The role of crowding in contextual influences on contour integration

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Dakin and Baruch (2009) investigated how context influences contour integration, specifically reporting that near-perpendicular surrounding-elements reduced the exposure-duration observers required to localize and determine the shape of contours (compared to performance with randomly oriented surrounds) while near-parallel surrounds increased this time. Here, we ask if this effect might be a manifestation of *visual crowding* (the disruptive influence of "visual clutter" on object recognition). We first report that the effect generalizes to simple contour-localization (without explicit shape-discrimination) and influences tolerance to orientation jitter in the same way it affects threshold exposure-duration. We next directly examined the role of crowding by quantifying observers' *local uncertainty* (about the orientation of the elements that comprised our contours), showing that this largely accounts for the effects of context on global contour integration. These findings support the idea that context influences contour integration at a predominantly local stage of processing and that the local effects of crowding eventually influence downstream stages in the cortical processing of visual form.

Keywords: contour integration, contour-shape processing, context, visual crowding

Introduction

There is a long-standing interest in how the visual system links estimates of local image-structure into global, complex forms. With respect to the visual processing of contours, it is now clear that the integration of their constituent components requires cooperative interactions between feature detectors distributed across space with different orientation preferences (Field, Hayes, & Hess, 1993). An outstanding question, which much research in the last decade has focused on, is how the visual system can link the elements of a contour, while avoiding linkage with irrelevant background structure, to produce a salient structure that "pops-out." In psychophysical studies using the "path paradigm" (Field et al., 1993), observers' task is to detect the presence of a smoothly curved contour (path), composed of a series of oriented Gabor patches, embedded in an array of similar but randomly oriented background-elements. These studies highlight the crucial parameters for contour integration, the most important being contour-element rotation. Specifically, contour detection performance is best if elements match the local orientation of the contour ("snakes") but relatively poor if elements are oriented perpendicular to the contour ("ladders"; Bex, Simmers, & Dakin, 2001; Field et al., 1993; Hess, Ledgeway, & Dakin, 2000; Ledgeway, Hess, & Geisler, 2005). The poorest performance, however, is obtained with elements oriented at 45° relative to the contour (Ledgeway et al., 2005). Other crucial parameters are path curvature (Field et al., 1993), interelement distance (Kovacs & Julesz, 1993), element-density (Li & Gilbert, 2002; Pennefather, Chandna, Kovacs, Polat, & Norcia, 1999), exposure-duration (Roelfsema, Scholte, & Spekreijse, 1999), similarity in phase (Dakin & Hess, 1999; Hess & Dakin, 1999; Keeble & Hess, 1999), and spatial frequency of the contour-elements (Dakin & Hess, 1998, 1999).

Outside of the field of contour integration, several studies have investigated the impact of contextual information on our sensitivity to local and global image-structure. For example, with respect to the detection of local structure (isolated elements), it has been shown that the detection of an oriented target in a field of identical elements depends on the distance from distracters to the target and also nonmonotonically on

distracter-density (Casco & Campana, 1999; Sagi, 1990). In terms of global processing (of groups of elements), recently Kingdom and Prins (2009) investigated the effect of texture-surround on contour shape-coding and reported results consistent with contour-shape mechanisms being inhibited by nearby parallel but not orthogonal texture orientations. The authors suggest that the processing of contour-shapes involves those neurons in the visual cortex that are inhibited by similar orientations outside their classical receptive fields.

Dakin and Baruch (2009) looked at the interaction of contextual effects between contour and background, and within the contour itself by examining how contour integration is influenced by the orientation structure of the context immediately surrounding the contour. Specifically, they manipulated the relative orientation of background distracter-elements compared to their nearest contour-element (weighted by contour-distracter distance) to generate surround conditions ranging from near-parallel to near-perpendicular. Using "S"-shaped contours, they measured observers' ability to perform a combined contour-localization and explicit shape-discrimination task, and showed robust psychophysical effects that were consistent with facilitation and suppression of contour structure in the presence of near-perpendicular and near-parallel surrounds, respectively. More recently, the same pattern of results has also been shown for straight contours (Schumacher, Quinn, & Olman, 2011). Specifically, the authors reported that parallel flankers reduced performance for intermediate and large Gabor spacings and sizes, whereas orthogonal flankers increased contour detection for small Gabor spacings and sizes.

Dakin and Baruch (2009) proposed that a two-stage filtering model of contour integration (incorporating an orientation-opponent stage after first-stage filtering) could account for such effects of context. However, given that their task had two components (contour-localization and explicit shape-discrimination), it is possible that the effects of context they showed are actually more related to one component than the other. Moreover, as a consequence of the display size used in this study, many of the contours would have been presented quite distant from the fovea (mean eccentricity, ~3.5°), and it is possible that this contributed to the effect. Indeed, Hess and Dakin (1997, 1999) showed that contour integration in the peripheral visual field is limited in a manner that suggests it could be relying on the output of large receptive fields. Recently, May and Hess (2007) reported a selective loss of sensitivity for "ladders" in the periphery and suggested that this result arises from a phenomenon known as *crowding*.

Crowding refers to the disruptive effect of "clutter" (task-irrelevant flanking features) on our ability to recognize (not detect) objects (for recent reviews, see Levi, 2008; Whitney & Levi, 2011). The effects of crowding are particularly evident when objects are presented in the peripheral visual field (Levi, 2008). Crowding does not simply induce a loss of information but involves an active change in the appearance of objects (Greenwood, Bex, & Dakin, 2010). Current accounts of crowding involve some form of *averaging* of the attributes, such as orientation (Parkes, Lund, Angelucci, Solomon, & Morgan, 2001) or position (Dakin, Cass, Greenwood, & Bex, 2010; Greenwood, Bex, & Dakin, 2009), of features falling within the flanking and target regions. In the paradigm of Parkes et al. (2001), for example, observers' ability to judge the orientation of a near-vertical Gabor element presented in the periphery is compromised when the target is crowded by vertical Gabor flanking-elements but is actually *improved* when a small (subthreshold) orientation cue is added to flankers. This is strong evidence that the orientation cue arising from flankers is incorporated into the crowded percept of the target through a process which is, or at least looks like, averaging.[1] In terms of crowding of orientation, similarity between flankers and target influences the magnitude of crowding (more similar flankers crowd more), and the effect of similarly oriented flankers is to induce observers to make target reports that are consistent with the target-orientation having been averaged with the orientation of the flankers (Parkes et al., 2001).

Several studies have reported crowding in tasks involving fine *discrimination* of contrast, spatial frequency, and orientation (Andriessen & Bouma, 1976; Parkes et al., 2001; Wilkinson, Wilson, & Ellemberg, 1997). Little or no effect of crowding has been found for *detection* tasks (Andriessen & Bouma, 1976; Parkes et al., 2001; Wilkinson et al., 1997). However, May and Hess (2007) have suggested that the failure to detect peripheral ladders could be a form of crowding caused by inappropriate feature integration by large integration fields in the periphery (Pelli, Palomares, & Majaj, 2004). In particular, they showed that a "crowding-based" model could account for the poor detection of ladders in periphery. More recently, Chakravarthi and Pelli (2011) directly tested the proposal by May and Hess (2007) that the association field in contour integration and the combining field (i.e., the *critical spacing* area) in crowding might be one and the same. They asked observers to perform a contour integration task and a crowding task on the same stimulus and found that observers were equally sensitive to alignment (i.e., the Gestalt *goodness of continuation*) in both tasks. In particular, better alignment increased binding (grouping), which led to improved performance for contour integration but worse performance under crowding. The authors conclude that the same binding mechanisms underlie contour integration and crowd-

ing. This suggestion is consistent with a growing consensus (Dakin et al., 2010; Livne & Sagi, 2007; May & Hess, 2007) that contour integration and crowding are related. Greenwood et al. (2010), for example, emphasized the remarkable similarity between the averaging processes that characterize crowding and the processes of contour integration, which group local elements into spatially extended edges (Field et al., 1993). This work fits with a proposal from Livne and Sagi (2007) that contour integration can explain configural effects, created by the global arrangement of flankers, on crowding.

In this study, we sought to clarify and extend several aspects of the earlier Dakin and Baruch's (2009) study. First of all, we wished to determine whether context affects simple contour-localization without explicit shape-discrimination. This is important in order to better understand the level at which contextual effects exert their influence. In particular, we wished to determine if the effects reported by Dakin and Baruch (2009) were an inevitable consequence of that study having had observers make an explicit contour-shape discrimination. To this end, we measured threshold exposure-duration in a two-alternative forced choice (2AFC) localization task (Experiment 1) where observers had to indicate which side of an image contained a contour (either snake or ladder). We note that, because our task requires only contour-localization (without explicit shape-discrimination), it is also less cognitively demanding (Pennefather et al., 1999) and thus can be useful to test contour integration in a clinical population. This is essentially a "standard" contour integration task where the global shape of the contour (which is not known in advance and changes from trial to trial) is not informative in itself. Note that we are not saying that this is a *pure* localization task. Indeed, contour integration clearly requires at least a partial representation of both location and shape. While we do not rule out any role for contour-shape processing, our underlying assumption is that explicit shape-discrimination is not possible without some forms of shape localization.

The second aspect we investigated is the generality of the effect of context (Experiment 2) by measuring its influence on estimates of a different threshold measurement (maximum tolerable orientation jitter) in addition to threshold exposure-duration. It is important to have a threshold orientation jitter measure to allow comparison of our results to the final experiment (Experiment 3) where we attempted to determine what role crowding might play in our task. We did this by measuring orientation-discrimination of a single tilted target flanked by two similar elements (at eccentricity and element-spacing comparable to our contour experiments) to estimate orientation uncertainty of our contour-elements in different surrounds. We then compared contextual effects on threshold estimates from the second and third experiments. The core assumption of our approach is that contour integration involves an explicit progression from local to global structure. Specifically, in order to segment a contour made of individual elements from background-noise, the visual system must first extract local information and then integrate local inputs into coherent global structures, such as spatially extended contours (Field et al., 1993). In this framework, the effects of context at a local level (e.g., orientation uncertainty) can influence downstream global processes such as contour integration and localization.

Experiment 1: effect of context on the exposure-duration required for contour-localization

In the first experiment we wished to determine if the effects of context on a combined contour-localization and explicit shape-discrimination task (reported by Dakin & Baruch, 2009) extend to a simpler contour-localization task (without explicit shape-discrimination). The motivation for the choice of a simple contour-localization task was to provide a closer link to existing studies (Field et al., 1993) and, at the same time, use a less cognitively demanding task (Pennefather et al., 1999).

Methods

Observers

Six observers (VR, SCD, MST, EA, EI, ALF), of which four were naïve to the purposes of the study (MST, EA, EI, ALF), participated in Experiment 1. All had normal or corrected-to-normal vision. Four of them (VR, SCD, MST, EA) were experienced psychophysical observers.

Apparatus

Experiments were run on an Apple MacBook computer under the Matlab programming environment (MathWorks, Natick, MA) and incorporated elements of the Psychophysics Toolbox extensions (Brainard, 1997; Kleiner, Brainard, & Pelli, 2007; Pelli, 1997). Stimuli were presented on a CRT monitor (LaCie [Paris, France] Electron Blue 22-inch). The monitor was calibrated with a Minolta photometer and

linearized in software, giving a mean and maximum luminance of 50 and 100 cd/m^2, respectively. The display resolution was 1024 × 768 pixels, and the refresh rate was 75 Hz.

Stimuli

Test stimuli (Figures 1 and 2) consisted of *snake*- and *ladder*-contours composed of seven spatial-frequency, band-pass, Gabor micropatterns embedded in a field of distracter Gabors (Field et al., 1993). In snake-contours, Gabors were coaligned with an underlying contour-spine, whereas in ladder-contours, they were oriented at 90° relative to the contour-spine. The separation of contour-elements was 56 arcmin (i.e., 3.5λ), and the whole-stimuli subtended 12.8° square containing on average 220 elements ($\sigma = 3.9$ elements). All elements were in cosine phase, had a peak spatial frequency (SF) of 3.75 c/deg with an envelope σ of 5.7 arcmin, and were presented at 95% contrast.

We adapted the methodology previously used by Dakin and Baruch (2009) to generate the contour. Rather than constraining contours to be "S"-shaped (required in Dakin & Baruch, 2009 for the 2AFC shape-discrimination task), we used standard contours with a 15° path angle where the sign of the orientation difference between subsequent elements was randomized. To ensure elements were clearly located in either the left or the right half of the image, we forced the middle/fourth element of our seven-elements paths to (a) pass through a region within ± 0.53° of the center

of a given image-half and (b) to have an orientation within ± 45° of vertical. In addition, contours were generated such that no one element of the contour passed within 0.9° of the edge of the image and such that the contour did not cross itself.

We made our stimuli by first inserting two contours—one in the left and one in the right half of the image—and then dropping distracter-elements in the background maintaining a minimum interelement separation of 40 arcmin (matching the mean-distance of any element, within contour or background, to its nearest neighbor). Unlike standard contour detection paradigms, but similar to Dakin and Baruch (2009), we manipulated the orientation of distracter-elements depending on their proximity to their nearest contour. Specifically, we had three surround conditions, each with a different mean orientation of surrounding-elements relative to contour-elements: random, near-parallel, and near-perpendicular (Figure 2). We refer to the random surround condition—where the orientation of distracter-elements was not modified depending on contour distance—as the "baseline" condition. The near-parallel and near-perpendicular conditions were generated as in Dakin and Baruch (2009). In brief, we first computed the distance of each background-element to its nearest contour-element. Then, we used the inverse of the Gaussian function ($\sigma = 1.0°$) of the distance between distracters and contour-elements to set the orientation of distracter-elements, offset by 0° (near-parallel) or 90° (near-perpendicular).

At this point in the stimulus generation procedure, we have an image containing two contours (e.g., two
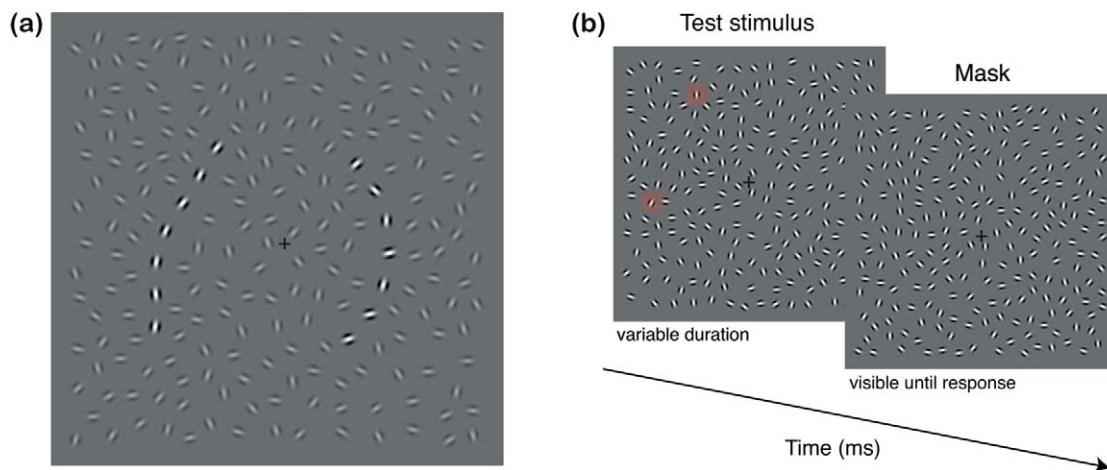

Figure 1. (a) An example of the stimuli from the first experiment (with the contrast of distracters reduced for illustrative purposes). Observers had to report which side of the image contained a structured contour. In this case, the contour is surrounded by near-perpendicular elements, which generally enhance detectability. Note that the random-path on the right was generated in essentially the same way as the structured contour, except that the orientation of path-elements was randomized prior to presentation. Because of this, the orientation of distracters surrounding the random-path is comparable to the context of the structured contour. (b) A typical trial of Experiment 1. The test stimulus, which contained a structured contour either on the left or on the right (here the first and the last elements of the path are shaded to assist the reader in finding the contour) was immediately followed by a mask with randomly oriented elements. This display persisted until observers had made a response.
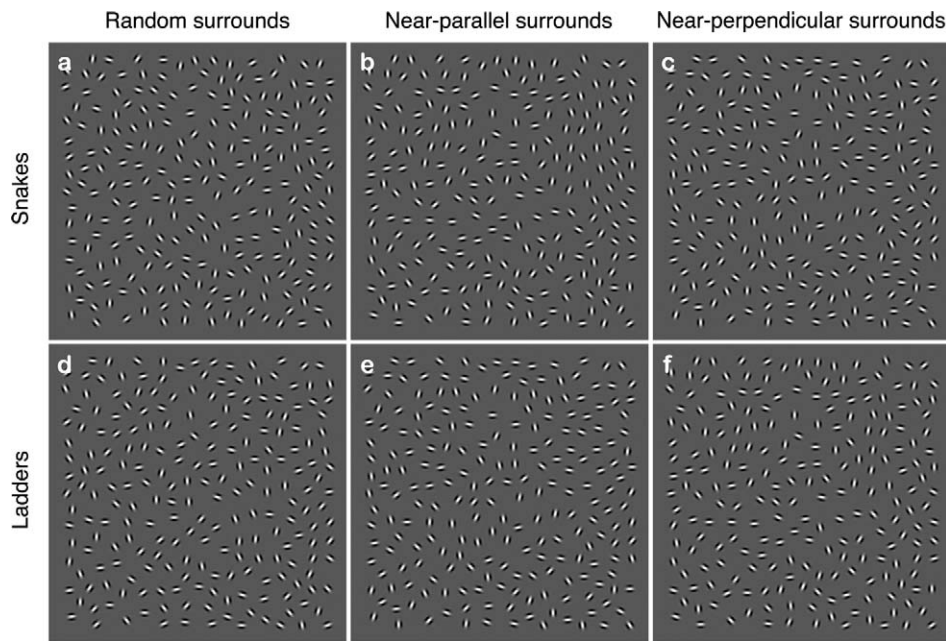
Figure 2. Examples of the surround conditions and contour types tested in Experiment 1. The upper row shows *snakes* embedded in either (a) random, (b) near-parallel, or (c) near-perpendicular surrounds. The lower row shows similar stimuli but with *ladders*. Note that each surround condition is defined by the orientation offset of the immediate surrounding-elements relative to the contour-elements. In these examples, contours always have the same global orientation and the same location (right upper part of the image).

snakes), one on either side of fixation, where the distracter-elements surrounding each have been subject to the same contextual constraints (w.r.t. the contour on each side). We made our "random contour" by simply randomizing the orientation of the elements of one of these contours. The observers' task was then to report the side of the image containing the structured contour (either snake or ladder). Figure 1a shows an example (with the contrast of surround reduced for the purpose of illustration). Stimulus presentation was immediately followed by a mask composed of a field of randomly oriented elements (with on average the same number and separation of Gabors as the test stimulus). This display persisted until observers had made a response (Figure 1b).

Design

We used a within-subjects design. The independent variable was the orientation offset of the contour's immediate context, defined as the mean orientation of the surrounding-elements relative to the orientation of the contour-elements (and not to the contour-spine). We tested three levels of orientation offset (Figure 2): 0° (surrounding-elements near-parallel to the contour-elements, Figures 2b and 2e), 90° (surrounding-elements near-perpendicular to the contour-elements, Figures 2c and 2f), and random (surrounding-elements randomly oriented, Figures 2a and 2d). The dependent

variable was the minimum exposure-duration of the test stimulus that led to 75% correct contour-localization (*threshold exposure-duration*, see Procedure). Note that this is a slightly lower performance criterion than used previously (Dakin & Baruch, 2009) which will lead to generally slightly lower thresholds.

Procedure

Stimuli were viewed binocularly at a distance of 129 cm from the display. Observers fixated a centrally presented marker during presentation of test and masking stimuli. They were presented a test stimulus (for a variable exposure-duration) containing a structured and a random contour embedded within distracter-elements and located right and left of the fixation marker. This screen was immediately followed by a mask, which contained randomly oriented Gabors and remained on the screen until observers made a response (using the computer keyboard) to the question "Which side of the stimulus contained the structured contour?" Visual feedback (the contrast-polarity of the fixation marker) indicated a correct or incorrect response. The exposure-duration of the test stimulus was controlled by an adaptive staircase procedure (QUEST, Watson and Pelli, 1983) with correct and incorrect responses respectively causing reduction and increase in exposure-duration. The procedure converged on the exposure-duration that led to 75%
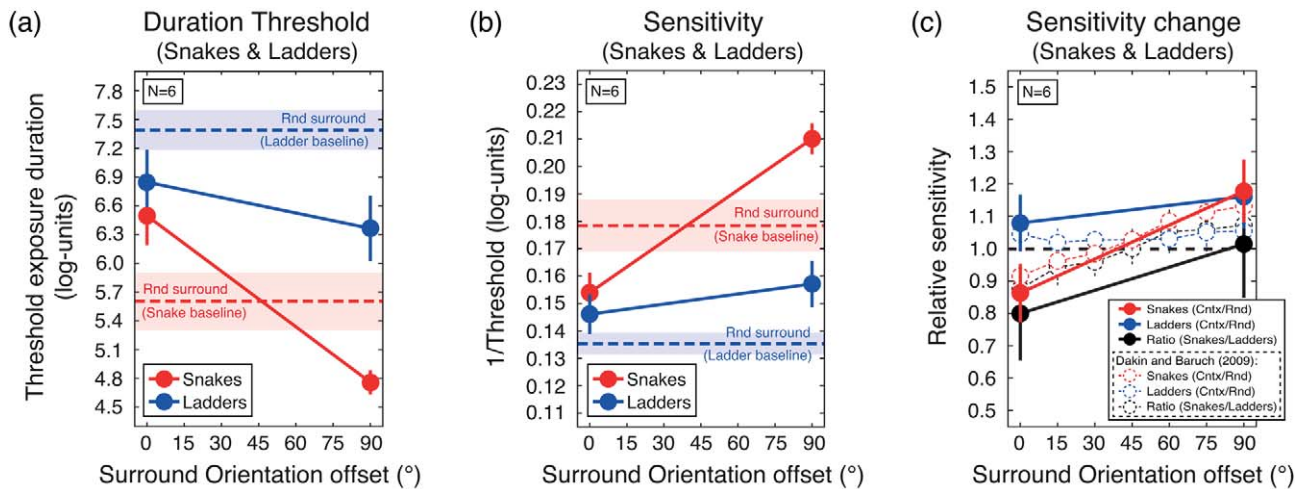
Figure 3. Results from the first experiment averaged across six observers. Red and blue symbols denote performance with snakes and ladders, respectively, measured with random surrounds (dashed lines) and as a function of surround orientation (filled circles). Dashed symbols indicate data from Dakin and Baruch (2009). Error bars represent standard errors. (a) Threshold exposure-duration (the minimum exposure-duration supporting 75% correct contour-localization) in log-units. Thresholds for snakes are reduced in the presence of near-perpendicular surrounds (90° orientation offset) and increased when the surround is near-parallel (0° orientation offset). Thresholds for ladders decrease in presence of any of the two surrounds. (b) Sensitivity (1/threshold exposure duration). There is a reduction and elevation in snake-sensitivity with near-parallel and near-perpendicular surrounds, respectively. Ladder-sensitivity is increased in the presence of any of the two surrounds. (c) Ratio of sensitivities for organized (*Cntx*, i.e., near-parallel or near-perpendicular) versus random surrounds (*Rnd*) with snakes and ladders. The ratio of these two relative sensitivities (black symbols) compares the effect of surround on snakes and ladders and indicates that, for snake-localization, there is an extra sensitivity loss with near-parallel surrounds.

correct contour-localization. We refer to this measure as the *threshold exposure-duration*. Snakes and ladders were tested in separate runs, each of which comprised all three orientation offset levels of the elements surrounding the contour.

For each type of structured contour (snake and ladder), observers completed three runs of 135 trials each (45 trials per surround condition). Thus, for each observer, we obtained the mean threshold exposure-duration for each type of structured contour embedded in a particular kind of surround over 135 trials. Before data collection, every observer completed a practice session of at least 135 trials for each type of contour (in separate runs). All observers started with a run of "snake" stimuli. Order of the other runs has been counterbalanced between observers.

Statistical analysis

To test the effect of contour-elements' orientation and the effect of the immediate surround, we carried out a two-way repeated-measures ANOVA, with factors *type of contour* (two levels: snakes and ladders) and *immediate surround* (three levels: random, near-parallel, and near-perpendicular), on the log-transformed threshold-values. Bonferroni correction has been used to

adjust *p*-values for multiple comparisons. Alpha-value was set to 0.05 for all statistical tests.

Results and discussion

Figure 3a presents results (averaged across six observers) from various conditions tested in the first experiment. Graphed data are mean thresholds exposure-duration (the minimum presentation time supporting 75% correct contour-localization) in log-units. Sensitivity-values (the inverse of mean thresholds in log-units) and normalized sensitivity (ratio of sensitivities for organized, i.e., near-parallel or near-perpendicular, versus random surrounds) across observers are plotted in Figures 3b and 3c. In Figure 3c, data from Dakin & Baruch (2009), recalculated on the log-transformed performance-values, are also presented. Note that, for threshold exposure-duration, the smaller the number, the less time observers need to attain the criterion level of performance (75% correct contour-localization). The inverse is true for sensitivity (the smaller the number, the lower the sensitivity to the contour).

The ANOVA on log-transformed threshold-values show a significant effect of the factors *type of contour* ($F_{1,5} = 308.3$, $p < 0.001$) and *immediate surround* ($F_{2,10} = 10.40$, $p = 0.004$) as well as a significant interaction

($F_{2,10} = 6.78$, $p = 0.014$). The significant effect of the factor *type of contour* indicates substantially poorer performance with ladders than snakes, consistent with previous findings (Bex et al., 2001; Dakin & Baruch, 2009; Field et al., 1993; Ledgeway et al., 2005). Specifically, in the baseline condition (random surrounds), ladder-threshold is about 1.3-times higher than snake-threshold (both in log-units). The significant effect of the factor *immediate surround* clearly indicates a substantial influence of context on contour-localization. However, the significant *type of contour × immediate surround* interaction suggests a different effect of context on localization of snakes and ladders. Specifically, as indicated by Figure 3a and post-hoc comparisons, there is substantial reduction ($t_5 = -3.82$, $p = 0.025$) and modest elevation ($t_5 = 3.11$, $p = 0.05$) in snake-threshold in the presence of near-perpendicular and near-parallel surrounds, respectively. These results indicate that observers need *less time* to correctly localize snakes in the presence of near-perpendicular surrounds compared to random surrounds. By contrast, they need *more time* for snake-localization in the near-parallel surround condition than in the baseline condition (random surrounds). In contrast, ladder-localization is modestly facilitated by the presence of any of the two organized surrounds ($p > 0.05$). Thresholds for snakes and ladders are not significantly different from one other when measured with near-parallel surrounds.

Figure 3c presents the ratio of sensitivities for organized (i.e., near-parallel or near-perpendicular) versus random surrounds with snakes and ladders (i.e., sensitivities for snakes and ladders in organized surrounds normalized to the corresponding performance with random backgrounds). The ratio of these two relative sensitivities (black symbols) compares the effect of surround on snakes and ladders and indicates that, for snake-localization (without explicit shape-discrimination) there is an extra sensitivity loss with near-parallel surrounds (Snakes/Ladders ratio = 0.8).

Taken together, these results suggest that the immediate context a contour arises in has a direct influence on simple contour-localization (without explicit shape-discrimination). These effects of context are broadly consistent with those found by Dakin and Baruch (2009) in their combined contour-localization and explicit shape-discrimination task (represented with dashed symbols in Figure 3c). The authors found a reduction in snake-sensitivity when the surround was near-parallel compared to random (relative sensitivity equal to ~0.9) and an increase in snake-sensitivity in the presence of near-perpendicular compared to random surrounds (relative sensitivity equal to ~1.15). For ladders, instead, they reported a relative sensitivity of ~1.05, both with near-parallel and with near-perpendicular surrounds. We also find that perfor-

mance with snakes is consistent with facilitation in the presence of near-perpendicular surrounds (relative sensitivity equal to 1.18) and suppression in the presence of near-parallel surrounds (relative sensitivity equal to 0.86), and that ladder-localization tends to be higher in the presence of any organized surrounds (relative sensitivity equal to 1.08 and 1.16 with near-parallel and near-perpendicular surrounds, respectively). The comparison between our results and Dakin and Baruch's (2009) findings indicate a substantial and consistent effect of context on contour integration (if one accepts that integration is effectively probed by the localization task, which was common to this and the earlier study).

Experiment 2 examines if the effect of context generalizes to another threshold-based measure of performance (i.e., threshold orientation jitter, which reflects the tolerance to orientation jitter along the contour-path).

Experiment 2: effect of context on tolerance to orientation jitter in snake-localization

Both Experiment 1 and the earlier study by Dakin and Baruch (2009) used threshold exposure-duration measure as a practical psychophysical procedure for measuring performance. Threshold-based paradigms have advantages over standard "path paradigms" that use percent correct measure, which are limited in that e.g., they do not allow calculation of performance-ratios across conditions. In order to be able to quantify the contribution to contextual effects from the influence e.g., of crowding (Experiment 3), it would be desirable for our performance measure to be expressed in units not of time but of tolerable orientation uncertainty. Furthermore, a similar effect of context on other threshold measures would argue for generality of the findings from Experiment 1. Finally, a fixed-exposure-duration paradigm has the potential to lead to faster threshold measurement that would be useful in the clinical field (reducing "test-stress" and the probability of eye movements).

Methods

Observers

The same six observers of Experiment 1 (VR, SCD, MST, EA, EI, ALF) served as participants in Experiment 2.

Apparatus

We used the same apparatus and display parameters as in Experiment 1.

Stimuli

In Experiment 2, we used only *snakes* as structured contours because, in pilot trials, we found that even modest levels of orientation jitter reduced ladder-localization to chance but with large intertrial differences (rendering staircases unusable). Increasing the fixed exposure-duration helped but greatly extended test-time (precluding e.g., possible clinical translation). For this reason, here, we measure performance only for localization of snakes. The parameters of the Gabors and the methodology to create contours and manipulate the immediate surround (random, near-parallel, near-perpendicular) of contours were the same as in Experiment 1. As before, stimuli contained a structured and a random contour embedded within distracter-elements and located right and left of the fixation mark.

Prior to stimulus presentation, we jittered the orientation of the elements within the structured contour. We did this by generating Gaussian random offsets using standard deviations in the range 0 to 90°. (Note that this is the generating standard deviation; the true/wrapped standard deviation will be lower.) A generating Gaussian standard deviation of 90° will produce a near-isotropic distribution of orientations. The level of orientation jitter was under control of an adaptive staircase procedure (QUEST, Watson & Pelli, 1983), as described in the Procedure. The orientation of distracter-elements was not modified further based on the new (noisy) contour orientation structure (where the orientation of each contour-element had been drastically altered). As in Experiment 1, the mask was composed of a field of randomly oriented elements (with the same number and separation of Gabors as the test stimulus, on average).

Design

The experiment had a within-subjects design. The independent variable was the *surround orientation offset*: the mean orientation of the surrounding-elements relative to the contour-elements (three levels: random, near-parallel, near-perpendicular). Note that these offsets are relative to the contour-elements *without* any orientation jitter. The dependent variable was the maximum orientation jitter along the contour-path supporting 75% correct contour-localization (*threshold orientation jitter*, see Procedure).

Procedure

The procedure was similar to Experiment 1, except for (a) the duration of the test stimulus, which was fixed (1,000 ms), and (b) the variable controlled by the adaptive staircase procedure (Watson & Pelli, 1983), which was orientation variability along the contour-path (rather than exposure-duration, as before). We selected a relatively long fixed exposure-duration of 1,000 ms because pilot experiments revealed that the minimum exposure-duration for all observers to perform snake-localization at 75% correct with a high level of orientation jitter (~15°) was around this value. Note that, by using this duration, our experiments can be more closely related to existing studies on contour integration (Field et al., 1993), where this same duration has been used.

Correct and incorrect responses led to an increase or a decrease in orientation jitter, respectively. The procedure converged on the orientation jitter that led to 75% correct contour-localization. We refer to this measure as the *threshold orientation jitter*. Each run comprised all three surround-orientation conditions (random, near-parallel, near-perpendicular). Observers completed at least three runs of 135 trials each (45 trials per surround condition). In this way, for each observer, we obtained the mean threshold orientation jitter in each surround condition over at least 135 trials.

Statistical analysis

To test the effect of the immediate surround, we carried out a one-way repeated-measures ANOVA, with factor *immediate surround* (three levels: random, near-parallel, and near-perpendicular), on the log-transformed threshold-values. *P*-values have been adjusted for multiple comparisons using the Bonferroni correction. Alpha-value was set to 0.05 for all statistical tests.

Results and discussion

Figure 4a presents results from the second experiment averaged across six observers. Graphed data are thresholds orientation jitter (in log-units), which are a measure of tolerance to orientation jitter along the contour-path. Thus, the smaller the number, the less orientation jitter observers tolerate and the poorer (more noise-sensitive) their performance. We first note that observers tolerate a higher degree of orientation jitter along the contour in the presence of near-perpendicular than random surrounds. By contrast,
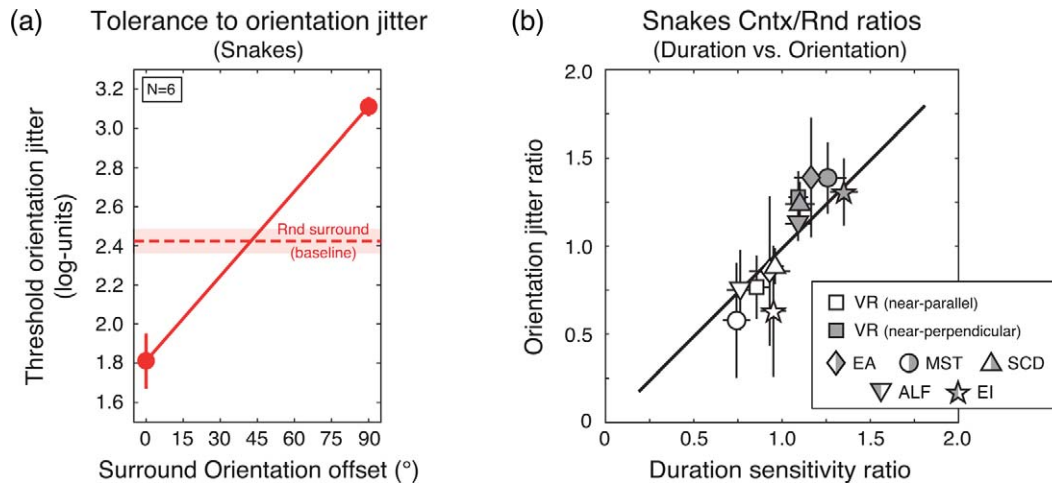
Figure 4. (a) Results from the second experiment, averaged across six observers. Plotted data are thresholds orientation jitter in log-units (the maximum orientation jitter supporting 75% correct contour-localization). Plotting conventions are as in Figure 3; error bars represent standard errors. Note similarity to Figure 3b. Observers tolerate a higher degree of orientation jitter along the contour-path with near-perpendicular than random surrounds. Near-parallel surrounds, instead, decrease tolerance compared to the baseline. (b) Comparison of results from Experiments 1 and 2. Graphed data are individual duration sensitivity ratios and threshold orientation jitter ratios in the near-parallel (white symbols) and near-perpendicular surrounds (grey symbols), representing performance with organized surrounds (Cntx, i.e., near-parallel or near-perpendicular) relative to random surrounds (Rnd). Error bars represent standard errors. The black line is the 1:1 line. Note that, as duration sensitivity ratios increase, orientation jitter ratios also increase.

they tolerate less orientation jitter with near-parallel than random surrounds. The ANOVA on the log-transformed thresholds confirms that the factor *immediate surround* has a significant effect on snake-localization ($F_{2,10} = 60.08$, $p < 0.001$). Post-hoc comparisons indicate lower tolerance to orientation jitter in the presence of near-parallel than random surrounds ($t_5 = -5.39$, $p = 0.006$) and higher tolerance with near-perpendicular than random surrounds ($t_5 = 8.22$, $p < 0.001$).

Figure 4b compares results from Experiments 1 and 2. Graphed data are individual performance in near-parallel (white symbols) and near-perpendicular surrounds (grey symbols) relative to performance with random surround (i.e., divided by performance in the random surround condition). Specifically, we used duration sensitivity (in log-units) for Experiment 1 and threshold orientation jitter (in log-units) for Experiment 2 because, in both cases, higher values mean better performance. Note that, as ratios in Experiment 1 increase, ratios in Experiment 2 also become larger ($r_{10} = 0.90$, $p < 0.001$). This means that, as duration sensitivity to the contour increases, and thus observers need less time for localization (lower threshold exposure-duration reflected in higher Cntx/Rnd ratios on the x-axis), then the tolerance to orientation jitter along the contour increases (higher Cntx/Rnd ratios on the y-axis).

Taken together, the results of Experiments 1 and 2 indicate similar effects of context on threshold exposure-duration and threshold orientation jitter for

snake-localization, arguing for the general finding that perpendicular surrounds promote contour-localization while parallel surrounds also affect contour-localization (i.e., not just *shape processing*).

Previously, several studies have demonstrated that contour detection decreases as a function of increasing orientation jitter of local contour-elements (Field et al., 1993; Geisler, Perry, Super, & Gallogly, 2001; Hess & Dakin, 1999; Hess & Field, 1995). These studies, however, did not explicitly measure threshold orientation jitter, but rather percent correct contour detection (accuracy), which do not allow calculation of performance ratios across different conditions. Two recent studies (Kuai & Yu, 2006; Schumacher et al., 2011) directly measured tolerance to orientation jitter in contour detection tasks. Kuai and Yu (2006) measured threshold orientation jitter with closed circular contours and showed that observers tolerated on average 12° of orientation jitter, both at 4° and at 20° of eccentricity. More recently, Schumacher et al. (2011) used a threshold orientation jitter measure to quantify the spatial scale of the orientation-dependent surround effects on contour detection. They also confirmed the contextual effect found by Dakin and Baruch (2009); however, their observers tolerated a higher degree of orientation jitter (~27° with randomly oriented distracters) than ours (~11° in the random surround condition). The higher detection performance they showed likely results from their use of straight contours falling on fixed positions.
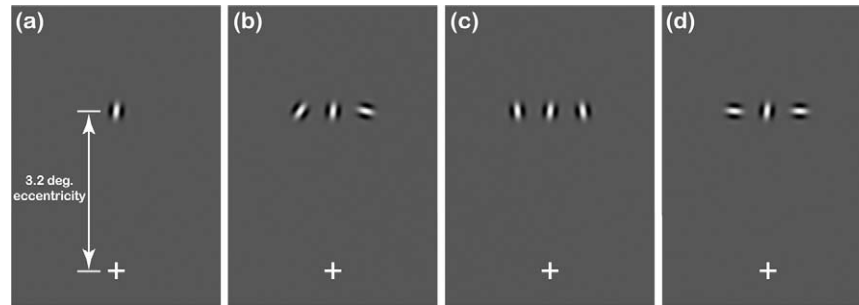
Figure 5. Examples of stimuli from the third experiment. Observers judged the orientation of the central Gabor. The target for the orientation judgment (in these examples 6° clockwise-tilted) was presented either in isolation (a) or with two flankers, whose orientation could be random (b), near-parallel (c), or near-perpendicular (d) relative to vertical. When flankers are near-parallel, the orientation-discrimination task becomes very difficult if one fixates on the marker. This is typical of the near-parallel condition that induces very high levels of crowding compared to the isolated-target condition.

We designed our experiments to emphasize the effect of context on contour-localization (and not contour-shape discrimination). However, because our experiments require that observers decide which side of a display contours lie on, in the presence of distracting elements, it is possible that the strategy they adopt involves finding multiple "candidate" contours (on both sides of the pattern) and then deciding which is the most "contour-like." For this reason, we cannot state that the effect of context we observed in the previous experiments is entirely limited by contour-localization. In order to see how much of our effects were attributable to changes in how well contours could be localized, we performed a control experiment using the same stimuli as Experiment 2 but in the absence of background-elements. Two expert observers (VR and SCD) and two naïve observers (ALF and BR) again reported whether the more "contour-like" path was on the left or on the right side of the display. We expect a higher tolerance to orientation jitter when there is no background because, in this case, there is no localization uncertainty (i.e., it is not necessary to localize candidate contours on each side of the display). In this condition, the tolerance to orientation jitter is much higher (~37°) than in the conditions with surrounds (random: ~11°; near-parallel: ~6°; near-perpendicular: ~23°). These findings are consistent with contour-localization limiting performance in the main experiment.

Experiment 3: the role of crowding in the effect of context on contour integration

In the course of these and earlier experiments (Dakin & Baruch, 2009), contours would frequently fall in the parafovea (typically 3 to 4° eccentricity). At these eccentricities and with the interelement spacing used in our contour-stimuli, we would expect that *visual crowding* would interfere with the representation of the local orientation of Gabor-elements (Levi, 2008). Because several groups have linked contour integration and crowding (Chakravarthi & Pelli, 2011; Dakin et al., 2010; Livne & Sagi, 2007; May & Hess, 2007), we next sought to directly investigate the contribution of crowding to the effect of context on contour integration.

To this end, we had first to estimate the observers' local uncertainty as to the orientation of the elements that make up the contours. We did this by measuring orientation-discrimination (2AFC, clockwise versus anticlockwise) with Gabors of similar size/SF, mutual-separation, and eccentricity as contour-elements in Experiments 1 and 2. The target was either an isolated Gabor or a Gabor presented with two flankers (Figure 5). Flankers could be randomly oriented, near-parallel, or near-perpendicular relative to vertical orientation.

Methods

Observers

The same observers of Experiments 1 and 2 (VR, SCD, MST, EA, EI, ALF) participated in Experiment 3.

Apparatus

We used the same apparatus and display parameters as in Experiments 1 and 2.

Stimuli

In Experiment 3, we used Gabors with the same parameters as those used in the contour experiments previously described (cosine phase, peak spatial fre-

quency = 3.75 c/deg, envelope $\sigma = 5.7$ arcmin, 95% contrast). The target for the orientation judgment (clockwise or anticlockwise of vertical) was either an isolated Gabor (*isolated-target condition*) or a Gabor presented with two flankers (see following paragraphs). In all conditions, the target fell in the parafovea (upper side of the screen, 3.2° eccentricity). We repeatedly tested the same location in the visual field because we aimed at determining the role of *local orientation uncertainty* in the effects of context on contour-localization, without additional uncertainty, e.g., arising from element-localization. Additionally, we picked the upper visual field, where crowding is maximized, in order to make a liberal estimate of the contribution of crowding. Note that we did not include conditions that involved contour-like targets since within-contour flankers (inevitably) are cues to the identity of the target. Here we focus on conditions where flankers are noninformative in order to quantify local orientation uncertainty about individual elements *in the absence of global (multielement) cues.*

In the *flanker-pair conditions,* target and flankers fell on the same horizontal axis and element separation was 40 arcmin (matching the minimum interelement separation used in the contour-localization experiments). Flanker orientation could be random, near-parallel, or near-perpendicular relative to vertical (the orientation around which target orientation-discriminations were made). We obtained near-parallel and near-perpendicular flankers by adding orientation noise (Gaussian-distributed, $\sigma = 22°$) to perfectly parallel and perpendicular flankers. The value $\sigma = 22°$ corresponds to the average standard deviation of the orientation difference between a given contour-element and its nearest surrounding background-element (computed using stimuli from the near-parallel condition of the contour-localization experiments). This matched the orientation statistics of our crowding stimuli and contour-localization stimuli (so that, for example, the orientation offset of a near-parallel flanker relative to vertical in Experiment 3 was, on average, the same as the orientation difference between a given contour-element—without any orientation jitter—and its nearest near-parallel background-element in Experiments 1 and 2).

We manipulated the target tilt (clockwise or anti-clockwise of vertical), preselecting seven tilts (−6°, −4°, −2°, 0°, +2°, +4°, and +6° in the isolated-target condition; −9°, −6°, −3°, 0°, +3°, +6°, and +9° in the random, near-parallel, and near-perpendicular flanker-pair conditions) to fit psychometric functions. These values were selected based on pilot data that indicated they bracketed the psychometric function for the observers tested under these conditions of crowding. Note that the orientation of flanking-elements was not modified further based on the target tilt manipulation.

Design

We used a within-subjects design and tested four conditions: (1) isolated-target, (2) target plus randomly-oriented flanker-pair, (3) target plus near-parallel flanker-pair, and (4) target plus near-perpendicular flanker-pair. In each condition, the independent variable was the degree of tilt of the target, which had seven levels: −6°, −4°, −2°, 0°, +2°, +4°, and +6° (in the isolated-target condition) and −9°, −6°, −3°, 0°, +3°, +6°, and +9° (in the random, near-parallel, and near-perpendicular flanker-pair conditions). The dependent variable was the probability to report that the target was tilted clockwise of vertical.

Procedure

Stimuli were viewed monocularly (with observers' dominant/sighting eye) at a distance of 129 cm from the display. Observers fixated a centrally presented marker during presentation of the test stimulus, which appeared peripherally in the upper portion of the screen (3.2° eccentricity) and lasted 100 ms. This relatively short duration was selected because ~100 ms is the shortest time at which we showed an effect of context on contour-localization. Observers indicated (using the computer keyboard) whether the target was tilted clockwise or anticlockwise of vertical. Visual feedback (the contrast-polarity of the fixation marker) indicated a correct or incorrect response. We used the method of constant stimuli to present different levels of target tilt. The four conditions (each testing seven target tilt-levels) were presented in the same run, and observers completed at least two runs of 448 trials each (16 trials per tilt-level in each condition). Raw data were fit with cumulative Gaussian functions to give an estimate of bias (the μ parameter) and threshold orientation-discrimination (the σ parameter).

Statistical analysis

To test the effect of flankers, we carried out a one-way repeated-measures ANOVA, with factor *flanker-condition* (four levels: no-flankers, random flankers, near-parallel flankers, and near-perpendicular flankers), on the log-transformed threshold-values. The presence of a statistically significant bias was assessed with one-sample *t*-tests on the μ parameters of the best-fitting psychometric functions. Paired-samples *t*-tests have been used to compare the results of Experiments 2 and 3. *P*-values have been adjusted for multiple comparisons using the Bonferroni correction. Alpha-value was set to 0.05 for all statistical tests.
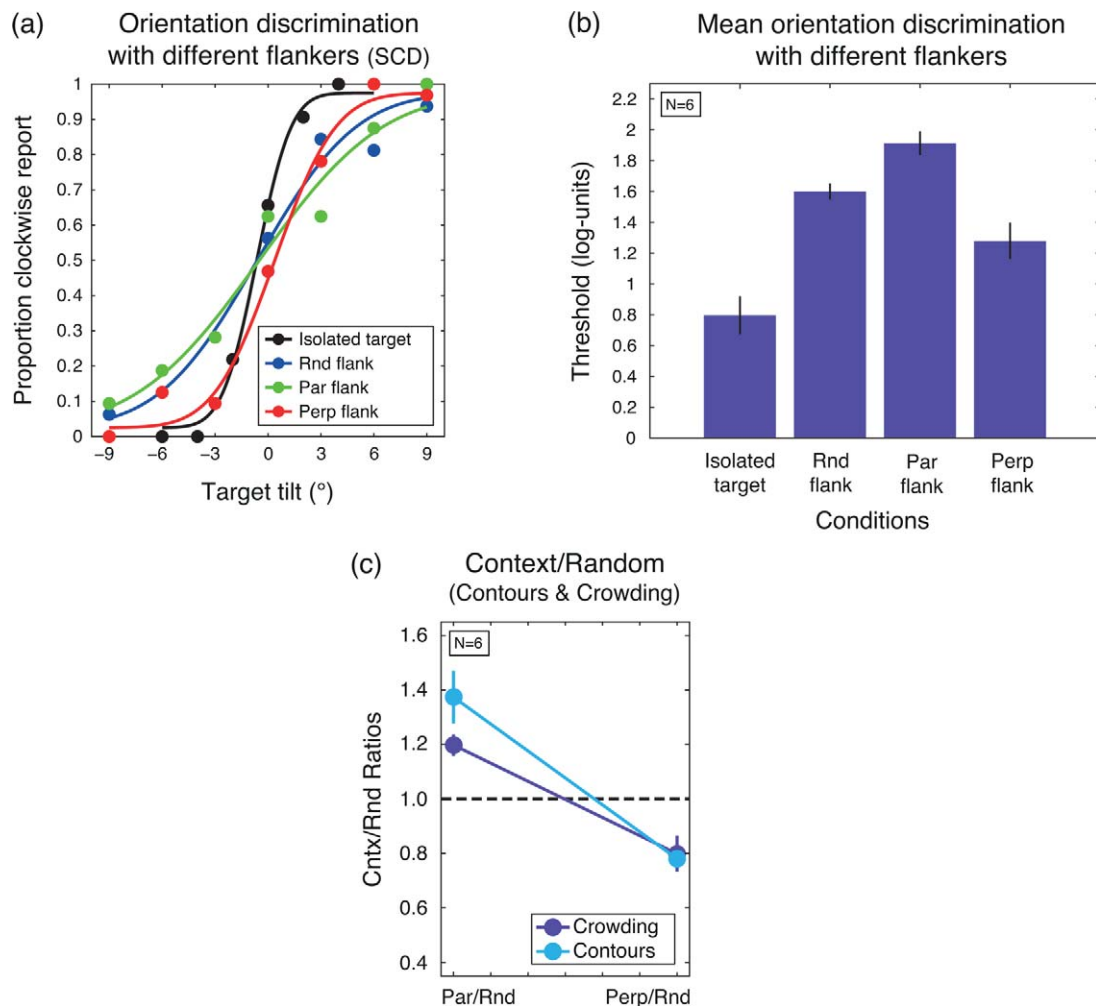
Figure 6. (a) Psychometric function from one observer (SCD) in each condition tested in Experiment 3 (black = isolated target; blue = random flankers; green = near-parallel flankers; red = near-perpendicular flankers). The graph presents the proportion of "clockwise" responses as a function of the target tilt. (b) Mean thresholds orientation-discrimination (in log-units) for each condition tested in Experiment 3. Error bars depict standard errors. The presence of any surrounds (random, near-parallel, near-perpendicular) greatly increases thresholds. (c) Comparison between Experiments 2 and 3. Plotted data are Context/Random ratios (i.e., Parallel/Random and Perpendicular/Random), which represent a measure of *global contour-localization uncertainty* (light blue lines and circles) and a measure of *local orientation uncertainty* (violet lines and circles). The local orientation uncertainty introduced by crowding largely accounts for both contextual effects on global contour-localization.

Results and discussion

Figure 6b presents mean thresholds orientation-discrimination (in log-units) across six observers for each condition tested in the third experiment. Thresholds are the standard deviation parameter (σ) of the best-fitting psychometric functions. The one-way repeated-measures ANOVA on the log-transformed thresholds indicates a significant effect of the factor *flanker-condition* ($F_{3,15} = 45.49$, $p < 0.001$). Post-hoc comparisons show that the presence of randomly oriented flankers doubles threshold compared to the isolated-target condition ($t_5 = 10.70$, $p < 0.001$). Near-parallel and near-perpendicular pairs of flankers,

instead, cause on average a 2.5-time ($t_5 = 12.71$, $p < 0.001$) and a 1.6-time ($t_5 = 3.82$, $p = 0.037$) threshold-elevation, respectively. On average, observers' orientation-judgments are unbiased in all conditions ($p > 0.05$), which means their reports are symmetrically distributed around the stimulus midpoint. These trends are reflected in Figure 6a, which plots example psychometric functions from observer SCD in the four conditions tested.

Note that our finding that near-perpendicular flankers crowd less than random flankers is inconsistent with a model of crowding based strictly on orientation averaging (under which theory one would always predict that the larger the orientation difference between target and flanker, the larger the amount of crowding). Instead, it

implies that target-flanker similarity is important and would be consistent with an averaging process that uses something more akin to maximum likelihood estimation (van den Berg, Roerdink, & Cornelissen, 2010). Note also that the fixed position of the stimulus (above the fixation cross) has no role in explaining lower thresholds with near-perpendicular than random and near-parallel flanker-pairs. Indeed, a control experiment (run on the first author VR) with the stimulus randomly presented above or below fixation produced an identical pattern of results.

Figure 6c compares results from Experiments 2 and 3. Specifically, for both experiments, we plotted Context/Random ratios (i.e., Parallel/Random and Perpendicular/Random). We calculated these ratios using *thresholds orientation-discrimination* (in log-units) for the crowding experiment (Experiment 3) and *1/thresholds orientation jitter* (in log-units) for the contour-localization experiment (Experiment 2). In this way, in both cases, we have a measure of uncertainty: *local orientation uncertainty* for Experiment 3 and *global contour-localization uncertainty* for Experiment 2. The data suggest that the *local* orientation uncertainty (on individual elements) introduced by crowding from different types of flankers influences contour-localization (which involves *global* processing), largely contributing to the contextual effects we showed in Experiment 2. Indeed, for the near-parallel conditions, the global contour-localization uncertainty is not statistically different from the local orientation uncertainty ($t_5 = 2.03$, $p = 0.099$). Similarly, for the near-perpendicular conditions, the global contour-localization uncertainty is not statistically different from the local orientation uncertainty ($t_5 = -0.30$, $p = 0.779$).

Taken together, the results of Experiments 2 and 3 indicate that the modulation of crowding of local contour-elements largely accounts for both contextual effects on contour-localization. Within a framework that assumes an explicit progression from local to global processing, this supports the idea that context influences contour-localization at a predominantly local stage of processing and, more generally, is consistent with the notion that the local effects of crowding eventually influence downstream stages involved in the cortical processing of global visual form (such as contour integration).

As already discussed in the Stimuli section, we picked the upper visual field, where crowding is maximized, in order to make a liberal estimate of the contribution of crowding. However, it has been shown that crowding is influenced not only by the position of the stimuli in the visual field but also by their position relative to fixation (Pelli et al., 2004; Toet & Levi, 1992). This may potentially have an impact on the relative effects of different types of flankers (i.e., on the Context/Random ratios). To check for this possibility, we run a control experiment with Gabors on the radial axis from fixation (instead of circumference). Six observers, four of who also participated in Experiment 3, again discriminated the orientation of a target Gabor, which appeared on the right of fixation either in isolation or surrounded by two flankers (as before, flankers were randomly oriented, near-parallel or near-perpendicular to vertical). Observers who did not participate in Experiment 3 also performed the task with stimuli up of fixation. This allowed us to compare the mean Context/Random ratios (i.e., Parallel/Random and Perpendicular/Random calculated on the log-transformed threshold-values) over six observers across the two axis-conditions (i.e., circumference versus radial axis). Results show no significant effect of the axis-condition on contextual modulation; neither the Parallel/Random ratios ($t_5 = -0.77$, $p = 0.477$), nor the Perpendicular/Random ratios ($t_5 = 1.30$, $p = 0.250$) differ between axis-conditions. These results suggest that the relative contextual effects on local contour-elements do not depend on the position of the stimuli relative to fixation.

General discussion

We measured observers' ability to perform a contour-localization task (that did not require explicit contour-shape discrimination). We report a reduction and substantial increase in snake-sensitivity in the presence of near-parallel and near-perpendicular surrounds, respectively, whereas ladder-sensitivity was modestly increased in the presence of any of the two surrounds (Experiment 1). We also find that context has a similar effect on the exposure-duration required to localize the contour (Experiment 1) and on our tolerance to orientation jitter (Experiment 2). Finally, we report that the local orientation uncertainty (on individual elements) introduced by crowding (Experiment 3) largely contributes to contextual influences on contour processing.

Context affects simple contour-localization without explicit shape-discrimination

In this study, we first sought to determine whether context could affect simple contour-localization *without* explicit shape-discrimination. Our data provide evidence that context influences the localization of contours in noise also when the task does not require an explicit shape-discrimination. In this regard, it is interesting to discuss the implications of our results, particularly in the light of previous findings on the effects of context on contour-shape processing.

It is known that near-parallel surrounds disrupt shape processing in the absence of location-uncertainty

as is evident by the reduction in contour-shape adaptation that one observes in the presence of near-parallel surrounds (Kingdom & Prins, 2009). The authors suggested that the most likely underlying mechanism for the parallel effect is based on the operation of neurons in the primary visual cortex (V1), which show iso-orientation surround suppression, feeding their responses directly into shape-coding neurons in higher visual areas.

At first glance, Dakin and Baruch's (2009) findings are also consistent with an effect of context on contour-shape processing. However, as in that study the authors used a combined contour-localization and explicit shape-discrimination task, their results could reflect, at least in part, an effect of context on the localization component. Our finding that context has a substantial effect on a simple contour-localization task (without explicit shape-discrimination) suggests that Dakin and Baruch's (2009) results were not an inevitable consequence of that study having had observers make an explicit contour-shape discrimination. Instead, the fact that our effects are consistent with those reported by Dakin and Baruch (2009), not only in direction but also in magnitude, indicates that the effects of context generalize to a simple contour-localization task that does not require explicit shape-discrimination. This in turn suggests that the immediate context that a contour arises in has a substantial and consistent effect on contour integration—if one accepts that integration is effectively probed by the localization task, which was common to our and Dakin and Baruch's (2009) study. Given that local orientation uncertainty (about each individual contour-element) can largely account for the effects of context on contour-localization (see Experiment 3), we speculate that the underlying mechanism may be primarily based on early visual processes (possibly occurring in V1).

Context effects generalize across different performance measures

Taken together, results from Experiments 1 and 2 indicate that the effect of context generalizes across threshold measurements. In particular, we showed that context affects threshold orientation jitter and threshold exposure-duration in a similar way. Note that the disruptive effect of near-parallel surrounds cannot be attributed to observers mistaking the parallel surround along the random-path as target-snake (a more likely possibility when measuring threshold orientation jitter where the target-snake is not perfectly smooth). Indeed, a control experiment where an organized surround was present only in the vicinity of the target-snake and not the random-path showed the same amount of "interference" from near-parallel surrounds. In particular, we modified

the stimuli of Experiment 2 such that Gabors on the opposite side of the target-snake were all randomly oriented and again asked observers (VR, EI, ALF) to localize the contour (as before, we tested random, near-parallel, and near-perpendicular surround-conditions). We report a halving in tolerance to orientation jitter with near-parallel compared to random surrounds (mean threshold $\pm$ SE = 6.08° $\pm$ 1.25° versus 12.41° $\pm$ 0.55°), as observed for the same three participants in Experiment 2 (mean threshold $\pm$ SE = 5.97° $\pm$ 0.63° versus 11.95° $\pm$ 0.57°). Having said that, in the following section, we discuss the implications of our result that crowding of local contour-elements largely accounts for the effects of context on global contour-localization.

Crowding of local contour-elements affects global contour-localization

Our results indicate that the modulation of crowding of local contour-elements is comparable in magnitude to the effects of context on global contour-localization. This is consistent with context influencing contour-localization at a predominantly local stage of processing. While the local effects of crowding likely influence downstream stages in the processing of contours such as contour-localization (under the assumption of an explicit progression from local to global), our results do not provide explicit evidence that crowding directly affects multiple levels of processing. Indeed, for the localization of contours embedded in background-noise, our results are consistent with crowding exerting its influence at a predominantly local stage, probably before the integration of individual elements into extended global structures. We note that this mirrors an earlier finding that, for an orientation averaging task, crowding affects the processing of local elements and not the efficiency of global pooling (Dakin, Bex, Cass, & Watt, 2009). While this implicates early visual areas in crowding, we cannot also rule out a role for later visual areas, especially given the existence of extensive feedback projections between areas (Anderson, Dakin, Schwarzkopf, Rees, & Greenwood, in press; Freeman & Simoncelli, 2011).

Modeling the effects of context on contour-localization

To perform our contour-localization task, the visual system must first extract local information and then *integrate* local inputs into spatially extended contours. Therefore, contour-integration modeling is relevant to our study. Several computational models of contour integration have been proposed (Elder & Goldberg, 2002; Field et al., 1993; Geisler et al., 2001; May &

Hess, 2007) whose performance is consistent with human observers' ability to localize contours within noise (Field et al., 1993). We now briefly consider how our finding of a robust effect of context on contour-localization, which is largely accounted for by local uncertainty about the orientation of each contour-element, might be used to compare and further constrain these models.

The "association field" model (Field et al., 1993) defines the necessary geometric relationships required for linking adjacent local filters. According to Field et al. (1993), the responses of local filters to individual elements are combined only if conjoint constraints on position and orientation are satisfied. Facilitatory connections between filters occur only if they have locations and orientations mutually consistent with the presence of a contour. On the opposite, those filters with locations and orientations inconsistent with the presence of a path tend to inhibit each other. This implies that the amount of nearby aligned and correctly oriented contour-structure is crucial to determine the association output. Colinearity increases the strength of the association whereas an increase in distance, curvature, or misalignment from cocircularity leads to weaker association. This model does not directly take into account contextual effects on contour-localization. Nevertheless, we can make some predictions, at least for snakes (the model indeed cannot account for ladder-localization). For snake, a less-accurate local orientation-discrimination (due to higher orientation uncertainty introduced by crowding, see Experiment 3) with near-parallel compared to random surrounds would affect colinearity, curvature, and/or co-circularity between contour-elements. This would lead to weaker association outputs between contour-elements, which can potentially account for the near-parallel "disadvantage" we report in Experiments 1 and 2. The local orientation discrimination for each element of the snake would be more precise with near-perpendicular than random surround (lower levels of crowding from surrounding-elements, see Experiment 3), thus leading to stronger association outputs between contour-elements and accounting for the near-perpendicular "advantage" (see Experiments 1 and 2).

May and Hess (2007) developed a contour integration model based on an association field algorithm in which snake and ladder associations compete directly for ownership of the elements. In their model, ladder associations are half as strong as snake associations, implying great impairment for ladder particularly in the periphery where the association field is larger than in fovea. This architecture can account for the near-parallel surround-effect we obtained for snakes. In this case, indeed, there would be additional quite strong snake-associations (between contour- and surrounding-elements or possibly also between surrounding-ele-

ments) that would likely interfere, thus disrupting contour-localization performance. Remember that our data indicate a substantial contribution of local uncertainty to the effects of context on contour-localization. Therefore, we need to assume that a high probability of incorrect linkages between contour- and surrounding-elements follows from imprecise orientation discrimination about each contour-element (which in turn results from the local uncertainty introduced by flanking-elements). When the snake is surrounded by near-perpendicular elements, instead, the orientation uncertainty about each contour-element would be low (see Experiment 3) and thus the strong snake association corresponding to the target-contour would "win" over the weaker ladder associations from the surround. This model can also account for the result that snakes with near-perpendicular surrounds are easier to spot than when they are within random-surrounds. Indeed, we reported lower orientation uncertainty with near-perpendicular than random flankers (Experiment 3). This would lead to a more accurate discrimination of the orientation of the contour-elements, which in turn would lead to fewer incorrect links between contour- and background-elements when the surround is near-perpendicular compared to random.

Note that, for ladders, we were not able to obtain a performance measure expressed in units of tolerable orientation uncertainty (see Stimuli section of Experiment 2), which would have been desirable to quantify the contribution of crowding (in terms of local orientation uncertainty) to the contextual effects on ladder-localization. Nevertheless, it is interesting to speculate what could account for the modest increase in ladder-localization with near-parallel compared to random surrounds. Near-parallel surrounds should increase orientation uncertainty among ladder contour-elements, thus reducing sensitivity. However, even if here we focused only on *orientation* uncertainty, we cannot rule out an influence of context on *position* uncertainty. In this framework, the presence of near-parallel surrounding-elements would induce some reduction in position uncertainty. If we apply May and Hess's (2007) model in these circumstances, for ladder surrounded by near-parallel elements, snake-associations perpendicular to the direction of the path would be stronger than ladder-associations running parallel to the path. Therefore, the modest facilitation from near-parallel surrounds in ladder-localization (Experiment 1) might reflect a sort of texture-segmentation. Note that this interpretation implies a change in processing strategy from contour-localization to texture-segmentation when the contour is a ladder (compared to a snake) in near-parallel surrounds. If snake-associations are stronger than ladder-associations, one could argue that, in the case of ladder surrounded by near-perpendicular elements, observers

actually detect nearly-snake paths in the surrounds rather than the ladder-target. If this were the case, no facilitation would have been observed as the same type of surround was present on both sides of the display.

Geisler, Perry, Super, and Gallogly (2001) modeled contour detection performance using a local grouping rule derived from the co-occurrence statistics of the local orientation structure of edges within natural scenes, in combination with a simple integration rule based on transitivity that links local groupings of contour-elements into longer contours. This work was the first to establish that the principles of contour integration (as expressed by the association field model) agree with the statistical properties of contours within natural scenes. For example, pairs of local orientation estimates are more likely to arise from the same contour if they are tangent to a common circle (i.e., if they are cocircular; Geisler et al., 2001). Elder and Goldberg (2002) used a similar statistical characterization of the orientation structure of natural scenes to derive a comprehensive set of grouping rules. Such approaches use an orientation structure derived from edge structure of natural scenes (derived using either automated edge-detection or manual segmentation) and, as such, are focused on conjoint orientation/position statistics *within contours*. Our results suggest that—inasmuch as psychophysical paradigms can constrain the likely mechanisms of contour integration—such approaches will fail to predict contour salience with different surrounds. That said, the approach is sufficiently general that there is no reason that statistical properties of structure surrounding contours might not be incorporated into grouping rules.

Clinical implications

If context strongly influences contour-localization performance, then this has interesting implications for the specific mechanism underlying poor contour detection in some clinical populations. For example, the contour detection deficit in schizophrenia has largely been attributed to poor integration (e.g., Silverstein, Kovacs, Corry, & Valone, 2000). However, recently we have reported evidence that poor contour detection in schizophrenia likely originates from imprecise discrimination of *local* orientation and abnormal processing of visual context (Robol et al., in preparation).

Note that the results of the present study suggest that, in clinical populations, it might be simpler to just test crowding of local elements (rather than contour-localization in different surrounds). However, this may lead to misleading conclusions. Indeed, we have recently reported (Robol et al., in preparation) that

patients with schizophrenia show no impairment in contour-localization with near-parallel surrounds but the same amount of "facilitation" with near-perpendicular surrounds as healthy matched controls. This pattern of contextual modulation was not expected on the basis of the *generally* weaker proneness to crowding we reported for patients (whereby the "perpendicular facilitation" should have been greater for patients than controls).

Conclusion

Context affects contour-localization, with near-parallel and near-perpendicular surrounds decreasing and increasing performance, respectively. The effect generalizes across threshold measurements, which may have clinical implications. Finally, the *local* orientation uncertainty introduced by crowding influences contour-localization (which involves *global* processing) and largely accounts for the effects of context. These findings are consistent with the suggestion that context influences contour processing at a predominantly local stage of processing and also with the notion that the local effects of crowding influence global cortical processing of visual form.

Acknowledgments

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Footnote

[1]Intuitively, it is unlikely that the visual system computes detailed local information only to discard it by spatially extensive pooling. Rather it seems more

likely that the local information was never there but a crude representation (resembling an average) was.

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