Crowding is reduced by onset transients in the target object (but not in the flankers)

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In peripheral vision, objects that are visible in isolation become difficult to identify in clutter. This *crowding* effect is typically strong when objects are similar in a given dimension (e.g., color) and weak when they differ. Here we examine the selectivity of crowding for temporal differences—namely, the transient signals associated with object onsets and offsets. Observers judged the orientation of a peripheral Gabor target surrounded by four flankers. Midway through each trial, selected elements "blinked" off and on again. Performance was poor (crowding was strong) when all Gabors blinked simultaneously or when only the flankers blinked. In contrast, performance improved dramatically when the target alone blinked despite the continued presence of the flankers. This asymmetric release from crowding occurs across a range of blink durations and target–flanker separations. A similar release was found when the target onset was delayed relative to the flanker onsets, though varying the target offset had little effect. This suggests that blinks (composed of offset *and* onset events) reduce crowding specifically because they separate target and flanker *onsets*. Finally, with luminance pedestals added to the Gabors, crowding was reduced by blinks in the target pedestal only when the target Gabor was present; pedestal blinks before/after the stimulus Gabors (as precues/postcues) had no effect. That is, transients do not simply cue the target location. The asymmetry of this effect (reduced crowding with target transients, no effect with flanker transients) also precludes explanations based on *similarity* or *grouping*. We attribute our findings to the isolation of the target in transient (vs. sustained) visual channels.

Introduction

Although objects in our peripheral vision can be scaled to become visible in isolation, these same objects are often difficult to recognize in clutter. We refer to this as *crowding* (Bouma, 1970; Pelli, Palomares, & Majaj, 2004; Levi, 2008). Crowding is typically stronger in peripheral vision than in the fovea, though it is elevated in foveal vision during development (Atkinson, Anker, Evans, & McIntyre, 1987; Jeon, Hamid, Maurer, & Lewis, 2010) and particularly so in cases of strabismic amblyopia (Flom, Weymouth, & Kahneman, 1963; Levi & Klein, 1985). The disruption to visual recognition in these cases provides a clear motivation to understand how to reduce crowding–or avoid it altogether. However, although much is known about the selectivity of crowding with static stimuli, the dynamic properties of crowding are far less understood. Because the visual world is ever-changing, we sought to examine whether crowding is modulated by the transient signals that occur when objects appear and disappear.

Previous research has identified several ways to reduce crowding. The simplest is to increase the spatial separation between the target object and its surrounding flankers: Close flankers will impair target recognition; more distant flankers will not. The *critical spacing* at which this transition occurs increases with target eccentricity (Bouma, 1970) and is greater with flankers along a radial axis with respect to fixation than with flankers along the tangential axis (Toet & Levi, 1992). Significant variation has also been observed both across the visual field and across observers (Petrov & Meleshkevich, 2011). Because the critical spacing depends on the *perceived* position of flanker elements rather than their *physical* position (Dakin, Greenwood, Carlson, & Bex, 2011; Maus, Fischer, & Whitney, 2011), this spatial tuning is likely to develop late in the visual hierarchy, consistent with a range of proposed mechanisms for crowding more generally (He, Cavanagh, & Intriligator, 1996; Pelli et al., 2004; Freeman & Simoncelli, 2011).

The second way to reduce crowding is to add feature differences between the target and flanker objects. Crowding affects the recognition of a diverse range of visual features: everything from orientation (Wilkinson, Wilson, & Ellemberg, 1997) and color (van den Berg, Roerdink, & Cornelissen, 2007) to complex objects, like faces (Martelli, Majaj, & Pelli, 2005). Typically, crowding is strong when target and flanker objects are similar along a given dimension and weak when they are not. This has been observed for features such as contrast polarity and color (Kooi, Toet, Tripathy, & Levi, 1994), depth (Butler & Westheimer, 1978; Kooi et al., 1994), orientation (Wilkinson et al., 1997), spatial frequency (Chung, Levi, & Legge, 2001), and even holistic similarity for faces (Louie, Bressler, & Whitney, 2007; Farzin, Rivera, & Whitney, 2009). These effects have been interpreted first as evidence that crowding is tuned for target–flanker similarity (Kooi et al., 1994) and second as evidence that crowding depends on the grouping between target and flanker elements (because manipulations outside of the local context can yield similar modulations, e.g., Livne & Sagi, 2007; Sayim, Westheimer, & Herzog, 2008; Saarela, Sayim, Westheimer, & Herzog, 2009; Manassi, Sayim, & Herzog, 2012). Consistent with both approaches, the feature-based release from crowding appears to be symmetric in the sense that the direction of the feature difference is immaterial: A black target among white flankers shows as much release as a white target among black flankers (Kooi et al., 1994).

In the temporal domain, crowding appears to be modulated by both separation and similarity. First, much like the effect of spatial separation, crowding is reduced by the separation of target and flanker objects in time. The *flanker preview* effect in particular demonstrates that crowding is reduced when the flankers are presented before the target compared with their simultaneous presentation (Huckauf & Heller, 2004; Scolari, Kohnen, Barton, & Awh, 2007). Flankers presented after the target can also reduce crowding, though this is less effective than previewing (Huckauf & Heller, 2004). Second, if we consider the temporal properties of objects as a feature (like color or depth), then crowding is also tuned for temporal similarity. Although there is little selectivity for the direction of motion, there is some reduction in crowding when target and flanker objects differ in temporal frequency (Bex & Dakin, 2005). The precise pattern of selectivity varies between observers, but the magnitude of release for a given temporal frequency difference is linked with its salience in a visual search task (Gheri, Morgan, & Solomon, 2007). Altogether then, crowding is tuned for both temporal distance and target–flanker differences in temporal frequency.

The clear temporal selectivity of crowding led us to explore whether it is similarly modulated by the abrupt temporal changes associated with object appearance, disappearance, and substitution. A large body of work demonstrates that the visual system is highly sensitive to these transient events, although their effect on crowding is unknown. In visual search tasks for instance, objects with an abrupt onset will "pop out" (Yantis & Jonides, 1984) with a strength that is greater than that of other feature differences, such as color and contrast polarity (Jonides & Yantis, 1988; Theeuwes, 1991). Transient events are also strong attractors of attention in change-detection tasks (Phillips & Singer, 1974; O'Regan, Rensink, & Clarke, 1999; Kanai & Verstraten, 2004) and powerful modulators of the temporal alternations in binocular rivalry (Blake, Westendorf, & Fox, 1990; Wilson, Blake, & Lee, 2001). In all of these cases, transient onset signals show greater perceptual prominence than transient offsets (Phillips & Singer, 1974; Yantis & Jonides, 1984; Wilson, Blake, & Lee, 2001). This sensitivity likely reflects the independent operation of channels in the visual system selective for either transient or sustained object presentations (Kulikowski & Tolhurst, 1973; S. J. Anderson & Burr, 1985; Snowden & Hess, 1992; Cass & Alais, 2006). It has been further proposed that the transient system is more directly involved in visual awareness than the sustained system (Motoyoshi & Hayakawa, 2010). Indeed, adaptation of the transient system has been used to decrease observers' awareness of the flankers in a cluttered array, thereby reducing crowding (Wallis & Bex, 2011).

Given the exquisite sensitivity of the visual system for these transient events, we examined whether onset and offset signals could also alter the strength of crowding. Ordinarily, manipulations of the transient onset of target and flanker elements would require

their separation in time, thereby confounding both temporal similarity and separation. Because prior studies suggest that the temporal selectivity of crowding follows both these dimensions (as above), we sought to examine the influence of onset and offset transients independently of their occurrence at the onset and offset of the stimulus itself. We did so by applying a brief "blink" to selected stimulus elements midway through stimulus presentation. These blinks involved an abrupt reduction to zero contrast and the abrupt restoration to their prior contrast after some duration. Importantly, the placement of these blinks at the midpoint of the trial allowed us to examine their influence on crowding separately from the transients at the beginning and end of each trial, which were constant across all conditions. To foreshadow our primary result, we find an interesting asymmetry whereby transient events in the target object reduce crowding and transients in the flankers (or all elements together) do not.

Experiment 1

We first examined whether a brief "blink" event could reduce crowding when applied to the target, the flankers, or all elements at once. Because we expected that these blinks might vary in visibility, a range of blink durations was examined.

Method

Observers

Five observers were tested in this first experiment: two of the authors (JG and BS) and three naïve observers. All had normal or corrected-to-normal visual acuity and gave written consent.

Apparatus

Experiments were programmed in MATLAB (Mathworks, Inc.) on an Apple iMac computer running PsychToolbox software (Brainard, 1997; Pelli, 1997). Stimuli were presented on a ViewSonic G220f 21-in. CRT monitor with 1024 × 768 pixels resolution and a refresh rate of 100 Hz. The monitor was calibrated using a Minolta photometer and linearized in software to give a mean and maximum luminance of 50 and 100 cd/m^2, respectively. Stimuli were presented binocularly and viewed from a distance of 57 cm with responses made via keypad. No feedback was provided. The same apparatus was used for all four experiments.

Stimuli and procedures

In each trial, observers were presented with either a single target Gabor or a target surrounded by four flanker Gabors. All Gabor elements had a spatial frequency of 2 c/° with 0° phase presented within a Gaussian envelope with a standard deviation of 0.32° and a peak of 50% Weber contrast above the mean luminance. Observers were required to make a two-alternative forced choice regarding the orientation of the target Gabor (left/right of vertical). The target orientation was varied between 75° and 105° in 11 steps of 3° according to the method of constant stimuli. In each trial, the flanker orientations were randomly selected from a range between 70° and 110° with a mean centered on 90°. This variation allowed some degree of heterogeneity in our stimuli (both to minimize adaptation and to ensure that the target tilt was not an isolated cue) whilst also ensuring that any averaging of the flanker orientations with that of the target (Parkes, Lund, Angelucci, Solomon, & Morgan, 2001; Greenwood, Bex, & Dakin, 2009) would have no cumulative effect on bias over the course of the experiment.

Stimuli were presented at 10° eccentricity in either the left or right visual field. This location was randomly selected in each trial to minimize the effects of contrast adaptation at each point. When present, flankers were placed at a center-to-center separation of 1.6° from the target, well within the standard critical spacing for 10° eccentricity (Bouma, 1970; Toet & Levi, 1992). A white Gaussian blob with a spatial standard deviation of 0.1° was presented at the center of the screen as a fixation point. Stimuli were followed by masks presented on both sides of the screen, each consisting of a circular aperture with a 15° diameter and a cosine edge, filled with white noise that was filtered to have a 1/f energy spectrum. This was presented for 200 ms, after which observers were required to make a response.

In all, five conditions were tested. The first two were "standard" crowding conditions: an *uncrowded* condition with an isolated target stimulus (a single Gabor) presented at 10° and a *no-blink* crowding condition in which four flanker Gabors surrounded the target. In both of these conditions, stimulus presentation was for 400 ms with no stimulus changes, followed by the mask. The remaining three "blink" conditions had the flankers present, with a temporal event midway through stimulus presentation. The temporal event was a brief blink in element presentation—a reduction of stimulus contrast to zero for a given period, as depicted for two example trials in Figure 1. In the *all-blink* condition, the blink was simultaneously applied to all five elements in the stimulus array (see part 1 of Movie 1). In the *target-blink* condition, the blink was applied solely to the target while the flankers remained present throughout (see Figure 1A and part 2 of Movie 1). The reverse was true for the *flankers-blink* condition in which all four
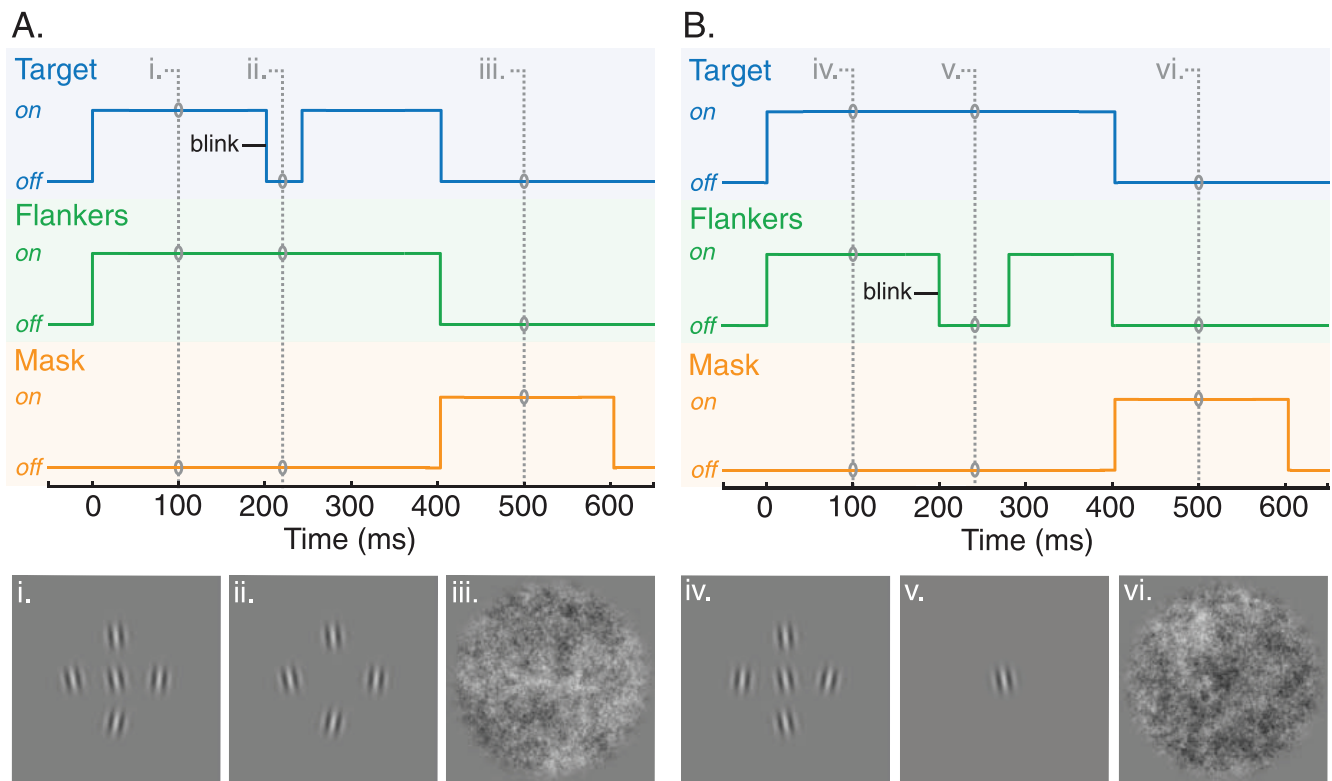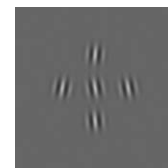
Figure 1. The time course and stimulus appearance of example trials in Experiment 1. (A) An example *target-blink* trial. The target Gabor contrast is plotted as a function of time via the blue line (whose height ranges from "off" at zero contrast to "on" at 50% Weber contrast). A 40-ms blink is depicted, beginning 200 ms after stimulus onset. The four flankers, indicated by the green line, share their initial onset with the target and remain present throughout the 400-ms trial. After the final target/flanker offsets, a noise mask was presented for 200 ms as shown by the yellow line. The appearance of stimuli in this trial is shown at three time slices, indicated by gray dashed lines and inset panels depicting (i) the full stimulus array as it appeared before and after the blink, (ii) stimuli in the *target-blink* phase, and (iii) the post-mask. (B) An example trial in the *flankers-blink* condition with an 80-ms blink. Gray lines indicate three time slices with inset panels depicting (iv) the full stimulus array, (v) the isolated target during the *flankers-blink* phase, and (vi) the postmask.

flankers blinked simultaneously while the target remained unchanged (Figure 1B and part 3 of Movie 1).

For the three blink conditions, blinks with four durations were tested: 10, 20, 40, and 80 ms. In each case, the offset of stimulus contrast (to begin the blink) occurred 200 ms after the initial stimulus onset (as depicted in Figure 1). The restoration of stimulus contrast (the "onset" portion of the blink) then occurred 10–80 ms afterward. In all cases, the final stimulus offset always remained at 400 ms after the initial stimulus onset. The four blink durations were tested in separate blocks with each of the three blink conditions interleaved within. With eight repetitions per target orientation, there were 264 trials per block. The *uncrowded* and crowded *no-blink* conditions were presented in separate blocks of 88 trials each. Each block was repeated three times, all randomly interleaved, to give 3,696 trials per observer. Breaks were taken when required.

Results and discussion

Responses were scored as the proportion of trials in which the target orientation was reported to be

Movie 1. Stimuli from three example trials in Experiment 1. The first part shows an example *all-blink* trial. Target and flanker stimuli share a common onset before a brief "blink" is applied to all elements (here with a 40-ms duration). Stimuli are then restored before the mask replaces all elements 400-ms after the initial onset. The second part shows a *target-blink* trial where the blink is applied to the target only (again for 40 ms), while the third part shows an example *flankers-blink* trial where the blink is applied solely to the flankers.
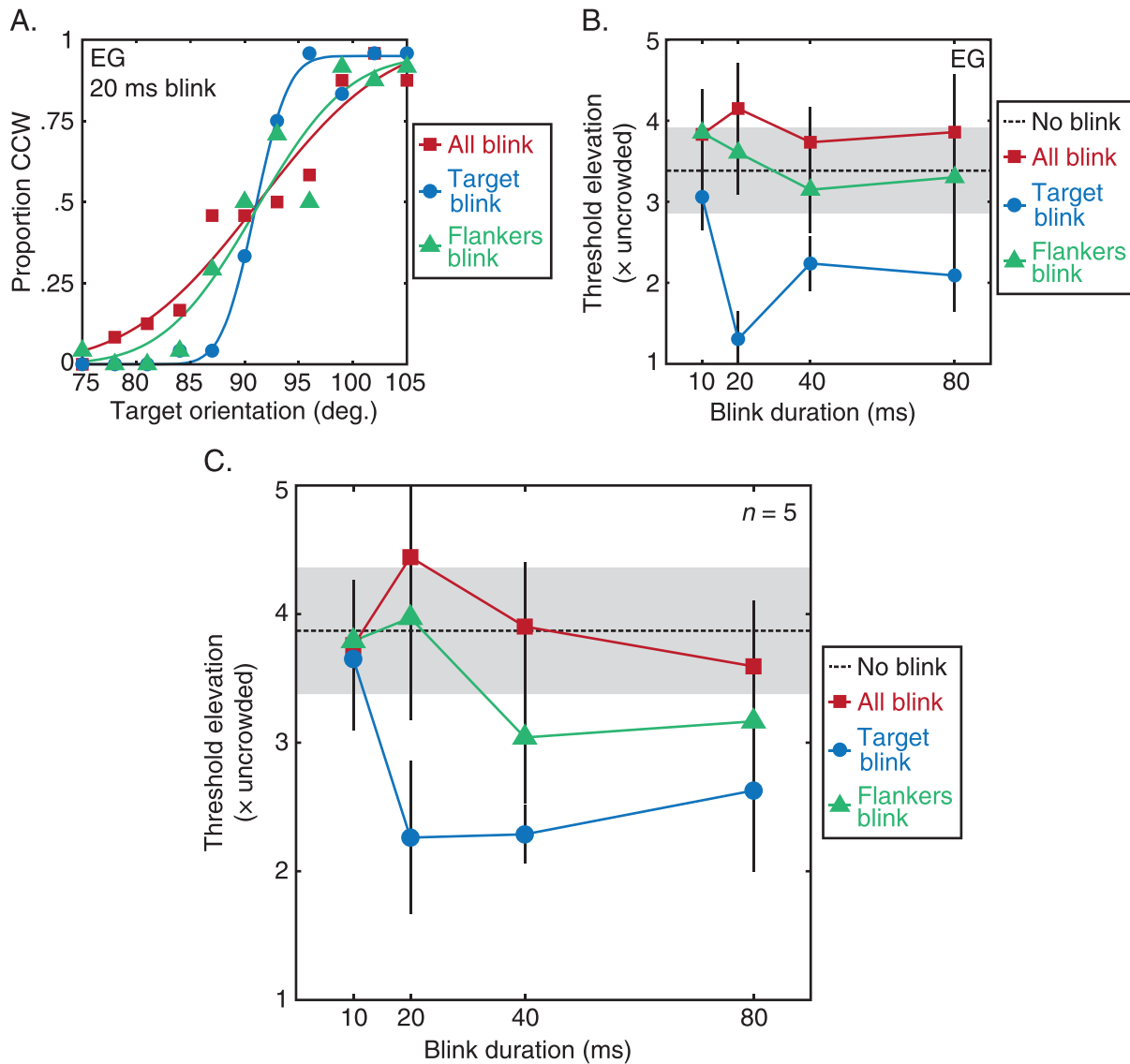
Figure 2. Results from Experiment 1. (A) Example responses and psychometric functions for observer EG in the 20-ms blink condition. Only the three blink conditions are shown, in which the blink was applied to all elements (red squares), just the target (blue circles), or just the four flankers (green triangles). Responses are plotted as the proportion of trials in which the target orientation was reported as counterclockwise of vertical. (B) Threshold elevation values (crowded thresholds divided by uncrowded thresholds) for example observer EG. The dashed black line shows the threshold elevation resulting from a crowded array without blinks. The gray region and black error bars give the standard error of the mean derived from bootstrapping. With blink durations longer than 10 ms, blinks applied to the target (blue circles) decrease threshold elevation strongly, while blinks applied to all elements (red squares) or just the flankers (green triangles) are far less effective. (C) Threshold elevation values averaged across the five observers and plotted as a function of blink duration, as in panel B. Here the gray region and black error bars give the standard error of the mean between observers. The pattern of results is identical to that seen for the example observer.

counterclockwise of vertical. Psychometric functions were fit to the data using a three-parameter cumulative Gaussian (fitting the midpoint, slope, and ceiling/lapse rate). Example functions are presented in Figure 2A for observer EG in the 20-ms blink condition with each of the three blink conditions shown (where either all elements, just the target, or the four flankers had a blink midway through the trial). It can be seen that these conditions do not induce any changes in bias; curves remain centered on the vertical decision boundary, consistent with the average flanker orientation being maintained at 90°. However, there is a clear difference in slope, with the *target-blink* condition yielding a steep function (indicating better orientation discrimination) compared with the shallow curves of the other two blink conditions.

Thresholds were taken as the orientation difference required to shift performance from 50% counterclockwise responses by ±25% (e.g., to 75% counterclockwise). For each observer, threshold elevation scores were then obtained by dividing crowded thresholds by uncrowded thresholds. These scores are shown for observer EG in Figure 2B with the average values for all five observers shown in Figure 2C. A value of one here indicates uncrowded levels of performance. The dashed black line depicts performance in a crowded array when no blinks occurred, i.e., the standard level of crowding. Performance for the three blink conditions is plotted as a function of the blink duration.

A similar pattern is evident for both observer EG and the averaged data set. At 10 ms, the threshold elevation in all three blink conditions is equivalent to the standard crowding condition; transients of this duration thus have little effect on crowding regardless of the element to which they are applied. A difference emerges with 20-ms blinks. Here, blinks in the target (blue) improve performance considerably. For the averaged data, threshold elevation is reduced to almost half that seen in the *no-blink* condition. In contrast, blinks in all elements together (red) or in the flankers alone (green) have no effect on the degree of crowding (i.e., performance is similar to the *no-blink* condition). With longer blink durations, the improvement in performance in the *target-blink* condition remains clear; performance is maintained at a level that is approximately twice the uncrowded threshold. In contrast, the *all-blink* and *flankers-blink* conditions deviate only slightly from the degree of crowding induced in the *no-blink* baseline.

To analyze the data, we conducted a three-way, mixed-effects ANOVA with blink condition and blink duration entered as fixed effects and the observers entered as a random effect (suggested by Howell, 1997, p. 485). This produced a significant main effect for both blink condition, $F(2, 24) = 7.60$, $p = 0.002$, and duration, $F(3, 24) = 3.71$, $p = 0.043$, and a significant interaction between the two, $F(6, 24) = 4.78$, $p = 0.003$. There was no main effect of observer, $F(4, 24) = 2.16$, $p = 0.064$, nor were any of the interactions with the observers significant (all $ps > 0.05$). Our primary interest, however, is in whether the blink conditions significantly improved performance relative to the crowded *no-blink* baseline. For these planned comparisons, 95% confidence intervals were computed around the mean difference (with paired samples) for all observers. Comparisons between the *target-blink* and *no-blink* conditions reveal significant differences (that do not include zero) for the 20-ms (−2.66, −0.55), 40-ms (−2.32, −0.85), and 80-ms (−2.15, −0.33) blink durations but not with 10 ms (−1.12, 0.69). At each of these same durations, confidence intervals for the difference between the *flankers-blink* and *no-blink* conditions all

include zero: 10 ms (−0.62, 0.46), 20 ms (−0.99, 1.19), 40 ms (−1.70, 0.04), and 80 ms (−2.17, 0.76). That is, although transient events in the target significantly reduce crowding, the same transient events in the flankers do not.

Our results thus demonstrate that crowding is tuned for the transient events associated with the appearance and disappearance of objects. This release from crowding differs from that observed previously with stimulus dimensions such as contrast polarity, where a black target among white flankers yields as much release from crowding as a white target among black flankers (Kooi et al., 1994). In the present case, brief temporal events in the target produce a strong reduction in crowding despite these same events having no effect when applied to the flankers alone or to all elements simultaneously. We will consider the basis for this shortly.

Note that the improvement in the *target-blink* condition occurs despite the fact that the blinks actually decreased the presentation time of the target. Similarly, the null effect in the *flankers-blink* condition occurs despite the target being uncrowded during the blink. We suspect this asymmetry would disappear with longer blink durations as observers became increasingly likely to catch uncrowded glimpses of the target; informal examination with blink durations of 160 ms did indeed allow such improvements in performance. At the other end of the scale, the lack of effect with 10-ms flashes is likely due to the temporal gap being below perceptible limits. Indeed, even in the fovea, temporal gap–detection thresholds for double-flash stimuli are typically above 10 ms (Dunlap, 1915; Purcell & Stewart, 1971). Nonetheless, as soon as the blinks become apparent within the target (somewhere above 10 ms but below 20 ms), there is a strong reduction in crowding.

It is also worth remarking on the phenomenology of this effect. Several observers reported that, at stimulus onset, a jumbled or unclear crowded array was initially seen. When a *target blink* occurred midway through the trial, it appeared as if the target orientation suddenly emerged from this jumbled array. In these cases, two distinct orientations were seen in the target location: one before the blink and one afterward. When this occurred, observers were instructed to report the second orientation, which they indicated was clearer than the first. We suspect that the initial perceived orientation was that induced by crowding (Greenwood, Bex, & Dakin, 2010), likely the average of target and flanker orientations (Parkes et al., 2001; Greenwood et al., 2009), with the veridical orientation then replacing this percept after the target blink. Readers can potentially experience this themselves by viewing Movie 1 in their peripheral vision; the target orientation should be clearly visible in the *target-blink* demonstration and difficult to determine otherwise.

Experiment 2

Our results demonstrate that transient events can reduce crowding when they occur in the target object. We next sought to examine whether this occurs at all target–flanker separations where crowding is present, in part to ensure that the effect was not limited to specific stimulus parameters. We were also motivated by suggestions that target–flanker differences (e.g., in color) may reduce the critical spacing for crowding (Scolari et al., 2007). As above, the critical spacing is the target–flanker separation at which flankers no longer produce crowding, a value that is typically half the target eccentricity (Bouma, 1970) with a radial/tangential anisotropy (Toet & Levi, 1992). Although some have observed reductions in the critical spacing (Scolari et al., 2007), it is not clear whether this reflects a reduction in the region of interference for crowding or simply a general improvement in performance at all separations (Pelli & Tillman, 2008). With this in mind, we examined the effect of transient blink events on the critical spacing for crowding with 20-ms blinks tested at a range of target–flanker separations.

Method

The majority of stimulus parameters and procedures were as in Experiment 1. Omitting the previous *no-blink* crowded condition, we tested four conditions: uncrowded performance and the *all-blink*, *target-blink*, and *flankers-blink* conditions. When blinks occurred, they were 20 ms in duration and commenced their offset at 200 ms (with a time course like that depicted in Figure 1A). When present, flankers were placed at one of six center-to-center separations from the target: 1.6°, 2.0°, 2.8°, 4.4°, 6.0°, or 7.6°. All four flankers were placed at the same separation in any given trial. Each separation was tested in a distinct block with the three blink conditions randomly interleaved within to give 264 trials per block. Uncrowded performance was measured in a separate block of 88 trials. Observers completed each block three times to give a total of 5,016 trials each. Four observers were tested: one of the authors (JG) and three newly selected naïve observers. All had normal or corrected-to-normal visual acuity.

Results and discussion

As before, responses were scored as the proportion of trials in which the target orientation was reported as counterclockwise of vertical. Psychometric functions were fit to data in each condition, with threshold elevation scores obtained by dividing thresholds in each blink condition by the uncrowded baseline for each observer. The mean threshold elevation values for all observers in the three blink conditions are plotted in Figure 3A as a function of the target–flanker separation. Crowding is strongest at the closest separations (1.6° and 2.0°), particularly in the *flankers-blink* and *all-blink* conditions where thresholds are elevated to over four times uncrowded levels at their peak. There is clearly less crowding in the *target-blink* condition at the closest separations, again demonstrating the performance improvements afforded by transient events in the target. The difference between these conditions decreased when flankers were separated from the target by 2.8°, largely due to the overall level of crowding declining substantially. Performance in all conditions was close to uncrowded levels once the flankers were 4.4° or further from the target.

A three-way, mixed-effects ANOVA (separation × blink condition × observer) confirms the above pattern with significant main effects of separation, $F(5, 30) = 12.22$, $p < 0.001$, and blink condition, $F(2, 30) = 5.38$, $p = 0.046$. The interaction between these factors was also significant, $F(10, 30) = 5.91$, $p < 0.001$, likely driven by the reduced crowding in the *target-blink* condition at close separations. The main effect of observer was nonsignificant, $F(3, 30) = 2.79$, $p = 0.077$, although there were significant interactions between observer and spacing, $F(15, 30) = 3.79$, $p < 0.001$, as well as observer and blink condition, $F(6, 30) = 2.94$, $p = 0.022$. These individual differences become most apparent in the critical spacing values below.

To quantify the effect of transients on the critical spacing for crowding, we fit bilinear functions with a sloped section and a flat minimum to each condition. These functions had three parameters: the slope, the overall y-intercept, and the x-value of the junction. Similar bilinear fits have been employed elsewhere (Yeshurun & Rashal, 2010), and Figure 3A demonstrates that these fits clearly capture the variation in threshold elevation across our range of target–flanker separations. From this, we can take the point at which crowding ceases to occur (the critical spacing) as the junction between the two lines. This gave critical spacing values for the averaged thresholds of 3.20° and 3.16° for the *all-blink* and *flankers-blink* conditions, respectively, and 2.98° for the *target-blink* condition (indicated by arrows in Figure 3A). These values are plotted in Figure 3B along with those from the fits to each of the four observers' individual data. Although critical spacing values vary across observers, variations across the blink conditions are typically slight and not consistent in direction. The same results were obtained when different functions (such as Weibull functions) were used in place of the bilinear fits. From this, we conclude that the primary
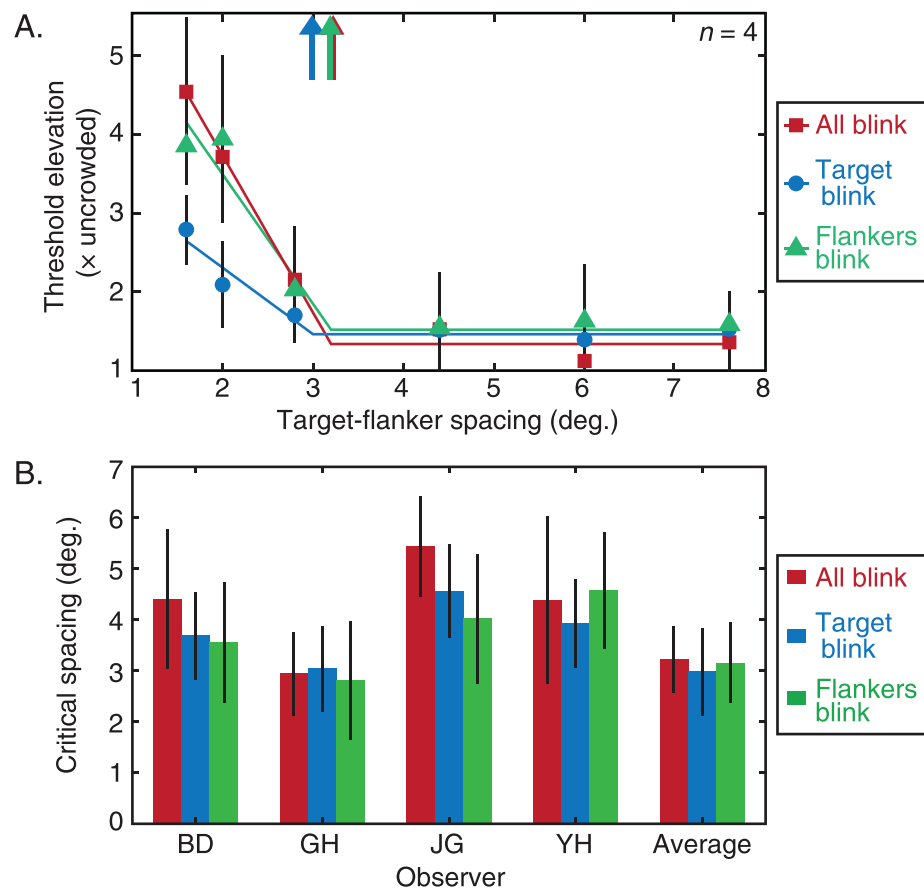
Figure 3. Results from Experiment 2. (A) Threshold elevation for the three blink conditions, plotted as a function of the center-to-center separation between target and flanker elements. Crowding is strongest at the three closest separations, although the *target-blink* condition (blue circles) produces less crowding than the *all-blink* (red squares) or *flankers-blink* (green triangles) conditions. Lines show the best-fitting bilinear function, each with sloped and straight sections that reflect the decrease in crowding with increasing target–flanker separation. Arrows on the top axis show the critical spacing for each condition (i.e., the junction point of the bilinear fits). Error bars give the standard error of the mean between observers. (B) Critical spacing values for the averaged thresholds in panel A (far right) and for fits to thresholds for each of the four observers (indicated by their initials). Error bars are derived from bootstrapping. The three blink conditions produce little consistent variation in the critical spacing required to relieve crowding.

effect of target transients is an improvement in performance at each separation in which crowding occurs and not a change of the range over which crowding operates.

This finding differs from prior work showing that feature differences in domains such as color can reduce the critical spacing for crowding (Scolari et al., 2007). Others have argued that these reductions may be an artifact of defining the critical spacing by a fixed performance criterion (e.g., 90% correct), which makes it difficult to distinguish changes in overall performance from changes in the critical spacing (Pelli & Tillman, 2008). With percent-correct data, an improvement in overall performance would shift the entire function upward to give an artificial reduction in the estimated critical spacing. The threshold values obtained in the present study are less prone to this effect because ceiling effects are easier to avoid (as long as the range of target orientations is sufficient), and the

critical spacing can be fit to any asymptotic performance level. Regardless, our results show that transient events have a beneficial effect on performance within the range of separations in which crowding occurs, without changing that range, and with no effect on performance outside of this range (i.e., the effect is specific to crowding and not a general improvement in performance).

Note that our average values of critical spacing are smaller than the 5° extents that would be predicted by the "Bouma law" of 0.5 × the target eccentricity (Bouma, 1970; Pelli et al., 2004). We suspect this is due to the location of our stimuli along the horizontal meridian in the left and right visual fields, which has been found to be less prone to crowding than the vertical meridian (Liu, Jiang, Sun, & He, 2009; Petrov & Meleshkevich, 2011; Wallis & Bex, 2012).

Experiment 3

Experiments 1 and 2 demonstrate that transient blink events in the target can reduce crowding. Because these blinks contain both an onset and an offset signal, we next examined whether one was preferentially driving this effect. Prior work demonstrates that visual onsets are strikingly effective at capturing attention in a visual search task (Yantis & Jonides, 1984; Jonides & Yantis, 1988) whereas offsets have comparatively little effect. Onset transients are similarly far more effective in driving change-detection performance than offsets (Phillips & Singer, 1974). Here we examine whether the same is true for the release from crowding.

To this end, we compared a brief 20-ms blink in element contrast (as in Experiments 1 and 2) with the two components of these blinks: a delayed onset of the relevant stimulus element(s) or a premature offset. Each of these temporal events could be applied either to the target or to the four flankers. This not only allowed us to examine the influence of these events in both target and flankers, but also provided a parallel with previous reports of the *flanker preview* effect (Huckauf & Heller, 2004; Scolari et al., 2007). Namely, flankers presented in advance of the target have been found to give less crowding than flankers presented simultaneously with the target. We note that when flankers are presented prior to the target, the subsequent arrival of the target yields an onset transient that could provide a benefit similar to our blinks. Because both effects could thus be understood within a common framework, we sought to compare them directly in Experiment 3.

Method

The majority of stimulus parameters were identical to the first experiment with the exception of the stimulus time course. Here we compared three temporal events: a *blink* composed of an abrupt offset in stimulus contrast for 20 ms before its abrupt restoration, a delayed *onset* in which the selected element(s) were absent at stimulus onset and abruptly appeared midway through the trial, and a premature *offset* in which the selected element(s) appeared at stimulus onset but were abruptly removed midway through the trial. The time course of these three events is depicted in Figure 4A. Note that the *blink* condition had two stimulus periods of 190 ms with an intervening 20-ms blink. The *onset* condition contained only the latter portion of this time course with a delayed onset at 210 ms after the beginning of the trial. The *offset* condition involved a common onset for all elements and an offset 190 ms after stimulus onset. In all cases, the postmask

noise stimulus appeared 400 ms after the initial stimulus onset (as in previous experiments).

When crowded (with a target–flanker separation of 1.6°), these three temporal events could be applied either to the target or to the four flankers simultaneously. The remaining element(s) were presented for the full 400-ms duration. For illustration, Movie 2 depicts one *target-onset* trial and one *flanker-offset* trial. Because these manipulations altered the presentation time of the relevant element(s), particularly when applied to the target, we also examined the effect of these three temporal events on the target in isolation. Thus, in total, there were seven crowded conditions (the three temporal events applied to either the target or the flankers and a *no-blink* condition) and four uncrowded conditions (the three temporal events and a *no-blink* condition). The *no-blink* conditions were tested in separate blocks with 88 trials per block. The three temporal events were randomly interleaved in a given block, and the application of these events to distinct elements (uncrowded targets, crowded target, or the flankers) was tested in separate blocks of 264 trials each. Observers completed each block three times to give 2,904 trials in total. One of the authors (JG) and the three naïve observers from Experiment 1 participated in this experiment.

Results and discussion

Responses were again scored as the proportion of trials in which the target orientation was reported as counterclockwise of vertical, with psychometric functions fit to the data and thresholds derived as above. When the target was presented alone (i.e., uncrowded), thresholds in the *blink*, *onset*, and *offset* temporal conditions (1.7°, 1.8°, and 1.3°, on average) did not differ substantially from the static baseline (1.5°). Thus, although the stimulus duration varies from 210 to 400 ms across conditions, these durations are evidently long enough that this has minimal effect.

Threshold elevation scores were obtained by dividing thresholds in each temporal condition with the relevant uncrowded baseline, separately for each observer. Threshold elevation values are shown for observer EH in Figure 4B with the average values for all four observers shown in Figure 4C. Performance varies similarly in the two plots. With *no blink* in the crowded array (dashed black line), identification of the Gabor target is four times worse (on average) than uncrowded levels. The *blink* condition (blue bars) shows that a 20-ms blink in the target again improves performance substantially, with threshold elevation dropping to twice the level of the average uncrowded threshold. Indeed, 95% confidence intervals around the difference between these *target blink* values and the crowded *no blink* baseline do not include zero (−2.46, −1.32).
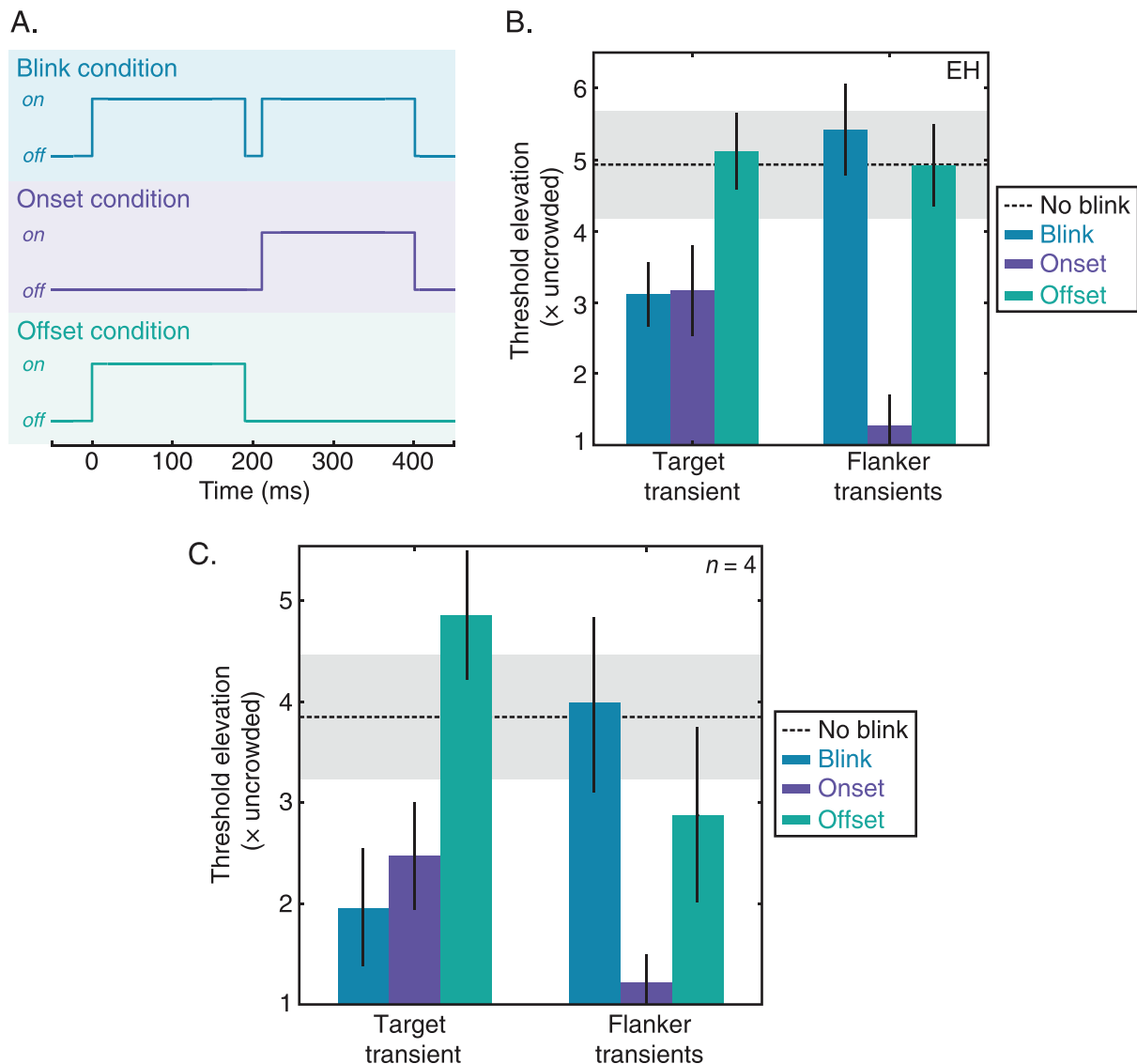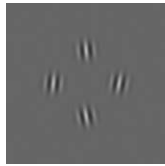
Figure 4. Procedures and results from Experiment 3. (A) The time course of the three temporal conditions. The *blink* condition was identical to the 20-ms blink condition of Experiments 1 and 2. The *onset* condition involved a delayed onset of either the target or the flankers, appearing at 210 ms after stimulus onset and disappearing together with the remaining elements. For the *offset* condition, all elements shared a common onset with either the target or flankers then disappearing 190 ms later. These events could be applied to either the target or the flankers with the other elements present throughout. All stimuli were followed by a noise mask. (B) Threshold elevation scores for observer EH for the three temporal conditions, as applied to the target or flanker elements. Crowded thresholds with no blinks are shown as a dashed black line. Threshold elevation for the *blink* condition is shown in blue, the *onset* condition in purple, and the *offset* condition in green. Error bars and the gray region indicate the standard error of the mean derived from bootstrapping. (C) Average threshold elevation values for the four observers, depicted as in panel B. Here error bars and the gray region indicate the standard error of the mean between observers.

Applying the same blink to the flankers gave no improvement in crowded performance, with confidence intervals around the difference with the *no-blink* baseline that clearly include zero (−1.38, 1.62). This replicates the asymmetric pattern of release evident in Experiments 1 and 2.

When applied to the target, the *onset* delay (purple bars) also produced a substantial improvement in performance, with a significant difference from the

crowded *no-blink* baseline: 95% confidence intervals around the mean difference do not include zero (−2.50, −0.25). That is, crowding is reduced when the target onset is delayed relative to that of the flankers, with a similar magnitude to that obtained with blinks of the target. Contrast this with the *offset* condition (green bars) for the target; there is no improvement in performance when the target onset is simultaneous with that of the flankers and its offset occurs independently

Movie 2. Stimuli from two example trials in Experiment 3. The first part shows an example *target onset* trial: the flanker elements appear first, with the target onset 210 ms later. All elements then share a common offset 400 ms after the initial stimulus onset, with a mask presented for the final 200 ms. The second part shows an example *flankers offset* trial: all elements share a common onset, with the disappearance of the flankers 190 ms later. The target remains and a mask then follows.

190 ms later. Indeed, performance here did not differ from the *no-blink* baseline: 95% confidence intervals cover zero (−0.34, 2.70). The effect of the blink is thus largely attributable to the onset transient, with little contribution from the offset event.

The importance of the isolated target onset can also be seen when the onset and offset events were applied to the flankers. When flankers were delayed in their *onset* (purple) so that the flankers arrived 210 ms after the target, performance was indistinguishable from uncrowded levels. There is thus a strong reduction relative to the crowded *no-blink* baseline, and indeed the confidence intervals do not include zero (−4.02, −1.23). Of course, a key aspect of this improvement in performance could be that the target spends 210 ms in the uncrowded state. However, this amount of uncrowded time is identical in the *flankers-offset* condition (green), where all elements arrived simultaneously and the flankers disappeared 190 ms later. Here, there is only a slight improvement in performance that does not differ significantly from the *no blink* baseline (−2.57, 0.24). The difference between these conditions can be understood by considering the timing of the target onset relative to that of the flankers. In the *flankers-onset* condition, the target onset is isolated when the trial commences before the flankers arrive. In the *flankers-offset* case, all elements share their onset before the flankers disappear. The common factor is once again the presence of a target onset signal that is temporally separated from the onset of the flankers.

Together, our results suggest that the most effective way to temporally modulate crowding is to separate the target onset from that of the flankers. This is evident in all of the conditions in which crowded performance improved: the *target-blink*, *target-onset*, and *flankers-onset* conditions all involve the onset signal for the target occurring either before or after that of the flankers. In contrast, the *target-offset*, *flankers-blink*, and *flankers-offset* conditions involve a target onset that occurs at the same time as that of the flankers, with either subsequent changes in the flankers or an isolated

offset signal in the target. Performance in each case is poor. We take from this that crowding is reduced by transients only when they isolate the target onset within a given time window.

The dominance of onset signals in this experiment is consistent with prior studies in visual search and change detection (Phillips & Singer, 1974; Yantis & Jonides, 1984). This finding also presents an alternative explanation of the *flanker preview* effect, whereby flankers presented prior to the target onset reduce crowding relative to their simultaneous presentation (Huckauf & Heller, 2004; Scolari et al., 2007). We suggest that this can be attributed to the target having an isolated onset transient, as opposed to a preview of the flankers per se. Our *target-onset* condition in particular is similar to the negative stimulus–onset asynchronies found to be beneficial by Huckauf and Heller (2004). Although there is a "flankers only" preview period in this condition, however, there is no such preview in the *target-blink* condition, which gives an equally robust release from crowding. We suggest that the release in both cases is due to the isolation of the target onset from that of the flankers.

Interestingly, although crowding is reduced when flankers precede the target (as above), flankers that follow the target with short-onset asynchronies have been found to produce strong crowding (Huckauf & Heller, 2004). In our data, however, the *flankers-onset* condition (in which flankers follow the target) yields similar (if not improved) performance over the *target-onset* case (in which the target follows the flankers). This is likely due to the longer onset asynchronies used herein. If we suppose that the accurate recognition of the target requires a given period of time after its isolated onset transient, then flanker onsets presented within this period will likely have a disruptive effect (as they would with simultaneous presentation). These interactions could then be avoided either with longer onset asynchronies or by presenting the flanker onsets before that of the target.

Experiment 4

Thus far, we have examined the effect of transient events only at the midpoint of stimulus presentation. Here we examine the time course of this effect. This also allows us to consider an alternative interpretation of our results. Rather than promoting the temporal separation of the target from the flankers, our blink events could improve crowded performance by cueing the target location. Prior demonstrations that transient onsets can improve visual search times (Jonides & Yantis, 1988; Theeuwes, 1991) are consistent with this idea. For this to be true of crowding, however, one has
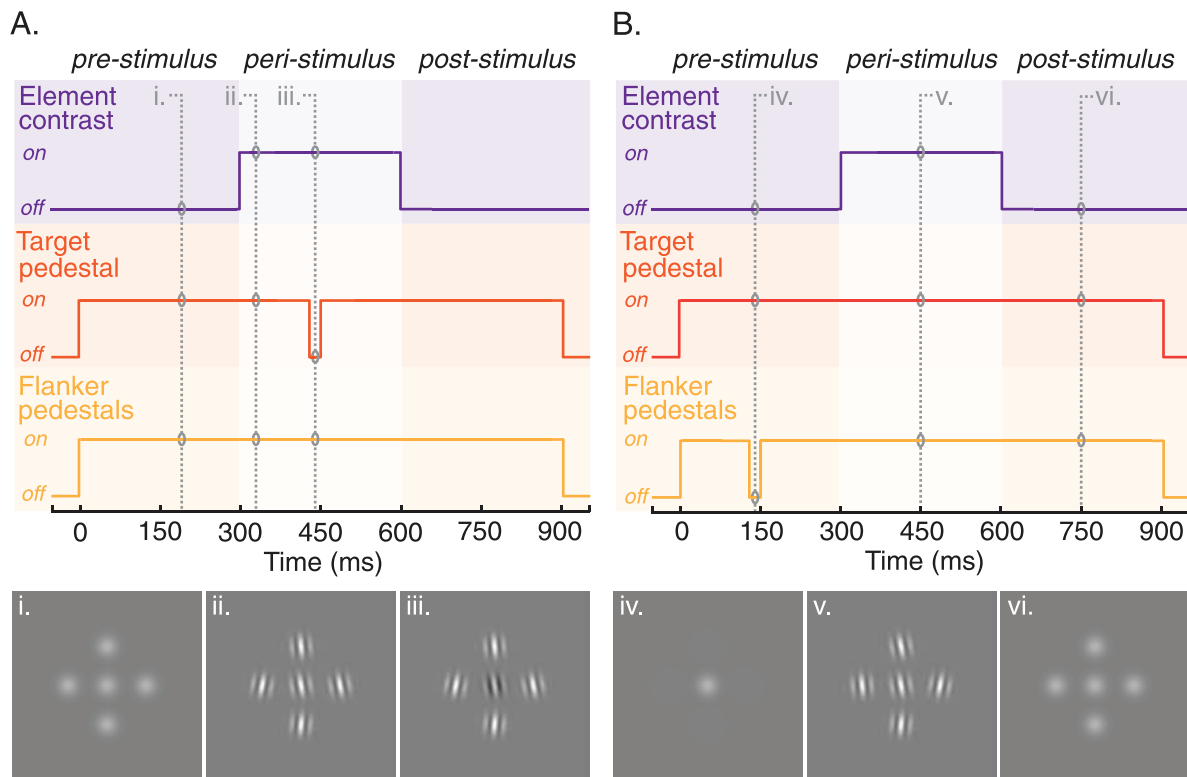
Figure 5. The time course of trials in Experiment 4. (A) Schematic of an example *target-blink* trial. The contrast of the five Gabor elements is shown in purple, the target luminance pedestal in red, and the flanker pedestals in orange. Trials had three distinct periods. In the pre-stimulus period, five luminance pedestals were present with the stimulus Gabors then appearing after 300 ms. At 600 ms, the Gabors were removed, and the pedestals remained for 300 ms. A mask replaced all stimuli at 900 ms. The blink in this trial is applied to the target pedestal and begins at 430 ms with an onset at 450 ms. Insets i through iii depict the stimulus appearance at the three time points shown by the gray dashed lines. (B) An example time course for a *flankers-blink* trial in which the luminance decrement is applied to the flanker pedestals in the pre-stimulus phase. Stimulus insets iv through vi show the stimuli at three key points in this trial.
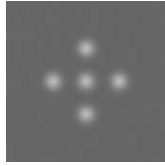
to first assume that there is some uncertainty regarding the location of the target. Some have indeed argued for a contribution from position uncertainty, most notably in theories where crowding relates to mislocalizations of the attentional spotlight (Strasburger, 2005). It has also been shown that positional cueing can reduce crowding when the temporal properties of the stimulus are carefully controlled (Yeshurun & Rashal, 2010). Transient onset signals could therefore serve a similar role in simply cueing the target location.

If transients do serve as positional cues, then their occurrence before stimulus onset should facilitate performance just as well as their occurrence during stimulus presentation. To examine this, luminance-increment pedestals were added to each of the target and flanker locations. These pedestals were present before, during, and after the presentation of the stimulus Gabors. This allowed us to apply the blink events to the luminance pedestal (rather than the Gabor contrast) and equate the strength of transient events at time points in the pre-stimulus, peri-stimulus, and post-stimulus time periods. As above, a positional cueing

account predicts that pre-stimulus cues should be just as, if not more, effective than peri-stimulus cues with a potential benefit for postcues as well. In contrast, were the effects to require transients that specifically contain the to-be-detected orientation signal, then these blinks should have their greatest effect within the peri-stimulus period with some development of this effect around the initial stimulus onset.

Method

The majority of stimulus parameters were as in the first experiment. The key difference was the addition of luminance pedestals to each of the target and flanker locations. These pedestals were Gaussian blobs with the same spatial standard deviation as the Gabor elements and a luminance increment of 15 cd/m^2 above the background (30% Weber contrast). This pedestal was added to the Gabors when present with the Gabor contrast increased to 70% to ensure visibility.

Movie 3. Stimuli from three example trials in Experiment 4. The first part shows a *target blink* trial with a blink in the peri-stimulus period (430-450 ms after the initial trial onset, as in Figure 5A). The second part shows a *target blink* trial with a blink in the pre-stimulus period (130-150 ms after trial onset), similar to the time course in Figure 5B (albeit for the target pedestal and not the flanker pedestals). The third part shows a *flankers blink* trial with a post-stimulus blink, 730-750 ms after trial onset.

Each trial was 900 ms in duration with three distinct periods, depicted in Figure 5. The luminance pedestals were present for the entirety of this duration except during the 20-ms blink (when it occurred). The pre-stimulus period lasted 300 ms and consisted solely of the luminance pedestals. The peri-stimulus period involved both the luminance pedestal and the Gabor elements, again for 300 ms, and the post-stimulus phase involved another 300 ms of the luminance pedestals alone. The blink, when present, lasted 20 ms and applied only to the luminance pedestal. It could be applied either to the target, the flankers, or all five elements at once. Thus, if the blink occurred in the peri-stimulus period, the luminance pedestal was removed to leave the Gabor element modulated around the background luminance with the pedestal returning after 20 ms. The time course for an example *target-blink* trial is shown in Figure 5A with inset examples to show the appearance of the peri-stimulus blink (see also part 1 of Movie 3). If the blink occurred in the pre-stimulus or post-stimulus phases, the Gaussian elements were removed to leave the mean luminance with the Gaussian abruptly restored 20 ms later. An example pre-stimulus *flankers-blink* trial is shown in Figure 5B. The second part of Movie 3 similarly shows a *target blink* in the pre-stimulus period, and the third part depicts the *flankers-blink* condition in the post-stimulus period. In all conditions, the 900-ms stimulus presentation was followed by a noise mask for 200 ms.

Blinks in this experiment could occur at one of six times throughout the 900-ms trial duration: 150 or 250 ms after trial onset (pre-stimulus); 350, 450, or 550 ms (peri-stimulus); or 750 ms (post-stimulus). Because the results of Experiment 3 suggest that it is the onset transients that drive the observed reductions in crowding, the above time points refer to the point at which the stimulus reappeared (i.e., the onset with the offset occurring 20 ms prior to this) unlike in previous experiments in which we have referred to the blink point via the element offset. Blinks were applied in three conditions: *target blink*, *flankers blink*, and *all*

blink as in the first two experiments. These three conditions were randomly interleaved within the same block with each block testing blinks at a fixed time point. An additional two *no-blink* conditions were tested: one uncrowded and one crowded. In each case, stimuli were presented for the full 900 ms with pre-stimulus and post-stimulus pedestals, but without the blink. These *no-blink* trials were tested in separate blocks. To reduce testing time, the range of target orientations was decreased to values between 78° and 102° in nine steps separated by 3°. Each was presented eight times to give 216 trials per block in the *blink* conditions and 72 trials in the *no-blink* conditions. Observers completed each block three times to give 4,320 trials each. Two of the authors (JG and BS) and two new naïve observers took part in this experiment.

Results and discussion

As before, thresholds were derived from the psychometric functions fit in each condition and converted into threshold elevation scores by dividing crowded thresholds by the uncrowded baseline. These values, averaged across the four observers, are plotted in Figure 6 as a function of the blink onset time throughout the 900-ms trial duration. Pale background colors divide the time course into the pre-stimulus, peri-stimulus, and post-stimulus periods. The dashed black line plots the threshold elevation in the crowded *no-blink* condition with a gray region showing the standard error of the mean between observers. Red data points show the effect of blinking all elements simultaneously. When compared with the *no-blink* crowded baseline, it is clear that doing so has little effect on performance regardless of the time at which these blinks occur. The green points show that blinking the flankers at various time points also produces no consistent improvement in performance.

Performance varies more widely in the *target-blink* condition (blue points). In the pre-stimulus period, there is clearly no benefit to having a blink in the luminance pedestal 150 ms after the trial onset (and 150 ms before stimulus onset). Performance improves slightly with blinks at 250 ms, just 50 ms before stimulus onset. Within the stimulus period, this slight improvement in performance is maintained 50 ms after onset before improving again to reach its peak magnitude at 450 ms midway through presentation. This benefit is reduced for blinks at 550 ms. After the stimulus, there is clearly no benefit to blinking the luminance pedestal.

The difference between the three conditions is evident in the results of a three-way, mixed-effects ANOVA (blink condition × time × observer). The main effect of blink condition was clearly significant,
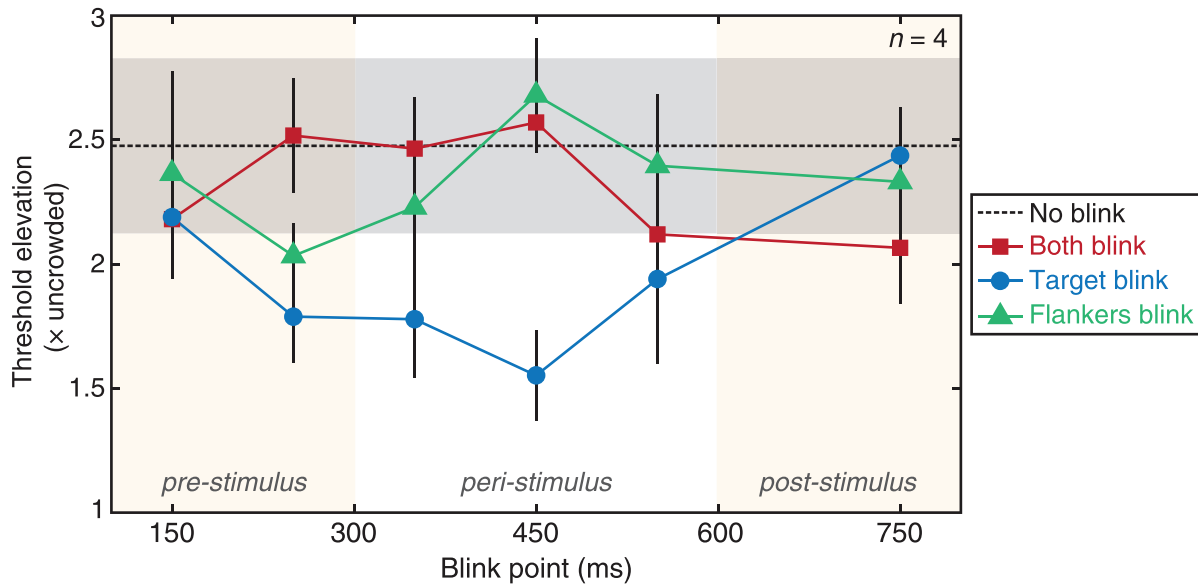
Figure 6. Results from Experiment 4, examining the time course of transient effects on crowding. The pale vertical blocks divide the 900-ms trial duration into the three pre-stimulus, peri-stimulus, and post-stimulus time periods. Threshold elevation values, averaged across the four observers, are plotted as a function of the onset time of the blink. The dashed black line shows performance in the *no-blink* crowded baseline, and the three temporal conditions are shown with red squares (*both blink*), blue circles (*target blink*), and green triangles (*flankers blink*). Error bars and the gray region show the standard error of the mean. Notice that performance only improves to below the gray *no-blink* region in the *target-blink* condition in and around the peri-stimulus time period.

$F(2, 30) = 8.78$, $p = 0.016$, although the main effects of time, $F(5, 30) = 0.47$, $p = 0.792$, and observer, $F(3, 30) = 1.96$, $p = 0.188$, were not. The main effect of blink condition is clearly driven by the performance improvements in the peri-stimulus period of the *target-blink* condition, and indeed the interaction between blink condition and time was significant, $F(10, 30) = 6.24$, $p < 0.001$. Interactions with observer were nonsignificant (all $ps > 0.05$). As before, however, our primary interest is whether performance in each blink condition was improved over the *no-blink* crowded baseline; 95% confidence intervals around the difference between these conditions reveal a close but significant difference at 250 ms $(-1.36, -0.02)$ and highly significant differences at 350 ms $(-0.95, -0.45)$ and 450 ms $(-1.51, -0.33)$. *Target-blink* thresholds are clearly lower than the baseline in these cases. This was not the case for *target-blink* thresholds at 150 ms $(-0.80, 0.23)$, 550 ms $(-1.44, 0.47)$, and 750 ms $(-0.93, 0.88)$. That is, there is a small benefit from transient events in the target in the 50 ms before and after stimulus onset and a clear effect 150 ms after stimulus onset.

These results demonstrate a temporal window within which transient onsets in the target can reduce crowding. The benefit begins 50 ms prior to stimulus onset, improves when blinks occur midway through stimulus presentation (150 ms after the onset of the stimulus Gabors), and declines thereafter. Importantly, there is clearly no effect of precueing the stimulus 150

ms before the onset of the oriented Gabors nor after the stimulus offset as a postcue. The rapid buildup of this effect is consistent with prior results demonstrating that rapid alternations of stimulus contrast polarity can nonetheless still allow the release from crowding (Chakravarthi & Cavanagh, 2007). It is only when the time after the transient is insufficient to process the target orientation that this effect breaks down (e.g., at 550 ms where the target is present for only 50 ms following the blink).

The lack of effect at 150 ms after trial onset (in the pre-stimulus period, 150 ms before the target onset) runs contrary to the predictions of crowding theories based on position uncertainty: If there had been uncertainty about the target location, cueing the target location should have improved performance at all pre-stimulus time points. The lack of position uncertainty in our paradigm is perhaps unsurprising given that the luminance pedestals were presented in the correct location of the visual field for 300 ms prior to stimulus appearance. The Gabors themselves were also presented for 300 ms—sufficient time to orient attention and to overcome any of the gross positional uncertainty that may have been present regarding the stimulus array. We note that prior results demonstrating benefits from reducing position uncertainty used extremely brief presentation times (Yeshurun & Rashal, 2010), which may heighten position uncertainty and perhaps even elevate the degree of crowding that is present (Tripathy, Cavanagh, & Bedell, 2013). In our case, the transient
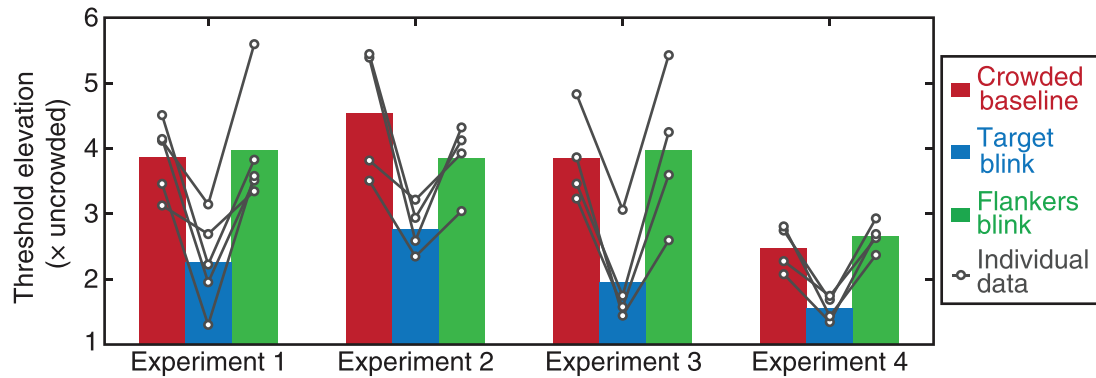
Figure 7. The asymmetric release from crowding in each of the four experiments. Threshold elevation values have been taken from three matched conditions in each experiment. Colored bars show the mean across observers for these three conditions: a crowded baseline (either the *no-blink* or *all-blink* condition; red bars) and *target-blink* (blue bars) and *flankers-blink* (green bars) conditions. Individual threshold elevation values for these same conditions are superimposed as white points with gray lines. Stimulus parameters are similar in each experiment: a target–flanker separation of 1.6° and blink durations of 20 ms that occurred midway through stimulus presentation.

blink events are clearly not functioning as location cues.

There was nonetheless a significant improvement in performance at the time point 50 ms prior to stimulus onset. Rather than being the result of position cueing, we suggest that at this time point there is an association between the target Gabor and the onset transient in the Gaussian placeholder. This could reflect the decay time of transient signals within visual cortex; V1 cells, for instance, show an initial transient burst of activity that lasts from 50 to 100 ms (Müller, Metha, Krauskopf, & Lennie, 2001). Repeated transients within this time would be difficult to distinguish from one another. Indeed, judgments of temporal order can yield thresholds well in excess of 50 ms (Rutschmann, 1966; Stelmach & Herdman, 1991). If both the isolated transient onset and the whole stimulus onset were to occur within this window, the combined transient response could then allow the differentiation of the target signal from that of the flankers in the same way as occurs midway through the stimulus time course. We suggest therefore that this release from crowding shares a common basis with that obtained in the peri-stimulus period and that neither can be attributed to position cueing.

Test–retest reliability

Overall, we have demonstrated a release from crowding when there is an isolated onset transient in a crowded target. The reduction is substantial, reducing crowded thresholds from the *no-blink* baseline by up to 49.1% (maximally in Experiment 3). Indeed, because our four experiments include a common set of

conditions, we are able to formally demonstrate the reliability of both the transient-based release from crowding and its asymmetry. Specifically, all four experiments had conditions with a target–flanker separation of 1.6° and blinks of 20-ms duration that occurred midway through stimulus presentation, applied either to the target or the flankers. Each also measured uncrowded thresholds and a baseline for crowded performance (either with no blinks or with all elements blinking simultaneously).

To present these data together (and examine the reliability of the transient-based release from crowding), threshold elevation scores were taken from each of the four experiments to give three conditions for each. For Experiments 1, 3, and 4, threshold elevation values from the *no-blink* condition were taken as a "crowded baseline" along with threshold elevation values from the *target-blink* and *flankers-blink* conditions. For Experiment 2, the *all-blink* condition was taken as a crowded baseline (because *no-blink* thresholds were not tested) again with the *target-blink* and *flankers-blink* conditions. Data from Experiment 4 were taken from the peri-stimulus conditions in which the blink occurred at 450 ms—note that this experiment also differs from the others in stimulus duration and contrast. Data from Experiment 1 includes thresholds from five observers, and the other experiments include four. Different sets of naïve observers were tested in Experiments 1, 2, and 4 (those in Experiments 1 and 3 were the same).

Figure 7 plots the average of these threshold elevation values for each of the four experiments as colored bars with individual threshold elevation values superimposed as white points with gray lines. In each case, there is strong crowding in the baseline condition (red bars) in which either all elements blinked

(Experiments 1, 2, and 4) or in which no blink occurred (Experiment 3). A blink in the target element reduces crowding substantially (blue bars) whereas blinks in the flankers (green bars) continue to produce strong crowding. Although there is some variation in the overall level of threshold elevation (most notably in Experiment 4 where parameters differ the most), the asymmetry in the release from crowding is evident in each case. It is also evident in the threshold elevation values for each of the individual observers. Accordingly, 95% confidence intervals around the mean difference between the *target-blink* condition and the crowded baseline reveal significant differences in each case: Experiment 1 (−2.66, −0.55), Experiment 2 (−3.44, −0.09), Experiment 3 (−2.46, −1.32), and Experiment 4 (−1.51, −0.33). And, in each case, the *flankers-blink* condition does not differ significantly from the crowded baseline: Experiment 1 (−0.99, 1.19), Experiment 2 (−1.70, 0.33), Experiment 3 (−1.38, 1.62), and Experiment 4 (−0.53, 0.89). That is, in each case, transient events in the target reduce crowding, and transient events in the flankers do not.

General discussion

We report three key findings. First, transient "blink" events in stimulus contrast can reduce crowding. Midway through the presentation of a crowded array, if the target is briefly removed from the display and then returned, there is a dramatic reduction in crowding. This release is asymmetric; blinks applied to the target will release crowding, and blinks applied to the flankers (or all elements together) will not. We observe this effect with blinks as brief as 20 ms in duration (Experiment 1) and over the range of target–flanker separations where crowding is seen (Experiment 2). Perhaps reassuringly, this means that when a new object appears (abruptly) in the visual field, its recognition is unlikely to be affected by nearby objects that were already present.

Our second key finding is that the beneficial effect of transient blinks is largely derived from the target onset and not its offset (Experiment 3). This suggests that the temporal modulation of crowding depends specifically on the temporal separation between the onsets of target and flanker objects. Our third key finding is the demonstration that this reduction in crowding is maximal for blinks that occur while the target orientation is present, with no advantage for blinks applied to luminance pedestals 150 ms before or after stimulus presentation (Experiment 4). From this, we exclude explanations of the transient-based reduction in crowding that rely on spatial cueing of the target location. Together, these findings present several

challenges to current conceptions of the mechanisms that underlie the release from crowding.

Our results demonstrate that, in addition to being selective for temporal frequency differences (Bex & Dakin, 2005; Gheri et al., 2007), crowding is also tuned for the occurrence of transient onset events. This is consistent with the suggestion that crowding can be reduced through adaptation of the transient system and the concurrent dampening of flanker onset signals (Wallis & Bex, 2011). As discussed in relation to Experiment 3, our results also provide an explanation for the *flanker preview* effect (Huckauf & Heller, 2004; Scolari et al., 2007). That is, the strong release when flankers are presented in advance of the target is likely derived from the isolation of the target onset from the flanker onsets, as with our blinks. The reduced benefit with flankers that follow the target can be attributed to the disruptive effect of the flanker onsets during the period of target recognition. Notice that, in aligning our findings with these prior studies, we depict transient onsets both as a *feature* associated with individual objects (i.e., their spatiotemporal profile) and as an *event* that occurs at a particular time. In this way, the transient-based release from crowding encapsulates both aspects of the temporal selectivity of crowding–it requires tuning for both separation *and* similarity. We consider the potential mechanisms of this below.

Although our results align with the temporal selectivity of crowding, the effect of transient onsets differs from the reductions in crowding observed with features such as color and orientation. With color, for instance, a red target among green flankers gives as much release as a green target among red flankers (Kooi et al., 1994). With transients, we see an asymmetry: Target transients relieve crowding, and flanker transients do not. This is inconsistent with the idea that crowding is selective for *similarity* in its simplest sense; were this true, a temporal difference should have improved performance regardless of whether the transient was applied to the target or the flankers. The inadequacy of target–flanker similarity as an explanatory concept is also evident in the several stimulus dimensions, including luminance contrast, size, and eye of origin (Kooi et al., 1994; Chung et al., 2001; Tripathy & Cavanagh, 2002; Pelli et al., 2004), for which target–flanker differences do not affect the magnitude of crowding. In these cases, one could argue that crowding is simply not tuned for similarity along these dimensions. The asymmetry in our case demonstrates that crowding is clearly tuned for temporal onset events, and yet the pattern of release is inconsistent with predictions based purely on target–flanker similarity.

Similar objections apply to explanations of the release from crowding based on *grouping*; i.e., that crowding occurs when the target is grouped together

with the flankers (Livne & Sagi, 2007; Saarela et al., 2009; Sayim, Westheimer, & Herzog, 2010; Manassi et al., 2012). In our case, it would appear that, although transient onsets can ungroup the target from the flankers, these same transient signals fail to ungroup the flankers from the target. Although grouping can clearly modulate the strength of crowding, it is insufficient on its own to explain the release from crowding in our case. This is consistent with recent work suggesting that crowding and grouping can operate over distinct spatial scales (Sayim & Cavanagh, 2013).

We attribute this asymmetry to the operation of the "transient" temporal channel within the visual system. A large body of work suggests that these detectors show band-pass tuning for high temporal frequencies in comparison with a "sustained" channel that is more low-pass in its selectivity (Kulikowski & Tolhurst, 1973; S. J. Anderson & Burr, 1985; Snowden & Hess, 1992; Cass & Alais, 2006). An unblinking stimulus with a sufficiently long presentation time (e.g., the 300–400 ms used herein) would thus activate both sustained and (at onset) transient detectors. With the target and flanker signals present in both sets of channels, there would be crowding as usual. A blink in the stimulus, midway through the presentation, would then stimulate the transient channels a second time. When applied to the target alone, this would isolate the target signal (with no flankers) in the transient channel, while the sustained channel would still contain both target and flanker signals. If we assume that stimulus identification can occur somewhat independently in each channel (Kulikowski & Tolhurst, 1973; S. J. Anderson & Burr, 1985; Snowden & Hess, 1992; Cass, Van der Burg, & Alais, 2011), then the isolated target signal in the transient channel would allow the accurate identification of the target orientation. In contrast, a blink event in the flankers would isolate the task-irrelevant flanker signals within the transient channel and leave both target and flanker signals in the sustained channel. Without an isolated target signal, performance would be poor, leading to the asymmetry that we observe. It is in this sense that our proposed mechanism requires selectivity for *both* temporal distance and temporal similarity: The target onset transient must be temporally separated from the flanker onset signals (at stimulus onset) *and* show a temporal frequency profile that differs from that of the flanker signals. The resulting asymmetry may be further enhanced by the higher contrast gain associated with transient responses (Müller et al., 2001) or if transient detectors were to disproportionally inhibit the output of sustained detectors (Breitmeyer & Ganz, 1976; Cass & Alais, 2006).

To take this explanation further, we propose that crowding is strong when the target and flankers activate

mechanisms with common tuning properties. It is reduced when stimulus differences allow the representation of the elements within separate channels. The separation of the target and flanker signals in this way would not only render them less susceptible to pooling processes (Parkes et al., 2001; Greenwood et al., 2009), but could also facilitate their isolation by attentional processes (He et al., 1996). One way to think about this reduction in crowding is that the separation of target and flanker signals via feature differences may increase their cortical separation, given the physical segregation of dissimilarly tuned neurons in the brain. This cortical separation may be similar to that produced by the spatial separation of target and flanker elements, given the retinotopy of visual cortices (Mareschal, Morgan, & Solomon, 2010). Indeed, crowding is reduced when stimuli are physically close but cortically distant through their placement on either side of the hemifield representations in the visual cortex (Liu et al., 2009). The selectivity of crowding in the temporal domain may operate in a similar fashion, with increases in temporal distance and decreases in temporal similarity both serving to reduce the overlap in channel activation between the target and flanker signals.

This account of our finding bears some resemblance to the asymmetries found in visual search tasks. Namely, it is typically easier to search for the presence of a feature among distractors lacking this feature (e.g., a Q target among Os) than to search for a target lacking a feature that distractors possess (Treisman & Souther, 1985; Treisman & Gormican, 1988). Features such as motion can also produce asymmetries of this nature—it is easier to search for a moving target among stationary distractors than vice versa (Verghese & Pelli, 1992; Royden, Wolfe, & Klempen, 2001)—making it likely that transients would operate similarly. Because search tasks typically require only the detection of the target (and not its identification), search asymmetries have been attributed to our ability to detect activity within the relevant feature map for the target (Treisman & Souther, 1985). For instance, a target defined by orientation and motion is easily detected among stationary distractors (defined only by orientation) because the mere presence of motion denotes the target. A stationary target among distractors defined by motion and orientation does not possess this isolated feature and must therefore be found through serial scanning. With crowding, although the task typically requires the identification of the target (as in the present study), isolated activity within a given channel/feature map would nonetheless allow the segregation of the target signal from the flankers (as described above) as well as a "target present" response in a visual search task. The asymmetry in our crowding experiment may thus be considered as an analogue of visual search

asymmetries in the domain of identification rather than detection.

Treisman and Souther (1985) also point out that visual search asymmetries are specific to features that can be removed without replacing another value on the same dimension; we might call these *additive* features. This is contrasted with *substitutive* features, such as color, with which the removal of one value (e.g., red) is necessarily replaced by another (e.g., green). Investigations of the feature-based release from crowding have tended to use the latter type of substitutive feature, such as color, and the pattern of release has been accordingly symmetric (Kooi et al., 1994). In our case, transient onset events could be considered to be an additive feature; as above, the onsets would provide added activation of the transient channels without necessarily affecting activity in the sustained channels. We suggest that similar additive features would allow further asymmetries in the release from crowding.

What remains unclear is whether the release from crowding depends on processes that occur early or late in the visual system. In other words, is the release from crowding something that is part of the crowding process (e.g., based on the selectivity of pooling mechanisms), or is it a prefilter that occurs in the initial stages of visual processing? Evidence favoring a late mechanism comes from the observation that the release from crowding with one feature difference (e.g., orientation) can reduce crowding for other feature judgments (Greenwood, Bex, & Dakin, 2012). This suggests that the release from crowding occurs after feature binding (Treisman & Gelade, 1980) has taken place. The modulations in crowding strength via Gestalt factors (Livne & Sagi, 2007; Saarela et al., 2009; Sayim et al., 2010; Manassi et al., 2012) are also consistent with a higher-level basis for this release.

In contrast, there are several reasons to suspect that the release from crowding using transients could arise from lower-level processes. For instance, onset transients are monocular in origin (Phillips & Singer, 1974; Kanai & Verstraten, 2004), suggesting that their representation arises either in V1 or earlier in the visual system. The fact that onset transients facilitate processes such as visual search, change detection, and binocular rivalry (Phillips & Singer, 1974; Yantis & Jonides, 1984; Blake et al., 1990) as well as the potential relationship to search asymmetries above also suggests that this release mechanism could be a general process rather than something specific to crowding. If the orientation signals were carried within the transient channels themselves (Breitmeyer & Julesz, 1975; S. J. Anderson & Burr, 1985), then it is possible that the transient-based release from crowding could indeed arise early in the system; the target signal would be isolated early on, and crowding would not occur. However, if the target orientation were coded sepa-

rately from the transient activation (e.g., because the transient system may be too broadly tuned for orientation to allow this discrimination; Cass & Alais, 2006), then an association must be made between the transient activation and the target orientation, and the release from crowding must then occur after feature binding as outlined above. Although we cannot distinguish between these possibilities, it may in fact be the case that the release from crowding operates over several levels in the visual system, as has been suggested for crowding more generally (Whitney & Levi, 2011; E. J. Anderson, Dakin, Schwarzkopf, Rees, & Greenwood, 2012).

Keywords: crowding, peripheral vision, transients, orientation, temporal dynamics

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