When target onset follows that of non-targets it is coded as negative, and asynchronies of -20, -40 and -100 ms were studied. In these trials there are therefore also three distinct displays: the background, the background plus non-targets, and finally the background plus both target and non-target elements. A timeline illustrating a positive SOA of 100mS is shown in Fig. 1d. The target appears on one side only, chosen at random. The location of the target within its array varied randomly over trials. The task and stimuli used are therefore comparable to those used in several prior studies of pop-out (e.g. Nothdurft, 1992, 2000, 2002), in that they require the rapid detection of a contrasting element within a very large set of elements (about 160 in our experiments). Accurate detection under such conditions is assumed to predominantly reflect fast pre-attentive processes rather than post-attentive serial search processes.

Apparatus

A Cambridge VSG (Visual Stimulus Generator) was used for all experiments. Stimuli were displayed via a Cambridge Control VSG2/3 card and a Panasonic P110 21-inch monitor operating at a 100 Hz refresh rate.

Procedure

All experiments used a spatial two-alternative forced choice (2AFC). The task was to attend to the new elements and to detect the odd one out. On each trial a display sequence lasting 1.3 s was shown (except for some at 1.05 s in experiment 1), and observers were told to indicate whether the target was in the left or right array by pressing the appropriate response key. No feedback was given.

All possible conditions within an experiment occurred at random across trials within blocks, such that each possible condition occurred three times within each block. Each block of trials was completed within about 8 minutes. For each subject the interval between blocks ranged from a few minutes to a few days.

Observers

Fourteen observers were used overall, from three to six being used in each experiment. All observers had normal or corrected to normal vision (including colour vision). The authors

(PH, WP) and two other observers (RE, MH) were aware of the hypotheses being tested, and of the design of the experiments. Seven were male (PH, WP, DB, RB, AC, BH, NG); and seven were female (RE, MM, AC, SF, DF, JS, MH). All were told as much about the general nature of the experiments as was necessary to enable them to give informed consent to act as participants.

Experiment 1: The effect of a pre-existing background on pop-out from synchronized onsets

Abrupt onsets are highly salient, and the question we asked is whether a set of new elements is organized into figure and ground as reflected by pop-out. If so, then pop-out should occur even when there is a pre-existing background of similar elements. There are several reasons for predicting that pop-out will apply to abrupt onsets. First, if subjects can perform a search task by attending to a distinct set of elements, e.g. as distinguished by colour, then reliable pop-out from within that set can occur (Wolfe, 2003). Pop-out may therefore occur within a set of elements that are distinguished by their abrupt onset. There is evidence that in attentive visual search paradigms subjects can voluntarily ignore old elements that are presented prior to a set of new elements containing the target (Watson & Humphreys, 1997; Watson, Humphreys & Olivers, 2003). If they can also do so in the paradigm studied here than performance will not be affected by either the presence or the luminance of the prior background elements. Second, pop-out occurs rapidly (Treisman, 1988), so there may be time for it to affect the transient component of response, and there is some evidence that it does (Vidnyánszky et al., 2001). Third, pop-out, as studied previously, only requires sufficient contrast in one feature dimension. The uniformity of width and length of the elements in Fig. 1b does not prevent pop-out due to contrast on other dimensions. If onset time is just another variable on which features may differ then synchrony of onset should not prevent pop-out due to other contrasts. Fourth, when temporal stimulus cues to grouping or segregation have been put in conflict with non-temporal cues the non-temporal cues have been found to be dominant (Leonards, Singer, & Fahle, 1996; Fahle & Koch, 1995; Kiper, Gegenfurtner, & Movshon, 1996). Grouping by synchrony in our paradigm should therefore not prevent pop-out due to non-temporal contrasts. Fifth, contrasting elements pop-out from brief displays, so, if brief displays produce only the transient component of neural response, then pop-out applies to the transient activity produced by abrupt onset. Sixth, computational theories using pre-specified feature hierarchies can segregate many textured inputs effectively (Sagi, 1995), and the mechanisms by which they achieve this operate on transient as well as upon sustained activity.

There are therefore several reasons for predicting that pop-out will apply to abrupt onsets. There is at least one reason for predicting that pop-out from abrupt onsets will be impaired if they are synchronised, however. It has been hypothesised that synchronization of neural activity specifies sets of signals to be processed as a whole (e.g. Gray, König, Engel, & Singer, 1989; Gray, 1999). There have been many psychophysical tests of this synchronization hypothesis (Fahle, 1993; Alais et al., 1998; Usher & Donnelly, 1998; Lee & Blake, 1999; Leonards et al., 1996; Leonards & Singer, 1998; Lee & Blake, 2001). Most show some role for timing in perceptual grouping, but some show that temporal cues have little effect when in competition with non-temporal cues (Leonards et al., 1996; Fahle & Koch, 1995; Kiper et al., 1996). These psychophysical studies therefore show that stimulus timing can be a cue to grouping, but they do not show any special status for timing amongst the many other cues that are also effective. They neither confirm nor refute the synchronization hypothesis, however, because it is not clear whether the timing of the relevant neural activity in those studies was locked to external stimulus timing. Our paradigm addresses this problem because the transient neural activity that signals onset needs to be, and is, transmitted rapidly through all relevant levels of processing. This implies a close relation between the timing of abrupt onsets and of their internal signals. The synchronization hypothesis therefore predicts that pop-out will not apply to a set of abrupt onsets that occur simultaneously, because their synchrony will cause them to be seen as a whole.

To strengthen the grounds for expecting pop-out, and thus provide a stronger test of the synchronization hypothesis, target elements in this experiment differed greatly from all other new elements on both colour (red vs green) and orientation (horizontal vs vertical). As we wanted large non-temporal contrasts, no attempt was made to achieve isoluminance of the red and green elements, so they also differed in luminance. This contrast in multiple dimensions does not require conjunction search. Targets and non-targets contrasted on each of the dimensions independently. The luminance of background items was varied from a level at which they were not visible to a level equal to that of the new elements. To examine the effects of display duration new elements (including the target) were displayed for either 50 or 300 ms.

Methods

Displays were similar to that shown in Fig. 1, where the target event differs from the other new elements in orientation, colour, and luminance. A background of green and red, horizontal and vertical line elements was first displayed. Each array location was filled with probability 0.7, with the features of each element being selected at random. After 1s, between 9 and 13 new elements were added to random locations within each of the two arrays such that the same total number of new elements was added to each of the two arrays. All new non-target elements were identical to each other and contrasted with the target element on all three non-temporal features. The orientation and colour of this target varied randomly from trial to trial. The displays covered 575 x 275 pixels in total, with each line element being 15 x 3 pixels. This produced a display size of 28 x 13 cm, i.e. ~ 21^{o} horizontal extent at a viewing distance of ~ 75 cm (so each line element ~35 min arc). Green line element luminance was ~73 cd/m^2, red line element luminance was ~21.5 cd/m^2.

The task was to attend to the new elements and to detect the odd one out. Observers made 24 responses to each of 4 target types (red vertical, red horizontal, green vertical, green horizontal) in each of 7 conditions that varied in the luminance of the pre-existing background with the lowest not being visible and the highest being identical to that of the new elements. The brightness ratios of background items to new ones were 1, 0.5, 0.25, 0.125, 0.063, 0.032 and 0.008, with the measured luminance being linear down to a ratio of 0.032 for both green and red channels (line fit r=0.999 for both red and green). This required 8 blocks of trials, within which each possible condition occurred 3 times. Six observers were used (MH, JS, AC, NG, DF, BH). There was diffuse lighting present in the test room.

Results

Results for individual observers are shown in Fig. 2, with averages in Fig 3. Results from horizontal and vertical targets did not differ and were combined. A number of effects are evident.

Figs. 2 and 3 about here

----

1. When the background was not visible or clearly of lower luminance than the new elements then target detection was reliable at close to 100%. However, when the background and new items did not differ in luminance, all observers' performance falls, though all but one remain above chance. Therefore, as predicted by the synchronization hypothesis, participants had difficulty in detecting one odd element within a set of synchronous onsets when there was no luminance difference to distinguish the new items from the old.

2. The form of the dependence of performance on background luminance is much the same for the two post-onset display durations but there are some differences. When background and target have the same luminance, there is little or no difference between average performance with a 50 ms post-onset display duration and that with a 300ms duration. When the background is dimmer, particularly at a ratio of 0.25 to that of the new items, performance at 300ms is better than that at 50ms. Given even longer display times, performance with this brightness difference should be at ceiling, as demonstrated by Fig. 1. With a 50ms post-onset display duration, performance at a luminance ratio of 0.25 is not significantly better than the equal luminance condition.

3. Performance is close to 100% even when the background elements are present, but dim (up to 0.1 of the luminance of new items in the 300ms condition). Under these conditions the background items can be seen but appear much dimmer than the new items.

4. The results show that pop-out from a 50 ms flash with no visible background is at ceiling, but that from onsets within a background of equivalent elements is much lower. If contrast detection tasks using brief displays (e.g. Nothdurft, 2002) reflect pop-out within sets of neural transient responses, and if contrast detection within a set of elements distinguished only by being new also reflects pop-out within transient responses, then pop-out from onsets within a background of equivalent elements, should have been much the same as that from. a 50 ms flash with no visible background. They were not, possibly because brief displays produce some sustained neural activity that lasts long enough to support detection. It would therefore be of interest to compare performance in our paradigm with that obtained from brief flashes when followed by a masking stimulus as used by Nothdurft (2002).

Experiment 2: Target onsets distinguished by asynchrony only

Experiment 1 shows that pop-out does not occur reliably from within a subset of elements that appears simultaneously with luminance equal to the background (ie all observers were significantly below 100%). If this is because synchronous signals are processed as a whole, then asynchronous signals should be segregated, even if they contrast in no other way. It is known that onset asynchrony can be an effective cue to figure-ground segregation, but different paradigms produce different measures of the asynchrony required to produce segregation. This experiment therefore studied the effect of SOA to determine how much asynchrony is required for pop-out from abrupt visual onsets.

Methods

As in Experiment 1, a background of green and red, horizontal and vertical elements was first displayed. Each array location was filled with probability 0.7, with the features of each element being selected at random. The luminance of these background elements was identical to that of the new elements (equal to the brightest condition of Experiment 1), so new elements were distinguished from background only in being new. After 1s, a target element was added to a random location within one array. The orientation and colour of this target varied randomly from trial to trial. Simultaneously, or 20/40/100 ms before or after the target, between 8 and 12 non-target elements were added to random locations within each of the two arrays such that the same total number of new elements was added to each of the two arrays. All new elements, including the target, were identical except for the time of onset. 300ms after the target appeared, the whole display was removed

Three observers (WP, RE, RB) were tested, each making 48 responses to each of 4 target types (red vertical, red horizontal, green vertical, green horizontal) in each of 7 SOA conditions (-100, -40, -20, 0, 20 40 100 ms) conditions. This required 16 blocks of trials, within which each possible condition occurred 3 times.

Fig. 4 about here

Results

There were no significant differences between performance for horizontal and vertical targets, so results from these conditions were combined and are displayed in Fig. 4. They show that, as expected, segregation in this paradigm can occur on the basis of onset asynchrony alone. Performance at an SOA of 0 was, necessarily, at chance. Asynchronies of more than 40 ms produce reliable pop-out, but asynchronies of 20 ms or less do not. The width of the temporal window separating perceptual grouping from perceptual segregation in this experiment therefore seems to be well defined, and to lie at about 40 ms for observers RE and RB, and between 40 and 100ms for WP. These results are consistent with those of Bowen, Lindsey and Smith (1977), who found a minimum ISI of 20ms to resolve two pulses when separated by a change of colour and luminance, increasing to around 60ms, dependent on colour contrast, with no luminance change.

The display duration of the non-target new elements covaries with SOA in this experiment. For example, when the non-target new elements appear 100ms earlier than the target element they are displayed for 400 ms as their offset is synchronized with that of the target. The target is always displayed for 300 ms which therefore differs from that of the non-targets at non-zero SOA's. Onset asynchrony is likely to be the effective cue supporting performance, however, because when one element pops-out then it is usually clear whether it appears before or after the other elements. In addition response selection often seemed to precede stimulus offset. As a further check we repeated this experiment with one subject leaving the display present until response, and obtained essentially the same dependence of performance on SOA (results not shown). Experiment 4 provides further evidence that SOA is the effective cue, and indicates that it is the asynchrony between cortical events that is relevant rather than that of external stimulus events.

Experiment 3: The effect of SOA when target onsets also contrast with non-target onsets in orientation, colour, and luminance

The asynchrony required for segregation in Experiment 2 is longer than that found in some other paradigms. Experiment 3 therefore asks whether shorter asynchronies will be effective when the target element also contrasts with other new elements in several non-temporal features.

Methods

Displays were as in Experiment 2, except that the target event differed from all other new elements in orientation, colour, and luminance, as well as in onset time. All new non-target elements were identical to each other and contrasted with the target on all three non-temporal features. As for Experiment 2, the target appeared 1 second after background and the whole display was removed 300ms later, luminance was at display maximum. The background consisted of green and red, horizontal and vertical elements, each array location filled with probability 0.7, with the features of each element being selected at random.

Observers made 48 responses to each of 4 target types (red vertical, red horizontal, green vertical, green horizontal) in each of 7 SOA conditions (-100, -40, -20, 0, 20 40 100 ms) conditions. This required 16 blocks of trials, within which each possible condition occurred 3 times. Four observers were used (RB, RE, SF, AC).

Results

There were no significant differences between performance for horizontal and vertical targets, so results from these conditions were combined. They show that many errors occurred at or near synchrony (Fig. 5). This replicates the findings of Experiment 1, and again shows that targets often fail to pop-out from synchronous onsets, even when they contrast greatly with other onsets on several non-temporal features.

The effect of SOA was much as in Experiment 2, so adding non-temporal contrasts had little effect on sensitivity to onset asynchrony. For green targets there was no significant difference between performance at SOAs of –20 ms and 0 ms, but both were significantly worse than at 20 ms and –40 ms ($p<0.01$, all significance calculations were done by resampling methods, using 1000 samples[1]). For red targets there was no significant difference between performance at SOAs of 20 ms and 0 ms, but both were significantly lower than at –20 ms and 40 ms ($p<0.01$). The asynchrony required for reliable pop-out is therefore around 40 ms. There may be some asymmetry around synchrony in that detection of red targets in a green background at an SOA of +20 and +40 ms is worse than that at –20 and -40 ms, while the detection of green targets in a red background shows the opposite effect. The significance of this was assessed by fitting a Gaussian curve to the results, again using resampling methods[2]. The estimated mean for the red targets is 7.0 ms, significantly different from zero ($p<0.01$), while the estimate for green targets is 2.5 ms, not significantly different from zero.

Experiment 4: The effect of SOA when targets contrast with non-targets only in luminance

As the above results show that relative timing has a large effect on pop-out from abrupt onsets, the question arises as to whether it is the timing of stimulus events that matters, or the timing of the cortical activity produced. To obtain evidence on this we used the relationship between stimulus luminance and the latency of transient cortical activity. Psychophysical and neurophysiological studies both show that the latency with which stimulus events produce cortical activity reduces with luminance. It has been suggested that if grouping depends on the relative timing of cortical responses then such latency differences may contribute to grouping (Gawne et al., 1996; Opara & Wörgötter, 1996; von Ferber & Wörgötter, 2000). We test this suggestion using latency differences to determine whether grouping depends upon the synchrony of stimulus events or of the cortical responses that they generate.

If it is the relative timing of cortical responses, rather than of stimulus events, that matters then bright target onsets will be grouped with non-targets that occur earlier, and dim targets with those that occur later. Conversely, using feature contrasts that are not associated with latency differences, such as those produced by differences in diagonal orientation, will remove any asymmetry, and performance will be worst at zero SOA. This experiment and the next test these predictions.

Methods

The stimuli and display sequences were as for Experiment 3, except that all line elements were diagonal, rather than being horizontal and vertical, and all were green. Background line elements were at 45° or 135° and were either bright (~73 cd/m^2) or dim (~8.5 cd/m^2), with each of the four possible combinations equally probable. The orientation

---

[1] E.g. to compare 0.7 and 0.8 on 96 observations, generate 96 random numbers in the range 0-1 and count the number less than 0.7, then do the same for 0.8. If there are more below 0.8, count as a "win" for 0.8. Repeat 1000 times. If 0.8 has more than 990 "wins", then it is significantly higher than 0.7, with $p< 0.01$, one-tailed.

[2] Data from +/- 100 ms were ignored as being mostly due to random errors. For the other 5 data points, generate points on a histogram with probability of 1-pc, where pc is the proportion correct at that time. So for the red targets at timing offset 0, pc=0.78. The value of 0.78 comes from a total of 384 observations, so put a point on the histogram for time = 0 with probability of 0.22, 384 times. Do this for each of the five times and then fit a Gaussian to the histogram. Repeat this 1000 times to get this many estimates for the mean. If > 995 of these estimates are above zero, then the true mean is greater than zero with $p< 0.01$, two tailed.

and luminance of the target element varied randomly across trials. The new non-target elements differed from the target element in luminance but not in orientation.

As above, the task was to attend to the new elements and to detect the odd one out. Each observer made 48 responses to each of 4 target types (bright 45°, bright 135°, dim 45°, dim 135°) in each of 7 SOA conditions (-100, -40, -20, 0, 20, 40, 100 ms) conditions. This required 16 blocks of trials, within which each possible condition occurred 3 times. Four observers were used (PH, WP, DB, RE).

Fig. 6 about here

Results

There were no significant differences in performance for left and right diagonal targets, so results from these conditions were combined. Performance of all four participants is shown in Fig. 6. As expected, detecting the onset of a bright target amongst several dim non-targets was much easier than detecting the onset of a dim target amongst several bright non-targets. The detection of a dim target was strongly dependent on SOA, but performance was not worst when target and non-target onsets were synchronous. Instead, as the synchronization and latency hypotheses predict, performance was worst when target onsets preceded non-target onsets. Fitting of Gaussian curves to these data, using the resampling method described above, gave an estimated mean (for the offset timing that gives worst performance) of 9.2 ms for the dim targets and -7.8 ms for the bright targets, both differing significantly from zero in the directions predicted by the hypothesis that it is the synchrony of cortical activity that determines grouping.

Thus, as predicted by the hypothesis that it is the synchrony of cortical activity that matters, the onset of bright elements interfered most with the detection of a dim target when they occur about 10 ms later (Fig. 6), which is approximately the latency difference expected for the difference in luminance used (Gawne et al., 1996). The small asymmetries found in the effects of SOA around synchrony in Experiment 3 may therefore be due to the luminance differences between red and green elements, and the latency differences that this entails.

Experiment 5: The effect of SOA when targets contrast with non-targets only in orientation

A contrast in diagonal orientation was chosen for this experiment because although it has been shown to be a salient contrast there are no grounds for supposing that differences in diagonal orientation are associated with latency differences. Therefore on the synchrony hypothesis performance should be worst at zero SOA.

Methods

The stimuli, display sequences, and procedures were all as for Experiment 4, except that the non-target elements differed from the target element in orientation rather than in luminance. The background again contained all four combinations of angle and luminance, randomly distributed. Observers made 48 responses to each of 4 target types (bright 45°, bright 135°, dim 45°, dim 135°) in each of 7 SOA conditions (-100, -40, -20, 0, 20, 40, 100 ms) conditions. This required 16 blocks of trials, within which each possible condition occurred 3 times. Four observers were used (PH, WP, DB, RE).

Results

There were no significant differences in performance for left and right diagonal targets, so results from these conditions were combined. Performance of all four participants is shown in Fig. 7. Detecting onsets that contrast in orientation was a little easier when all onsets were bright, rather than when all were dim. Detection in both cases was strongly dependent on SOA, however, and performance was worst in both cases when target and non-target onsets were synchronous. There was a small asymmetry when all new elements were bright, in that performance at an SOA of 20 ms was significantly worse than at –20 ms ($p<0.01$). This asymmetry is in the opposite direction to that observed for bright targets in Experiment 2. No asymmetry was observed in this experiment when all new elements were dim, however. Performance at SOAs of 20 ms and -20 ms did not differ significantly. In both cases, performance at asynchronies of 40 ms or -40 ms was significantly and substantially better than at synchrony. Fitting of Gaussian curves by resampling yielded an estimate of 1.5 ms for dim elements, not significantly different from zero, and 6.4 ms for bright elements, which does differ significantly from zero ($p<0.01$). While this deviation from zero is not as marked as those obtained in Experiment 4 (0 is still the lowest point on the average results) it was not predicted and we do not have an explanation.

Discussion

These results show that synchronized onsets tend to be seen as a whole, even when they contain a target that contrasts strongly with all others on several non-temporal features. They also show that asynchronous onsets tend to be segregated, even when homogeneous on all non-temporal features. These findings are therefore evidence that the timing of activity is a major signal for grouping abrupt onsets. In contrast to previous studies (e.g. Leonards, Singer, & Fahle, 1996; Fahle & Koch, 1995; Kiper, Gegenfurtner, & Movshon, 1996), they imply that perceptual organization can depend more upon temporal than upon non-temporal cues, possibly because, in our paradigm, the timing of the relevant neural activity is closely locked to external stimulus events. Thus, though we assume that other interpretations are possible[3], we see our results as providing strong prima facie support for the synchronization hypothesis.

---

[3] One referee pointed out that a logical possibility is that the arrival of a new set of stimuli could trigger a new "snapshot" of information on the retina, thus mixing the background and new items in the transient signal.

By using stimulus events that evoke transient cortical responses with different latencies we have also found evidence that it is the timing of cortical activity that determines grouping, rather than the timing of external events. This supports suggestions that segregation can be based on latency differences (Gawne et al., 1996; Opara & Wörgötter, 1996; von Ferber & Wörgötter, 2000).

As noted above, our results contrast with previous findings showing that grouping can depend more on spatial than on temporal cues (e.g. Fahle & Koch, 1995; Kiper et al., 1996). Beaudot (2002), for example, noted that it has been 'shown that large temporal asynchrony has no significant effect on figural binding, compared to, for example, small spatial displacement which can destroy it.' The opposite occurred in our paradigm. Pop-out from abrupt onsets depended significantly upon small asynchronies, even when targets were distinguished by a maximal orientation contrast. It was still sensitive to asynchrony even when large contrasts in orientation, colour, and luminance were combined. A simple explanation for the greater dependence on temporal relations in our paradigm is that it requires the use of neural activity that is time-locked to input, whereas the previous paradigms do not. Most previous psychophysical studies of the role of temporal cues in grouping have used continuous patterns of change, such as flicker or jitter. Such changes may not continuously produce transient bursts such as those produced by abrupt onsets. It would be metabolically expensive and of doubtful utility to maintain activity at the high level of such transient bursts during the whole course of such continuous patterns of change. Physiological (Singer & Phillips, 1974) and psychophysical evidence (Phillips & Singer, 1974) indicates that when onsets and offsets occur rapidly one after the other then they interact so as to reduce or remove the transient burst. It is therefore likely that large transient bursts are produced only at the onset of flicker or jitter. Sustained neural responses to such sustained patterns of change may be closely time-locked to the stimulus at early stages of processing, or in pathways specialized for the processing of motion or flicker, such as the magnocellular pathways, but this does not apply in general, and in particular not to the higher levels of the parvocellular pathway (Rager & Singer, 1998; Leonards & Singer, 1998). Performance in paradigms studying the perception of sustained patterns of change could therefore be based upon sustained neural activity that is not closely time-locked to the external stimulus.

Though the findings reported here support the synchronization and latency hypotheses, two caveats are necessary. First, evidence for the relevance of synchronization is not evidence against a role for firing rate. There is good evidence that both are used, and that they are mutually supportive (Watt & Phillips, 2000). To see how this could be so, first note that prespecified feature detectors work better with simplified uncluttered inputs, but inputs are often cluttered. At each level of processing, operations such as dynamic grouping and contextual modulation simplify the data received by each local processor by organizing it into figure and ground and by assigning salience. Second, the asynchrony required for segregation in our experiments was a few 10s of ms rather than a few ms. This is consistent with the size of the coincidence window (i.e. the width of the cross-correlogram peaks) found in many neurophysiological studies of internally determined synchronization, which ranges from 5 to 50 ms (Engel & Singer, 2001). Furthermore, the latencies with which a single stimulus produces transient bursts of activity in different cortical regions and visual pathways varies by a few 10s of ms (e.g. with latencies in the magnocellular pathway being less than those in the parvocellular pathway) (Lamme & Roelfsema, 2000). Recurrent interactions between feedforward and feedback activity also occur on the timescale of a few 10s of ms (Bullier, 2001; Hupe et al., 2001; Pascual-Leone & Walsh, 2001). As all of these activities need to be processed as a whole, this suggests that activities occurring within a few 10s of ms are grouped. Asynchronies of a few ms might be used to signal segregation of the sustained signals that follow transient bursts, but whether this is so or not, our results show that the perceptual segregation of transient bursts requires asynchronies of a few 10s of ms, even when combined with other strong feature contrasts. Some other psychophysical paradigms that have been used to study this issue have also failed to find evidence for grouping due to asynchronies of a few ms (Kandil & Fahle, 2001). Asynchronies of a few ms may nevertheless have a functional role (Diesmann et al., 1999). For example, the RF inputs to some local processors, such as those involved in motion perception, may be specifically arranged to give them high temporal sensitivity. Some prior studies of the role of temporal relationships in grouping may therefore be reflecting this special sensitivity, rather than the general use of synchronization as signal of dynamic grouping.

The sensitivity of performance to asynchronies of 10 ms or less that has been observed in some visual grouping tasks (e.g. Usher & Donelly, 1998; Lee & Blake 2001; Leonards , Singer & Fahle, 1996) may be due to the translation of the temporal differences into spatial differences by ocular microtremor (Wallis, submitted). Such eyemovements would not affect performance in our task, however, and this may explain why, in our paradigm, we do not find any effects of such small asynchronies.

Our discussion so far has implied that pre-attentive grouping processes either apply to transient activity or they do not, and that synchronization either is the signal for grouping or it is not. We must also consider the possibility that some pre-attentive grouping processes apply to abrupt onsets and some do not, and that some groupings are signalled by synchronization and some are not. Watt and Phillips (2000) argue that it is necessary to distinguish between pre-specified groupings that are computed rapidly by feedforward connectivity and groupings that are created by an interaction between the particular input and grouping operations. They refer to the latter as dynamic grouping, and review evidence that it occurs both pre- and post-attentively. Pre-specified groupings are those that combine inputs within what is known as the receptive field (RF) so as to determine the cell's RF selectivity. Dynamic groupings of these activities are influenced by inputs from far beyond the RF, via connections that have been referred to as contextual field (CF) connections. Both Phillips and Singer (1997) and Watt and Phillips (2000) argue that it is only dynamic groupings that are signalled by synchrony. On this view therefore, the perceptual organization of abrupt onsets will depend upon pre-specified grouping processes but not upon dynamic grouping processes. This does not imply that all pre-attentive grouping applies to onsets, as there is good reason to suppose that much pre-attentive grouping is dynamic (Watt & Phillips 2000).

Observers in Experiments 1 and 3 showed some ability to detect non-temporal feature contrasts in synchronized activity when several strong non-temporal cues were combined. This could in part be due to short-term visual memory processes, particularly when the target appears in the vicinity of the fixation point. It could also be due in part to the detection of local feature contrasts by rapidly operating feedforward RF connections. If all figure-ground organization were due to such connections, however, then it would apply to transient as well as to sustained activity. One way to interpret these results is therefore to hypothesize that detection of a contrasting element within a set of onsets depends only in part on dynamic grouping. To the extent that it does so, it depends on their temporal relations. Our results can therefore be seen as support for the distinction between dynamic groupings and the pre-specified groupings that determine RF selectivity. This requires a distinction to be drawn that is usually ignored in discussions of 'binding'. Grouping is not achieved in only one way, but involves groupings that are pre-specified as well as those that are specified only after the data to be grouped are known (Watt & Phillips, 2000). Local contrasts of orientation, for example, may be computed by pre-specified RF connections that have a limited spatial range. More flexible dynamic groupings may require more open operations that depend on CF connections and use synchrony to signal the groupings created. This predicts that some segregation of synchronous activities will occur, and that to the extent that this is due to pre-specified RF computations it will be less flexible and creative than that which is computed dynamically.

Similar predictions are suggested by evidence for two kinds of grouping mechanism: one achieved via rapidly operating but spatially constrained segmentation mechanisms; and, one via segregation processes that are slower but less spatially constrained and more flexible (e.g. Forte et al., 1999; Nothdurft, 2000). One interpretation of the results reported above is therefore that fast local segmentation mechanisms apply to the transient activity that signals abrupt change as well as to sustained patterns of activity, whereas the slower dynamic segregation processes that also include non-local relations apply only to the sustained activity. Synchronization of neural activity to within about 20 ms could be a signal for grouping in both cases, however, with this being determined by the external input rather than by internal criteria in the case of transient bursts.

Paradigms designed to study pop-out are in some ways similar to those designed to study serial visual search in that both involve detection of one item amongst several others. There are also major differences, however. Pop-out paradigms are usually designed to study texture segmentation involving rapid pre-attentive processes that apply in parallel across the visual field (e.g. Nothdurft, 1991; 1992), and performance in these paradigms has been related in detail to single unit neurophysiological studies of primary visual cortex (e.g. Kastner, Nothdurft & Pigarev, 1997, Nothdurft, 2002). In contrast, visual search paradigms are designed to study higher-level post-attentive processes that operate serially across object representations (e.g. Treisman, 1988). The paradigm reported here can be compared and contrasted with a version of visual search in which participants first view a set of to-be-ignored nontargets, and must then decide whether a pre-specified target appears in a second set that is added to the first after 1 sec or so (Watson & Humphreys, 1997). Targets are not distinguished by any low-level feature contrast that would produce fast and accurate performance that is independent of the number of items, so participants must search for the target, and the central independent variable measured is the search rate calculated from RTs across conditions that vary only in the number of items present. These search rates indicated that in some conditions participants could ignore the first set of items, and search only through the second set. This effect has come to be called the preview benefit in visual search, and has excited widespread interest, many further studies (Watson, Humphreys & Olivers, 2003), and much debate (Jiang, Chun & Marks, 2002; Donk & Theeuwes, 2001).

The preview benefit paradigm may have some relevance here, as, like ours, it involves the detection of an element that is present in a set of items that is added to a prior set. In their study of the preview benefit in visual search, Olivers, Watson, Humphreys (1999) concluded that old items can be completely excluded from the search through a set of new items. If that were so in our paradigm then performance would not have been affected by the luminance of the prior set of items, but Experiment 1 found that it was, and it would have been highly accurate in all conditions of Experiments 2 - 5, which it clearly was not. This difference between their results and ours is no surprise, however, as the paradigms differ in several ways. In our paradigm, but not theirs, processing of the prior set of items is made necessary by the task as the target is not defined in the final set of items alone. The pop-out item differs in one or several low-level features from all the other new items, but is identical on all non-temporal features to many of the items in the initial set. Furthermore, as our focus is on pre-attentive pop-out rather than on visual search we use displays with about 160 elements, specify the target only as 'the odd one out', display the array containing the target only briefly, and calculate detection accuracy rather than search rates. These differences do not rule-out any contribution from a preview benefit effect to performance in our paradigm,but they do suggest that it does not make a major contribution. This is also implied by findings showing that in the serial search paradigm singletons within the new set of items are not easily detected when they share non-temporal features with the old items (Olivers & Humphreys, 2003). Similarly, the differences that there are between the two paradigms do not rule-out a contribution to performance in preview benefit paradigms from the transient neural responses produced by abrupt changes and from processes of temporal segmentation. Donk and Theeuwes (2001) present evidence indicating that prioritisation by abrupt onsets can make a substantial contribution to the preview benefit. Jiang, Chun and Marks (2002) present evidence that grouping and segmentation through synchrony and asynchrony also make a substantial contribution to performance in the preview benefit paradigm. Our results provide further evidence for the importance of both abrupt onsets and temporal segmentation. This is not evidence against the existence of a top-down process of visual marking that inhibits old items in visual search paradigms, such as that hypothesized by Watson, Humphreys and Olivers (2003), however. Bottom-up processes of temporal segmentation and top-down attentional processes are in no way mutually exclusive, and their relative contributions to performance in various paradigms needs to be clarified by further research.

Overall, our results suggest an important role for the synchrony of cortical activity in signalling the groupings reflected by pop-out. In contrast to previous findings they show that temporal cues to grouping can override non-temporal cues. We suggest that this is because in our paradigm timing of the relevant internal activity is locked to stimulus events, whereas in the previous studies it was not. We do not assume that no other explanation for these results is possible, but they do support a strong prediction made by the synchronization theory, and this prediction contrasts with that made on several other grounds.

Acknowledgements

Ruth Elvish and Michelle Heron helped with running the experiments. Michael Cook, Roger Watt, and Florentin Wörgötter gave valuable advice on earlier drafts of this paper. We are grateful to Adam Reeves and two anonymous reviewers for much advice in clarifying the presentation.

References

Alais, D., Blake, R., & Lee, S.-H. (1998). Visual features that vary together over time group together over space. *Nature Neuroscience, 1*(2), 160-164.

Beaudot, W. H. A. (2002). Role of onset asynchrony in contour integration. *Vision Research, 42*(1), 1-9.

Bergen, J. R., & Julesz, B. (1983). Parallel versus serial processing in rapid pattern discrimination. *Nature, 303*, 696-698.

Bowen, R.W., Lindsey, D.T. and Smith, V.C. (1977) Chromatic two-pulse resolution with and without luminance transients. *Journal of the Optical Society of America, 67*, 1501-7.

Bullier, J. (2001). Feedback connections and conscious vision. *Trends in Cognitive Sciences, 5*(9), 369-370.

Castelo-Branco, M., Goebel, R., & Neuenschwander, S. (2000). Neural synchrony correlates with surface segregation rules. *Nature, 405*, 685-689.

Colby, C. L., & Goldberg, M. E. (1999). Space and attention in parietal cortex. *Annual Review of Neuroscience, 22*, 319-349.

DeCharms, R. C., & Merzenic, M. M. (1996). Primary cortical representation of sounds by the coordination of action-potential timing. *Nature, 381*, 610-613.

Diesmann, M., Gewaltig, M.-O., & Aertsen, A. (1999). Stable propagation of synchronous spiking in cortical neural networks. *Nature, 402*, 529-533.

Donk, M. & Theeuwes, J. (2001) Visual marking beside the mark: prioritizing selection by abrupt onsets. *Perception and Psychophysics*, 63 (5), 891-900.

Engel, A. K., & Singer, W. (2001). Temporal binding and the neural correlates of sensory awareness. *Trends in Cognitive Sciences, 5*(1), 16-25.

Fahle, M. (1993). Figure-ground discrimination from temporal information. *Proceedings of the Royal Society of London B., 254* , 199-203.

Fahle, M., & Koch, C. (1995). Spatial displacement, but not temporal asynchrony, destroys figural binding. *Vision Research, 35*(4), 491-494.

Forte, J., Hogben, J. H., & Ross, J. (1999). Spatial limitations of temporal segmentation. *Vision Research, 39*, 4052-4061.

Gawne, T. J., Kjaer, T. W., & Richmond, B. J. (1996). Latency: another potential code for feature binding in striate cortex. *Journal of Neurophysiology, 76*(2), 1356-1360.

Gawne, T. J., & Martin, J. M. (2000). Activity of primate V1 cortical neurons during blinks. *Journal of Neurophysiology, 84*(5), 2691-2694.

Gray, C. M. (1999). The temporal correlation hypothesis of visual feature integration: still alive and well. *Neuron, 24*, 31-47.

Gray, C. M., König, P., Engel, A. K., & Singer, W. (1989). Oscillatory responses in cat visual cortex exhibit inter-columnar synchronization which reflects global stimulus properties. *Nature, 338*, 334-337.

Hupe, J.M., James, A.C., Girard, P., Lomber, S.G., Payne, B.R., & Bullier, J. (2001). Feedback connections act on the early part of the responses in monkey visual cortex. *Journal of Neurophysiology, 85*(1), 134-145.

Irwin, D. E., Colcombe, A. M., Kramer, A. F., & Hahn, S. (2000). Attentional and occulomotor capture by onset, luminance and colour singletons. *Vision Research, 40*(10-12), 1443-1458.

Jiang, Y., Chun, M. & Marks, L. E. (2002) Visual marking: selective attention to asynchronous temporal groups. *Journal of Experimental Psychology: Human Perception and Performance*, 28 (3), 717-730.

Kandil, F. I., & Fahle, M. (2001). Purely temporal figure-ground separation. *European Journal of Neuroscience, 13*, 2004-2008.

Kastner, S., Nothdurft, H. C., & Pigarev, I. N. (1997) Neuronal correlates of pop-out in cat striate cortex. *Vision Research*, 37, 371-376.

Kiper, D. C., Gegenfurtner, K. R., & Movshon, J. A. (1996). Cortical oscillatory responses do not affect visual segmentation. *Vision Research, 36*(4), 539-544.

Lamme, V. A. F., & Roelfsema, P. R. (2000). The distinct modes of vision offered by feedforward and recurrent processing. *Trends in Neurosciences, 23*, 571-579.

Lamme, V. A. F., & Spekreijse, H. (1998). Neural synchrony does not represent texture segregation. *Nature, 396*, 362-366.

Lee, S.-H., & Blake, R. (1999). Visual form created solely from temporal structure. *Science, 284*, 1165-1168.

Lee, S.-H., & Blake, R. (2001). Neural synergy in visual grouping: when good continuation meets common fate. *Vision Research, 41*, 2057-2064.

Leonards, U., & Singer, W. (1998). Two segmentation mechanisms with differential sensitivity for colour and luminance contrast. *Vision Research, 38*(1), 101-109.

Leonards, U., Singer, W., & Fahle, M. (1996). The influence of temporal phase differences on texture segmentation. *Vision Research, 36*(17), 2689-2697.

Nothdurft, H-C. (1991) Texture segmentation and pop-out from orientation contrast. *Vision Research*, 31, 1073-1078.

Nothdurft, H.-C. (1992). Feature analysis and the role of similarity in preattentive vision. *Perception and Psychophysics, 52*(4), 355-375.

Nothdurft, H.-C. (2000). Salience from feature contrast: temporal properties of saliency mechanisms. *Vision Research, 40*, 2421-2435.

Nothdurft, H.-C. (2002). Latency effects in orientation popout. *Vision Research, 4*2, 2259-2277.

Olds,E.S., Cowan, W.B. and Jolicoeur, P. (2000) The time course of pop-out search. *Vision Research, 40*, 891-912

Olivers, C. N. L. & Humphreys, G. W. (2003) Visual marking inhibits singleton capture. *Cognitive Psychology*, 47, 1-42.

Olivers, C. N. L., Watson, D. G. & Humphreys, G. W. (1999) Visual marking of locations and feature maps: Evidence from within-dimension defined conjunctions. *Quarterly Journal of Experimental Psychology*, 52A(3), 679-715.

Opara, R., & Wörgötter, F. (1996). Using visual latencies to improve visual segmentation. *Neural Computation, 8*, 1493-1520.

Pascual-Leone, A., & Walsh, V. (2001). Fast backprojections from the motion to the primary visual area necessary for visual awareness. *Science, 292*, 510-512.

Patel, A. D., & Balaban, E. (2000). Temporal patterns of human cortical activity reflect tone sequence structure. *Nature, 404*, 80-84.

Phillips, W. A., & Singer, W. (1974). The function and interaction of 'on' and 'off' transients in vision. I. Psychophysics. *Experimental Brain Research, 19*, 493-506.

Phillips, W. A., & Singer W. (1997). In search of common foundations for cortical computation. *Behavioral and Brain Sciences, 20*(4), 657-683.

Rager, G., & Singer, W. (1998). The response of cat visual cortex to flicker stimuli of variable frequency. *European Journal of Neuroscience, 10*(5), 1856-1877.

Roelfsema, P. R., Engel, A. K., Konig, P., & Singer, W. (1997). Visuomotor integration is associated with zero time-lag synchronization among cortical areas. *Nature, 385*, 157-161.

Sagi, D. (1995). The psychophysics of texture segmentation. T. V. Papathomas, C. Chubb, A. Gorea, & E. Kowler (Editor), Early vision and beyond . Cambridge, MA.: MIT Press.

Shadlen, M. N., & Movshon, J. A. (1999). Synchrony unbound: A critical evaluation of the temporal binding hypothesis. *Neuron, 24*(1), 67-77.

Singer, W. (1999). Neural synchrony: a versatile code for the definition of relations. *Neuron, 24*, 49-65.

Singer, W., & Phillips, W. A. (1974). The function and interaction of 'on' and 'off' transients in vision. II. Neurophysiology. *Experimental Brain Research, 19*, 507-523.

Steinmetz, P. N., Roy, A., Fitzgerald, P. J., Hsiao, S. S., Johnson, K. O., & Niebur, E. (2000). Attention modulates synchronized neuronal firing in primate somatosensory cortex. *Nature, 404*, 187-190.

Treisman, A. (1988). Features and objects: The Fourteenth Bartlett Memorial Lecture. *The Quarterly Journal of Experimental Psychology, 40A*(2), 201-237.

Usher, M., & Donnelly, N. (1998). Visual synchrony affects binding and segmentation in perception. *Nature, 394*, 179-182.

Vidnyánszky, Z., Papathomas, T.V. & Julesz, B. (2001) Contextual modulation of orientation discrimination is independent of stimulus processing time. Vision Research 41(22): 2813-2817

von der Malsburg, C. (1999). The what and why of binding: the modeller's perspective. *Neuron, 24*, 95-104.

von Ferber, C., & Wörgötter, F. (2000). Cluster update algorithm and recognition. *Physical Review E, 62*(2-A), 1461-1464.

Wallis, G. A spatial explanation for synchrony biases in perceptual grouping: Consequences for the temporal binding hypothesis. (submitted to *Perception and Psychophysics*, Nov 2003)

Watson, D. G., & Humphreys, G. W. (1997) Visual marking: Prioritizing selection for new objects by top-down inhibition of old objects. *Psychological Review*, 104, 90-122.

Watson, D. G., Humphreys, G. W. & Olivers, C. N. L. (2003) Visual marking: using time in visual selection. *Trends in Cognitive Sciences*, 7 (4), 180-186.

Watt, R. J., & Phillips, W. A. (2000). The function of dynamic grouping in vision . *Trends in Cognitive Sciences, 4*(12), 447-454.

Wilson, J. T. L. (1981). Visual persistence at both onset and offset of stimulation. *Perception and Psychophysics, 30*(4), 353-356.

Wolfe, J.M (2003). Moving towards solutions to some enduring controversies in visual search. *Trends in Cognitive Sciences,* 7(2): 70-76.

Ziebell, O., & Nothdurft, H.-C. (1999). Cueing and pop-out. *Vision Research, 39*, 2113-2125.

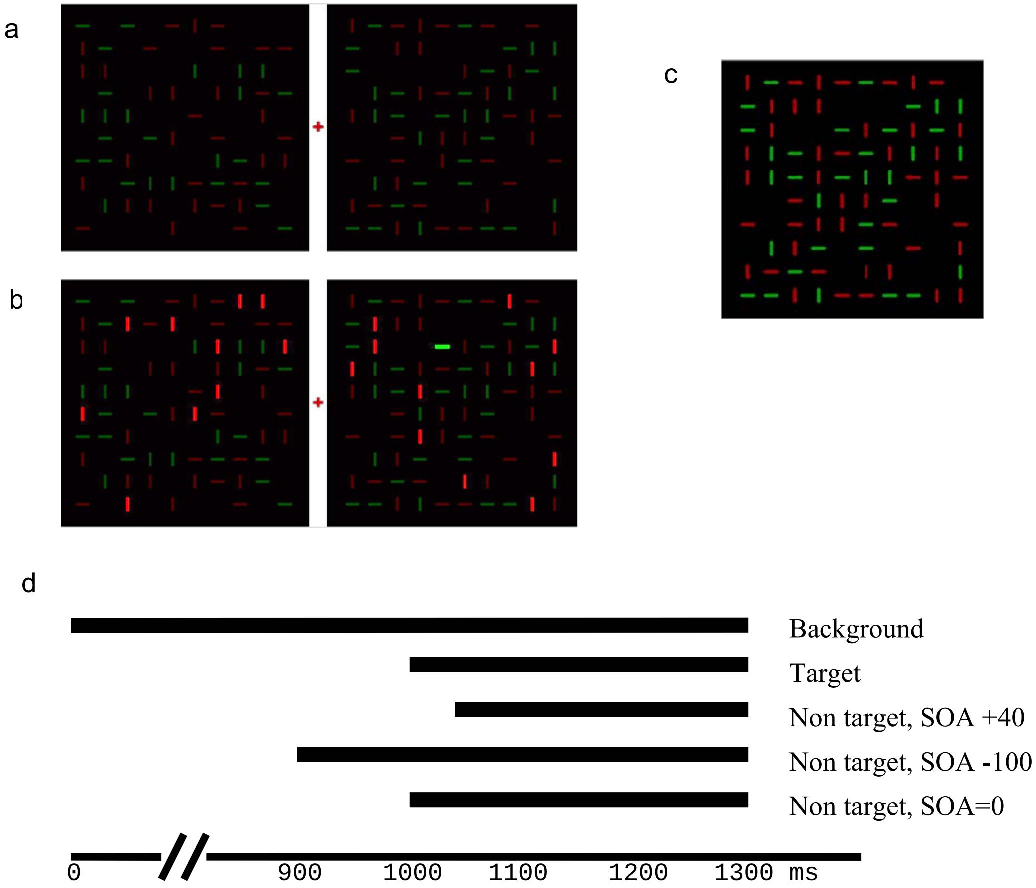

Figure 1. (a) In Experiment 1, a background of green and red, horizontal and vertical elements was first displayed. Observers are asked to look at the central fixation point. (b) After 1 s, new items are displayed, with one (the target) differing from the others in both colour and orientation. Task is 2AFC, which side has the odd item? All items are removed 50 or (shown in (d)) 300ms after target onset. In this example, the background luminance is much lower than the new items (which are always all at 100%), allowing easy detection. (c) When background is at full luminance, shown here for right panel from (b), it is not possible to identify the target element from the static display. (d) Generalised timeline for the display for all experiments: Background items appear at time zero, followed 1 second later by the target element. Other new, non-target elements appear up to 100ms before or after the target. 1300ms after the start, the whole display is removed. In experiment 1, SOA is always zero (target and other new elements appear simultaneously) but in some versions the display lasts only 1050ms in total, switching off 50ms after the new items appear.

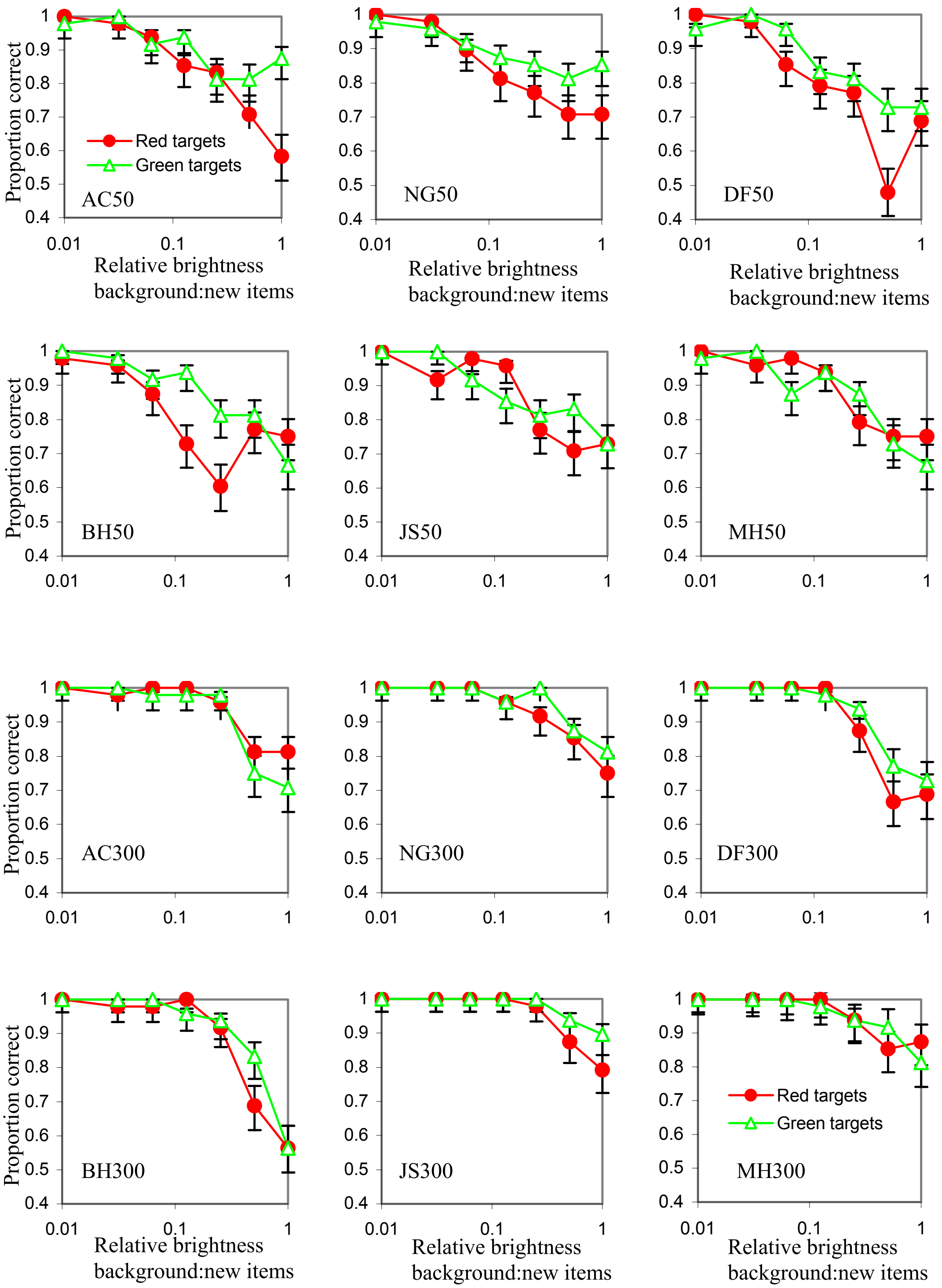

Figure 2. Results from each of the six observers in experiment 1. The display was terminated 50ms (upper panels) or 300ms (lower panels) after the onset of the new items.

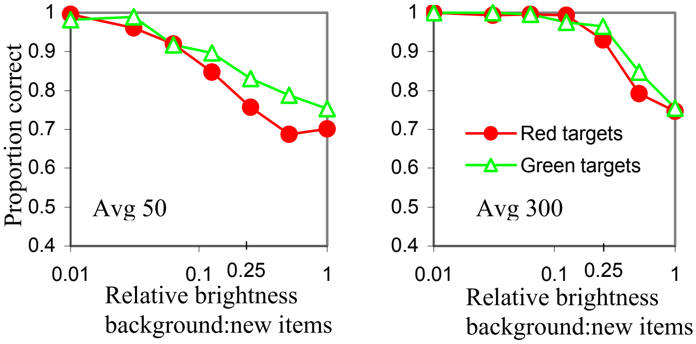

Figure 3. Averaged results from Experiment 1, for the 50 ms post-onset display duration on the left panel, and 300 ms duration on the right.

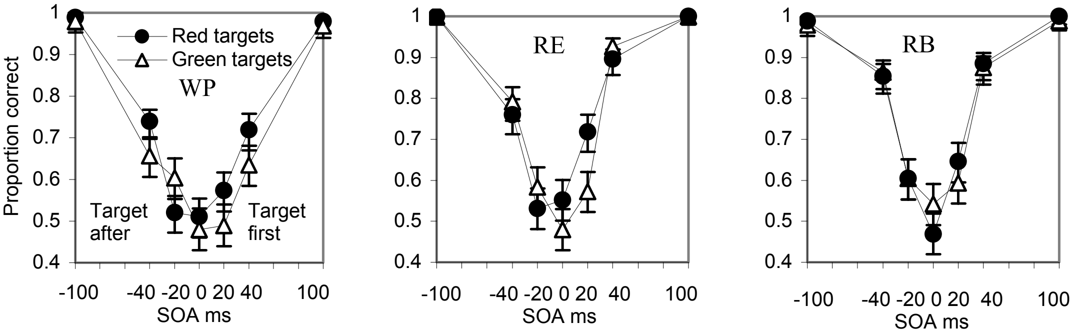

Figure 4. Results for the three observers in Experiment 2. Random background field of green and red, horizontal and vertical lines, to which new items are added after 1 second. Target differed from other new items only in onset time, task is to say which side the odd new item was on. SOA: stimulus onset asynchrony between target and other new items.

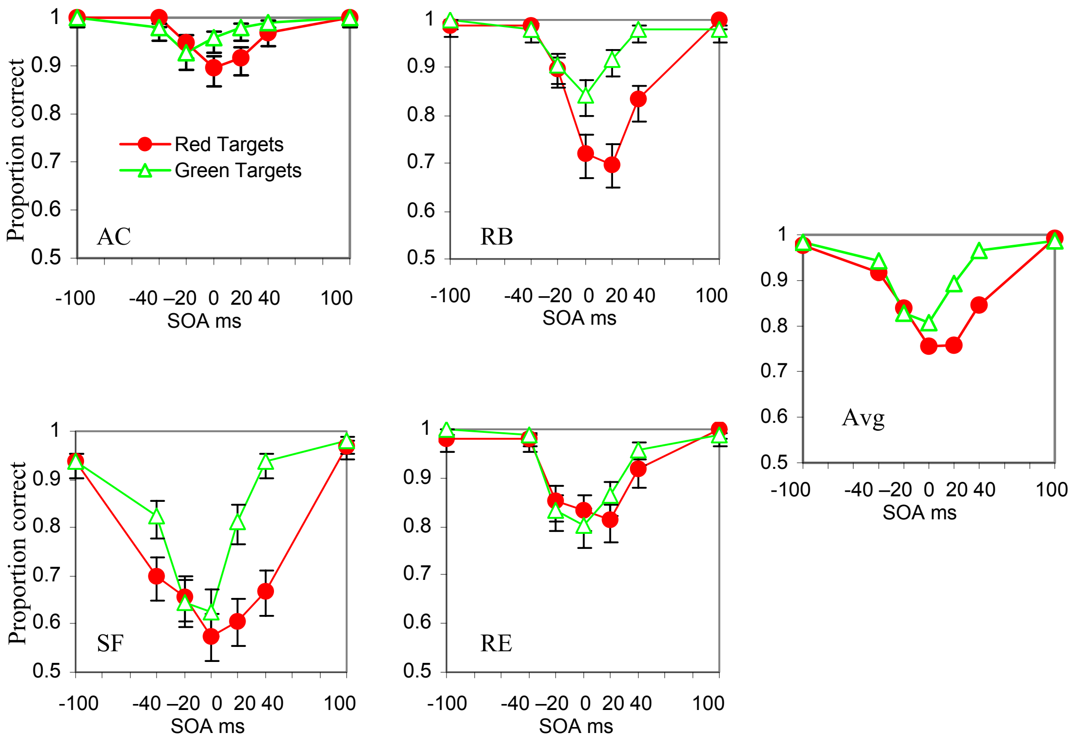

Figure 5. Results for 4 observers, and average, for experiment 3. Random background field of green and red, horizontal and vertical lines, to which new items are added after 1 second. Target differed from other new items in colour, orientation and luminance (red being dimmer than green) and with variable onset time, task is to say which side the odd new item was on. SOA: stimulus onset asynchrony between target and other new items.

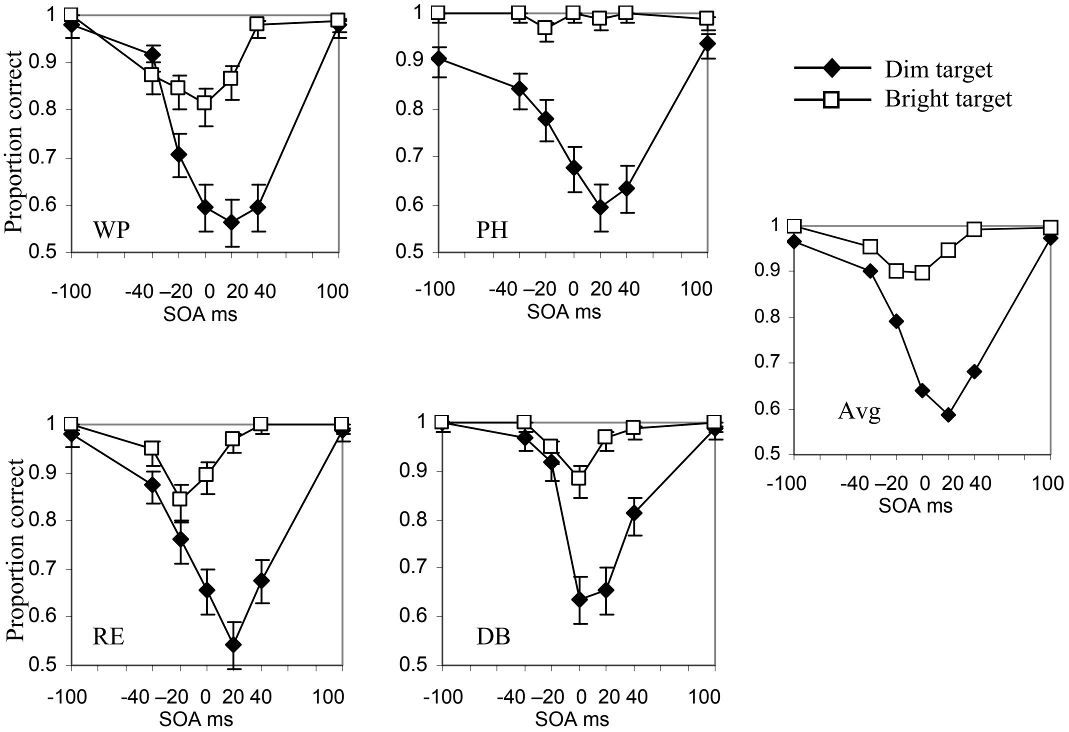

Figure 6. Results for 4 observers, and average, for experiment 4. All elements were green, with each at 45^{o} or 135^{o} and either bright (~73 cd/m2) or dim (~8.5 cd/m2). Each of the four possible combinations occurred in the initial background display with equal probability. The new elements were all of the same orientation but one, the target, differed in luminance. Task is 2AFC, which side is the odd new item? SOA: stimulus onset asynchrony between target and other new items.

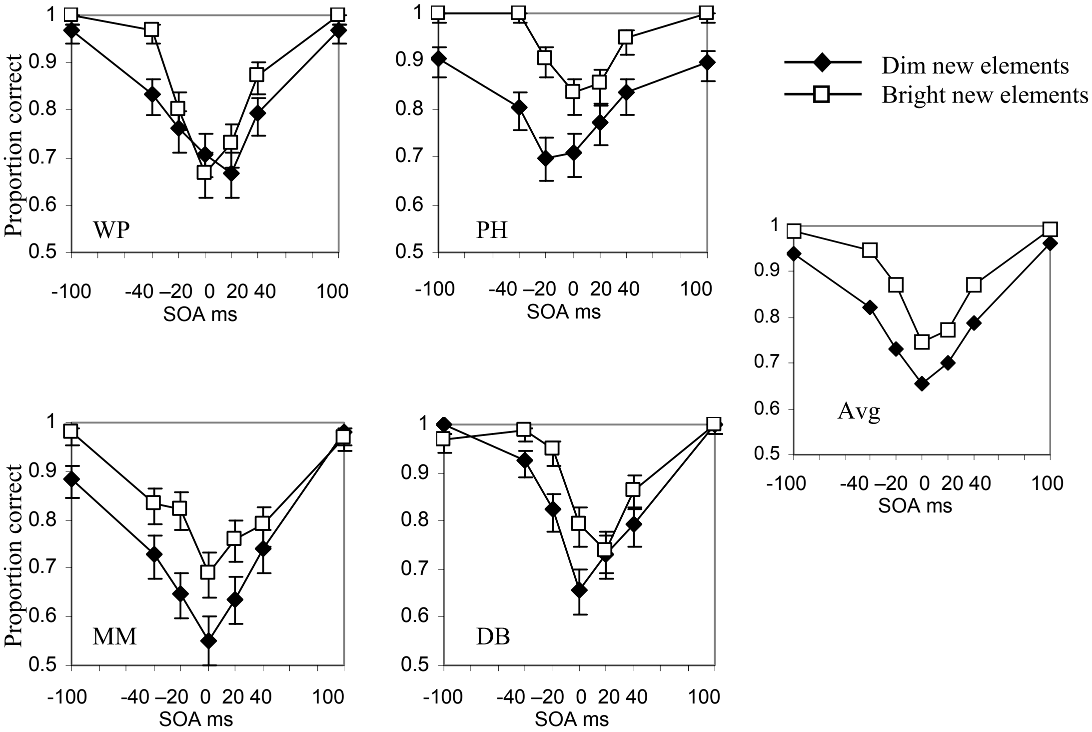

Figure 7. Results for 4 observers, and average, for experiment 5. All elements were green, with each at 45° or 135° and either bright (~73 cd/m2) or dim (~8.5 cd/m2). Each of the four possible combinations occurred in the initial background display with equal probability. The new elements were all of the same brightness but one, the target, differed in orientation. Task is 2AFC, which side is the odd new item? Filled diamonds: dim new elements, open squares: bright new elements. SOA: stimulus onset asynchrony between target and other new items.