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Non-linear integration of crowded orientation signals

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ABSTRACT

Crowding of oriented signals has been explained as linear, compulsory averaging of the signals from target and flankers [Parkes, L., Lund, J., Angelucci, A., Solomon, J. A., & Morgan, M. (2001). Compulsory averaging of crowded orientation signals in human vision. *Nature Neuroscience, 4*(7), 739–744]. On the other hand, a comparable search task with sparse stimuli is well modeled by a 'Signed–Max' rule that integrates non-linearly local tilt estimates [Baldassi, S., & Verghese, P. (2002). Comparing integration rules in visual search. *Journal of Vision, 2*(8), 559–570], as reflected by the bimodality of the distributions of reported tilts in a magnitude matching task [Baldassi, S., Megna, N., & Burr, D. C. (2006). Visual clutter causes high-magnitude errors. *PLoS Biology, 4*(3), e56]. This study compares the two models in the context of crowding by using a magnitude matching task, to measure distributions of perceived target angles and a localization task, to probe the degree of access to local information. Response distributions were bimodal, implying uncertainty, only in the presence of abutting flankers. Localization of the target is relatively preserved but it quantitatively falls in between the predictions of the two models, possibly suggesting local averaging followed by a max operation. This challenges the notion of global averaging and suggests some conscious access to local orientation estimates.

1. Introduction

Identifying a target in a cluttered visual scene can be a very difficult task. Moving the stimulus to the periphery of the visual field, decreasing the size of the elements and the distance among them makes such a task even harder. This effect is called crowding.

In a study that is directly connected to our present investigations, Parkes, Lund, Angelucci, Solomon, and Morgan (2001) have investigated the effect of crowding on simple feature processing. They measured the effect on orientation discrimination thresholds of flanking a small tilted target in the periphery with a number of oriented elements all displaced within the spatial range of crowding. Keeping the overall number of elements fixed, they increased gradually the number of flankers that were tilted like the target. They observed that thresholds were reduced linearly (on log–log scales) with increasing number of tilted flankers, even though observers knew that they only had to judge the target that was sitting centrally on the array of Gabor patches (see Fig. 1). In a separate task, they tilted three out of nine elements according to a vertical vs. a horizontal configural arrangement and observers were asked to identify the orientation of the configuration; a task implying that observers localized individual patches. This task was very difficult to perform. The results of this study have led to the suggestion that crowding of individual features, such as orientation, can be explained as a compulsory averaging of information from targets and flankers before the site of conscious evaluation of the target tilt (Parkes et al., 2001). In its strictest form, this model assumes that the system averages orientation estimates for all targets and flankers. Since in this task the number of elements (tilted plus vertical) was fixed to nine, the overall amount of noise is constant, while the signal that each tilted patch should carry, in order for the observer to reach threshold, decreases linearly with the number of positive signals (i.e. tilted flankers) introduced (for details see Parkes et al., 2001). A fundamental consequence of this model is that, within the range of crowding, it is impossible to segregate individual visual targets by having access to their information in isolation. A similar averaging rule has been suggested in the domain of textural integration and visual search (Baldassi & Burr, 2000; Dakin & Watt, 1997; Morgan, Ward, & Castet, 1998). However, in the domain of visual search a very similar effect on orientation discrimination thresholds is predicted by a version of the Max of Outputs rule (Palmer, 1994; Palmer, Ames, & Lindsey, 1993) developed for 'two-tailed' orientation discrimination tasks, in which the target randomly assumes one of two possible values around a reference (e.g. CW or CCW tilts away from vertical). This model assumes that each

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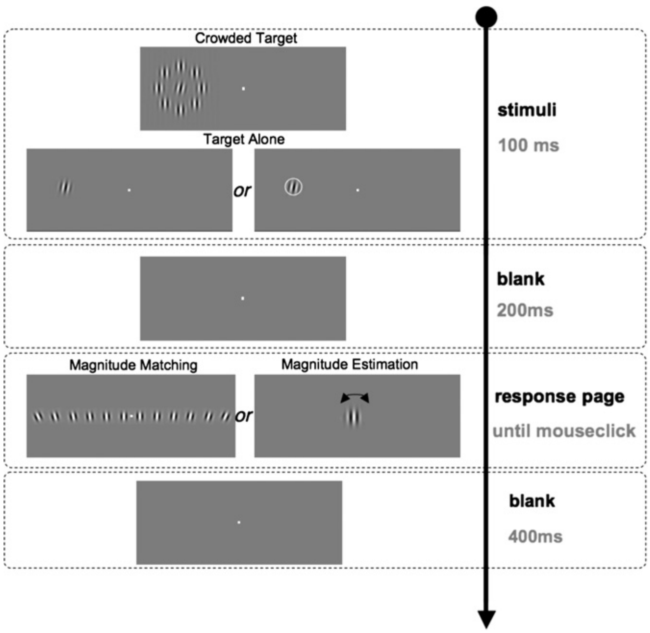

Fig. 1. Experimental sequence and stimuli. The stimuli matched exactly the parameters of Parkes et al. (2001) but were shown according to a vertical, rather than horizontal reference. After the stimulus display, a response page was shown requiring one of two alternative tasks. In the magnitude matching task, observers were presented with 12 response probes whose tilt corresponded to the stimulus set from which the target tilt was sampled. In the magnitude estimation task the response page consisted of a probe resembling the target (but two times larger) that could be rotated by lateral motion of the mouse. Immediately after the response a blank page of 400 ms was displayed and the following trial started automatically. No feedback of any kind was given. One of the observers was tested with an outlining circle to reduce intrinsic uncertainty.

stimulus in the array is monitored by at least two detectors (one for each direction of tilt), whose output is noisy. There is no further perceptual processing of the display (such as averaging or summation) and the decision rule is based on the preferred direction of the detector yielding the strongest response. Because of noise, there are two main consequences of adding distractors (or flankers) to the display. The first is that the more vertical elements are included in the computation, the more likely it will be that one of these neutral elements will be signaled as more tilted than the target, in either the same or the opposite tilt direction. In the latter case the observer produces an error. The second is that increasing the number of elements increases the maximum response from each of the two detectors. This is reflected in the response distributions as a lack of responses at small tilts and an increase of responses at high tilt. In other words, the distribution of maxima from the two oppositely tilted detectors monitored in the task becomes more and more bimodal as the number of displayed elements increases. Baldassi and Verghese (2002) have shown that this model quantitatively explains both the thresholds and the change in shape of the psychometric function with set size better than an Averaging model. Furthermore, Baldassi and Burr (2004) have shown that it fits well with the observed pop-out of a luminance target at threshold and with the flattening of the set size function at high set sizes. Using a novel psychophysical technique that probes the internal stimulus representation directly, Baldassi, Megna, and Burr (2006) were able to demonstrate that in sparse search displays the distribution of reported tilts follows strictly the predictions of the Signed–Max model. In particular, they reported a unimodal response distribution at set size 1 and an increasingly more bimodal distribution at physical or cue-defined set sizes higher than one. Interestingly, the use of an amount of external noise in the set size one condition so high as to match the sensitivity of set size eight broadened the width (i.e. the standard deviation) but not the shape of the distribution, which remained unimodal.

This study is aimed to discriminate between two possible integration rules in crowding of oriented signals: a linear averaging rule vs. a non-linear max-of-outputs rule. Since the predicted response distributions differ substantially in the two models, in order to pursue this goal we measured internal response distributions in an orientation crowding task by relying primarily on the magnitude matching technique used by Baldassi et al. (2006) in the context of search. In both the present and a previous study (Baldassi et al., 2006) we have observed that the measure of the target displayed in isolation showed a response distribution of gaussian shape, whose parameters depend strictly on the physical signal (i.e. different tilt offsets from vertical) and on the noise, converging with the standard psychometric measures. However, in the presence of multiple stimuli, response distributions revealed the integration rule used to combine several inputs at the decision stage, by showing predictable patterns of shape change. Therefore, we assume that any change on the shape of the distributions with different crowding conditions should reflect the underlying integration rule. In particular, if crowding of oriented signals relies on compulsory, linear averaging of noisy information, the measured internal response distributions should broaden when flankers are displayed, as they are vertical and add only noise, with no change in shape. On the contrary, if the limits come from integration rules different from Averaging, this should reflect into a change of shape of the distributions when the number of flankers varies.

We did not have specific reasons to commit in advance to a Max or to any other non-linear integration rule for the crowding task. However, using a number of converging measures, we show that the orientation signal carried by a crowded target is combined in a non-linear fashion and departs in many ways from the predictions of an Averaging model, revealing the signature of some form of uncertainty over the target identity, combined with an inefficient use of detectors at very small scales.

2. General methods

2.1. Stimuli and procedure

The parameters of the stimuli used in our study were designed to reproduce exactly the display used by Parkes et al. (2001). Stimuli were generated in Matlab, using Psychophysics Toolbox extensions for Macintosh (Brainard, 1997; Pelli, 1997) and presented with a Mac G3 computer on a 17" Sony display at 75 Hz refresh rate. The individual elements were Gabor patches (12 c/deg sinusoidal gratings of 90% contrast and 29 cd/m^2 mean luminance, windowed within a circular Gaussian aperture of $\sigma = 0.083°$ space constant), at 2.5° eccentricity. A stimulus set comprised 1 central target that was always tilted clockwise (CW) or counterclockwise (CCW) from vertical and that could be displayed alone or surrounded by eight flanking elements. When flankers were displayed, they were either all vertical or a proportion of them (2, 5 or 8) could carry the same signal of the target; thus, in different conditions there were one, three, six and nine out of nine tilted elements, one of them was the central patch, always tilted. The center-to-center separation of the central target from each flanker was equal to $\lambda 3\sqrt{2}$ (where λ is one cycle of the carrier grating of the Gabor stimulus).

In the intrinsic uncertainty control experiment, the Gabor patches were surrounded by a white annulus of 62 cd/m^2 with a radius equal to about 2σ of the encircled Gabor.

In the main experiments, the target assumed one out of 12 possible orientations (six for each direction of tilt, clockwise or counterclockwise) ranging between ±32°, in step sizes equal to one octave, and presented the same number of times in random order within a block according to the method of constant stimuli. This was a necessary expedient to measure unbiased response distributions. After the stimulus, each trial included a response page that allowed the collection of the subject response, according to the magnitude *estimation* or the magnitude *matching* procedure. Different observers used different procedures. In the magnitude matching measures, observers were asked to indicate the perceived direction and magnitude of tilt of the central target by clicking with the mouse on one of the 12 response probes representing the entire set of possible signals. In the magnitude estimation task the response page was a probe similar to the target (but twice as large) that could be rotated as a knob by lateral motion of the mouse until it matched the perceived tilt of the target. Once the perceived match was reached, the subject clicked and the current probe angle was scored. Immediately after the response a blank page of 400 ms was displayed and the following trial started automatically. No feedback was provided.

In both tasks, we expected the distribution of reported tilts to probe the distributions of internal noisy states of representation of the tilt, enabling to assess more directly the mechanism of crowding of orientation information.

In the location experiment the paradigm was slightly varied so that one of the flankers was tilted like the target and observers were required both to locate it – by mouse clicking on its location – and to estimate the magnitude of its tilt. This second response was required to check that the modifications introduced in the task did not alter the observers' strategy when judging the tilt of the targets relative to our previous experiments. Note that in this condition there are two targets, the central one and one randomly selected from the crown of the eight flankers.

In the threshold and magnitude estimation tasks, the overall number of trials, executed in blocks of variable length (60–120) was about 600, with variability depending on the stability of the results and the particular condition. One of the observers (CB) performed many more trials (∼1800) as he participated in the pilot phase of the experiment. In the location task observers executed 320 trials.

2.2. Data analysis

We analyzed the data by classifying clockwise vs. counterclockwise responses in a standard binary fashion to produce psychometric functions that were fit with a cumulative gaussian function to estimate thresholds, corresponding to the level of tilt producing 75% of correct tilt direction judgments. Responses were scored correct if the sign of the tilt was correctly identified, irrespective of the magnitude match.

For each observer and each condition, the identification responses scored by the psychometric function were binned into three classes of discriminability: below threshold (less than 67% correct), near threshold (67–83% correct responses) and above threshold (greater than 83% correct). Only distributions for near thresholds angles are presented here as they provide the best information about the shape of the response distributions, free from floor or ceiling effects (Baldassi et al., 2006). The response distributions for the magnitude matching procedure were simply constituted by the histogram of perceived tilts given a target angle (i.e. they were drawn by collapsing all the physical angles yielding near threshold accuracy). For the magnitude estimation procedure, response distributions were drawn by binning the selected probe tilts into classes providing the best match with the tilts of the magnitude matching procedure. A response distribution (Figs. 3 and 4) has two sides, one for correct identifications, that is reported tilts sharing the same direction of off-vertical tilt with the target, and one for identification errors, that is tilts perceived in the opposite direction of the target.

2.3. Observers

Eight observers participated in the experiment, four of which executing only the location experiment. They had normal or corrected to normal vision and they were all naive to the goal of the study, except for one who was the author (CG). Data for different target sizes were collected in separate blocks.

3. Results

3.1. Thresholds vs. number of targets

Parkes et al. (2001) used a simple binary task to show that increasing the number of tilted patches carrying the same tilt helped performance following a slope of 1 on log–log coordinates. This result implies crowding; in fact the surrounding elements influence thresholds even though the observers knew they only had to judge the tilt of the central element. The result was explained as compulsory averaging of orientation signals of target and flankers. In order to compare the outcome of our measures of response distribution to the results shown in Parkes et al. (2001), we first verified Parkes et al. (2001) results with our magnitude matching technique.

Fig. 2 shows the orientation discrimination thresholds of two observers for judging the direction of tilt of a central Gabor patch

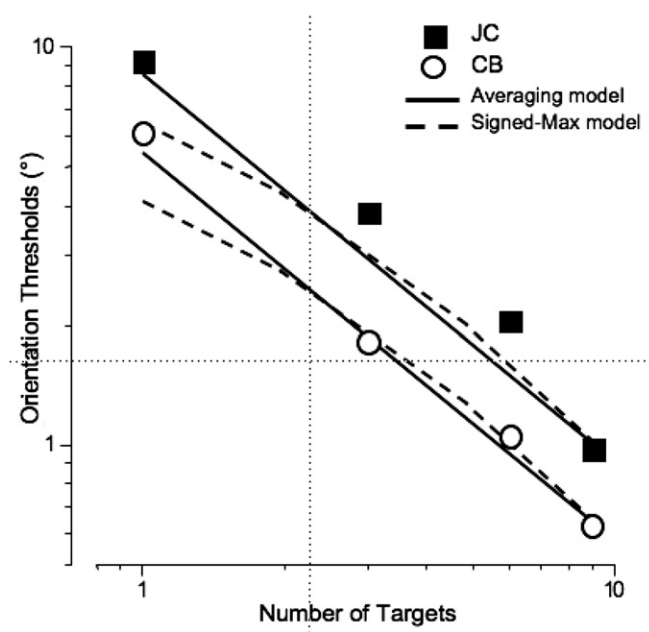

Fig. 2. Threshold estimation from the magnitude matching procedure. The graph represents orientation thresholds as a function of the number of targets, in log–log axes. The symbols represent the measures for the two observers, while the continuous and the dashed lines are the predictions of the Averaging and of the Signed–Max model, respectively. Orientation sensitivity (reciprocal of threshold) increases with the number of patches having the same tilt as the target. The rise of performance on log–log axes is close to the predictions of both models for all but the target alone condition, which is well predicted by the Averaging model while the Signed–Max model predicts a performance better than the data. These data are a very good replication of those by Parkes et al. (2001), suggesting that the magnitude matching and estimation tasks do not alter the decision strategy in any way.

surrounded by an array of eight flankers, of which only a (variable) proportion carried the same signal of the target.

These results confirm and replicate the results of Parkes et al. (2001). In particular, the more tilted elements there were in place of vertical flankers, the better were the thresholds, implying an increase of orientation sensitivity, dropping to 1° for JC and 0.65° for CB. The rise of performance was very well predicted by the Averaging model (continuous line), as shown by Parkes et al. (2001), even though the Signed–Max model did as well when the number of target was higher than 1. When only one target is present the latter model predicts a better performance than the data, consistently for both observers. In any case, the good match between our and Parkes et al.'s results legitimates the use of the magnitude matching technique to further characterize the mechanisms underlying crowding of oriented signals, in that it leaves the pattern of thresholds unaffected relative to standard, binary psychophysical tasks.

3.2. Matching and estimation of target tilt

In the second stage of our study, we measured the response distributions for a small peripheral Gabor target at or around threshold under different crowding regimes: the target alone condition and the crowded condition, in which the tilted target was flanked by eight vertical elements. Note that the latter condition is the one that elicits the strongest crowding effect both in Parkes et al. (2001) study and in our replication reported in the previous paragraph.

4. Measuring the target alone

This condition was used as baseline for both the measurement of the crowding effect and that of the response distribution. Three observers took part in this experiment: CB was tested with the magnitude matching paradigm, while GB and CG used the magnitude estimation paradigm. GB was also tested in a different condition with an outlining circle around each patch to reduce intrinsic spatial uncertainty Intrinsic uncertainty refers to an inefficient channel monitoring due to stimuli that are poorly defined and that elicit maximum activity in several independent sensory mechanisms, only one of which is actually sensitive to the stimulus (Pelli, 1985; Solomon, 2007a; Solomon, 2007b).

As reported in the Methods section, only distributions for near thresholds angles are presented here as they provide the best information about the shape of the response distributions, free from floor or ceiling effects (Baldassi et al., 2006).

Fig. 3 shows results for all observers in the target alone condition. The symbols show a histogram of the proportion of reported tilts for target tilts around threshold (i.e. about 75% of correct identifications). Empty symbols represent errors and black symbols correct identifications. The error bars represent the standard error of the mean (SEM) calculated by bootstrap (Efron & Tibshirani, 1994). When not shown, the SEM is smaller than the symbol.

All observers except one (GB), show unimodal, gaussian-like distributions as predicted by both models. The solid line represents the best fitting gaussian function underlying the distributions. The spread of these distributions was in all cases (except GB's in the basic condition) in good agreement with the threshold for the target alone of each observer, consistent with our assumption that the distributions we measured corresponded to the internal states generated by our stimulus as predicted by the Signal Detection Theory (Green & Swets, 1966). The criterion to decide whether a distribution was unimodal or bimodal was the following (Baldassi et al., 2006). The largest positive and negative responses were selected as potential peaks. If any data points between them were significantly lower than both these peaks (bootstrap t test, $p < 0.01$) then the distribution was classified as bimodal.

The bottom right panel of Fig. 3 shows GB's data in a slightly modified version of the task. In fact, we wondered if the bimodality shown in this observer could be attributed simply to a fault of the

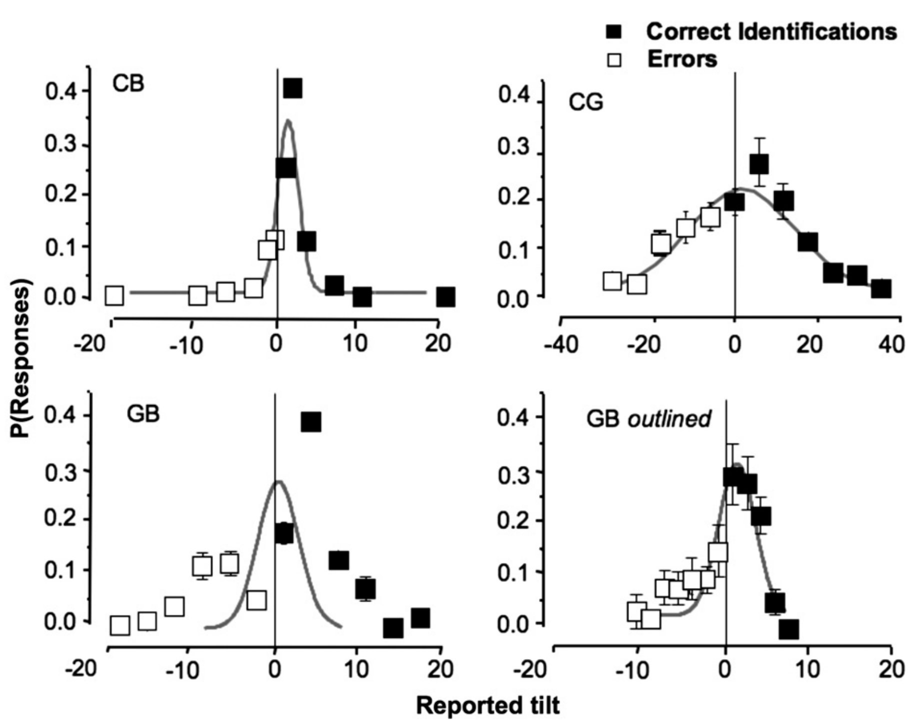

Fig. 3. Response distributions for the target alone condition. Each panel plots the proportions of responses for a target around threshold as a function of the reported tilt for three observers (GB was tested in two conditions, see text). Empty symbols, to the left of 0, represent errors, while filled symbols represent correctly identified tilt directions. Two out of three observers show unimodal distributions, well approximated by gaussian functions, as predicted by both models. Observer GB does not follow this pattern in the basic condition, but she does when the target location is clearly outlined by a circle around the target.

estimation task measurement, when observers had to report small tilts, or to a more subtle effect like the intrinsic uncertainty (Pelli, 1985) that could be generated by the fact that the target was a very small, isolated peripheral patch of high spatial frequency, even if it was displayed at high contrast. Indeed, even if the target had high contrast, observers sometimes reported not to see it clearly (or at all). To answer this question we re-ran this condition in observer GB with an outlining circle that cued clearly the location of the stimulus, possibly reducing intrinsic uncertainty about its location. The bottom right panel of Fig. 3 shows the response distribution of observer GB under this condition, showing a return to a gaussian, unimodal shape of the distribution. Therefore, the bimodality obtained by this observer in the basic condition is coherent with the effect of intrinsic uncertainty that was reduced by outlining its location.

5. Measuring the crowded condition

Results for the crowded condition are shown in Fig. 4. Again, proportions of responses for three observers are plotted as a function of the reported tilt. The bottom right panel reports the distributions of GB with outlining circles around both target and flankers; we reasoned that in the crowded condition the flankers should reduce themselves the positional uncertainty about the target location, but this measure was performed to control for potential artifacts from the outlining circles. In this case the pattern of distributions changes drastically compared with the Target Alone condition. In all cases the criterion for bimodality was met, with larger tilts preferred to smaller tilts for both errors and correct identifications.

This pattern was very close to that obtained in the uncrowded condition of visual search (Baldassi et al., 2006). We therefore modeled the data simulating both the Averaging model (solid lines) and the Signed–Max model (dashed lines). The only parameter used was the internal noise for one element (i.e. the threshold for the target alone), that was successful in describing the response distributions for the target alone. The MonteCarlo simulations rule out the strict Averaging model, since it predicts unimodal distributions independently on the presence of the flankers. The Signed–Max model was a very good fit of the data in two out of three observers. In the two conditions tested in observer GB, even though the bimodality is clear (and significant, based on the bootstrap test), the prediction of the Signed–Max model, represented by dashed lines, underestimates the width of the empirical function. Possibly, this indicates some additional source of noise in the computation, that is often found in set size modulations (Wilken & Ma, 2004) or the use of a hybrid model, in which the max rule is applied to regional rather than global orientation estimates (see below).

5.1. Locating individual crowded stimuli

The data shown so far seem to support an uncertainty explanation of this sort of crowding. However, we still cannot completely rule out that this pattern was due to a version of the Averaging model that combines outputs from independent, first stage filters after a non-linear transformation, such as squaring (Heeger, 1992). If the output from each local element is raised to a power greater than 1 before the averaging stage, then the element with the strongest output will count more and more with increasing the exponent. The response distribution generated by a similar averaging rule will lose linearity, approximating the one predicted by the Signed–Max rule, showing a bimodality that sharpens with higher exponents. We then decided to test if observers would be able to locate the target.

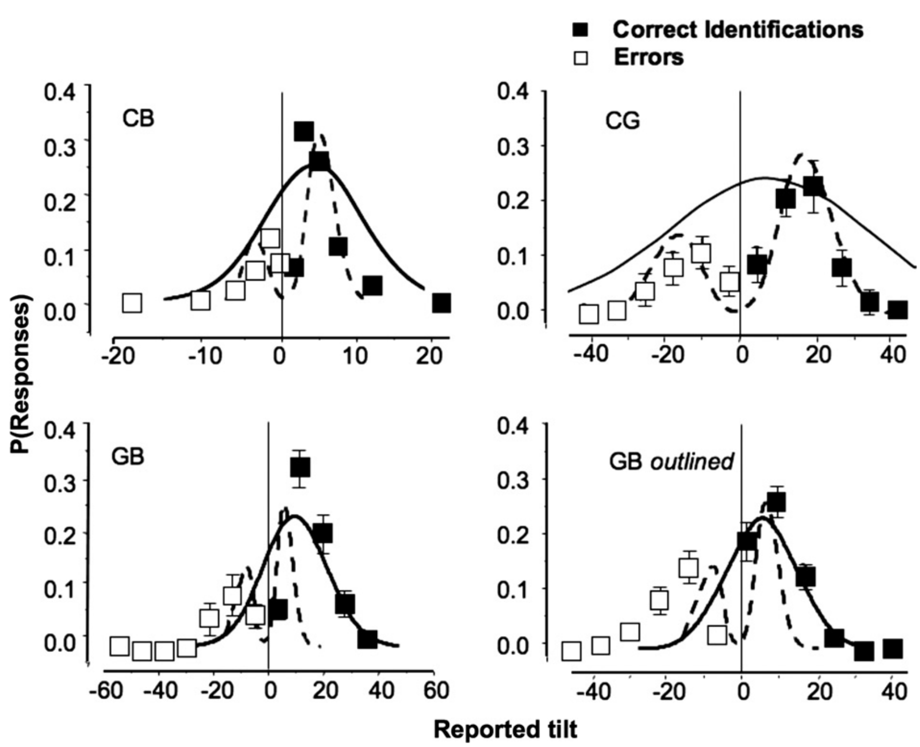

Fig. 4. Response distributions of the crowded condition. Each panel plots the proportions of responses as a function of the reported tilt for three observers (GB was tested also with outlined patches). Symbols are like those of Fig. 3: empty symbols, to the left of 0, represent errors, while filled symbols represent correctly identified tilt directions. The solid line represents simulation for the Averaging model, while the dashed line represents simulation for the Signed–Max model. All observers exhibit a low rate of responses for small tilts and an increase for larger tilts implying bimodality, but the tails of the empirical distributions are generally larger than the predictions of the Signed–Max model, possibly implying that the flankers introduced additional sources of noise.

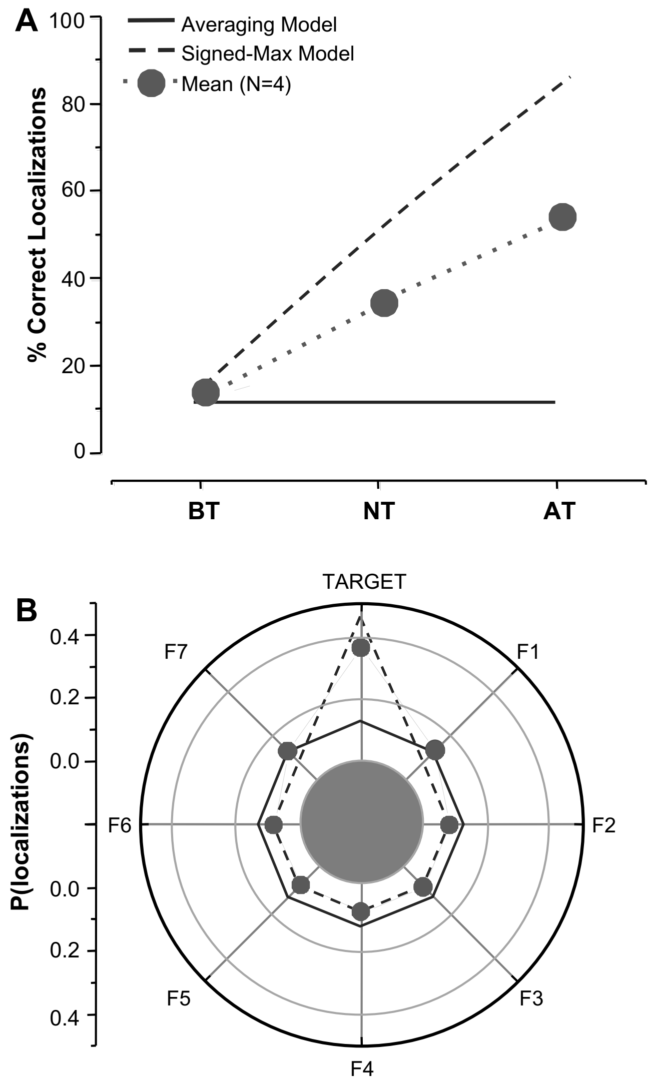

Fig. 5. Results for the location task. Panel A plots percent of correct localizations as a function of different target tilts leading to different identification performances (BT = below threshold, NT = near threshold, AB = above threshold). Localization performance, represented by the circles, improves significantly with target tilt, against the Averaging prediction (solid line), but less rapidly than the predictions of a Signed–Max model (dashed line) that locates the target based on the strongest output. Panel B shows the proportion of responses for each location when the target tilt was correctly identified. Note that the axis goes to negative values, corresponding to the central gray circle, an artifact we have introduced to increase the visibility of the results without altering its significance (error bars are in all cases smaller than the symbols). Polar angle reflects the selected position, relative to the tilted flanker position, that in the plot is normalized to its North location. Flankers are numbered in a clockwise, progressive order (*F*1–*F*7). The symbols show the mean of four observers and its standard error. The solid line shows the guessing rate, coincident with the predictions of the Averaging model, while the dashed line indicates the prediction for the Signed–Max model. For correct identifications, the position of the target was reported significantly more often ($p < 0.01$) than the other locations and the locations adjacent to the target are reported more often than those farther away (Tukey test $\alpha = 0.05$).

Fig. 5A shows the proportion of correct localization, independent of the identification response (CW or CCW), at different identification performance levels relative to threshold (BT = below threshold; NT = near threshold; AT = above threshold). The mean of our four observers (standard errors are smaller than the symbols) clearly show a consistent and significant pattern of improvement of localization performance with increasing discriminability. Performance departed from guessing (coinciding with the predictions of the Averaging model, the solid line), but it was not as efficient as predicted by an uncertainty model (dashed line) that selects the location with the strongest output. Fig. 5B shows a polar representation of the selected locations relative to the target when the target tilt was correctly identified. The tilted flanker location was normalized to be plotted at the North location, and each gray circle is the mean of the four observers (with SEM). The solid line shows the pattern of random localization that coincides with the predictions of the Averaging model, while the dashed line shows the predictions of the Signed–Max model, represented by a peak of localization responses at the target position while the other seven locations are randomly selected. When observers identified the tilt of the two targets, they could also locate the tilted flanker significantly more often than the other locations (ANOVA test, $p < 0.01$, $F = 79.3628$, Tukey test $\leqslant 0.05$), ruling out the Averaging model. The only difference between the data and the predictions of the Signed–Max model was in the 'nearby flanker' errors shown in the data.

It thus appears that observers are not limited to a global average orientation, and are able to locate tilted targets in crowded arrays with some degree of accuracy. These localization results diverge from those obtained by Parkes et al. (2001), who found that observers were unable to identify the configuration of three tilted elements in a crowded array. One possible reason for our divergent results is our size of target angles. Parkes et al. did not report the size of theirs, they only stated that performance "did not improve with target tilt." When our targets were Below Threshold, our observers' localizations were no better than chance. Perhaps Parkes et al's target tilts were similarly small.

6. Discussions and conclusions

In this study we investigated the mechanism underlying crowding of orientation signals, previously explained by compulsory averaging before awareness. The study by Parkes et al. (2001), to which our work is directly connected, reported a linear decrease of thresholds with increasing number of targets from an array of nine oriented signals. In our study, we replicated the effect but increased the scope of the results by concurrently measuring the distributions of perceived magnitude. The distributions showed bimodality of perceived tilts, which is a signature of non-linear combination of information from the elements composing a crowded display.

For further evidence of conscious access to local orientation signals, we tested the observers' locating ability, that was well better than chance as predicted by the Averaging model. Whereas location would be impossible without some conscious access, performance fell below the Max rule predictions (see Fig. 5). Perhaps observers used some hybrid strategy, averaging orientation estimates in different regions of the stimulus array, and then applying a max rule to those averages. Another possibility is that, when identifying target tilt, observers use some non-linear combination of tilt estimates (e.g. the max rule); but their localization responses are based on texture borders. Targets form a texture border with each adjacent distractor. On trials in which only one of these borders can be detected, observers may select the adjacent distractor, rather than the target's true location (Solomon & Morgan, 2001). Mislocalization to adjacent elements can be associated to the illusory conjunction effect, the condition in which the observer combines different characteristics of nearby elements susceptible to spatial crowding (Treisman & Schmidt, 1982), or to the similar phenomenon of feature inheritance (Herzog & Koch, 2001).

To conclude, based on the results of this study, we propose that uncertainty contributes to the sensitivity impairment in the presence of flankers to a peripheral target, but it is not the sole cause. In our crowding task, what may be happening is that the system cannot avoid basing its decision on a channel representing a flanker, or group of flankers, if it produces a response stronger than that representing the target. What remains to be determined are (i) the size of the regions in which orientation estimates are averaged, (ii) the number of these regions that influence observer's responses and (iii) the exact form of the decision rule. In any case, we have enough evidence to suggest that identification of a crowded target's tilt is not limited to an array's global average orientation. Some form of uncertainty plays a role.

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