

Crowding Changes Appearance

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Summary

Crowding is the breakdown in object recognition that occurs in cluttered visual environments [1–4] and the fundamental limit on peripheral vision, affecting identification within many visual modalities [5–9] and across large spatial regions [10]. Though frequently characterized as a disruptive process through which object representations are suppressed [11, 12] or lost altogether [13–15], we demonstrate that crowding systematically changes the appearance of objects. In particular, target patches of visual noise that are surrounded (“crowded”) by oriented Gabor flankers become perceptually oriented, matching the flankers. This was established with a change-detection paradigm: under crowded conditions, target changes from noise to Gabor went unnoticed when the Gabor orientation matched the flankers (and the illusory target percept), despite being easily detected when they differed. Rotation of the flankers (leaving target noise unaltered) also induced illusory target rotations. Blank targets led to similar results, demonstrating that crowding can induce apparent structure where none exists. Finally, adaptation to these stimuli induced a tilt after-effect at the target location, consistent with signals from the flankers “spreading” across space. These results confirm predictions from change-based models of crowding, such as averaging [16], and establish crowding as a regularization process that simplifies the peripheral field by promoting consistent appearance among adjacent objects.

Results

Although the conditions required for crowding are well established—including peripheral viewing [17, 18], close target-flanker proximity [2, 10, 17], and high target-flanker similarity [5, 19]—exactly how crowding occurs is unclear. A distinction can be drawn between models of crowding that rely on information loss, with crowded items either suppressed [11, 12] or lost [13–15], and change-based models such as averaging [16] and flanker substitution [20–22]. The former predict that crowding should have purely random effects; the latter predict a systematic interaction between target and flanker elements. Change-based models are therefore better able to explain the correlation between target identification errors and the structure of flanking elements [9, 16, 22–25]. However, these systematic effects could reflect behavioral strategies that, for instance, lead observers to report the average of a stimulus array under conditions of high uncertainty or to simply report the flankers because of information loss at the target location.

Clear demonstration of a genuine change in the appearance of crowded targets has yet to be made.

Because flankers necessarily drive systematic effects, the clearest expression of target change is likely to occur when the target is noisy or even absent. To examine this, we constructed target patches of isotropic bandpass-filtered noise flanked by oriented Gabor stimuli (Figure 1A; see [Experimental Procedures](#)). We report that crowding induces target noise patches to appear oriented, matching the appearance of flankers to an extent that is indistinguishable from physically oriented stimuli. This can be seen in Figure 1A (see also [Movie S1](#) available online). The appearance of the target noise patch is apparent when fixated directly, but peripheral viewing of the stimulus (by fixating one of the green asterisks monocularly) should make the target appear oriented—the stimulus may now appear to be composed of five oriented patches, or the target may blend with the flankers to form a single oriented texture.

To examine observers’ perceptual experience of these stimuli, we utilized a change-detection paradigm. Because observers can detect changes in crowded targets despite being impaired in their identification [26], change detection offers an indirect but effective measure of the percept of crowded stimuli without requiring subjective judgments (which are difficult to specify and/or quantify). Observers reported when a crowded noise patch was swapped for an oriented Gabor, either with or without concurrent changes in the flankers (Figure 1B). Because temporal transients can signal change [27, 28], stimulus contrast counterphased, with all changes taking place when stimuli passed through zero contrast (Figure 1C). On an equal proportion of trials, the noise target either persisted (no-change or flankers-change conditions; [Movies S1 and S2](#)) or was swapped midway for an oriented Gabor (target-change and both-change conditions; [Movies S3–S5](#)). False alarms (the frequency of change reported when there was none) were determined from the no-change condition and were below 10% for both uncrowded (Figure S1) and crowded noise patches (Figure 2A; black line). Under crowded conditions, changes between noise targets and Gabors (target change; blue points in Figure 2A) were rarely detected when the substituted Gabor matched the flanker orientation (with performance approaching the false alarm rate). We postulate that this is a consequence of the perceptual similarity between substituted Gabors and the illusory orientation of the crowded noise. Accordingly, changes were easily detected when substituted Gabors differed from the perceived target orientation.

This explanation assumes that observers compared their percepts from the two stages of each trial. However, these results could also arise from flankers inhibiting the Gabors introduced in the second stage of target-change trials [11, 12]—because crowding is orientation tuned [5], introduced Gabors could be inhibited based on their similarity to the flankers. A reduction in the visibility of these Gabors through masking [17, 29–31] might also produce these results. To control for this possibility, we included trials in which the flankers rotated in the second stage to match the introduced Gabors (both change; Figure 1B). If performance in the

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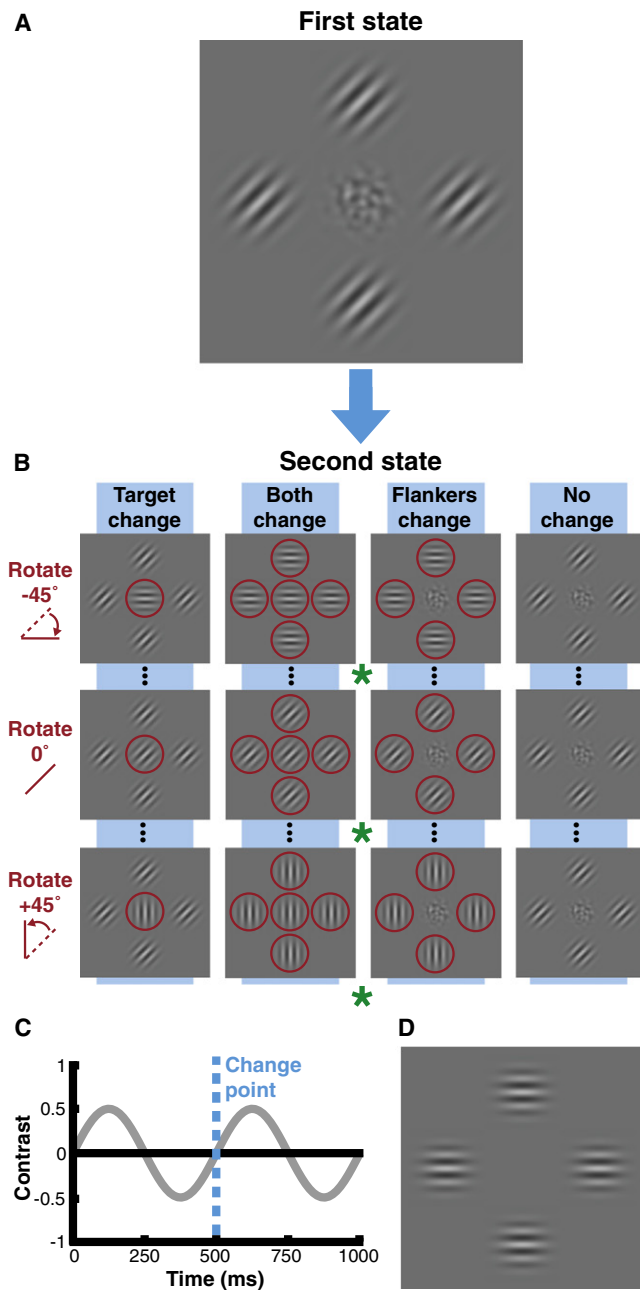


Figure 1. Stimuli and Procedure for the Change-Detection Experiments
(A) Experiments began with the target noise surrounded by four identical flankers at one of four orientations (45° depicted). Closing one eye and viewing the stimulus peripherally—by maintaining fixation on one of the green asterisks (depending on viewing distance)—allows one to see the effect of crowding: the target noise should become perceptually oriented.
(B) In one quarter of all trials, noise stimuli persisted throughout (no change). The remaining conditions involved a stimulus change (red circles). For the target-change condition, a Gabor was introduced at the target location, with an orientation between $\pm 45^\circ$ relative to the flankers. In the both-change condition, flankers rotated to match the introduced target. The flankers-change condition involved the rotation of flankers without a change in the target noise. All conditions were interleaved, and observers simply indicated whether the target had changed.
(C) Time course of a single trial. Stimuli counterphase flickered, with changes occurring midway through the trial when stimuli were at mean luminance.
(D) The initial stimulus configuration with a blank target (0° base depicted). Change conditions were as in (B), substituting blank regions for the noise patches.

target-change condition arose through inhibition of the introduced Gabors, performance in the both-change condition should be uniformly poor as a result of this target-flanker match. However, as shown in Figure 2A (red points), the pattern of data from the two conditions is identical, consistent with observers comparing the introduced Gabors and their percept of the crowded target. We also tested the spatial extent of these effects by varying target-flanker separation and report interference zones spanning 6° (Figure S2A). In line with prior estimates of crowding [2, 10, 17], this is equivalent to $0.4 \times$ the target eccentricity. Additionally, our stimulus configuration produces a minimal effect on detection thresholds (Figure S2B), contrary to the predictions of both masking and simple inhibition.

If, as we hypothesize, crowding induces the target noise to appear oriented, observers should also perceive an illusory rotation when the flankers rotate without a physical change in the target noise (flankers change; Figure 1B). This is indeed the case (green points; Figure 2A), with the highest rate of reported change occurring with large flanker rotations. The similarity between these data and observers' detection of introduced Gabors in other conditions suggests that these illusory changes are indistinguishable from physical changes. Our results are therefore mutually consistent with the notion that crowding alters appearance: here, isotropic stimuli assume an illusory orientation similar to the flankers'.

Because flanking elements are likely to drive this change in appearance, it might be possible to induce similar effects without a target. To test this, we repeated the procedure with a blank target instead of noise (Figure 1D). Viewed peripherally, this arrangement can give the faint appearance of oriented structure in the target region. For the change-detection paradigm, the target remained continuously blank in the no-change and flankers-change conditions and was swapped for a Gabor in the remaining conditions (as in Figure 1B). Results are plotted in Figure 2B and show a similar pattern to the crowded-noise experiment, albeit at a lower magnitude. As before, in target-change and both-change conditions, changes were most often missed when the substituted Gabor matched the flankers' orientation but were easily detected when substituted Gabors were dissimilar. However, both functions are now shifted upwards because of the lower likelihood of missed changes, consistent with the perceived orientation being more weakly induced in the target region. Similarly, the downward shift in the flankers-change data demonstrates a reduced rate of illusory changes, though the overall pattern was similar (with changes reported most often for large rotations). These results demonstrate that although target noise facilitates the expression of flanker-induced changes in appearance—perhaps similar to the way dynamic test patterns can reveal motion aftereffects [32]—a target is not required for crowding to occur.

Our results indicate that crowding can induce an orientation-selective change in the representation of the target. If this process engages the same low-level mechanisms that signal physical orientation, then prolonged viewing of our stimuli should induce adaptation. Ordinarily, adaptation to an oriented target produces a tilt aftereffect (TAE; [33]): the perceived orientation of subsequently viewed test stimuli is repulsed away from the adaptor. We examined whether crowding-induced changes in appearance could induce a TAE by having observers adapt to either (1) an uncrowded target Gabor, (2) crowded noise, or (3) a crowded blank region, followed by a single test Gabor on each trial (Figure 3A).

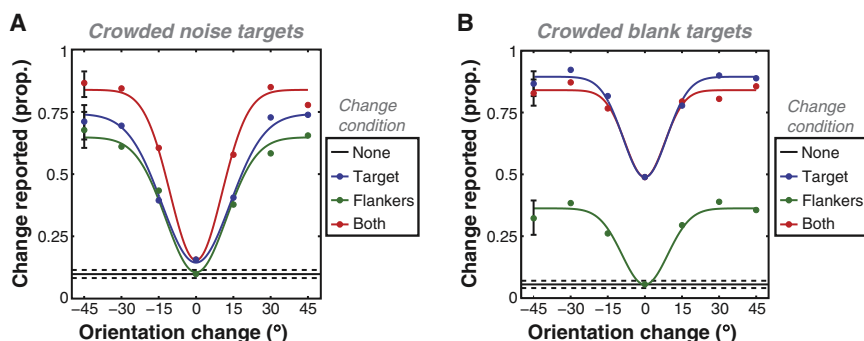


Figure 2. Crowded Change Detection

Data show the proportion of trials for which change was reported (pooled across three observers). Error bars indicate 95% confidence intervals.

(A) Change detection with target noise. Data are plotted as a function of the orientation change introduced, relative to the base orientation of the flankers. No-change trials gave a small proportion of false alarms (solid black line). In target-change (blue points) and both-change (red points) conditions, change detection was poor (approaching false alarm rates) when introduced target Gabors matched the initial flanker orientation (0° change). Detection improves with increasing orientation difference between the

introduced Gabor and the flanker orientation (i.e., the perceived orientation of the crowded noise). Large rotation of the flankers in the flankers-change condition (green points) also led subjects to report target change, consistent with the flankers inducing an illusory rotation of the target noise. (B) Change detection with a blank target, plotted as in (A). The pattern of results is similar to that observed with crowded noise (i.e., introduced Gabors were most often missed when they matched the initial flanker orientation), albeit with a lower magnitude (meaning both fewer errors overall and a lower frequency of illusory rotations).

Subjects indicated the apparent orientation of the peripheral test pattern by rotating a Gabor (at fixation) to match their percept. Postadaptation responses were then subtracted from preadaptation responses to measure the TAE.

As shown in Figure 3B, adaptation to an isolated target Gabor produced a robust TAE, with a maximum repulsion of $\pm 10^\circ$ at test orientations differing by $\pm 10^\circ$ – 15° from the adaptor (consistent with prior studies of the peripheral TAE [34]). Following adaptation to either crowded-noise or crowded-blank regions, the same pattern was evident, peaking with a lower magnitude of $\pm 5^\circ$. Here, the perceived orientation of the test was repelled from the orientation of the adapting flankers rather than from any physical structure at the target location. This effect of adaptation was not restricted to perceived orientation, with some elevation of contrast-detection thresholds also evident (Figure S3). Concurrent eye tracking further demonstrated that eye movements during adaptation (which might have shifted flankers into the target vicinity) cannot explain these results (Figure S4). Rather, these aftereffects are consistent with earlier findings that the spatial

spread of adaptation becomes increasingly broad as adapting stimuli move further into the periphery [35]. We suggest that this spread in orientation signals contributes to crowding. Accordingly, manipulations that do not produce crowding (e.g., a target Gabor with orthogonal flankers [5]) produce a TAE that is indistinguishable from that induced with a similar target in isolation (Figure S5).

Discussion

Our results demonstrate that crowding produces a change in object appearance: when crowded by Gabors, patches of isotropic noise assume the orientation of the flankers. Using a change-detection paradigm, we report that Gabors introduced at the target location go largely unnoticed when their orientations match this illusory percept but are easily detected when they differ from it (Figure 2A). Rotation of the flankers also caused an illusory rotation of the target noise, consistent with a crowding-induced orientation that is indistinguishable from physically oriented stimuli. Similar effects were apparent

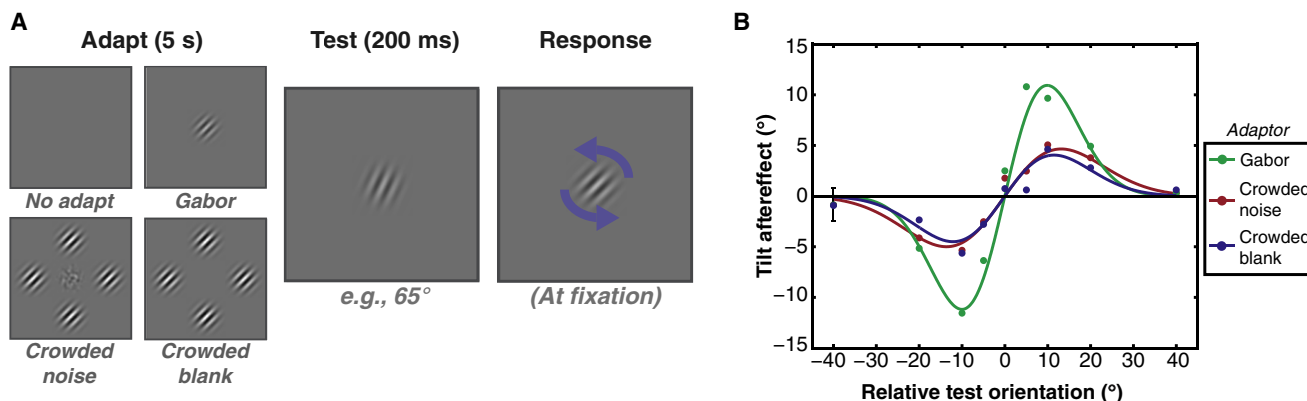


Figure 3. Adaptation to Crowded Stimuli

(A) Observers either remained unadapted or adapted to either a single 45° Gabor at the target location, a noise patch crowded by 45° flankers, or the flankers in isolation (“crowded blank”). Following 5 s adaptation, a Gabor was presented at the target location for 200 ms at one of several possible orientations. Observers rotated a response Gabor (at fixation) to match their percept of the test.

(B) Changes in perceived orientation after adaptation, averaged across three observers. Negative values indicate clockwise rotations and positive values indicate counterclockwise rotations; error bars depict ± 1 standard error of the mean. Adaptation to a single Gabor (green points) produced repulsion in perceived orientation that peaks at test orientations $\pm 10^\circ$ – 15° from the adaptor. Adaptation to either crowded noise (red points) or crowded blanks (blue points) produces the same pattern at a lower magnitude, consistent with the presence of an oriented signal at the target location.

with blank targets (Figure 2B), providing the first demonstration of crowding without a target. Finally, adaptation to both crowded-noise and crowded-blank regions produced a tilt aftereffect (Figure 3B), consistent with the flankers' orientation being introduced at the target location. Together, these results suggest that crowding is a process that actively promotes perceptual similarity between adjacent regions of the visual field.

These findings are inconsistent with several current explanations of crowding. First, models that rely on information loss through insufficient resolution of the attentional spotlight [13–15] predict little to no systematic target changes, contrasting with the strong percept elicited by our simple stimuli. Our results are also inconsistent with models in which target and flanker locations are lost through processes such as a misdirected attentional spotlight [23, 36]. Errors in positioning attention should be either constant (if localization errors are stimulus independent) or reduced in the presence of target noise (compared with blank targets, because the target noise would provide additional positional information). Gross spatial uncertainty thus incorrectly predicts either less crowding with noise targets or no effect of target identity at all. The robust TAE observed after crowded adaptation is also inconsistent with target-flanker mislocalizations, because attentional allocation should not affect retinotopic adaptation processes. In short, our results argue strongly against crowding models based solely on information loss.

Our results are also inconsistent with inhibition-based models of crowding [11, 12] and explanations based on masking [17, 29–31]. If the flankers suppressed the target, performance should have been uniformly poor in the both-change condition (Figure 1B) where the flankers rotated to match the introduced Gabor. That performance was identical to the target-change condition (Figure 2A) indicates that observers performed the task by comparing their percept of the crowded stimulus and the introduced Gabor. As an alternative, one could argue that the flankers inhibit dissimilar orientations to promote similarity in the target location. Although this could produce our results by creating an imbalance in the population response to the target noise, dissimilarity-based inhibition is inconsistent with the known selectivity of crowding. That is, stronger crowding is observed with increased target-flanker similarity and not vice versa [5, 19]. We can thus exclude inhibition as the primary mechanism of crowding. These results are similarly inconsistent with reductions in stimulus visibility related to masking, in conjunction with the broad spatial extent of our change-detection effects and the minimal effect on detection thresholds (Figure S2). Nonetheless, there is clearly some effect of clutter on stimulus visibility when flankers closely abut the target (Figure S2B; [17, 37]). These masking effects (on stimulus detection) may interact with crowding effects (on identification) at the closest target-flanker separations. An increase in the strength of masking could therefore cause crowded changes in target appearance to be reduced or even eliminated, though this was not the case with our stimuli.

The changes we observed in crowded target appearance are consistent with the correlation between target identification errors and the identity of flanking elements [9, 16, 22–25], suggesting that these systematic effects reflect a genuine change in the target representation rather than behavioral strategies aimed at overcoming uncertainty. These changes follow predictions from two change-based models of crowding. The first is flanker substitution, where either flanker features [11, 20] or flankers in their entirety [21, 22] replace

the target. The second is a compulsory average of target and flanker signals [16]. Both models require that flanker identities propagate into the target location but differ in the way that target and flanker signals interact. Substitution predicts that flankers overwrite the target and could thus predict both changes in appearance and orientation-selective adaptation. An average of target and flanker identities could similarly mimic our results, because averaging the flankers with noise (arising from either the visual system or the stimulus) would also replicate the flanker identity. Recent experiments demonstrate that a weighted average of noisily-encoded target and flanker feature positions can account for both the threshold elevation and the flanker-directed biases in judgments of the feature positions within letter-like elements, whereas flanker substitution predicts erroneously extreme feature positions [9]. We therefore favor an explanation where target flanker averaging produces both systematic and random aspects of crowding as a result of the inherent featural uncertainty of the periphery.

Several cortical mechanisms could subserve these effects. The first is propagation via lateral interactions within primary visual cortex [38]. Although this may appear to conflict with the minimal effects on the adaptive strength [13, 39] and contrast-detection thresholds of crowded targets [17, 29], our results suggest a potential reinterpretation of these results: crowding could produce a change in the identity of crowded targets without affecting their perceived contrast. However, the extent of horizontal connections scale to only $0.1\text{--}0.2 \times$ the target eccentricity [3], rather than the requisite $\sim 0.4\text{--}0.5 \times$ scaling seen here and elsewhere [2, 17]. A second possibility is that target changes occur through pooling within large receptive fields, likely within cortical areas such as V4 [40], though multiple regions may be involved through both feedforward and feedback connectivity [41]. We consider this to be the best current explanation of our findings.

Changes in the appearance of crowded targets bear a strong resemblance to the filling-in that occurs when regions of texture perceptually complete across either homogeneous target regions or the blind spot [42, 43]. Filling-in shares many characteristics with crowding, including an increased magnitude in the periphery, orientation tuning, binocular mechanisms, and occurrence across the blind spot (filling-in [42–45]; crowding [5, 19, 46]). Although the timescale of filling-in may be longer than crowding [45], it is likely that these processes are related. Changes in crowded target appearance may also underlie many effects in the change-detection literature [28].

Finally, the change-based processes observed herein demonstrate that crowding may not serve a purely disruptive role in visual perception. Rather than adding noise or suppressing target elements, crowding appears to explicitly promote perceptual similarity between adjacent regions of the peripheral visual field. This could involve the representation of large spatial regions as if they were texture (essentially preparing a statistical description [47, 48]), a process that could allow a more efficient representation of information given the low spatial sampling and high featural uncertainty of the periphery.

Experimental Procedures

Observers

Three experienced observers participated in the experiments: two of the authors (J.A.G. and S.C.D.) and one naive observer. All had normal or corrected-to-normal visual acuity.

Apparatus

Experiments were programmed with MATLAB (MathWorks) on a Macintosh computer running PsychToolbox [49]. Stimuli were presented on a cathode ray tube monitor (LaCie Electron Blue 22) with a resolution of 1152 × 870 pixels and a refresh rate of 75 Hz, fitted with a Bits++ box (Cambridge Research Systems) to give 14-bit contrast resolution. The monitor was calibrated with a Minolta LS110 photometer and linearized with look-up tables to give a mean and maximum luminance of 50 and 100 cd/m², respectively. Stimuli were viewed monocularly with the dominant eye from a distance of 57 cm. Experiments took place in a dark room, with responses made with either the keyboard (change detection) or mouse (adaptation).

Stimuli and Procedures

In all experiments, stimulus elements were either Gabors or patches of filtered noise (as in Figure 1A). Target noise stimuli were constructed from white noise that was convolved with a log Gaussian filter in the spatial frequency domain. This filtering was isotropic for orientation, with a peak spatial frequency of 2.5 cycles/degree (c/deg) and a bandwidth (s) of 1 octave. Gabor stimuli were also presented with a spatial frequency of 2.5 c/deg. The Gaussian window around both Gabors and noise elements had a standard deviation of 0.4°, and elements were presented at 50% Michelson contrast. All elements were counterphase flickered at 2 Hz with the same temporal phase (see Figure 1B).

Targets were presented 15° in the upper visual field. Under crowded conditions, four flankers were positioned above, below, to the right, and to the left of the target. Targets and flankers had a center-to-center separation of 2.75°, which, at 15° eccentricity, falls well within the region of interference [10, 17]. When targets were absent, the central noise patch was left blank at the mean luminance. Identical configurations were used for both change-detection and adaptation paradigms.

In the change-detection experiments, each 1 s trial was notionally divided into two 500 ms stages (Figure 1C). With target noise, the first stage contained the target noise patch surrounded by four Gabors (Figure 1A). Flanker orientations were always matched and were set initially to be either 0° (horizontal), 45° (tilted to the right), 90°, or 135°. After 500 ms, the counterphase time course of all elements reached mean luminance, and one of four conditions were initiated (Figure 1B). In the no-change condition, both target noise and flanking Gabors remained unchanged. For the target-change condition, the target noise was swapped for a Gabor element with an orientation that differed from the flankers by ±45° in 15° steps. The flankers-change condition left the central noise unchanged, with flankers rotated en masse by between ±45° relative to their initial orientation. Finally, the both-change condition involved both the appearance of a target Gabor and the rotation of the flanking Gabors so that the entire ensemble shared the same orientation. To examine the influence of isolated flankers, we also ran experiments with a blank target region (Figure 1D). Such trials were otherwise identical to those of the main experiment, incorporating the four change conditions (replacing target noise with a blank region where appropriate). In both cases, each orientation difference was presented 20 times for each change condition (five times at each of four base orientations), interleaved randomly to make 560 trials per block. Observers completed three blocks for each experiment, with crowded-noise and crowded-blank stimuli tested separately. Data were recorded as the proportion of trials in which change was reported and were pooled across observers (because all showed a similar pattern). Each data set was fit with an inverted Gaussian profile, and 95% confidence intervals were determined via a bootstrapping procedure with 1000 repetitions [50].

Stimuli were again at 15° eccentricity for the adaptation experiments, with similar parameters. Adaptation stimuli were either a single 45° Gabor at the target location, target noise surrounded by four flankers (each oriented at 45°), or the isolated flankers with a blank target region. Flankers were presented at 100% Michelson contrast to maximize crowding [19]. These stimuli counterphase flickered at 2 Hz for 5 s per trial, followed by a test interval for 200 ms. Test intervals contained a single Gabor at the target location with an orientation between 5° and 85°. A response Gabor then appeared at fixation, and observers adjusted its orientation with the mouse until it matched their percept of the peripheral test stimulus. This adaptation cycle then continued, with the first 10 trials discarded to enable the buildup of adaptation [13, 39]. Each test orientation was presented 20 times per block to give 190 trials, including practice. Observers repeated each adaptation condition three times in random order, with breaks taken when switching between conditions. For each test orientation, the mean perceived orientation was calculated. Data were again pooled across

observers and fit with the first derivative of a Gaussian, given the absence of attractive effects in the peripheral TAE [34].

Supplemental Information

Supplemental Information includes Supplemental Experimental Procedures, five figures, and five movies and can be found with this article online at doi:10.1016/j.cub.2010.01.023.

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Supplemental Information

Crowding Changes Appearance

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Supplemental Experimental Procedures

Change-Detection Experiments

Uncrowded Change Detection

The primary finding of this study is that patches of non-oriented visual noise appear oriented when crowded by Gabor flankers. This was demonstrated through the failure of observers to report trials in which crowded noise patches were changed into Gabors with an orientation that matched the flankers. In this section we present data from an uncrowded change-detection experiment that rule out performance anisotropies as an alternative explanation for this finding. Stimuli and procedures were similar to those of the main experiment, except that only a single target patch was present (Supplementary Fig. 1A). Each 1 s trial began with an isolated noise patch present for 500 ms, after which one of two conditions could be initiated. In the *no change* condition, the target noise remained present for the remainder of the 1 s trial. In the *target change* condition, a Gabor was introduced at the target location with a given orientation. Unlike the crowded conditions of the main experiment, orientations here are defined absolutely (0-179°), rather than relative to the flanker orientation. Each condition was presented 144 times in a given block; with each orientation in the *target change* condition presented 12 times. The three observers repeated each block three times.

As before, data were the proportion of trials in which change was reported. As all three observers showed an identical pattern of performance, data were pooled before a wrapped Gaussian profile was fitted and 95% confidence intervals determined using a 1000-repetition bootstrap [1]. The false alarm rate was determined from the *no change* condition, and was again less than 10% (Supplementary Fig. 1B; black line). In the *target change* condition, between 89-99% of changes were correctly reported, regardless of which target orientation was introduced (Supplementary Fig. 1B; blue points). This isotropic, near-ceiling performance stands in contrast to the pattern obtained when target-noise patches were crowded with oriented Gabors, as in the main text.

Crowding-Induced Change and Masking

Although it is often difficult to distinguish crowding from similar processes such as masking [2, 3], several lines of evidence support the notion that our change-detection effects originate from crowding. First, consider the effect of masking on the target-noise patches in the first half of each trial (Fig. 1A). Because masking reduces sensitivity to objects of similar spatial

structure [2, 3], it should reduce the effective contrast of similarly-oriented structure in the isotropic noise which, if it were to have a perceptual consequence, would lead the noise to appear oriented *orthogonally* to the flankers. In contrast, the actual appearance of crowded-noise patches was that their orientation matched the flankers (see data in Fig. 2A and the appearance of Fig. 1A in the periphery). Second, consider the effect of masking on the oriented Gabors introduced in the second half of *target change* and *both change* trials (Fig. 1B). In the *target change* condition, it is possible that the flankers could have masked the Gabors introduced to the target location, reducing the visibility of similarly oriented targets and thus producing the pattern of data in Fig. 2A. However, as outlined in the main text, this is not true for the *both change* condition. If impaired performance in the *target change* condition resulted from inhibition of the introduced Gabors, performance in the *both change* condition should be uniformly poor, as the flankers were always rotated to match the introduced Gabors. As shown in Fig. 2A (red points), this is not the case: the pattern of data was identical to that of the *target change* condition, consistent with observers comparing the introduced Gabors and their percept of the crowded noise.

In order to test for the involvement of masking more directly, we first observe a critical signature of crowding in our change-detection task. Namely, the distance over which target and flankers interact is equal to approximately half the target eccentricity [2, 4]. By contrast, the spatial extent of masking scales with target size, regardless of eccentricity, such that masks need to be either overlapping or in close proximity to the targets [2, 5, 6]. It follows that if our change-detection results are a consequence of crowding, these effects should be evident across a wide range of target-flanker separations. The magnitude of effects with crowded noise and blank targets should also decrease at the same rate with increasing target-flanker separation. To assess this, we re-ran the *no change* and *target change* conditions (using both noise and blank targets) as a function of target-flanker separation. Gabors in the *target change* condition were only introduced at the same orientation as the flankers, as this produces the strongest effect. Target-flanker separations between 2.75 and 11 deg. were tested in steps of 1.375 deg, both with crowded-noise and crowded-blank stimuli. Each target-flanker separation was presented 20 times for each change condition (five times at each of the four base orientations), interleaved randomly to make 560 trials per block. Observers completed three blocks, with crowded-noise and crowded-blank stimuli tested separately.

For each target-flanker separation, the proportion of change reported is plotted in Supplementary Fig. 2a for both crowded-noise (dark blue) and crowded-blank (light blue) stimuli. For both target types, increasing target-flanker separation produced a modest decrease in the rate of false alarms in the *no change* condition (dashed lines). In the *target change* condition, detection of change is poorest at small target-flanker separations, and improves markedly with increasing separation. The magnitude of this effect is approximately halved in the absence of a target, but both effects show an identical spatial extent, reaching a half-width at half-height of 5.7 deg. with blank targets and 5.8 deg. for crowded noise (shown with grey lines). This gives *interference zones* (the region around a target where the presence of flankers interferes with target recognition) proportional to $0.4 \times$ the target eccentricity (of 15 deg.), consistent with our effects arising from crowding [2, 4].

We next sought to examine whether our target-flanker configuration produced *masking*, i.e. whether there was a decrease in stimulus visibility, and if so, whether the spatial extent of this effect was similar to that produced by crowded change detection. Prior studies suggest that while crowding impairs object identification across large spatial extents (scaled with eccentricity), the same stimuli have a much smaller effect on contrast-detection thresholds

that occurs only when flankers are close to the target [2, 3]. We thus examined the effect of our target-flanker configuration on the detection of an oriented Gabor in the target location, using a paradigm that resembled the change-detection experiments as closely as possible. Each trial in this detection paradigm consisted of two 500 ms intervals (equivalent to the two halves of change-detection trials), separated by 500 ms. One interval contained a target Gabor at a given luminance contrast; the other remained blank. Each interval was delineated with a beep and an inversion of the contrast polarity of the fixation cross, with observers required to indicate which interval contained the target. Crowded detection thresholds were assessed with the addition of four vertically oriented flankers at 50% contrast, present in both intervals of the task. Target-flanker separations between 2.75 and 8.25 deg. were tested in steps of 1.375 deg. Thresholds were assessed by varying the Michelson contrast of the target using a QUEST staircase [7] that converged on 82% correct identification with a maximum of 45 trials per condition. Staircases for uncrowded detection and crowded detection at each target-flanker separation were interleaved in each run. This procedure was repeated three times for each of the three observers.

All observers showed the same pattern of performance and data were thus pooled, as presented in Supplementary Fig. 2b. When uncrowded, detection thresholds were around 4.5% Michelson contrast (solid black line). Under crowded conditions (green points), thresholds rose to around 18% at the closest target-flanker separation ($4\times$ uncrowded threshold). Importantly, this degree of masking is insufficient to account for our change-detection results: a four-fold elevation of thresholds would be unlikely to mask the visibility of either the target-noise or the target-Gabors introduced in the *target change* and *both change* conditions, which were presented at 50% Michelson contrast (i.e. $11\times$ detection threshold). Furthermore, this masking rapidly declines with increasing target-flanker separation – when fit with a cumulative Gaussian function, the half-width at half-height occurs at a 3.8 deg. separation. This corresponds to $0.25\times$ the target eccentricity, a modest spread that is only slightly broader than that of prior investigations [2, 3]. The slight increase in spatial extent over these prior studies is likely to reflect our use of four flankers, compared with two, which has been shown to increase the strength of masking [8]. Nonetheless, the effect on contrast-detection thresholds drops off considerably more rapidly than the effect of crowding on change detection.

A potential issue with the above analysis is the different nature of the data being compared in the two experiments. Differences in the range and magnitude of these effects could differentially affect the estimation of their spatial extent. To give each data set an equal footing, sensitivity measures were thus calculated for each experiment prior to normalization. For the change-detection data, a single measure of sensitivity (d') can be derived for each target type by subtracting z scores for the proportion of change in the *no change* condition (false alarms) from z scores for the *target change* condition (hits). For the masking paradigm, sensitivity can be determined from the inverse of the threshold elevation ratios obtained initially by dividing crowded thresholds by this uncrowded baseline. Both datasets were then normalized by subtracting the minimum and dividing by the maximum. The resulting values, ranging from 0-1 and fit with cumulative Gaussian functions, are plotted in Supplementary Fig. 2c. While this does alter the spatial spread of these effects slightly, with masking now reaching a half-width at half-height at 4.6 deg., crowded-blank stimuli at 6 deg. and crowded-noise at 6.6 deg., the relative spatial extent of these effects remains the same – masking still drops off at a faster rate than either of the change-detection effects.

Although the flankers clearly produce some degree of masking, these results demonstrate that masking cannot account for the entirety of the change-detection effects reported herein. First, a reduction in the visibility of structure oriented similarly to the flankers cannot explain either the subjective appearance of crowded-noise stimuli or data from the *both change* condition. Second, the magnitude of masking that we observe is modest and would have been insufficient to completely reduce the visibility of our target stimuli. Finally, masking shows a considerably smaller spatial extent than crowded change detection. This distinction fits with the more general dichotomy between crowding and masking – the former affects identification, while the latter affects detection [2, 3]. Given that our change-detection task requires observers to compare their percept of the two intervals, it clearly falls within the realm of target identification and thus suffers from crowding. Nonetheless, it is worth noting that this distinction is not absolute – configurations consistent with ‘crowding’, as in the present study, can nonetheless produce significant levels of masking. It is clear however that the effects of masking cannot completely encapsulate the effects of crowded change-detection.

Adaptation Experiments

Contrast Detection Thresholds

As outlined in the main text, our results suggest that crowding can produce an orientation-selective change in the representation of target stimuli. Consistent with this view, adaptation to both crowded-noise and crowded-blank stimuli produced a robust tilt aftereffect at the target location (Fig. 3). However, while these results are consistent with a spreading of the flanker signals, the latter result differs from previous studies that have examined the effect of crowded adaptors on contrast-detection thresholds. Specifically, adaptation to crowded Gabor targets has been shown to produce threshold elevation for the detection of similarly oriented Gabors that is either identical [9] or reduced in magnitude [10] compared with adaptation to uncrowded Gabors. Crowding in this case appears to have either no effect, or to operate as a suppression of the adapting signal, unlike the additive effect produced by the flankers in our experiments.

One reason for this discrepancy could relate to the more general debate regarding the locus of crowding and its effects on detection and identification. As above, although crowding impairs object identification, it has less impact on contrast-detection thresholds for the same objects [2, 3]. Were this to carry across to adaptation, crowded adaptors could affect post-adaptation identification with little-to-no effect on detection. Our use of the tilt aftereffect (measured via perceived orientation) might thus have biased our results towards these identification mechanisms, compared with prior work examining effects on post-adaptation detection thresholds. In order to test this hypothesis, we also examined the effect of adaptation to crowded-noise and crowded-blank stimuli on contrast-detection thresholds for oriented test stimuli in the target location.

As in the adaptation experiment in-text (Fig. 3), adaptation stimuli were presented counterphasing at 2 Hz for 5 s per trial, with the first 10 trials unrecorded to allow the build-up of adaptation. Observers adapted to either a single Gabor in the target location, crowded-noise stimuli, or the flankers in isolation (‘crowded-blank’ stimuli). Two temporally separated intervals were then presented, one blank and the other with a single target Gabor oriented at either 45° (as with the adaptor) or 135° (Supplementary Fig. 3a). Each interval was presented for 200 ms and separated by 500 ms, with observers required to make a two-interval forced-

choice decision regarding which interval contained the target Gabor (regardless of orientation). The Michelson contrast of the test Gabors was under the control of two interleaved QUEST staircases, one for each test orientation, set to converge on 82% correct. Each run was repeated three times for each observer.

Threshold elevation ratios were determined by dividing post-adaptation thresholds by unadapted thresholds. A value of 1 thus indicates no effect, with higher scores indicating stronger levels of adaptation. Supplementary Fig. 3b depicts these values for each observer, with the mean effect in grey. Adapting to a single Gabor produced a three-fold elevation of detection thresholds for similarly oriented test Gabors (45°), with much less effect on test Gabors of the opposite orientation (135°). Adaptation to crowded-noise stimuli also induced a clear elevation of same-orientation thresholds, with around half the magnitude of the effect induced by a physically oriented target. Orientation selectivity was also evident with little, if any, threshold elevation for the detection of test stimuli oriented at 135° . Threshold elevation was smaller again for the crowded-blank stimuli, with elevation values only marginally above 1, though some orientation selectivity is nonetheless evident. In sum, both types of crowding stimuli induced an orientation-selective elevation of post-adaptation detection thresholds, despite the absence of a physically oriented stimulus in the target location. This is again consistent with the induction of flanker signals within the target representation, with the magnitude of threshold-elevation values for crowded-noise and crowded-blank stimuli further consistent with the different effect sizes seen with these stimuli in the change-detection paradigm (Fig. 2). It follows that our adaptation results cannot be explained in terms of the more general detection/identification dissociation that occurs under crowding [2, 3].

Previously reported effects of adaptation to crowded Gabors [9, 10], can be reconciled with our own results by our demonstration that crowding can produce an orientation-selective *change* in the target representation. This would have been obscured in prior studies because the effect of adaptation was examined only for similarly- and orthogonally-oriented test stimuli. Rather, were crowding to change the target orientation, the strongest adaptation may in fact be found at intermediate orientations due to observers adapting to a different orientation for a large proportion of trials. This would shift the tuning curve of adaptation effects away from the original target orientation, which would appear as a reduction in threshold elevation at the target orientation. Alternatively, it is possible that such change initiates local competition between the target and flanker-introduced signals, which could produce both changes in appearance and reduced adapting strength. These processes would be evident only when a target signal is present to interact with the flanker signals and would thus have been obscured with our stimuli.

Eye Movements and the Tilt Aftereffect

One issue with adapting to crowded stimuli is the requirement that flankers be close to the target in order for crowding to occur [4, 11]. Consequently, small eye-movements could cause the flankers to fall on the retinal area that would ordinarily be responding to the target stimulus, possibly contributing to adaptation at that locus. To test this possibility, we repeated the tilt aftereffect experiment (Fig. 3a) and made concurrent measurements of eye movements. Stimulus parameters were identical to those of the main experiment, though stimuli were presented on a Sony Trinitron monitor with a resolution of 1152×864 and a 100-Hz refresh rate. Eye movements were recorded using a head-mounted Eyelink I infrared gaze-tracker (SensoMotoric Instruments, Teltow, Germany) running at 250 Hz, in conjunction with the Eyelink toolbox for Matlab [12]. Calibration was conducted at the beginning of each

block of trials, with drift correction every five trials. Movements of the right eye were recorded during the 5.7 s period of each trial containing the adaptation stimulus (5 s), inter-stimulus interval (0.5 s) and test stimulus (0.2 s). Additionally, if fixation strayed more than 1.5 deg. on either side of fixation, trials were aborted and re-commenced. Recordings were not made during the response phase. All other procedures were identical to those of the main experiment. One observer (JAG) participated in this control study.

Results are depicted in Supplementary Fig. 4a (blue points) and show an identical pattern to those obtained previously (red points, data for JAG only). As before, orientations tilted slightly clockwise of the flanker orientation (45°) were seen as tilted further clockwise than prior to adaptation, and vice versa for counter-clockwise orientations, regardless of whether eye movements were recorded. Fixational jitter greater than 1.5 deg. caused trials to be aborted on less than 1% of the total. Supplementary Fig. 4b shows the concurrently measured distribution of eye-fixation positions, plotted in degrees of visual angle relative to the fixation point (grey triangle). Data have been normalised so that frequencies fall between 0-1, and smoothed using a Gaussian function with a standard deviation of 1 pixel. The majority of fixation positions cluster tightly around the fixation point, with X and Y standard deviations of 0.37 and 0.38deg, respectively. This is well within normal limits [13, 14].

Estimating the effect of this retinal smear requires some assumptions. If we take ± 2 standard deviations around the fixation point, 95% of eye fixations were within ± 0.75 deg. of the fixation marker. Given the spatial frequency and luminance contrast of our stimuli, we can then take their perceived size as ± 2 standard deviations of the windowing Gaussian [15], to give a physical radius of 0.8 deg. Using these measurements, the impact of eye movements on our stimuli is shown schematically in Supplementary Fig. 4c. The target-noise patch is shown here with a rightwards flanker and a centre-to-centre separation of 2.75deg. Even when the estimated radius of our stimuli is added to the spatial extent of eye movements, the resultant shifts of the flankers would not exceed the separation between target and flanker stimuli. It is therefore unlikely that this fixational instability was sufficient to shift the flanker stimuli onto the region of the retina that would ordinarily be adapting solely to the target stimulus.

The Tilt Aftereffect and Uncrowded Stimuli

Although fixational eye movements were insufficient to move the flankers over the target location during adaptation, it is important that we consider the receptive field properties of the cells that would respond to these stimuli. In particular, it is well established that receptive fields grow in size as their location becomes increasingly peripheral [16], and as processing moves from V1 through to higher visual areas [17]. Given that our stimuli were presented at 15 deg. eccentricity, and that crowding may involve cortical regions beyond V1 [2, 18], it is likely that our stimuli activated cells with relatively large receptive fields. On the one hand, this is a potential model of the crowding process: the integrative operations typically seen in crowding tasks could result from a cortical resolution that is insufficient to represent the target and flanker stimuli independently [18, 19]. However, it could be that our stimuli simply adapt cells with large receptive fields in a manner unrelated to crowding. Given that our targets were either isotropic for orientation or absent altogether, the net effect could be adaptation to the flanker orientation (irrespective of whether crowding had occurred).

To test this hypothesis, we examined the effects of adaptation to a target stimulus surrounded by flankers that produce minimal crowding. Because crowding is tuned for orientation, flankers oriented orthogonally to the target produce little-to-no crowding, compared with

flankers oriented similarly to the target [20]. We thus compared the effect of adaptation to a single Gabor stimulus (oriented at 45° , as before) with that produced by adaptation to the same Gabor target surrounded by orthogonal flanking Gabors (oriented at 135° ; Supplementary Fig. 5a). If the adaptation effects observed herein are related to the flanker orientation, regardless of crowding, the tilt aftereffect should either be reversed, due to the orthogonal orientation of the flankers, or reduced considerably in magnitude. On the other hand, if the strength of the adapting signal depends on the strength of crowding, the magnitude of the tilt aftereffect should be similar in both cases. To further minimize crowding in the orthogonal-flankers condition, all elements were presented at 100% peak contrast [21]. Accordingly, the orientation of the target Gabor was readily detectable under these conditions. The remaining parameters were identical to those of the adaptation experiment in-text (Fig. 3), and only observer JAG participated in this control experiment.

Results are shown in Supplementary Fig. 5b, where adaptation to a single Gabor in the target location again produces a robust tilt aftereffect, with a large repulsive effect that peaked at test orientations differing by $\pm 10\text{-}15^\circ$ from the adaptor. An identical pattern was produced following adaptation to the same Gabor target surrounded by four orthogonally oriented flankers, despite the potential for the orientation of these flankers to either produce the opposite direction of repulsion or reduce the magnitude of target adaptation. Flankers that produce minimal crowding thus have a minimal effect on the adapting strength of oriented target stimuli. It follows that our results are unlikely to have been produced by adaptation of cells with large receptive fields in a manner unrelated to crowding. Of course, it remains possible that crowding itself could be produced by integration across large receptive fields, as we consider in the General Discussion.

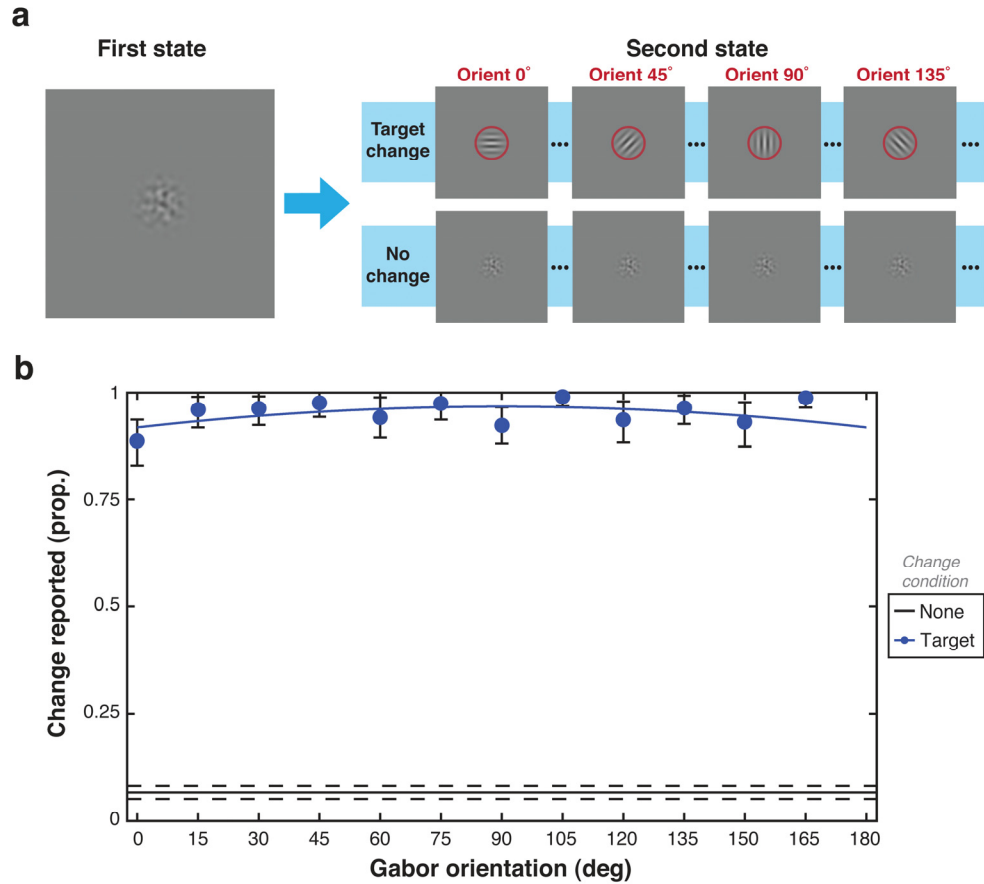


Figure S1. Uncrowded Change Detection

(A) Stimuli and procedure. Trials always began with target noise present, as in the main experiment. Here the noise was not crowded. Midway through each trial, the noise could either remain present (*no change*) or change into a Gabor (*target change*). All conditions were interleaved and observers indicated whether the target changed.

(B) The proportion of trials in which change was reported - pooled across three observers - is plotted separately for the *no change* and *target-change* conditions, the latter as a function of the absolute orientation introduced in the second stage. Error bars depict 95% confidence intervals. Performance is nearly identical across all orientations, indicating no difference in change-detection performance as a function of the introduced orientation.

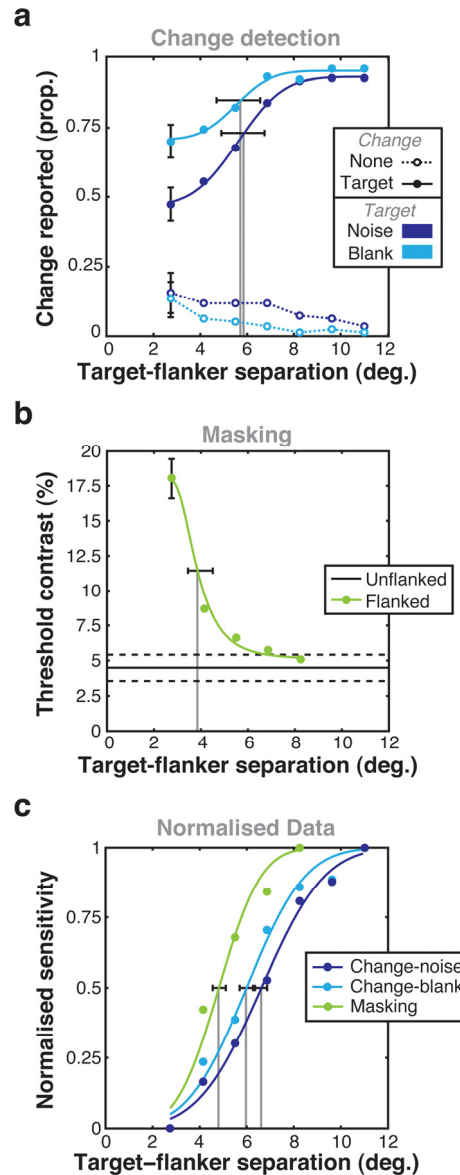


Figure S2. The Effects of Target-Flanker Separation

Data are pooled across three observers; error bars show 95% confidence intervals around the first data point of each series and the midpoints of each function, determined using bootstrapping.

(A) Change detection with crowded-noise (dark blue) and crowded-blank regions (light blue), plotted as the proportion of trials in which change was reported. Only the *no change* (dashed lines) and *target change* (solid lines) conditions were run, and introduced Gabors always matched the flankers. Change detection improves steadily with increasing target-flanker separation, with a half-width at half-height of 5.8 and 5.7 deg. for the crowded-noise and crowded-blank conditions, respectively (grey lines).

(B) Thresholds for detection of a Gabor target, with both unflanked (black line) and flanked (green points) configurations. Note that the x-axis shows the same target-flanker separations as panel A. Though there is some masking of target detection at the closest target-flanker separation, this rapidly declines to reach a half-width at half-height at 3.8 deg. separation (grey line), considerably less than that of crowded change detection.

(C) Normalized data for both masking and change-detection experiments. Sensitivity values were obtained by converting change-detection performance to d' and by inverting the threshold elevation ratios of the masking experiment. Data were normalized to between 0-1 by subtracting the minimum and dividing by the maximum. When fit with cumulative Gaussian functions, masking still drops off at a much faster rate than the two crowded-change conditions, with half-width at half-height values of 4.6, 6.0 and 6.6 deg., respectively.

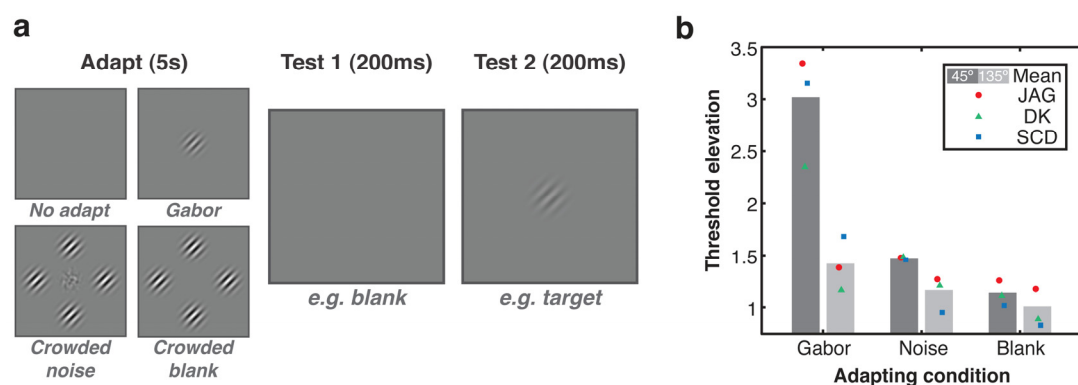


Figure S3. Adaptation and Detection

(A) Stimuli and procedure. As in the main experiment, observers were either (i) unadapted or adapted to (ii) a single Gabor in the target location (45° orientation), (iii) crowded noise stimuli with flankers oriented at 45°, or (iv) the flankers in isolation ('crowded blank'). Following 5-seconds of adaptation, two test intervals were sequentially presented for 200 ms each. One was blank and the other contained a single Gabor in the target location, oriented at either 45° or 135°. Observers indicated the interval containing the test Gabor.

(B) Threshold elevation values for the contrast-detection task. Results are shown for each observer, with mean values in grey. Adaptation to a single Gabor produced robust threshold elevation for detection of similarly oriented test stimuli (45°), with far less elevation for the opposite orientation (135°). Adaptation to crowded noise stimuli produced the same pattern at a smaller magnitude. Crowded-blank stimuli induced minimal adaptation, though some orientation selectivity is nonetheless evident.

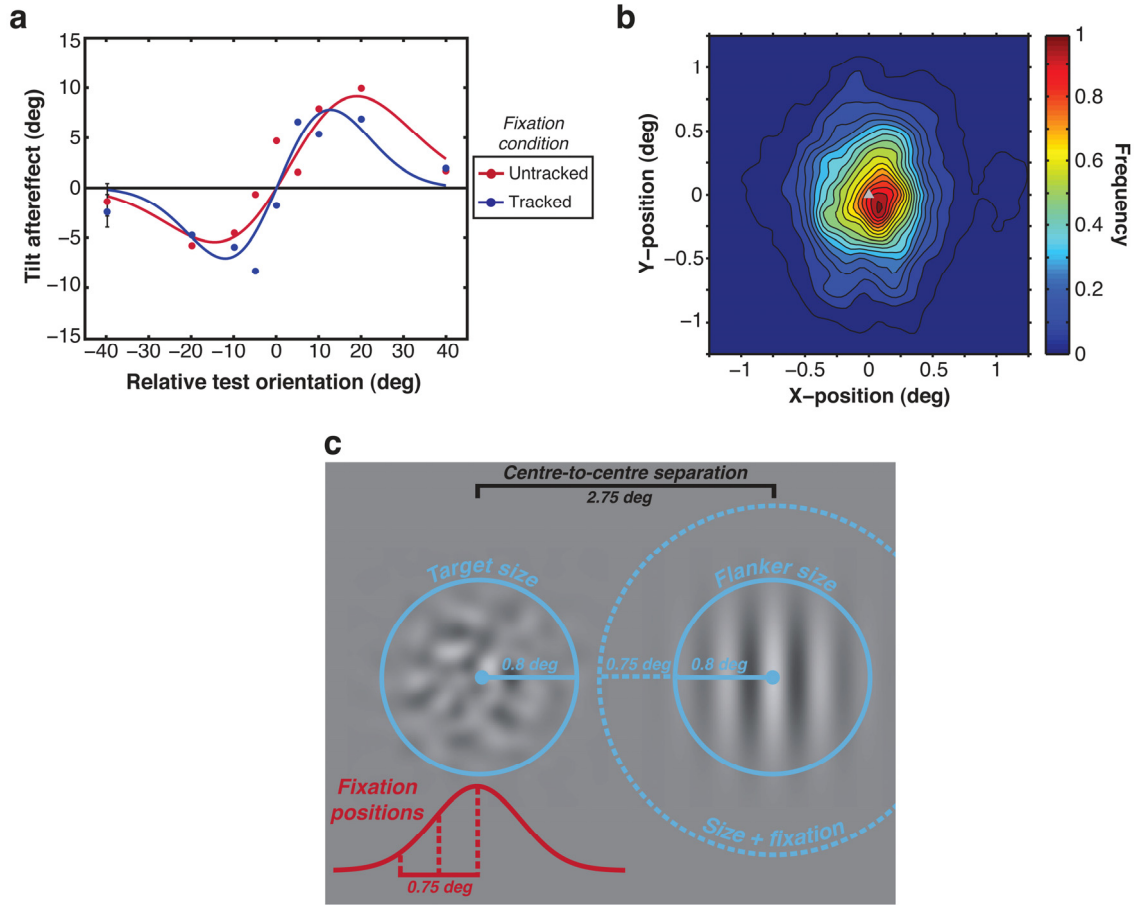


Figure S4. The Tilt Aftereffect and Eye Fixation

(A) The magnitude of the tilt aftereffect following adaptation to crowded-noise stimuli. Red points show the tilt aftereffect for JAG produced in the main experiment; blue points were measured with concurrent eye tracking. As before, negative values indicate clockwise rotations, positive indicate anti-clockwise rotations, and error bars depict ± 1 SEM. In both cases, adaptation to crowded-noise stimuli produces a repulsion in perceived orientation that peaks at test orientations ± 10 - 15° from the adaptor.

(B) The position of the right eye around fixation during adaptation and test intervals, relative to the fixation point indicated with a grey triangle at (0,0). Frequencies range between 0-1, and have been smoothed with a 1-pixel SD Gaussian function.

(C) A schematic view of the impact of eye movements on our stimuli. The radius of stimuli is estimated as 0.8 deg. (solid blue circles), given their spatial frequency and contrast, while the extent of eye movements is taken as ± 2 standard deviations around the mean, giving a smear of 0.75 deg. in all directions (red distribution). The combination of these factors is depicted as a dashed blue line around the flanker, which does not exceed the centre-to-centre separation between flankers and the target.

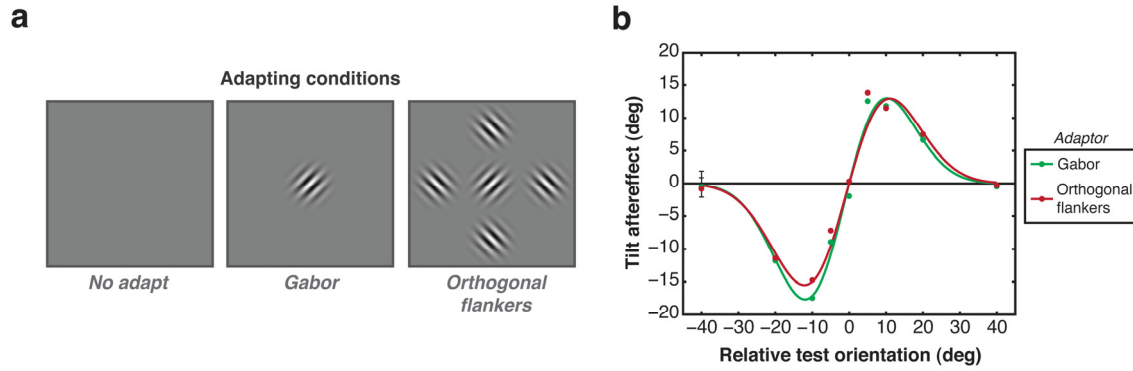


Figure S5. The Tilt Aftereffect and Uncrowded Stimuli

(A) Adapting stimuli: observers were either unadapted, or adapted to a single Gabor in the target location (45° orientation, 100% peak contrast) or a target Gabor at 45° surrounded by four flankers at 135° ('orthogonal flankers'). The latter stimulus produces minimal crowding due to the dissimilarity between target and flanker stimuli.

(B) Changes in perceived orientation after adaptation, for observer JAG. Adaptation to a single high-contrast Gabor (green points) produced repulsion in the perceived orientation of test stimuli that peaks at orientations ± 10 - 15° from the adaptor. An identical pattern is produced following adaptation to the orthogonal-flankers stimulus, despite the presence of the flankers.

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