A decisional account of subjective inflation of visual perception at the periphery

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Abstract Human peripheral vision appears vivid compared to foveal vision; the subjectively perceived level of detail does not seem to drop abruptly with eccentricity. This compelling impression contrasts with the fact that spatial resolution is substantially lower at the periphery. A similar phenomenon occurs in visual attention, in which subjects usually overestimate their perceptual capacity in the unattended periphery. We have previously shown that at identical eccentricity, low spatial attention is associated with liberal detection biases, which we argue may reflect inflated subjective perceptual qualities. Our computational model suggests that this subjective inflation occurs because under the lack of attention, the trial-by-trial variability of the internal neural response is increased, resulting in more frequent surpassing of a detection criterion. In the current work, we hypothesized that the same mechanism may be at work in peripheral vision. We investigated this possibility in psychophysical experiments in which participants performed a simultaneous detection task at the center and at the periphery. Confirming our hypothesis, we found that participants adopted a conservative criterion at the center and liberal criterion at the periphery. Furthermore, an extension of our model predicts that detection bias will be similar at the center and at the periphery if the periphery stimuli are magnified. A second experiment successfully confirmed this prediction. These results suggest that, although other factors contribute to subjective inflation of visual perception in the periphery, such as top-down filling-in of information, the decision mechanism may be relevant too.

Keywords Peripheral vision · Subjective perception · Perceptual decision making · Psychophysics · Signal detection theory

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Peripheral vision is limited in resolution and color sensitivity (Mullen, 1991; Noorlander, Koenderink, Den Olden, & Edens 1983; Strasburger, Rentschler, & Jüttner 2011). However, introspectively, peripheral vision does not seem so impaired; it does not seem to be achromatic, blurred, or dark. We experience a sense of vividness and detail outside of the center of gaze, despite a low processing capacity. This somewhat resembles the situation in endogenous spatial attention. For example, in inattentional and change blindness experiments, participants are often surprised at how poorly they detected (changes in) unattended targets, as if they feel they should have seen the targets despite the lack of attention (Simons & Chabris, 1999). It seems like humans overestimate their capacity to see both in the periphery of the visual field and when they are not paying attention. How can we reconcile the apparent contradiction between the high quality of visual experience and the relatively low brain processing capacity for peripheral vision?

We have recently investigated some of these phenomena within the framework of signal detection theory (Green & Swets, 1989; Macmillan & Creelman, 2004). We have previously shown that for stimuli at identical eccentricity, the lack of

attention can inflate subjective perception, specifically making detection criterion liberal (i.e., participants' propensity to report detecting a target is higher for unattended stimuli) (Rahnev et al., 2011). These findings have been explained by a signal detection theoretic model, according to which attention both increases the strength of the internal neural response and reduces its trial-by-trial variability (Bressler & Silver, 2010; Pestilli, Carrasco, Heeger, & Gardner 2011; Rahnev et al., 2011; Wyart, Nobre, & Summerfield 2012). This model has since gathered further empirical support from studies using transcranial magnetic stimulation and neuroimaging (Rahnev, Bahdo, De Lange, & Lau 2012; Rahnev, Maniscalco, Luber, Lau, & Lisanby 2012; Rounis, Maniscalco, Rothwell, Passingham, & Lau 2010).

Here we investigate to what extent the mechanism of subjective inflation of visual perception underlying lack of visual attention also applies to peripheral visual perception. In particular, we predicted that participants may use a relatively liberal detection criterion for the detection of periphery targets as compared to detection of targets in the center of the visual field, just as they did in Rahnev et al. (2011) under the lack of spatial attention. Although the emergent phenomena seem similar, the underlying physiology of eccentricity and lack of spatial attention may differ. In the case of peripheral vision, the reasons that led us to formulate the predictions are as follows. First, the architecture of the human retina already imposes limitations. On one hand, since the large majority of cones are concentrated in the foveal region, light at the central region of the retina is processed preferentially (Banks, Sekuler, & Anderson 1991; Curcio, Sloan, Kalina, & Hendrickson 1990). Also, each ganglion cell at the periphery receives information from up to hundreds of photoreceptors while at the fovea the correspondence is one-to-one (DeValois & DeValois, 1988). Second, the size of a ganglion cells' receptive field increases with eccentricity and the amount of cortex dedicated to process a stimulus (measured as the cortical magnification factor) decreases with eccentricity (Azzopardi & Cowey, 1993; Daniel & Whitteridge, 1961). These results imply that a visual stimulus presented in the periphery will be processed by fewer neurons and with larger spatial uncertainty than a centrally presented stimulus. Assuming that the overall sensory response is reflected by pooling of information over many neurons, peripheral vision may be similar to a lack of covert attention in that it may produce sensory responses with high variability. To test this prediction, we conducted a series of three psychophysical experiments in which participants were asked to detect the presence of a grating pattern embedded in noise.

Method

Participants

All participants were naive regarding the purposes of the experiments, had normal or corrected-to-normal vision,

signed an informed-consent statement approved by the local institutional review board, and received a monetary compensation of $10 per hour for their participation. Four participants participated in Experiment 1, 11 participants in Experiment 2, and 7 participants in Experiment 3. The mean age of the participants was 22 years.

Stimuli

Stimuli were generated using Psychophysics Toolbox (Brainard, 1997; D G Pelli, 1997) in MATLAB (MathWorks, Natick, MA, USA) and were shown on an iMac monitor (24-in monitor size, 1920 by 1200 pixels, 60 Hz refresh rate). Seated in a dimmed room (22 in from the monitor), participants were instructed to fixate at the center of the screen. "Target present" stimuli consist of gratings (2 cycles/degree) tilted in a random direction embedded in a white noise background. "Target absent" stimuli are just the noisy background. The total contrast of the stimuli was fixed at 30 % but the grating-to-noise ratio (grating contrast) varied, thus making the gratings more or less visible. The size of the stimuli was 5°.

Eye-tracking

Eye movements were monitored for all subjects in all experiments with a video-based eye tracker Eyelink 1000 (SR Research Ltd., Ontario, Canada). The observers' right eye was recorded at a sample rate of 500 Hz. Participants were instructed to keep their gaze at the center of the screen during trials. Trials in which gaze position was outside the center stimulus region (by any amount) at any time during stimuli presentation were discarded from the analysis. This strict control of fixation left out 20 % of the trials on average. However, we had similar results using all trials.

Data analysis

The experiments are variants of a "yes-no" detection task at the center and at 12° in the periphery of the visual field. The results can be summarized in terms of hits (stimulus was present and response was correct) and false alarms (stimulus was absent but the subject response was "yes"). Standard signal detection theory transforms hits and false alarms in a measure of sensitivity (d') and response bias (c) (Green & Swets, 1989; Macmillan & Creelman, 2004). The primary advantage of using d' instead of the hit rate or the percentage of correct responses is that d' is independent of a subject's criteria and thus measures objective performance capacity, whereas c is a subjective variable (Lau, 2008): some people may be very conservative (if he/she needs a lot of evidence to say "yes, I see it" and c is positive) or liberal (saying "yes, I see it" very often and c is negative). The distinction between

objective capacity and response bias is quite relevant to our study because we are comparing response bias at the center and at the periphery controlling for signal detection capacity.

Given each subject's hit and false alarm rates at a given location, we calculate d' and c according to standard signal detection theory (Macmillan & Creelman, 2004) formulas:

$$d' = z(HR) - z(FAR) \tag{1}$$

$$c = -\frac{1}{2}\left[z(HR) + z(FAR)\right] \tag{2}$$

where HR is the hit rate, FAR is the false alarm rate and z is the inverse of the normal cumulative distribution function.

Signal detection theoretic computational models

We modeled the behavioral results of Experiments 1 and 2 using models based on signal detection theory according to the following rules. First, every time a stimulus is shown, it produces in the mind of the observer an internal response drawn from a Gaussian probability density function. Given that the task involves displaying one central and one peripheral stimulus, on each trial two internal responses are produced, one for each location. If the target was absent, the mean of the distributions is set equal to 0 at both locations. If the target was present, the mean of the distributions is μ(cen) and μ(per) for the center and peripheral locations, respectively. Second, perceptual decisions are made by comparing the internal response to a criterion. When the internal response exceeds the decision criterion in the center (periphery), the observer's answer will be "yes" if asked to report the presence of a target in the center (periphery). Lastly, based on previous empirical evidence (Gorea & Sagi, 2000; Rahnev et al., 2011; Zak, Katkov, Gorea, & Sagi 2012), the decision criterion is common for central and peripheral decisions.

For all models, without loss of generality, the standard deviation for the peripheral distributions was set equal to 1. In summary, the possible free parameters are:

μ(cen) Mean of the central signal distribution
μ(per) Mean of the peripheral signal distribution
σ(cen) Standard deviation of the internal response distributions for the central stimulus
criterion Location of the common criterion level.

We considered four different models that differ in how eccentricity affects the internal response distributions:

1. Mean + variance modulation model (MEAN+VAR): Eccentricity changes the mean value and the standard deviation of the internal response distributions. Four parameters: μ(cen), μ(per), σ(cen), and criterion.

2. Variance modulation model (VAR): Eccentricity changes only the standard deviation of the internal response distributions. Three parameters: μ=μ(cen)=μ(per), σ(cen), and criterion.

3. Mean modulation model (MEAN): Eccentricity changes only the mean value of the internal response distributions. Three parameters: μ(cen), μ(per), and criterion (σ(cen)=σ(per)=1).

4. Null model (NULL): Eccentricity does not change the mean value or the standard deviation of the internal response distribution. Two parameters: μ=μ(cen)=μ(per) and common criterion.

Model fitting

We fit the models to the data using a maximum likelihood estimation approach that has previously been used within a signal detection framework (Dorfman & Alf, 1969). Briefly, the likelihood of a set of signal detection model parameters given the observed data can be calculated using the multinomial model. Formally,

$$L(\theta|data) \propto \prod_{i,j} P_\theta\left(R_i|S_j\right)^{n_{data}\left(R_i|S_j\right)} \tag{3}$$

where each R_i is a behavioral response a subject may produce on a given trial, and each S_j is a type of stimulus that may be shown on that trial. The expression "$n_{data}(R_i|S_j)$" is a count of how many times a subject actually produced R_i after being shown S_j. The expression "$P_\theta(R_i|S_j)$" denotes the probability with which the subject produces the response R_i after being presented with S_j, according to the signal detection model specified with parameters θ.

Given a set of parameters θ, the expression "$P_\theta(R_i|S_j)$" is calculated as follows. There are two possible stimuli (S_1="target absent" and S_2="target present") and accordingly two possible responses (R_1="absent" and R_2="present") for the center and periphery set of trials. For instance, if we are evaluating center trials and we assume that S_j gives rise to a Gaussian distribution with a mean μ_j and standard deviation σ_j, the expression "$P_\theta(R_1|S_j)$" equates to:

$$P_\theta\left(R_1|S_j\right) = \int_{-\infty}^{criterion} \frac{1}{\sqrt{2\pi\sigma_j^2}} \exp\frac{-\left(x-\mu_j\right)^2}{2\sigma_j^2} dx \text{ and } P_\theta\left(R_2\Big|S_j\right) \tag{4}$$

$$= 1 - P_\theta\left(R_1\Big|S_j\right).$$

Note that the models were not fit to summary statistics of performance such as percentage correct. Rather, models were

fit to the full distribution of probabilities of each response type contingent on each stimulus type. Various kinds of summary statistics (e.g., d', c, percentage correct, and so on) can be derived from this full behavioral profile of stimulus-contingent response probabilities.

We fitted all models under consideration to the observed data by finding the maximum likelihood parameter values θ. Maximum likelihood fits were found using a simulated annealing procedure (Kirkpatrick, Gelatt, & Vecchi 1983). Model fitting was conducted separately for each subject's data. The estimation procedure was reliable; subsequent repetitions of the model fitting procedure produced negligible variations in the parameter estimates for each model of each subject's data.

Formal model comparison

The maximum likelihood associated with each model characterizes how well that model captures patterns in the empirical data. However, comparing models directly in terms of likelihood can be misleading; greater model complexity can allow for tighter fits to the data but can also lead to undesirable levels of over-fitting, i.e., the erroneous modeling of random variation in the data. Therefore, we compared the models using the Bayesian Information Criterion (BIC). This measure provides a means for comparing models on the basis of their maximum likelihood fits to the data while correcting for model complexity. To better interpret the BIC values of a model, we calculated the normalized BIC weights (Burnham & Anderson, 2002), which are obtained by a simple transformation of BIC values. By definition, the BIC weight for model i quantifying the theoretical evidence in favor of model i can be expressed as:

$$BIC_w(model\ i) = \frac{e^{-\frac{1}{2}(BIC_i - BIC_{min})}}{\sum_{n=1}^{4} e^{-\frac{1}{2}(BIC_n - BIC_{min})}} \qquad (5)$$

where BIC_k is the BIC for model k and BIC_{min} is the lowest BIC exhibited by all models under consideration ("best model").

Similar results were obtained when we used the Akaike Information Criterion (AIC).

Experiment 1: Liberal detection bias for periphery targets
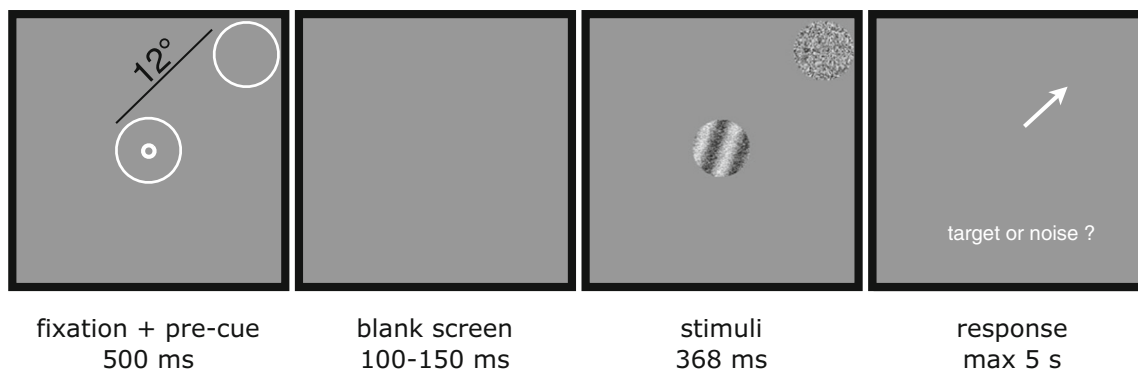
Experiment and task design

We adopted an intense single subject approach. The large amount of trials per subject at the expense of fewer participants ($N=4$) is especially suitable for model fitting. Each subject completed three sessions, with each session occurring on a different day. Each session consisted of 720 experimental trials separated into three blocks of 240 trials. Participants were allowed to have 60-s breaks after every 40 trials. Participants took approximately 75 min to complete a session. Task design is illlustrated in Fig. 1. Each trial begins with 500-ms presentation of a fixation cue at the center of the screen and two simultaneously-presented circles indicating the location of the upcoming stimuli. A blank screen is then presented for a random time varying from 100 to 150 ms, after which the target stimuli appear for 368 ms. The peripheral stimuli are always presented at an eccentricity of 12 ° towards the upper right corner of the screen. Finally, the stimuli disappear and an arrow indicates that the subject should report whether the target was present or absent at either the central or peripheral location. Participants had a maximum time of 5 s to respond. Target presence probability was 0.5 and the presence of a target at the center was independent of the presence of the target at the periphery. To stimulate subjects to distribute attention evenly at both locations, the orientation of the arrow was random, with 50 % of the trials assigned to each location. Participants were fully informed of these facts and completed 64 training trials at higher grating contrast than the actual experiment.

It may be argued that subjects may be inherently inclined to attend more to the central location, but this claim becomes difficult to be tested unless attention is operationally defined. Following previous definitions, here we define attention in terms of task relevance of the stimuli (Summerfield & Egner, 2009). It is in this sense that endogenous attention is stipulated to be equal between the central and peripheral stimuli.

Total contrast of stimuli was fixed to 30 % but the grating-to-noise ratio varied, thus making the gratings more or less visible. For each subject, we used a QUEST threshold determination procedure (Watson & Pelli, 1983) to find the grating-to-noise ratio that would produce about 75 % correct responses for the center and periphery stimuli. This procedure was performed using a two-interval forced-choice (2IFC) task to minimize decision biases (Macmillan & Creelman, 2004). The 2IFC task was similar to the detection task described above but the stimuli were presented in two intervals separated by a 0.1 s blank screen. The second presentation was opposite to the first one (if the target was present in the first presentation, it was absent in the second one and vice versa). Participants had to report in which presentation (first or second) the target was present at the location indicated by the arrow. Every 240 trials we controlled for task performance at both locations to make sure d' was in the range (1.5, 2.5). If d' was outside this range, grating contrast was slightly increased or decreased accordingly.

fixation + pre-cue   blank screen   stimuli   response
500 ms   100-150 ms   368 ms   max 5 s

Fig. 1 Task design for Experiment 1. Each trial began with a fixation circle at the center of the screen and two larger circles at the location where the stimuli appeared: one at the center and one at the periphery of the visual field (12 degrees towards the upper right corner). Following a variable-duration blank screen, the stimulus was shown for 368 ms, followed immediately by a response cue (white arrow) indicating the location at which participants were to provide a perceptual judgment

regarding the presence or absence of a grating. Central and peripheral stimuli were independent. The response cue was randomly assigned to the center or to the periphery, with 50 % of the trials at each location (see Experiment 1: Liberal detection bias for periphery targets – Experiment and task design for further details). Therefore, since both locations are equally relevant for the task, an optimal observer should distribute attention evenly to both locations (Summerfield & Egner, 2009)

Results

Detection criterion is more liberal at the periphery than at the fovea

Because sensitivity is usually better at the center of gaze, in an attempt to avoid the capacity to detect the target as a confounding factor, we titrated target contrast at both locations (see Experiment 1: Liberal detection bias for periphery targets – Experiment and task design). As a result, the between-subject average d' was equated at both locations (paired t test: T(6)=−0.42, p=0.69; Fig. 2a). However, subjective experience differed. Participants reported seeing the grating much more often at the periphery than at the center. The number of hits was significantly larger at the periphery than at the center (paired t test: T(6)=− −.37, p=0.01; Fig. 2b). Moreover, even when the stimulus was absent, participants still produced more false alarms in the periphery (paired t test: T(6)= −2.7, p=0.03), as if they imagined the target was there more often (Fig. 2c). This is reflected by a significant difference in the response bias c (paired t test: T(6)=6.15, p=8.5×10^{-4}; Fig. 2d): participants adopted a conservative subjective criterion for center trials (T(3)=5.19, CI=(0.25,1.04), p=0.01) and a liberal criterion for periphery trials (T(3)= −3.75, CI=(−0.3, −0.02), p=0.03). Similar results were obtained for each individual subject (Fig. 3).

### Perceptual internal response is more variable at the periphery

We tried to account for the liberal detection bias phenomenon with a model based on signal detection theory (MEAN+VAR model), as illustrated in Fig. 4a. The model assumes that the trial-by-trial variability and the mean value of the internal response differ with eccentricity. The rationale of the model is that information from the periphery may be processed with

larger internal noise that may lead to more frequent crossing of a subjective detection threshold. Based on previous empirical evidence (Gorea & Sagi, 2000; Zak et al., 2012), the model presupposes that participants use a single common criterion for detecting stimuli at both locations. This is a suboptimal strategy because to maximize the percentage of correct responses the ideal observer would make use of the fact that the target present probability is 0.5 and would set two different criteria, one for the center and one for the periphery location. These criteria would be located at a point where the "target absent" and "target present" distributions intersect (leading to a response bias c=0 for both locations).

The MEAN+VAR model was able to explain the behavioral results from Experiment 1 and provides a possible mechanistic account for the data (Fig. 4a and b). The parameter σ(cen) quantifies the increase or decrease of internal signal variance at the center relative to σ(per)=1. The between-subject average of σ(cen) – as estimated from model fitting – was 0.7, suggesting that eccentricity increases the variability of the internal responses.

One concern is that other models that differ in how eccentricity modulates the internal response distributions may also account for the data. Therefore, we performed a formal model comparison between the MEAN+VAR model and three other models in which eccentricity changes only the standard deviation (VAR model), only the mean value (MEAN model), or it doesn't change anything (NULL model). To determine formally which model offers the best description of the behavioral data, it is necessary to balance the model fit with model complexity. We calculated this tradeoff using the BIC. Similar results were obtained when we used the AIC. These measures provide a means for comparing models on the basis of their maximum likelihood fits to the data while correcting for potential overfitting due to model complexity (i.e., the number
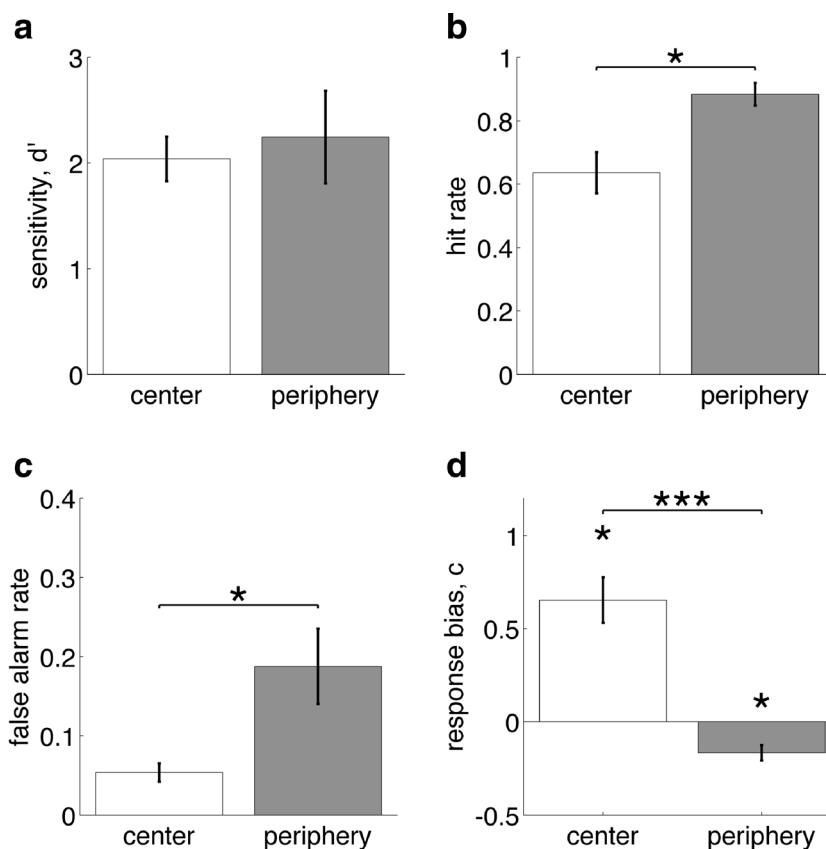
Fig. 2 Behavioral results for Experiment 1. (a) Detection sensitivity (d') was matched between central and peripheral stimuli (b-c) Participants tend to respond "yes, I see the grating" more often in the periphery than at the center for both stimulus present (hits) and stimulus absent trials (false alarms). (d) Response bias was suboptimal (c≠0) and different for central and peripheral detection being liberal (c<0) in the periphery and conservative (c>0) at the center. Solid bars indicate means and error bars S.E.M. *: $p<0.05$, ***: $p<0.001$
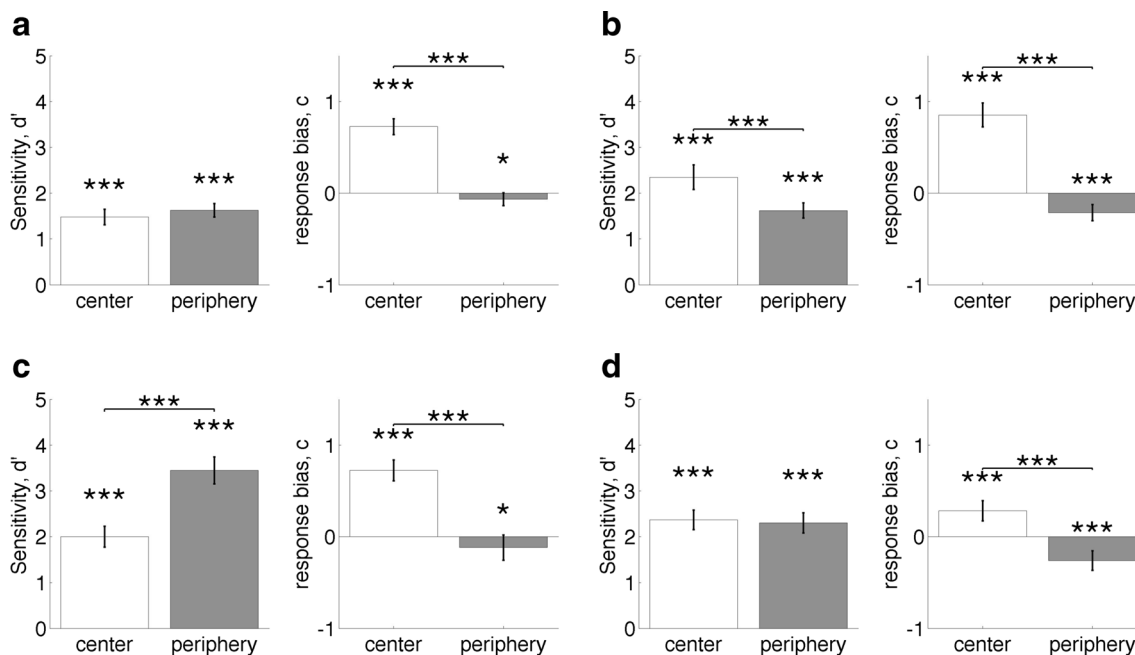
Fig. 3 Individual subject results for Experiment 1. Sensitivity (d') and response bias (c) for participants 1–4 (panels **a–d** respectively). All participants adopted a relatively conservative detection criterion in the center compared to the periphery, regardless of differences in sensitivity (subject 2 performed better in the center and subject 3 performed better in the periphery). Solid bars indicate means and error bars 95 % confidence intervals, estimated using bootstrap resampling methods (Efron & Tibshirani, 1994). *: $p<0.05$, **: $p<0.01$, ***: $p<0.001$
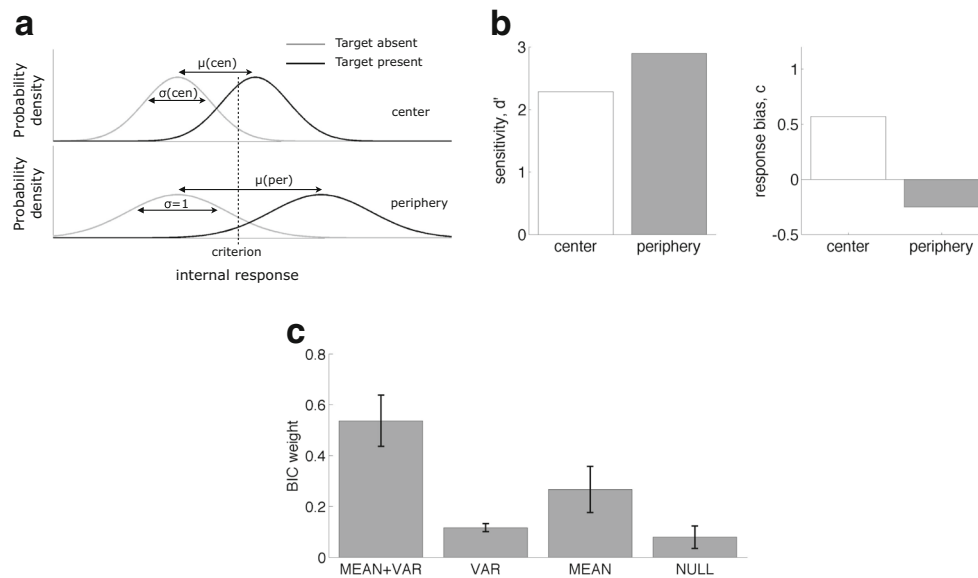
Fig 4 Model fitting results. (**a**) Representation of the MEAN+VAR model, based on Signal Detection Theory. Internal responses generated in the subject after stimulus presentation follow a Gaussian distribution. The degree of overlap between both distributions determines the observer's capacity to detect the target. According to the model, the standard deviation (SD, σ) and the distance between the means of the distributions (μ) are affected by eccentricity. If the internal response exceeds a common decision criterion in the center (periphery), the observer's answer will be "yes" if asked to report the presence of a target in the center (periphery). The distributions are plotted using the between-subject average of the parameters that maximize the likelihood of the model given the participants responses: μ(cen)=1.6; μ(per)=2.9; σ =0.7; criterion=1.2. (**b**) Model fits. The model was able to capture the pattern of the data (see Fig. 2a and c for comparison). (**c**) Formal model comparison. Bayesian

Information Criterion (BIC) weights were used to compare four models (Burnham & Anderson, 2002). We report the BIC between-subject mean weights that quantify the theoretical evidence in favor of each model such that the weights sum one. The MEAN+VAR model (eccentricity modulates the variance and the mean of the internal response distributions) fits the behavioral data better than the rest (in the MEAN model, eccentricity modulates only the mean of the internal response distribution; in the SD model eccentricity modulates only the variance, and in the NULL model eccentricity does not modulate the mean or the variance). Similar results were obtained when we used the Akaike Information Criterion (AIC). Between-subject mean AIC weights are 0.52, 0.12, 0.26, and 0.10 for the MEAN+VAR, VAR, MEAN, and NULL models respectively. For details, see Signal detection theoretic computational models and Model fitting in Method

of free parameters). We report the subject average BIC weights (Burnham & Anderson, 2002) which are obtained by a simple transformation of BIC values that quantify the theoretical evidence in favor of each model (see Method – Formal model comparison). The proposed "MEAN+VAR" model outperformed the three alternative models (Fig. 4c).

Experiment 2: Peripheral detection mimics center detection when periphery stimulus is scaled

What could be the neurobiological origin for the increased trial-by-trial variability in the periphery? It is well established that peripheral vision involves fewer cells than foveal vision: cortical magnification decreases and receptive field sizes increase with eccentricity (Azzopardi & Cowey, 1993; Daniel & Whitteridge, 1961). Given standard pooling mechanisms, the collective response of the activity of many neurons may have higher noise at the periphery, simply because it involves fewer neurons. This observation led us to a counterintuitive prediction regarding the model's possible neural implementation. If the trial-by-trial variability is determined in part by the

number of neurons recruited, we could reduce the differences in response bias between central and peripheral locations if we match their detection capacities not by titrating contrast, but by magnifying the peripheral stimulus. Moreover, our model predicts that if the variances of the central and peripheral distributions are similar, the criterion will be close to optimal. Experiment 2 was devised to test these predictions.
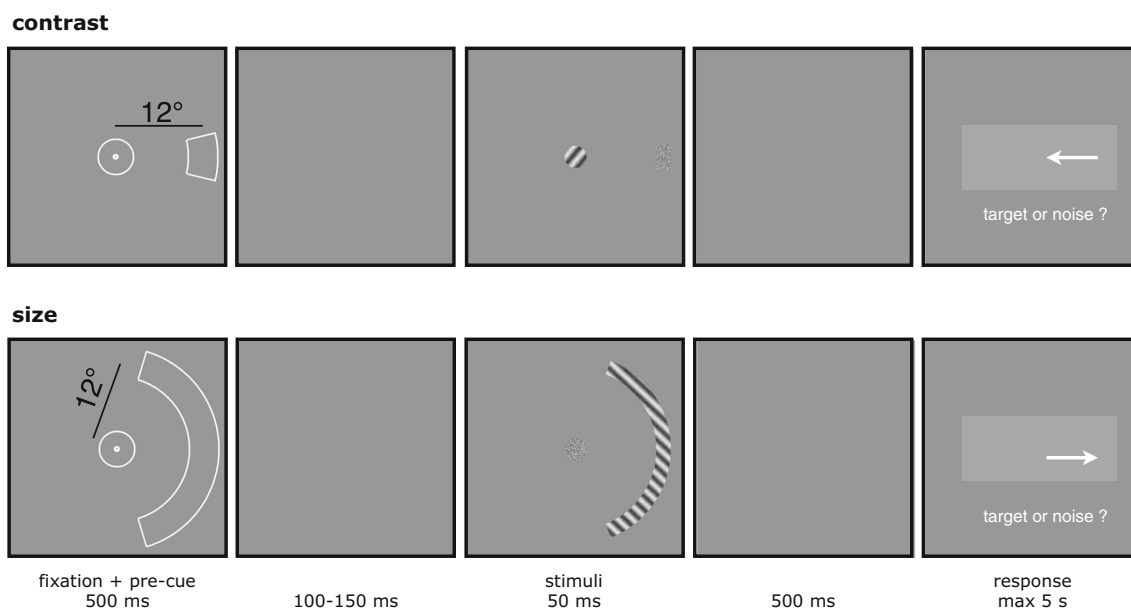
Experiment and task design

We recruited more participants (*N*=11) than in Experiment 1 but each subject performed fewer trials per condition. We therefore adopted a strict criterion to control for detection capacity. We only considered those participants whose d' at the center and at the periphery differ by less than 1 for all conditions (*N*=7). Each subject completed two experimental sessions. Each session consisted of 480 experimental trials separated into two blocks of 240 trials. The task was similar to Experiment 1 with several differences. First, there were two blocks of trials: in one block (half of the trials), the size of the central and peripheral stimuli was equal but the grating

contrast was titrated to equate sensitivity at the center and in the periphery, as in Experiment 1. In the other half, the contrast was the same at both locations, but the peripheral stimulus was eight times larger (inside an arc at equal eccentricity) than the central stimulus. We call these conditions "contrast" and "size" respectively (see Fig. 5). The order of the conditions was alternated from the first to the second experimental session and the order of conditions for the first session for each subject was chosen randomly. Second, stimulus presentation duration was reduced to 50 ms to avoid eye movements. Third, the peripheral stimulus was located towards the right, along the same horizontal line as the central stimulus. The "contrast" condition allowed us to replicate the results from Experiment 1 on a new set of participants.

Participants took approximately 80 min to complete a session. Different sessions always took place on different days. Participants completed 48 training trials at a higher grating-to-noise ratio than the actual experiment. In this case, we used the QUEST threshold determination procedure with a 2IFC task only, just as in Experiment 1, but we only used it to find the appropriate grating-to-noise ratio for the central stimuli. In the "contrast" condition, based on the experience of Experiment 1, the contrast in the periphery was defined as 1.4 times larger than at the center. In the "size" condition, the size of the peripheral stimulus was always fixed to eight times the size of the central stimulus. Overall, participants achieved equal performance at both locations using these settings (Fig. 6).
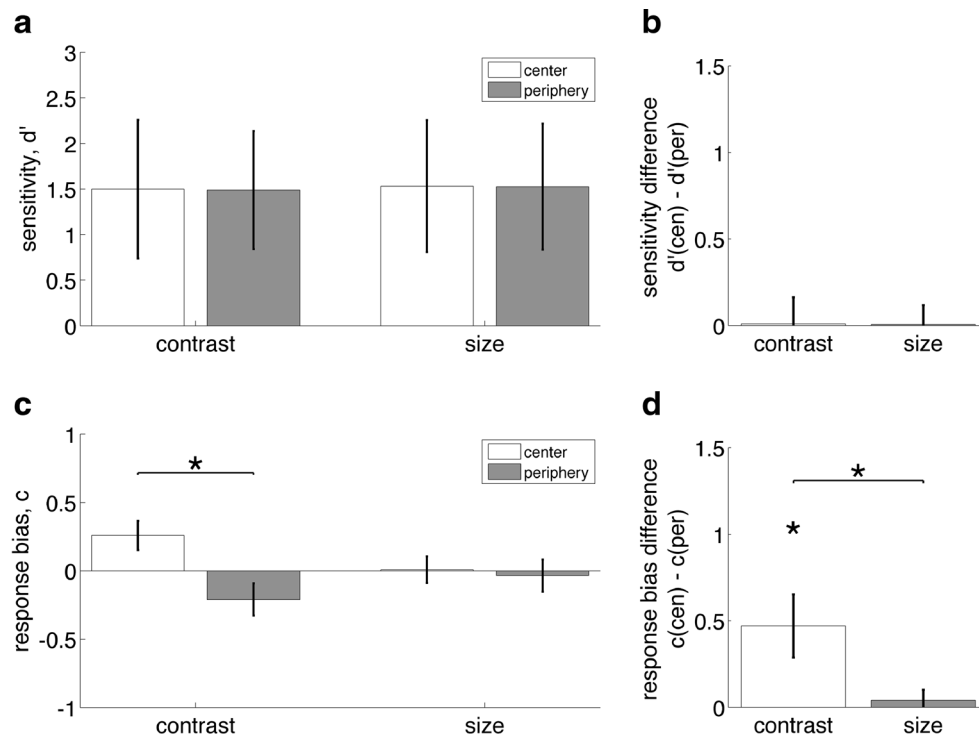
Results

In one-half of each experimental session, participants performed a detection task similar to that of Experiment 1 (Fig. 5, "contrast" condition), except that the stimulus duration was shorter (50 ms) and the peripheral stimulus was located at the same horizontal level. This half of the experiment was necessary to replicate the results of Experiment 1 with a new set of participants and slightly different experimental conditions. Indeed, as shown in Fig. 6 in the "contrast" condition, we replicated the results of Experiment 1: sensitivity was matched between the center and the periphery (paired t test: $T(12)=0.01$, $p=0.99$) and the criterion at the periphery was liberal relative to the criterion at the center (paired t test: $T(12)=2.94$, $p=0.01$). In the same experimental session, participants also performed the task in the "size" condition. As predicted, in this case, the detection bias effect disappeared completely. Participants' sensitivity was again matched for central and peripheral detection (paired t test: $T(12)=0.006$, $p=0.99$), but in this case detection criteria were statistically the same for central and peripheral trials (paired t test: $T(12)=0.28$, $p=0.78$). Moreover, as predicted, both the center and the periphery criterion approach the optimal value ($c=0$; t test, center: $T(6)=0.09$, $CI=(-0.23,0.25)$, $p=0.93$; t test, periphery: $T(6)=-0.29$, $CI=(-0.3,0.25)$, $p=0.78$). We also measured the difference in response bias at the center and at the periphery for each subject. As expected, this difference is positive in the "contrast" condition but not significantly different from zero in the "size" condition (Fig. 6d; paired t test: $T(12)=-2.23$, $CI=(-0.84, -0.01)$, $p=0.04$).

Fig. 5 Task design for Experiment 2. Each experimental session consisted of two blocks of trials in two conditions, "contrast" and "size". The conditions differ in how we calibrated central and peripheral stimuli to match detection performance at both locations. The "contrast" condition is similar to that of Experiment 1: we increased the grating-to-noise contrast of the peripheral stimuli by a constant factor of 1.4. In the "size" condition, grating-to-noise contrast was the same for both locations, but the size of the peripheral stimuli was eight times larger than the central stimuli. Both conditions led to matched sensitivity (Fig. 6). Also, compared to Experiment 1, the location of the peripheral stimuli was different (although at the same eccentricity, 12°), and the stimulus duration was shorter to facilitate fixation

Fig. 6 Results for Experiment 2. (**a-b**) Sensitivity (d') was matched for central and peripheral detection in the "contrast" and in the "size" conditions. (**c**) The "contrast" condition replicated the results for Experiment 1. In fact, participants adopted a conservative criterion (c>0) for detection of central gratings (*t* test against value zero: T(6)=2.42, CI=(−0.002,0.52), *p*=0.051) and a liberal criterion (c<0) in the periphery (*t* test against value zero: T(6)= −1.7, CI=(−0.5,0.08), *p*=0.12). In the "size" condition, response bias (c) was the same for central and peripheral detection (*t* test against zero value: center, T(6)=0.09, CI=(−0.23,0.25), *p*=0.93; periphery, T(10)= −0.29, CI=(−0.32,0.25), *p*=0.78). (**d**) In the "size" condition, the difference in response bias for central and peripheral decisions is reduced. This result is consistent with the hypothesis that making the peripheral stimuli larger recruits more neuronal resources, which, in turn, may lead to a less noisy trial-by-trial internal response. Solid bars indicate means and error bars SEM. *: *p*<0.05, **: *p*<0.01

However, 2×2 repeated measures ANOVA revealed no significant interaction between (center vs. periphery) and ("size", "contrast") (F(1,6)=3.97, *p*=0.09).

Experiment 3: The effect of trial-by-trial feedback

One remaining worry is that participants may have performed better had they had trial-by-trial feedback of their performance. That is, the differences in bias between center and periphery might just have been subjective tendency or cognitive strategy, but not an inherent constraint in the visual system. To further encourage participants to maximize accuracy, we ran Experiment 3 in which participants received trial-by-trial feedback of their performance at the periphery in one block of trials.
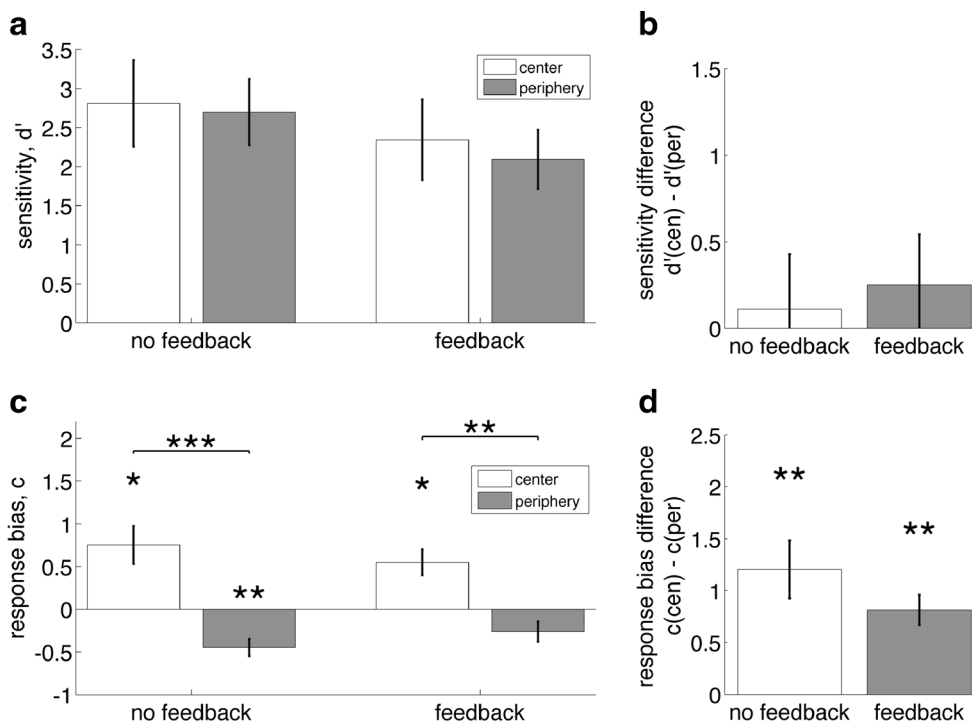
Experiment and task design

In Experiment 3 each subject completed two sessions, except for two participants who completed only the first session. Each session consisted of 480 experimental trials separated into two blocks of 240 trials. The task was similar to Experiment 2 in the "contrast" condition with a few differences. There were two

blocks of trials: one block with feedback and one without feedback. We call these conditions "feedback" and "no feedback". In both blocks, the size of the central and peripheral stimuli was equal but the grating contrast was titrated to equate sensitivity at the center and in the periphery, as in Experiment 1. In the "feedback" condition, participants received trial-by-trial feedback of their performance at the periphery: a low-pitched tone followed every incorrect response. The order of the conditions was alternated from the first to the second experimental session and the order of conditions for the first session for each subject was chosen randomly. The peripheral stimulus was located towards the right, along the same horizontal line as the central stimulus. The "no feedback" condition allowed us to replicate the results from Experiment 1 on a new set of participants. In the same experimental session, participants performed the task in the "no feedback" condition, in the remaining half of trials. The "no feedback" condition was necessary to replicate the results of Experiment 1 with a new set of participants.

Results

As shown in Fig. 7, we replicated the results of Experiment 1 in the "no feedback" condition. Sensitivity was matched

Fig 7 Behavioral results for Experiment 3: effect of trial-by-trial feedback. Task design for Experiment 3 was similar to Experiment 2 (Fig. 5) except that in both blocks of trials the stimuli had the same size. In the first block participants did not receive performance feedback (as in Experiment 1). In the second block, participants received trial-by-trial feedback of the periphery performance. (**a-b**) Sensitivity was matched in the center and periphery in both the "feedback" and the "no feedback" conditions (paired t test: T(8)= −0.1, CI=(−1.1,1.01), p=0.92) (**c-d**) Response bias for both conditions.. Essentially, trial-by-trial feedback of performance in the periphery did not have a significant effect on sensitivity or in decreasing response bias. Solid bars indicate means and error bars SEM. *: p<0.05, **: p<0.01, ***: p<0.001

between center and periphery (Fig. 7a and b; paired t test T(12)=0.16, p=0.88) while there is a significant difference in response bias (Fig. 7c and d: T(12)=4.97, p=3.10^{-4}). The addition of trial-by-trial feedback did not affect significantly sensitivity and bias. In the "feedback" condition, sensitivity was matched between center and periphery (Fig. 7a and b; paired t test T(12)=0.39, p=0.7) and response bias c differ significantly (Fig. 7c and d; paired t test T(12)=4.23, p=0.0012)

Discussion

Subjective inflation of visual perception at the periphery

Peripheral vision covers most of our visual field and provides coarse but invaluable information (Alvarez, 2011; Oliva, 2005). Despite its importance, visual information coming from the periphery is relatively coarsely analyzed in both the retina (Curcio et al., 1990) and the cortex (Azzopardi & Cowey, 1993; Daniel & Whitteridge, 1961). And yet, a long-standing and intriguing puzzle in vision science is the fact that we seem to be unaware of how poor our peripheral vision actually is. Subjectively, it feels like we can see colorful

and vivid details in the periphery, beyond the actual capacity. This is probably why we are often surprised at how difficult it is detect large changes in a visual scene (Simons & Levin, 1997), as if we overestimate our visual capacity outside the center of gaze.

We have investigated this phenomena within the framework of signal detection theory, as it allows us to formally distinguish between processing capacity (measured by d') and subjective strategy or response bias (measured by c). To summarize our results: subjects produced more hits and more false alarms in the periphery than at the center. They consciously saw the target much more often at the periphery than at the center. In fact, in Experiment 1, even though the target was present on 50 % of the trials, observers reported seeing the peripheral target in ~60 % of trials, but the central target was seen only ~40 % of trials.

A potential confounding factor is processing capacity. Maybe observers behave differently just because the quality of the information available to decode the stimulus differs. Therefore, when comparing the two conditions, we need to make sure we are comparing levels of subjective perception and not levels of processing capacity. To overcome this issue, we carefully controlled for task performance. Overall, observers performed equally well (in terms of measured d') in

the detection task at both locations. However, there was a significant difference in the subjective criterion c, which was liberal in the periphery and conservative at the center. Moreover, even if we consider only target absent trials where the physical stimuli were identical, observers produced significantly more false alarms in the periphery than at the center. These results were successfully replicated in Experiments 2 and 3 and thus confirmed our prediction that subjective perception is inflated at the periphery.

We argue that these results may intrinsically reflect the perceptual experience of peripheral vision, because they were robustly replicated even under trial-by-trial feedback, ruling out the alternative interpretation that this may just reflect a kind of high-level cognitive strategy or deliberate bias adopted by the participants.

Similarities between peripheral vision and inattention

We have previously found similar results in a study in which participants were asked to detect attended and unattended stimuli. Participants adopted a liberal response bias for detecting unattended targets (*i.e.* their propensity to report detecting a target is higher in unattended than in attended trials). Therefore, peripheral vision and inattention seem to suffer from a similar kind of subjective inflation at the perceptual level. In the case of attention, the behavioral results were successfully accounted for with a mechanistic model within the framework of signal detection theory. Here we show that the same model can account for our current findings. Most importantly, we found that the trial-by-trial variability of the internal responses was larger in the periphery than at the center. Therefore, assuming that participants used a single common decision criterion for detecting central and peripheral stimuli, the subjective threshold was surpassed more frequently for peripheral trials.

Beyond the psychophysical similarities, recent works also relate the neurobiology underlying visual inattention to peripheral vision. For example, it has been shown that the peak frequency of neuronal gamma-band synchronization increases when the stimuli that activates the neurons is attended as compared to unattended (Bosman et al., 2012). Likewise, other studies have shown that stimuli induced lower gamma peak frequencies for larger eccentricities (Lima, Singer, Chen, & Neuenschwander 2010; van Pelt & Fries, 2013).

Given the similarities between attention and central vision, one may wonder what is truly novel in the present work? That is, given that Rahnev et al. (2011) have already demonstrated that detection bias was relatively liberal for a spatial location outside the focus of endogenous attention, is it not trivial that peripheral vision is also associated with liberal detection bias? Is it not natural to assume that central vision just naturally attracts more endogenous attention? We think the answers are negative for several reasons. First, there are many kinds of

attention – endogenous, exogenous, spatial, feature, etc. – and it has been shown that there are important differences between them (Bisley, 2011; Carrasco, 2011; Scholl, 2001). Generalization of any experimental effect from one kind of attention to another is not trivial to begin with, let alone generalization from inattention to peripheral vision. More importantly, for endogenous spatial attention, one standard paradigm used is the Posner task (Posner, 1980), in which the likely location of stimulus occurrence is pre-cued. However, in Rahnev et al. (2011), the pre-cue did *not* inform subjects of the likely location of the stimulus. In fact, the pre-cue did not give any information regarding the upcoming stimuli. Rather, the pre-cue concerns the *task* that the subject will have to do,;specifically, to which stimulus they will have to respond. In this sense, "attention" in Rahnev et al. was defined entirely in terms of task relevance (Summerfield & Egner, 2009). In this study, "attention", defined in the same sense, was completely equal between the center and the periphery, thus one cannot say that central vision inherently draws more "attention"; this may be true in some other sense of the word but not in terms of the definition of attention used in Rahnev et al.; for task relevance both the center and the periphery were equally likely to be probed. Finally, we believe that the reason why peripheral vision is associated with higher variability of the internal response may be quite different from that under inattention. Whereas both peripheral vision and inattention in Rahnev et al.'s task may be associated with high variability, and hence liberal detection, the underlying physiological mechanisms for the variability in the peripheral vision case may be unique, as we discuss below.

Potential source of the increased variability in the peripheral internal response

Why is the internal response more variable in the periphery? We argue that part of the reason might be the reduced neuronal resources allocated to processing peripheral information. The receptive fields of neurons are larger in the periphery and the cortical magnification factor decreases with eccentricity, i.e., the central visual field is overrepresented relative to the periphery. Overall, these observations imply that fewer neurons, with larger spatial uncertainty, deal with peripheral vision. Since perceptual decisions are based on the collective response of many neurons, we can see how fewer neurons lead to more unstable or variable results. Recent work suggests that peripheral vision consists of summary statistics computed over local pooling regions (Balas, Nakano, & Rosenholtz 2009; Levi, 2008; Parkes, Lund, Angelucci, Solomon, & Morgan 2001; Pelli & Tillman, 2008). Also, several studies have shown that the decrease in performance with eccentricity for many visual functions can be minimized using properly scaled stimuli, a procedure called M-scaling (Anstis, 1998; Carrasco & Frieder, 1997; Strasburger et al., 2011; Virsu,

Näsänen, & Osmoviita 1987). The explicit purpose of M-scaling is to equalize the number of retinal ganglion cells and post-retinal cells stimulated at different eccentricities (Virsu et al., 1987). Based on this evidence, we hypothesized that if the peripheral stimuli were larger than the central stimuli, the underlying internal responses for the two may be matched in variability. In that case, even if participants are limited to using a common criterion, they would be able to calibrate its value close to a global optimum, maximizing accuracy in the detection task. This prediction was successfully confirmed in Experiment 2. The peripheral liberal detection bias disappeared completely under this "size" condition manipulation, even though in the same experiment we demonstrated the presence of this bias in the "contrast" condition in the same participants.

Limitations of the model

One limitation of our study is that the underlying neuronal mechanism we used to account for the larger variability in peripheral vision is highly simplistic. In reality, neurons may have a specific correlation structure (Cafaro & Rieke, 2010) that we have not taken into account here. Also, the pooling mechanism takes the form of simple averaging, which is unlikely to be exactly true. However, we believe the model serves as a proof of the simple concept behind it. That is, while the model may not be a fully realistic description of how periphery vision and perceptual readout work in general, it provides a simple mechanistic explanation of the phenomenon we are concerned with in this project.

Likewise, another assumption of the model is also probably overly simple: that participants use the exact same criterion for detection in both the center and the periphery. This assumption is supported by previous empirical work using similar experimental designs (Gorea & Sagi, 2000; Rahnev et al., 2011; Zak et al., 2012). We also note that, in another recent project, we directly tested this common criterion assumption between attended and unattended targets (Lau & Rahnev, 2011; Morales et al., 2014). In that study, we set up a situation in which if participants were to be constrained by this common criterion assumption, they would produce apparently highly suboptimal behavior, such as ignoring prior information about stimulus identity, under lack of spatial attention. The confirmation of such predictions gave some support to the assumption of a common criterion.

However, perhaps a more realistic view is that the two criteria attract each other to settle at a similar level (Zak et al., 2012), rather than being completely constrained to be identical; the identity assumption should be considered a computational convenience for implementation of the model. We have investigated this possibility elsewhere (Morales et al., 2014). Second, perhaps perceptual decisions are made not in an arbitrary internal evidence space (as assumed here), but in likelihood space (Eckstein, Peterson, Pham, & Droll 2009; Ma, 2010), where criteria are independently and appropriately placed. Future work that specifies these mechanisms will likely lead to more biologically realistic models.

Finally, a remaining important issue about the common criterion assumption is that it means the relative difference in detection bias may be specific to tasks in which the subjects have to simultaneously prepare for detection in two separate locations. Had the central and peripheral trials been blocked separately in different experimental sessions, subjects may well adopt different criteria for each block; whereas this is an empirical issue that we have not addressed, based on our model we would indeed expect results very different from the present ones as the common criterion assumption only stipulates that one cannot maintain multiple criteria *simultaneously*. However, we believe that this should not mean our results are contrived and entirely ad hoc with respect to the model. In everyday life, humans have to monitor for potential detection targets more often in multiple locations than in a single fixed and known location. In this sense, the requirement to simultaneously prepare for detection in separate locations may well be more ecologically relevant, despite its being relatively uncommon in most psychophysical tasks.

Final remarks

We acknowledge that there are other factors that contribute to subjective inflation of visual perception in the periphery. Here we focus on gratings detection but perhaps in everyday life the subjective inflation is more striking in the domain of color perception – a different topic that we have to save for future research. Also, as naturalistic stimuli are not completely unpredictable in structure, top-down filling-in of information would certainly play a role. However, in our psychophysics experiments this factor is unlikely to be at play, because the stimuli cannot be statistically predicted. Yet, we identify a decisional mechanism for bias in the periphery. Therefore, we argue that even in everyday peripheral vision, the decision mechanism may be relevant too, which is a fact that has been relatively neglected in previous research (for an example of an exception see Zhang, Morvan, & Maloney 2010). Overall, it is striking that despite the simplicity of our model, the observed result is mechanistically accounted for.

It has also been argued that the reason why we are usually unaware of the limitations of peripheral vision is that our brain appreciates the fact that we move our eyes (for example, see Boucart, Moroni, Thibaut, Szaffarczyk, & Greene 2013). In this sense, the subjective impression of a uniform visual field is an illusion, but of a useful kind. O'Regan (1992) argues that "the outside world is considered a form of ever present external memory that can be sampled at leisure via eye movements" However, at least introspectively, even when taking a single quick glance at a new scene, the perception of a detailed

periphery is still present. Our results are consistent with this idea because subjective inflation was present even when we carefully controlled for gaze fixation and the stimuli were presented as briefly as for 50 ms.

The reported mechanism of subjective inflation here may also speak to recent debates regarding the richness of our conscious perception. Whereas some authors speculate that the content of our conscious percept may be richer than what we can access, i.e., to report or to remember (Block, 2011; Lamme, 2010), others argue that this may not be so (Cohen & Dennett, 2011; Dehaene & Changeux, 2011; Kouider, de Gardelle, Sackur, & Dupoux 2010). This debate has somewhat led to an impasse: how can we assess the richness of information that we cannot report or remember? Whereas this may seem experimentally impossible to demonstrate, some authors feel that given that we can only access a few visual items at a time, it seems introspectively implausible that our conscious percept is so impoverished. Our results here may offer a partial resolution to this problem (Lau & Rosenthal, 2011). We need to distinguish between two senses of "seeing", one in terms of capacity, and one in terms of decision. Perhaps outside of central vision, we overestimate the richness of information at a late-stage, decisional level. This may explain the intuition behind the arguments that we can consciously perceive more than we can access. Perhaps we do not perceive more than we can access, we merely *think* we do because of this decisional inflation. As to whether this "thinking" contributes to our conscious phenomenology, this is discussed elsewhere in the context of philosophical theories of consciousness (Lau & Rosenthal, 2011).

In summary, peripheral vision contributes coarse but invaluable information. How the brain represents peripheral information and why we are not consciously aware of its larger limitations remain matters for further investigation. Here we speculate that subjective inflation of perception in the periphery may be a natural and unavoidable consequence, due to the structure of peripheral vision processing and limitations in our perceptual decision mechanism. At least in the case of our study, it seems that peripheral vision, being processed by fewer neurons, produces more variable responses. In turn, variable responses trigger subjective detection more often, in a potentially natural implementation of stochastic resonance (McDonnell & Abbott, 2009; Simonotto et al., 1997).

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