Collinear features impair visual detection by rats

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We measure rats' ability to detect an oriented visual target grating located between two flanking stimuli ("flankers"). Flankers varied in contrast, orientation, angular position, and sign. Rats are impaired at detecting visual targets with collinear flankers, compared to configurations where flankers differ from the target in orientation or angular position. In particular, rats are more likely to miss the target when flankers are collinear. The same impairment is found even when the flanker luminance was sign-reversed relative to the target. These findings suggest that contour alignment alters visual processing in rats, despite their lack of orientation columns in the visual cortex. This is the first report that the arrangement of visual features relative to each other affects visual behavior in rats. To provide a conceptual framework for our findings, we relate our stimuli to a contrast normalization model of early visual processing. We suggest a pattern-sensitive generalization of the model that could account for a collinear deficit. These experiments were performed using a novel method for automated high-throughput training and testing of visual behavior in rodents.

Keywords: contrast gain, detection/discrimination, learning, collinear, spatial vision, visual cognition

Citation: Meier, P., Flister, E., & Reinagel, P. (2011). Collinear features impair visual detection by rats. *Journal of Vision, 11*(3):22, 1–16, http://www.journalofvision.org/content/11/3/22, doi:10.1167/11.3.22.

Introduction

In this study, we consider a classic task of visual psychophysics, the discrimination between the presence and absence of a visual target at a known location. Human perception of oriented targets is influenced by the contrast, spatial frequency, and orientation of nearby stimuli, both in contrast discrimination tasks (Ejima & Takahashi, 1985; Xing & Heeger, 2001) and target detection tasks (Chen & Tyler, 2008; Polat & Sagi, 1993, 2007; Solomon & Morgan, 2000; Williams & Hess, 1998; Zenger & Sagi, 1996). This influence is typically largest when the surrounding stimuli match the orientation and spatial frequency of the target, both for annuli that completely surround a target and for discrete flankers (Cannon & Fullenkamp, 1996; Chubb, Sperling, & Solomon, 1989; Polat & Sagi, 1993). The influence of stimulus arrangement and phase is more variable and subject to experimental paradigms. The behavioral influence of flanking stimuli has occasionally been studied in non-human primates (Li, Piech, & Gilbert, 2006) but never in rodents.

The psychophysical effect of flankers may be caused by surround processing in visual neurons, whereby features outside of the classical receptive field modulate neural responses (Angelucci et al., 2002; Chisum & Fitzpatrick, 2004). The amplitude of neural responses in the retina, thalamus, and visual cortex are normalized to spatially nearby contrast (Carandini, Heeger, & Movshon, 1997; Heeger, 1992; Shapley & Victor, 1979), likely due to lateral connectivity at each level. In many cases, oriented stimuli in the surround suppress activity and suppress most when surround orientation matches the driving stimulus (Bonds, 1989; Cavanaugh, Bair, & Movshon, 2002; Polat, Mizobe, Pettet, Kasamatsu, & Norcia, 1998). However, some cells in the appropriate contrast conditions increase their spiking activity when the orientation of stimuli in the surround matches the driving stimulus (Li et al., 2006; Polat et al., 1998; Sillito, Cudeiro, & Murphy, 1993). In many physiology experiments, oriented surround stimuli are presented in an annulus. However, physiological surround effects can depend on the angular position of the flanker with respect to the target orientation, specifically influencing geometric arrangements like collinearity (Cavanaugh et al., 2002; Polat et al., 1998). Cortical circuits are likely to be involved in orientation-specific surround processing (Chisum, Mooser, & Fitzpatrick, 2003; Das & Gilbert, 1999; Gilbert & Wiesel, 1989). It remains unknown if the orientation-selective circuits described in cats and primates are also found in rats. Rodents have orientation-tuned cells in V1 but lack orientation columns (Ohki, Chung, Ch'ng, Kara, & Reid, 2005; Van Hooser, Heimel, Chung, & Nelson, 2006).

doi: 10.1167/11.3.22 Received December 7, 2010; published March 30, 2011 ISSN 1534-7362 © ARVO

From a theoretical perspective, there are several reasons it would be advantageous for representations of local features to be sensitive to nearby image context (Series, Lorenceau, & Fregnac, 2003). In natural scenes, local image features such as luminance, contrast, and orientation are correlated at nearby locations (Field, 1987; Geisler, 2008; Ruderman & Bialek, 1994). When features are spatially correlated, surround processing can optimize the fidelity or efficiency of image estimation (Barlow, 2001; Geisler, 2008). For example, divisive normalization from a nearby population of cells (Heeger, 1992) can allow a neuron to better adapt its sensitivity, reduce redundancy with its neighbors, and thus maximize information transfer (Schwartz & Simoncelli, 2001). Surround processing could also enhance salience of relevant features such as continuous contours (Field, Hayes, & Hess, 1993; Geisler, Perry, Super, & Gallogly, 2001; Sigman, Cecchi, Gilbert, & Magnasco, 2001) or statistically surprising features (Itti & Koch, 2000). These theories and others predict that different patterns in the surround should have distinct influences on a visual target's neuronal representation, even if lower order statistics like luminance and contrast are matched.

In the interest of developing a rodent model for the study of surround processing, we trained rats to report the presence or absence of an oriented target when sandwiched between two flanking stimuli. Rats have previously been trained on visual tasks including grating detection (Birch & Jacobs, 1979; Keller, Strasburger, Cerutti, & Sabel, 2000), motion discrimination (Douglas, Neve, Quittenbaum, Alam, & Prusky, 2006), orientation discrimination (Cowey & Franzini, 1979), and object recognition (Bussey et al., 2008; Minini & Jeffery, 2006; Zoccolan, Oertelt, DiCarlo, & Cox, 2009) but never on tasks with flanking stimuli. The presence of flankers made the task difficult for rats, presumably for both cognitive and perceptual reasons. In this study, we are interested in the differential effects of the arrangement of flankers when they are present. The flankers' contrast, size, and separation were held constant, while we varied their orientation, angular position, and sign in randomly interleaved trials. We ask if rats' detection performance is sensitive to the relative orientation, position, and sign with respect to the target. We report an effect specific to collinear arrangements irrespective of sign.

Results

Rats can report the presence of a small oriented grating in the presence of flankers

We developed an automated method to train rats to perform two-alternative forced-choice (2AFC) visual tasks (see Training protocol section). We trained 7 male Long–Evans rats to detect an oriented grating target. The target was presented in the middle of a CRT display, and subjects were required to select one of two response ports to indicate that the target was either present or absent (Figures 1a and 1b; photograph in Supplementary Figure S1).

The orientation of the target was tilted either clockwise or counterclockwise from vertical by a fixed angle; orientation was randomly chosen on each trial. Rats advanced automatically through a series of training steps that decreased target contrast, reduced its size, and increased its spatial frequency (Figures 1c and 1d, steps 5–8). After rats learned the basic detection task in the absence of flankers, a brief testing period assessed the influence of the target's contrast and spatial frequency was tested on a subset of the trained rats (Supplementary Figures S4a and S4c). This identified suitable parameters (see Supplementary Data 1) for the subsequent more difficult task involving distracting flankers.

Next, we added two "flanking" gratings on either side of the target location (Figures 1b and 1d, steps 9–10). The target was absent on 50% of trials. Flankers were absent on 5% of the trials. During testing (step 10), flanker contrast was fixed at 40% and spatial parameters of the stimuli were independently varied (θ_T, θ_F, ω, S_T, and S_F, as described in Figure 3). Rats learned to perform target detection even in the presence of distracting flankers (Supplementary Movie). We collected >20,000 trials per rat over 2–5 months of the testing step, which are further analyzed and summarized in Figures 4 and 5 and Supplementary Figures S3 and S5– S7. Throughout the testing step, performance on trials with flankers remained well above chance (e.g., step 10 in Figure 1c). Performance was stable over the period of data collection used for analysis (see Experimental procedures section).

The presence of flankers made the task substantially more difficult for rats (Supplementary Figure S3). This effect is significant for 7 of 7 rats individually (Agresti–Caffo 95% confidence interval) and the population as a whole ($p < 0.01$ on 2-way ANOVA; $p < 0.01$ on Friedman's test). Presumably, this is due to both cognitive and perceptual factors, which we have not disambiguated here but are considered elsewhere (Meier, 2010). A perceptual effect on detection could arise from spatial contrast normalization, a form of surround processing long observed in other mammals (see Introduction section). Flankers add contrast to the target's surround, which could lower the target's effective contrast through contrast normalization. We verified that lower target contrast impairs detection as expected (Supplementary Figure S4c), so detection should be sensitive to reduction in effective contrast. Flankers of higher contrast or closer proximity to the target should exert stronger contrast normalization, further reduce effective target contrast, and lead to larger impairments. Additional tests on a subset of rats confirmed both predictions (Supplementary Figures S4b and S4d). Thus, our task is a promising candidate for revealing effects that might depend on contrast normalization.

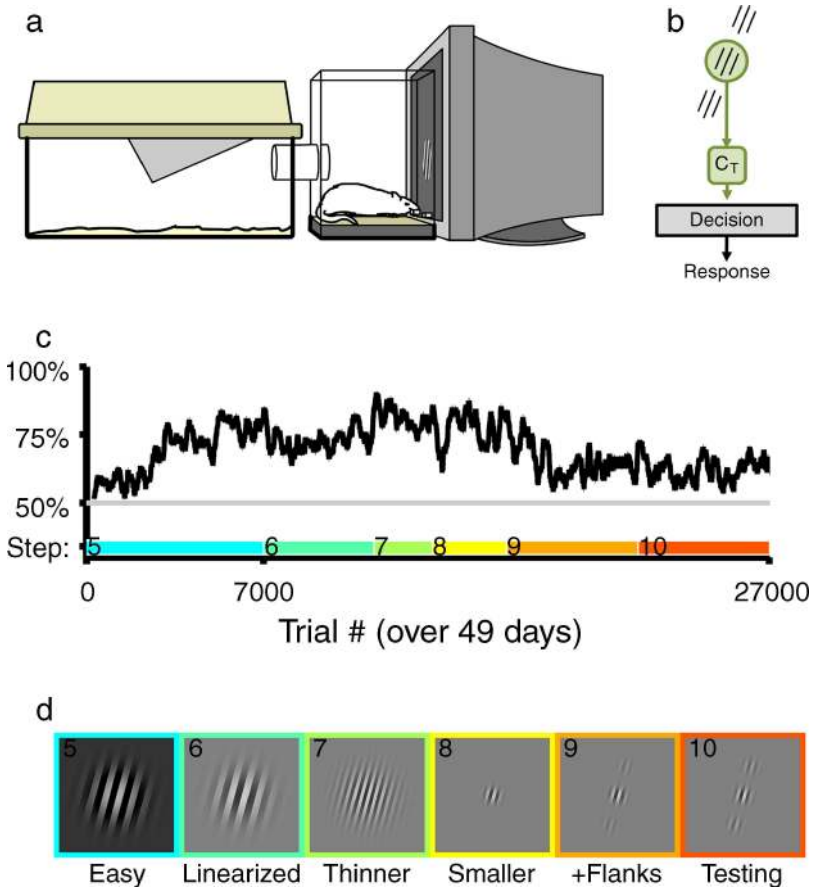

Figure 1. Training rats to detect an oriented target in the presence of flanking distracters. (a) A diagram of the training environment. Rats could initiate trials by licking a sensor centered in front of the display monitor. This immediately rendered a stimulus. Rats were rewarded with water for correctly reporting the presence or absence of a target by licking one of two response spigots located on the left or right side of the chamber. (b) A simple schematic indicating the final task the rat is being shaped to perform. The target location is denoted by a green circle. The target is present on 50% of the trials; the target contrast, C_T, is either 0 or 1. The target's presence, irrespective of the flanker configuration, informs the rat which decision will result in a water reward. (c) To achieve the final task that has small, low-contrast targets and distracting flankers, rats are shaped through a sequence of training steps that increase in difficulty. Performance for a single rat is plotted as a 200-trial running average, starting from the first easy visual trials (step 5) to the testing phase (step 10). The first four steps involved associating the response ports with rewards and did not involve any visual stimuli (see Supplementary Table S1 for details). When the rat's performance exceeded a preset criterion (>85% correct), he was automatically graduated to a new training step to ensure rapid progression and avoid over learning. (d) Sample stimuli from each step are color-coded to match the performance plot and named to emphasize the change from the previous training step. The addition of dim flankers (step 9) is displayed for a linearized contrast of 20% in (b) but was increased from 10% up to 30% in step 9. All testing was performed with 40% linearized flanker contrast. For simplicity, only one of the two orientations is shown, but all rats had equal training exposure to both. For more testing stimuli, see Figure 3. For a photograph of a rat performing the final task, see Supplementary Figure S1.

As indicated in the schematic of Figure 1b, the rat's decision and response in our task obviously depends on contrast at the target location. A more complete schematic (Figure 2) indicates that rats' decisions are also influenced by the presence of flankers. A contrast normalization component is indicated on the basis of past literature and in consistency with the data summarized above. The presence of flankers also affects performance for uncharacterized cognitive reasons, such as task confusion and compensating strategies. If performance is insensitive to the position and orientation of the flankers, a simple model like this would be sufficient.

Collinear flankers impair detection more than other arrangements

We next considered how performance depended on the arrangement of the flankers with respect to the target. There were two possible target orientations, as during training. Flankers always shared the same orientation and sign as one another and were located symmetrically on either side of the target location on an imaginary line tilted either clockwise or counterclockwise (Figure 3a). The target orientation ($\pm\theta_T$), flanker orientation ($\pm\theta_F$), and angular position of the flankers ($\pm\omega$) were chosen independently

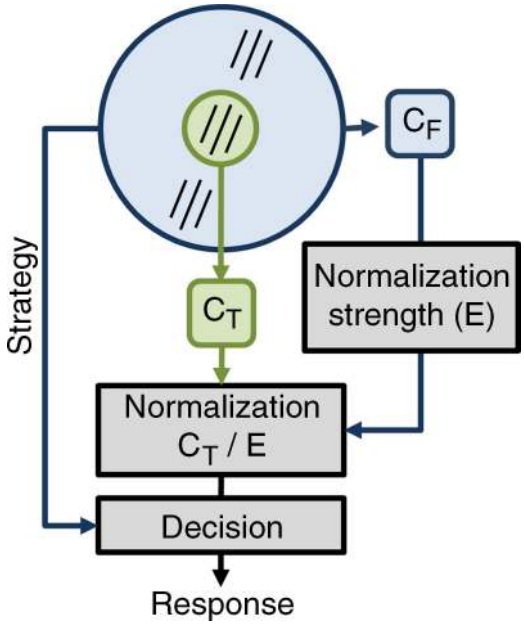

Figure 2. A schematic model indicating how the presence of flankers might influence rat's decisions. On this model, the contrast of the flankers (C_F) contributes to the normalization strength (E) such that the effective contrast of the target is reduced. The presence of spatial contrast normalization probably contributes to the deficits in performance associated with the presence of flankers. The presence of flankers also influences performance for cognitive reasons ("strategy"). This model is blind to orientation and position of flankers.

each trial for a total of 8 randomly interleaved stimulus configurations (Figure 3b). The luminance signs of both target and flanker gratings ($\pm S_T$, $\pm S_F$) were also randomized for each trial.

We use the term "collinear" to refer to stimulus configurations in which the target and flanker orientations are both aligned with the flanker angular position ($\theta_T = \theta_F = \omega$), irrespective of the relative sign. This configuration could engage visual processing that relates line segments that fall along a common contour. We label non-collinear conditions as follows: "popout$_1$" ($\theta_T = -\theta_F = \omega$), "popout$_2$" ($-\theta_T = \theta_F = \omega$), and "parallel" ($\theta_T = \theta_F = -\omega$). For examples, see Figure 3.

The main finding of our study is that the collinear condition is consistently harder for rats than any of the other three configurations (Figures 4a and 4b). This difference was true for each rat and significant at the population level even when adjusting for multiple comparisons ($p < 0.01$ by Tukey–Kramer on 2-way ANOVA for all three comparisons; two of these comparisons were also significant by the more conservative Tukey–Kramer on Friedman $p < 0.01$; see Supplementary Data 3 and Supplementary Figure S6). The other three conditions were not significantly different from one another (Supplementary Figures S5 and S6). In short, of all the flanker conditions tested, only the collinear condition was consistently most difficult.

All stimulus arrangements had the same flanker contrast and distance, so this difference cannot be explained by simple contrast normalization as illustrated in Figure 2. We consider next how the contrast normalization framework

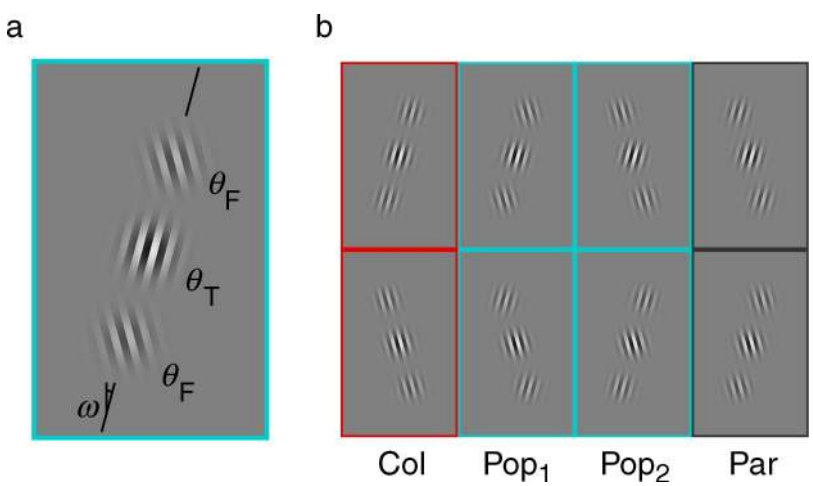

Figure 3. Grouping flanker stimuli into conditions. (a) A sample flanker stimulus, with labeled spatial parameters (θ_T, θ_F, ω). Flanker stimuli were generated by independently varying target orientation (θ_T), flanker orientation (θ_F), and the angular position of the flankers (ω). The two flankers always had the same orientation. (b) The different stimuli were grouped in four conditions that preserved geometric relationships. The top and bottom rows are mirror images of one another. In the collinear condition, the target and flanker orientations align with the angular position ($\theta_T = \theta_F = \omega$). Collinearity was disrupted by changing one of the parameters in each of the remaining flanker conditions: "popout$_1$" ($\theta_T = -\theta_F = \omega$), "popout$_2$" ($-\theta_T = \theta_F = \omega$), and "parallel" ($\theta_T = \theta_F = -\omega$). Each condition was equally likely during the testing. Every stimulus has a matching case in which the target was absent (not shown here, but see Supplementary Figure S2b). During all training and testing, the luminance sign of the target and flankers were randomized; the case of $S_T = S_F = +1$ is shown.

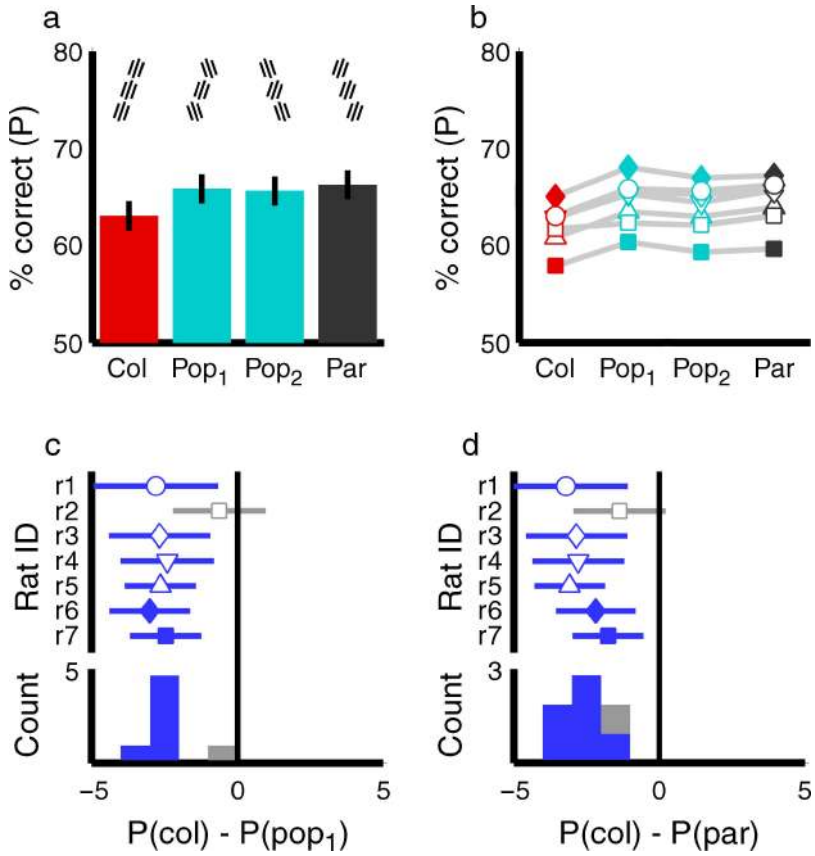

Figure 4. Collinear flankers impair detection more than other arrangements. (a) A single rat's performance (r1) on the four conditions: collinear and three patterns that disrupted collinearity. In popout$_1$, collinearity was disrupted by changing the flanker orientation (θ_F) to be different from the target(θ_T). Popout$_2$ maintained the same difference in flanker and target orientations ($|\theta_F - \theta_T|$) as popout$_1$, but the angular position of the flanker was different (ω). In the parallel condition, the collinearity was disrupted only by changing the angular position of the flanker. Error bars indicate 95% binomial confidence intervals. (b) Performance of all seven rats on all four conditions. (c) The difference in percent correct between collinear and popout$_1$ for all rats (r1–r7). Collinear is more difficult. Error bars indicate 95% confidence interval using a modified Wald interval described in methods (Agresti & Caffo, 2000). One rat's data are rendered gray to indicate that the difference in performance is not significant. The other six rats are rendered blue because they are each significant(Agresti–Caffo 95% confidence interval). Filled symbols indicate subjects in which the mapping between yes–no and left–right was inverted (see Training protocol section). Subjects with inverted training rules had no different effects. (d) The difference in percent correct between collinear and parallel. Again collinear is harder. For both comparisons ((c) and (d)), the difference between conditions is significant for six of seven rats individually (Agresti–Caffo 95% confidence interval) and for the population as a whole (2-way ANOVA with Tukey's, $p < 0.01$). For all possible pairwise comparisons, see Supplementary Figure S5.

could be extended to account for a collinear deficit at the level of early visual processing. The collinear flanker condition differs from the popout$_1$ condition only by flanker orientation, so the difference in performance (Figure 4c) suggests orientation-sensitive surround processing. This could be explained by a simple modification of the model in Figure 2, such that the strength of contrast normalization (E) is stronger when the contrast in the surround shares the target's orientation. Such a model could account for our result that the collinear flanker condition was harder than either popout condition, but could not explain why performance in the parallel condition was significantly better than collinear (Figure 4d), and indistinguishable from either popout (Supplementary Figure S5). Our data cannot be explained by simple orientation-dependent effect or by an angular position effect alone. Feature arrangement is important: flanker orientation and angular position interact. To capture differences between flanker conditions within the perceptual component of the model, it would be necessary to add a pattern-sensitive term (see Discussion section and Figure 6).

Flankers that are collinear to the target either had the same luminance sign ($S_F = S_T$), such that white bars of the target align with white bars of the flankers, or opposite signs, such that white bars align with black bars ($-S_F = S_T$). A reversal in sign is equivalent to a π shift in spatial phase. We could find no effect on performance of the relative or absolute luminance sign of the flanker and

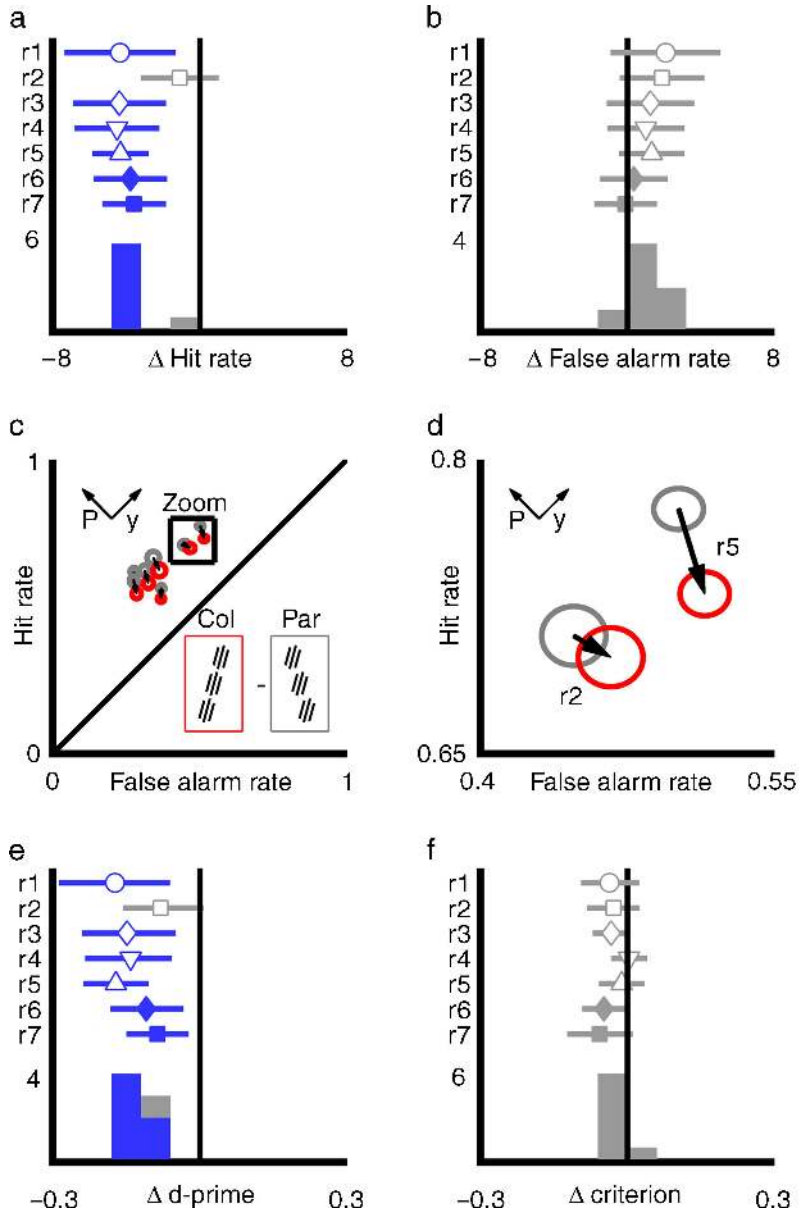

Figure 5. Collinear flankers cause rats to miss target. (a) The change in hit rate between collinear and parallel configurations, h(col) − h(par). Symbols left of the zero line indicate that the hit rate is lower when flankers are collinear. The effect is shown for each subject: the symbol location indicates mean difference in hit rate; horizontal lines indicate 95% confidence interval(Agresti & Caffo, 2000). For all but one rat, the deficit with flankers is statistically significant. (b) The change in false alarm rate, f(col) − f(par), using the same conventions as (a). Rats display more false alarms on the collinear stimuli. However, the change in false alarms was smaller than the change in hit rate shown in (a). (c) A geometric representation of the raw data in (a) and (b) is shown by plotting the Receiver Operator Characteristics (ROCs). The individual ellipses show the boundary of the 95% confidence intervals of a binomial distribution for hit rate and false alarm rate for one subject and condition. For each subject, an arrow in ROC space summarizes the difference between the collinear condition (red) and randomly interleaved trials of the non-collinear reference condition (parallel, gray). The arrow points to the change in responses induced by the collinear feature with respect to the reference condition. Most arrows consistently point down and to the right indicating a decrease in hits and a small increase in false alarms. (d) Detail of (c) to provide better resolution for a typical rat (r5) and an outlier rat (r2). Interestingly, histology (not shown) revealed that the rat displaying the outlier effect (r2) had a naturally occurring tumor that compressed and displaced about a quarter of the ventral thalamus. We do not know if this played a role in the animal's behavioral differences. (e) The difference in detection sensitivity between collinear and parallel conditions. Error bars are the 95% confidence intervals of samples drawn from a Monte Carlo Markov Chain. These d' measurements are consistent with the report in Figure 4d: collinear stimuli have targets that are harder to detect. (f) The change in criterion between collinear and parallel conditions. Negative values indicate that rats are more likely to report the absence of the target in the collinear condition. The change in bias is consistent for all rats but not significant for any individual rat (MCMC 95% confidence interval). The size of the bias difference is small compared to the change in d' shown in (e).

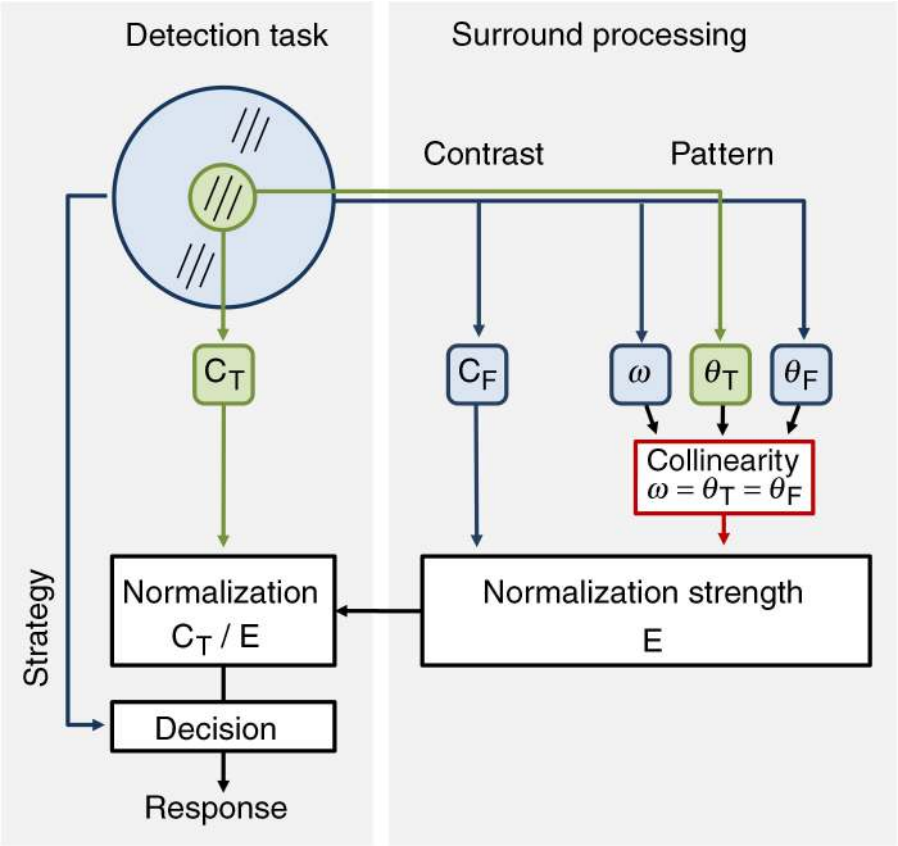

Figure 6. Schematic model of pattern-sensitive contrast normalization. The detection task is summarized in the left-hand region, unchanged from Figure 2. The contrast in the target region (C_T) is represented by a neural signal that is normalized by surround processing in early vision before the decision is made. Then, the rat responds left or right to indicate the target's presence or absence. In this model, cognitive effects of the surround ("strategy") depend only on the presence of flankers and insensitive to their configuration. Surround processing contains two aspects: sensitivity to contrast and sensitivity to pattern. In this study, surround contrast is determined by the experimental parameter for flanker contrast (C_F, same as Figure 2) and was held constant during testing. The pattern-sensitive component must include at least three terms to account for our data: the angular position of the flanker (ω), the orientation of the target (θ_T), and the orientation of the flanker(θ_F). While there are many ways that these terms could interact, we only require a dependence of collinearity to explain the rat's behavior. The processing of contrast and pattern in the surround is combined into a single normalization term (E). This determines the gain of the neural signal that is used for detection. An argument that the normalization term E could be interpreted as an expected contrast ($\hat{C}_T$) is considered in the Discussion section.

target gratings. In particular, whether the dark bars in the target aligned with the dark or light bars in the flankers, the specific impairment for the collinear configuration relative to other arrangements remained, and the amplitude of the effect was indistinguishable ($p > 0.05$, 2-way ANOVA; $p > 0.05$, Friedman's test; Supplementary Figure S7). In a pilot study, intermediate phase shifts also had no effect in a related task (Supplementary Figure S7). Therefore, we do not include phase as a parameter in Figure 6.

The arrangement of nearby features has been shown to affect behavior and early visual processing in other species (see Introduction section). This is the first demonstration of pattern sensitivity in a rodent, showing that such effects can occur even in species that lack orientation columns. This is also the first flanker study in any species in which both orientation and position were randomized in a single interleaved testing period, confirming that neither a position effect nor an orientation effect is sufficient to explain the collinearity effect.

Collinear flankers cause rats to miss target

Performance reflects both the ability to say yes when the target is present (hits) and the ability to say no when the target is absent (correct rejections). We find that the collinear condition decreases accuracy of both kinds. For each rat, the hit rate was lower for the collinear condition than the parallel condition (Figure 5a; vertical axis in Figures 5c and 5d). The false alarm rate was also higher for the collinear than the parallel condition (Figure 5b; red horizontal axis in Figures 5c and 5d). The average decrease in hit rate (3.7%, Figure 5a) was about three times larger

than the average increase in false alarms (1.1%, Figure 5b). The decrease in hit rate is significant for 6 of 7 rats (Figure 5a), whereas the increase in false alarms is significant for only 1 of 7 rats (Figure 5b). The same trends are found when comparing collinear flankers to either popout condition (not shown). The net effect is that collinear flankers cause rats to report "no" more often than other flankers. They cause rats to miss the target.

The hit rates and false alarms for collinear and parallel conditions are also shown in an ROC space (Figure 5c). Data from the one outlying rat (r2) is included next to a rat displaying a typical effect (r5) in the expanded view (Figure 5d). Although subjects differ in overall performance and bias, the effect of collinearity is similar for all subjects, indicated by the consistent direction of the arrows. The increase in misses is the dominant effect in the population.

Signal detection theory interprets these raw data in terms of sensitivity (d') and bias (criterion). Applying this framework, sensitivity is consistently lower when flankers are collinear (Figure 5e). This effect is significant for 6 of 7 rats (Agresti–Caffo 95% confidence interval) and for the population as a whole ($p < 0.01$ by Tukey–Kramer on 2-way ANOVA). Rats also show a consistent shift in criterion, reflecting the greater bias to say "no" for collinear stimuli (Figure 5f). The criterion shift is small compared to the change in sensitivity and is not significant for any rat. We cannot confirm that the assumptions of Signal Detection Theory hold in our study, but our conclusion (that collinear flankers cause misses) is observable in the raw data (Figures 5a–5d) independent of these assumptions.

Discussion

These data show that detection of visual stimuli by rats is sensitive to the configuration of the flanking elements. In particular, flankers collinear to the target impair performance compared with other configurations. Agreement in sign between target and flanker gratings was not required for this effect. This result suggests specialized processing of oriented image features that can be connected to form a continuous contour. It is noteworthy that this processing must occur in the absence of orientation columns, which are absent in rats (Ohki et al., 2005).

Contrast normalization is a powerful conceptual framework for explaining many surround effects in early visual processing. A pattern-sensitive generalization of contrast normalization could account for a collinear effect (Figure 6). In this model, the normalization strength (E) includes additional dependencies on the parameters of spatial configuration (θ_T, θ_F, ω). This extension of the model in Figure 2 allows the normalization strength (E) to be specific to orientation in the target location and sensitive to the specific arrangement of flanking features. The dominant effect of pattern in our data could be explained by a single factor that selects for the alignment of all three experimental parameters: $\theta_T = \theta_F = \omega$. In this model, collinearity increases the normalization strength leading to greater performance impairment. We offer this as one plausible and parsimonious model that makes direct predictions that can be tested physiologically.

Other perceptual and/or cognitive models could also account for our behavioral data, if they incorporate a "collinearity" term sensitive to the interaction of position and orientation of flankers. Collinear effects could be ascribed to higher visual processing areas. For example, mechanisms for binding features, processing gaps, or interpreting occlusions could play a role. In principle, collinearity could differentially influence cognitive factors such as arousal, attention, motivation, or task strategy. In order to account for the collinearity effect, these factors would have to switch on the timescale of seconds because trial types were randomly interleaved.

Collinear flankers cause rats to miss targets more than other flanker configurations (Figure 5a). This is consistent with perceptual masking (rats not seeing the target), but we are reluctant to attribute the bias change to a perceptual process alone or a decision process alone without a measurement of an internal signal that represents the target. For example, if rats suppress perception of a target due to a lateral mask or perceive a false target due to an illusory contour, they might learn to shift a downstream decision criterion to a new boundary that maximizes their reward rather than reporting their percept. Therefore, we do not think the change in bias observed in our data supports any strong conclusions about perception. Nevertheless, the data may constrain future models, so we report the raw values we observed for all conditions and rats in Supplementary Analysis 1 (Supplementary Figures S8a, S8d, and S8g).

Potential confounds

Our data show that rats' behavior is sensitive to the arrangement of oriented visual features above and beyond the effects of nearby contrast. In any flanker psychophysics study, one should address confounds that might arise from slow variation in performance, familiarity with stimuli, response biases, stimulus artifacts, cognitive confusion, or the influence of attention. Here, we address each of these potential confounds.

During the test period, each rat's performance was approximately stable. Of course, performance does fluctuate, probably due to slow variations in motivation. In addition, we cannot exclude a small effect of expertise learning. These correlations over time could influence blocked performance such that temporal variation would appear as differences across experimental conditions. For this reason, we randomly interleaved all condition types using the method of constant stimuli. This method also

balances subjects' exposure to long runs of the same flanker configuration (Figure 3b), which may be difficult to accomplish with adaptive psychometric methods.

Second, it is possible that the exposure to certain orientations, in the recent past or throughout a subject's life span, could influence their perceptual processing of that orientation (Kurki, Hyvarinen, & Laurinen, 2006). If we had only used a single target orientation in training or testing, we could not rule out effects of orientation-specific familiarity or adaptation. Therefore, subjects were exposed to the same distribution of target orientations and signs in the training steps as in the testing step. Moreover, whenever flankers were present they had the same distribution of properties as the target.

Third, if the rats' "yes" and "no" behavioral responses are inherently asymmetric, this would complicate interpretation. We avoided a go–no go trial structure because it is likely that a different circuitry is required to initiate versus inhibit a response. Instead, we used a 2-alternative forced-choice trial structure where both "yes" and "no" required initiation of a symmetric motor output. Reinforcement was also symmetric: correct trials were always rewarded and incorrect ones always initiated a timeout, regardless of the target's presence. As a further control, two subjects (r6 and r7) used the same experimental equipment as their brothers but were trained with an inverted rule, such that "yes" and "no" were mapped onto the opposite sides. The results for these rats were not different (Figures 4 and 5).

Fourth, target orientation or flanker properties might affect target visibility through artifacts of the monitor rather than processing in the brain. Specifically, it is known that vertical gratings presented on any CRT monitor have lower effective contrast than horizontal stimuli, because RGB guns follow rasterized horizontal scans and lack perfect temporal resolution (Garcia-Perez & Peli, 2001). Had we used gratings that were not symmetrically tilted about vertical, these artifactual differences in contrast could have been responsible for performance differences across conditions. We also designed the stimuli so that flankers and targets never shared horizontal scan lines to minimize their impact on each other's contrast.

Fifth, it is possible that subjects' errors are not due to perceptual difficulty but rather a failure to understand the intended task. We confirmed in 2/2 rats that their detection performance in all flanker conditions was sensitive to the target's contrast (Supplementary Figure S4c). Because their performance did not saturate with the contrast we used in our study, at least some incorrect responses were due to perceptual difficulty. We cannot rule out that cognitive difficulty may also have contributed to errors. For example, the decrease in performance when flankers are added (Supplementary Figure S3) could be explained if rats failed to understand that the target location contained the relevant feature and also responded to gratings in non-target locations. However, this confusion would not explain the consistent collinearity impairment observed in all individuals (Figure 4).

Finally, spatial or feature-specific attention may play a role in some flanker tasks (Freeman, Sagi, & Driver, 2004). In our task, to ensure that feature-specific attention would not give the rats a differential advantage between stimulus conditions, target orientation was randomly chosen in each trial. We did not employ a positional cue for target location because forward masking could affect target detection. In our task, flankers could improve allocation of spatial attention by reducing uncertainty about the target's location, ultimately improving performance compared to trials without flankers (Petrov, Verghese, & McKee, 2006). This could occur in our task, but if rats did benefit from spatial uncertainty reduction, other effects of the flankers overwhelmed this benefit, yielding net decreases in performance. Alternatively, rats' attentional allocation or visual representation might lack the spatial resolution to isolate flankers from the target location. These factors could explain the flanker-induced impairment (Supplementary Figure S3) but not the collinear specificity (Figure 4).

In summary, we have controlled for slow variations in behavior, balanced stimulus familiarity, used symmetric responses, avoided CRT artifacts, confirmed that targets are perceptually challenging to detect, and avoided confounds due to orientation-specific attention. We conclude that the rat visual system is sensitive to pattern above and beyond the effects of nearby contrast. We attribute this sensitivity to the rats' visual system, as opposed to other sources of variability in the environment or the rats' cognition.

Comparison to humans

In some perceptual tasks, the presence of collinear flankers improves human performance (Chen & Tyler, 2008; Polat & Sagi, 2007). Why did the collinear flankers impair behavior in rats as opposed to improve it? The term "facilitation" and "suppression" refer to either increases or decreases in performance at a fixed contrast, as in this study, or the ability to match a constant performance in a new condition using a lower or higher target contrast. In this study, collinear flankers suppressed detection in rats. On the other hand, collinear flankers facilitate detection for humans performing a two-interval forced-choice task in the lateral masking paradigm (Polat & Sagi, 1993; Solomon & Morgan, 2000; Williams & Hess, 1998) and dual masking paradigm (Chen & Tyler, 2008). We note that in different task paradigms, this facilitation is not found. The human study most similar to ours also used randomly interleaved trial conditions, fixed contrasts, a single stimulus yes/no paradigm, and oblique vs. collinear flankers but found no collinearity effect at the target–flanker proximity we used (their Figure 6, 3λ; Polat & Sagi, 2007). It remains to be determined whether this difference is attributable to a difference in species, training experience, or stimulus parameters: they used sinusoidal gratings and a single target orientation.

Human studies show that flanker effects change in magnitude or even sign, depending on the contrast regime—which is low contrast for detection tasks and higher for contrast discrimination. The pattern of results in both can be cast in a contrast normalization framework, though the different contrast regimes may involve disparate cellular and circuit mechanisms. The results above were obtained using a target contrast of 1.0 (where contrast is reported as the fraction of the linearized range of the display spanning 4–42 cd/m^2). This contrast is near detection threshold for rats at the spatial frequency we used (Supplementary Figure S4a). Collinear facilitation is reported to be strongest at lower target contrasts. Thus, we also analyzed the data collected from three lower contrasts (25%, 50%, 75%). In no case did any target contrast or any configuration of flankers improve detection compared to the target alone condition (data of Supplementary Figure S4c, analysis not shown).

In our data, we did not observe sensitivity to the relative sign of target and flankers. The two signs we used are equivalent to having one of two spatial phases. In human psychophysics, both phase-sensitive (Chen & Tyler, 1999; Ejima & Takahashi, 1985; Williams & Hess, 1998; Zenger & Sagi, 1996; Zenger-Landolt & Koch, 2001) and phase-insensitive (Chen & Tyler, 1999; Field et al., 1993; Xing & Heeger, 2001; Zenger & Sagi, 1996) collinearity effects have been described, perhaps reflecting the phase-sensitive (simple cell) and phase-invariant (complex cell) processing channels for orientation in V1. Differences among these studies that appear to be relevant include the distance of flankers from target (gap, no gap, or overlap) and whether the stimuli are presented in the fovea or periphery (Chen & Tyler, 1999). In rats, we only tested one distance with no overlap (3λ), one spatial frequency (0.22 cycle/deg), and two phases (aligned and reversed). We do not know what part of the retina rats used in the task nor whether rats' central vision (Heffner & Heffner, 1992) is more similar to foveal or peripheral vision in primates. While it may seem that phase sensitivity is useful for pattern processing, human psychophysics suggests that invariance to phase is a hallmark feature of contour integration (Williams & Hess, 1998).

Though flanker effects reported in the human literature depend on stimulus and task details, our results agree with the consistent key finding across human studies: performance under collinear conditions is special.

Relating our findings to natural scene statistics

There is a substantial literature theorizing that early visual processing is optimized for the statistics of natural scenes (Barlow, 2001; Field, 1987; Geisler, 2008). These optimizations can impair performance in tasks that violate natural scene statistics (Howe & Purves, 2005; Schwartz, Sejnowski, & Dayan, 2009; Weiss, Simoncelli, & Adelson, 2002). In light of this theory, it is noteworthy that the condition that most affects rats' target detection, collinear flankers, corresponds to the feature conjunction that is statistically most frequent in natural scenes. Combining this perspective with a contrast normalization model leads to a speculation about how a pattern-specific normalization pool could be acquired by learning, without requiring anatomic segregation of orientation channels.

Suppose the visual system computes a prediction of target probability based on some function of the image at other locations, and this prediction is used to adjust the local representation of target. The theory implies that those surrounds that make the strongest predictions about the target in natural images should influence the representation most and thus impair performance most in our task. This theory is neutral about whether predicted targets should be suppressed (reducing redundancy) or enhanced (propagating beliefs) at the level of early vision. The direction of this influence cannot be predicted and may be species specific. The framework of normalization developed above implies suppression of predicted features.

It is biologically plausible that the visual system could perform this computation. For example, sensitivity to the separate pairwise correlations of nearby local oriented features might be learned from the correlated firing of V1 neurons by activity-dependent mechanisms, without requiring orientation columns. Suppose that each local oriented feature's representation is normalized by the activity of all nearby local oriented features, in proportion to their statistical co-activation in natural images. In the statistics of natural images, contrast at one location is correlated with high contrast nearby (Ruderman & Bialek, 1994). The co-occurrence of oriented features depends on the relative orientation and position, and collinear features co-occur most often (Geisler et al., 2001; Itti & Koch, 2000; Sigman et al., 2001). Thus, all flankers should normalize, and collinear features should normalize the most (Schwartz & Simoncelli, 2001). In our task, we find that all flankers impair detection and collinear flankers impair the most.

In this framework, one can think of the normalization strength in our model (E) as representing a predicted contrast at the target location ($\hat{C}_T$) estimated on the basis of the contrast in the flanking region (C_F). This suggests that the function of divisive normalization is to reduce the effective contrast for expected features and amplify unexpected features, thereby maximizing information transfer for natural scenes (Ruderman & Bialek, 1994).

Future studies could further test this ecological interpretation by correlating behavioral impairment with natural co-occurrence statistics of flanking features at other positions and orientations. In particular, it will be of interest to explore parallel flankers at other positions and popout flankers with greater orientation differences. The more specific hypothesis of normalization makes the direct prediction that flanker features that are correlated with the target in natural images should reduce the firing rate of

neurons that respond to the target early in the visual system (such as thalamus or primary visual cortex). Surround processing has not been studied in these neurons in rodents. In cat and primate V1, surround stimuli generally reduce firing (Bonds, 1989; Carandini et al., 1997; Cavanaugh et al., 2002; Heeger, 1992; Polat et al., 1998; Shapley & Victor, 1979), but some cells fire more when flanked by collinear features (Li et al., 2006; Polat et al., 1998; Sillito et al., 1993).

Contrast normalization would reduce redundancy, leading to more efficient codes, but this is not the only goal of vision. Pure contrast normalization may even be at odds with other visual goals. Statistical inference from surround stimuli could contextually de-noise the signal, leading to better parameter estimation through the combination of weak signals. This would also exploit the correlated signals of the natural world (Barlow, 2001) but with opposing effects. We presume that both processes occur and interact in natural vision; different tasks may emphasize one or the other. We focus on the role of contrast normalization because it requires the least complexity to explain all of our data.

Rats as a model system for vision research

The impact of flankers on behavior has only been studied in humans and other primates, the physiology of the early visual system primarily in non-human primates and cats. Rats offer several advantages as a vision model. Rat husbandry is inexpensive and their behavior, neuroanatomy, and neurophysiology are extensively studied. We have demonstrated that they are easily trained to perform visual tasks that involve distracters and that their vision is sensitive to the spatial arrangement of features. This adds to the growing list of visual tasks demonstrated in rats (Birch & Jacobs, 1979; Cowey & Franzini, 1979; Douglas et al., 2006; Keller et al., 2000; Zoccolan et al., 2009). In this study, individual rats performed around 500 trials everyday with stable performance over months and require little human supervision. Many powerful techniques are more feasible in rats than primates or cats, such as genetic, transgenic, viral, histological, optical, intracellular, and pharmacological methods. We conclude that rats provide a valuable complementary model system for studying contextual visual processing.

Experimental procedures

Animal subjects

Data were collected from seven male Long–Evans rats (Harlan Laboratories). All experiments were conducted under the supervision and with the approval of the *Institutional Animal Care and Use Committee* at the University of California San Diego.

The rats included in this study were the 7 median performers from an initial cohort of 14 animals. Four animals were excluded from this study because they either remained at chance on the initial learning task or their performance never exceeded our automatic graduation criterion. They never saw flankers. Three of the remaining ten rats were high performers and were moved to another study before collecting a sufficient amount of data on the testing step. They performed 2, 7, and 16 sessions while other rats performed 60–150 sessions.

Training system

We designed custom hardware and software for automation and parallelization of training. A broad overview of its design and architecture can be found in Supplemental Experimental Procedures 2. Each station consists of a CRT display adjacent to a transparent cage that interfaces easily with slightly modified standard vivarium rat cages (Figure 1a). Rewards were spatiotemporally co-localized with response. Our initial training methods were adapted from previous studies of olfactory and auditory tasks in rats (Otazu, Tai, Yang, & Zador, 2009; Uchida & Mainen, 2003). Likewise, see other similar methods (Zoccolan et al., 2009). In our study, behavior was detected via three infrared beam break detectors (Optek OPB980T11) in stainless steel housings for protection against chew damage. Water was delivered to a rounded 16-gauge stainless steel tube positioned just behind each beam by computer-timed solenoid valve opening (80 ms, Neptune Research, 161PO21-11, 161T01, Cooldrive) from a pressurized source (~300 mm Hg, Infu-surg 4010, Ethox) through rigid tubing (CO_2 lines 8044, SurgiVet). Our reward volume was roughly 16 μl and was typically delivered within 10 ms of a correct lick response. Occasionally, rewards were larger, as described in the Training protocol section. Auditory feedback was provided with earbud headphones mounted on the sidewalls of the box. Different sounds indicated when a detector beam was broken and differentiated responses as request, correct, incorrect, and inappropriate (left or right licks with no preceding center request lick). To present visual stimuli, we used PsychToolbox (Kleiner, Brainard, & Pelli, 2007) to control standard OpenGL capable graphics cards (Nvidia GeForce 7600) via Matlab (Mathworks, Natick, MA). We did not track head position or gaze. The head position, head orientation, and eye level are fairly consistent from trial to trial within subject, as determined from direct observation.

Training protocol

We designed a series of shaping steps that gradually taught rats to perform the detection task with flankers.

An overview of the steps is provided in Supplementary Table S1. Details of the general training procedure such as water restriction, schedule, and environment can be found in Supplemental Methods 1. The specific shaping sequence used for the subjects in this study was given as follows.

Learning to lick. The goal of the first three steps was to teach the rats to use the detector/reward ports. We presented no visual stimuli, and rats obtain a reward by licking any port at any time. To encourage rats to move among the ports, only one consecutive reward was allowed per port. During step 1, the system occasionally stochastically generated a drop of water without any action from the rat, in order to generate interest in the ports. On step 2, these automatic rewards were turned off, so that rats must actively lick the ports. Rats graduated by sustaining 5 rewards per minute for 2 min. Step 3 was identical to step 2 except it required a stricter graduation; it need not be included in future studies. All rats in this study passed through step 3 in 1–2 sessions, with the exception of one rat that got stuck on step 3 for 6 sessions.

Learning two-alternative forced-choice (2AFC) task structure. From step 4 onward, trials had a 2AFC structure. A center lick initiated a trial (but was not rewarded), and the first subsequent lick at either the right ("target present") or left ("target absent") port determined the trial outcome. For 2 of the 7 rats, the present/absent port identities were reversed. Targets appeared on 50% of trials; for these trials, a response at the "present" port was rewarded. Otherwise, a response at the "absent" port was rewarded. The tone that accompanied each trial request provided the subject with confirmation that he had successfully initiated a trial and should proceed to ascertain and report target presence; a different tone and a flickering screen accompanied errors for the duration of the timeout penalty indicating the system was non-responsive. The gratings appeared on the same gray field background that was displayed between trials (after a response, during a reward, and before the next request).

We used two techniques to discourage guessing, side biases, and other undesirable behavior patterns. First, 50% of incorrect responses were followed by "correction trials." During correction trials, trials with new stimuli but the same correct answer are repeated until the rat responds correctly. Correction trials can induce a rational strategy of switching response after an error (if 50% of errors are followed by correction trials, always switching responses after an error gives 75% performance for those trials—above chance performance without reference to the stimulus). The rats did, in fact, bias their responses in this way, so trials immediately following errors, including correction trials, were omitted from analysis. Strategies that ignore the visual stimulus can only impair performance in any trial that did not follow an error trial.

Second, we gave increasing rewards for consecutive correct answers. The first correct response after an error yielded an 80-ms valve opening (approximately 16 μl). The 2nd to 4th consecutive correct responses earned 100-, 150-, and 250-ms rewards. Consecutive responses thereafter earned 250-ms rewards; the first incorrect response reset this schedule to the beginning value of 80 ms.

For step 4, the first step with visual stimuli, the target was a large full-contrast square-wave grating masked by a circular Gaussian (21.6° standard deviation from the reference viewing location, with spatial frequency of 0.11 cycle/deg, Figure 1d, same stimulus as step 5). We used square-wave gratings instead of sine-wave gratings because we speculate that contour integration mechanism might engage most strongly for sharp edges. The Gaussian was truncated at 4 standard deviations (about the limit of 8-bit discretization). The grating bars were slanted clockwise or counterclockwise from vertical with equal probability (±15° for r1–r5, ±22.5° for r6 and r7). Results from r1–r5 and r6–r7 were combined because the trends and effect magnitudes were not significantly different ($p > 0.05$, t-test; $p > 0.05$, Kruskal–Wallis). For this and subsequent steps, monitor resolution was set to 1024 × 768 pixels at 100 Hz.

Because this step was designed only to establish the 2AFC trial structure (center request followed by side response), the graduation criterion required only high sustained trial rates, *not* above chance performance.

Visual detection. Step 5 introduced a penalty timeout period for incorrect responses (1–6 s, hand-tuned for each rat), during which the "incorrect response" sound played and rats could not initiate a trial. Graduation from steps 5–8 required 85% correct performance on the previous 200 trials or 80% on the previous 500 trials. Graduation from step 5 represents the first evidence that rats can perform visual detection in our apparatus (Figure 1c).

Step 6 introduces a gamma correction table (previous steps leave the CRT's native gamma uncorrected) that linearizes the monitor's luminance output, so that the 2^8 gray levels correspond to equally spaced increments in cd/m^2 (see Supplemental Methods 3). After linearization, stimuli used a smaller luminance range and had a higher mean luminance than the earlier training steps. This reduced the effective contrast of the stimulus. All subsequent steps used linearized stimuli.

On step 7, grating spatial frequency increased to 0.22 cycle/deg (equivalent to $\lambda = 4.5°$, where λ is degrees per cycle, a standard unit for indicating flanker distance; Polat & Sagi, 1993). Pilot studies (Supplementary Figures S4c and S4d) identified this value as in the range where rats' detection performance was not saturated but strongly sensitive to target contrast (ranging from 60% to 75% as target contrast ranges from 50% to 100% of the linearized range). This was necessary in order to ensure that we could observe either performance improvements or impairments caused by flankers. This value is consistent with previous reports of rat acuity (Birch & Jacobs, 1979; Heffner & Heffner, 1992; Jacobs, Fenwick, & Williams,

2001; Keller et al., 2000; Prusky, West, & Douglas, 2000), which starts to roll off at 0.1 cycle/deg and shows no sensitivity above about 1.0 cycle/deg for high-contrast displays. Our Gaussian mask reduces contrast throughout the grating except at the centermost pixel.

Step 8 reduces the grating size by about 70%, so that the standard deviation of the Gaussian mask was 6.8°. Subjectively, this left about 3 visible periods in the grating. Flankers were not yet included, but at this grating size and spatial frequency, the monitor had room to display complete flankers (size and spatial frequency identical to the target) at a distance of up to 5λ.

Flanking targets were introduced at a distance of 3λ during step 9. Their contrast was slowly increased from 10% to 40% with training; each 10% was added after a performance criterion of 80% was reached. Performance remained above chance for higher flanker contrasts, but these were not chosen for testing because it is difficult to resolve differences in performance between conditions less than 60% correct. The increasing impairment of performance with flanker contrast could reflect either suppression of the target's apparent contrast below a detectable level or confusion of high-contrast flankers with rewarded targets. For this flanker distance and Gaussian mask size, flankers were non-overlapping and subjectively appeared separated from the target (Supplementary Figure S1). For each trial, the target orientation (θ_T), flanker orientation (θ_F), and angular position (ω) were randomly and independently chosen to be either ±15° (rats r1–r5) or −22.5° (rats r6 and r7).

Testing stimuli. Test stimuli were the same as those in step 9 with 40% contrast flankers (Figure 3). For the purposes of analysis, we grouped all the flanker conditions into four categories depending on the relationship of the flankers to the target (Figure 3b). During testing, error feedback and reward contingencies were not changed. Correction trials continued to occur after 50% of errors.

Performance stability, data filtering, and performance measures

Subjects performed 25,000–90,000 trials during the final testing phase, over the course of 67–136 training days. To assess the stability of performance over time, we calculated performance for each rat and condition in consecutive non-overlapping 500 trial windows. Considering the entire testing period, each subject's long-term performance trended slightly up or down, but this drift always amounted to <7% total change. The most unstable performance was exhibited by r5, whose behavior fell for unknown reasons from ~65% to ~55% for ~6000 trials (~12% of the data in his testing phase) and then recovered. Despite unstable performance over time, the influence of collinearity for this rat was typical of the population. The performance in 500-trial windows ranged between 52% and 72% for every rat and flanker condition, averaging 63% overall.

We excluded from analysis all trials following an error trial, because rats showed evidence of an alternation strategy after errors, perhaps due to correction trials (see above). Including non-correction trials that immediately followed errors reduces the effect of collinear flankers but not below significance; this did not alter any trends or influence our interpretation. Considering only trials in the central 80% of reaction times can remove many aberrant trials where rats were either not on task or very rapidly performing trials while apparently ignoring the visual stimulus. This improves performance and makes the collinearity effect appear stronger, but we do not filter the data in this way for the purposes of this publication.

We report performance in terms of percent correct (Figure 4), but we confirmed that the metric d' yields the same conclusions (Figure 5e, Supplementary Figure S8) and that the effects on performance are not an artifact of bias (Supplementary Analysis 1).

Statistical tests

The performance of individual rats in each flanker condition is assumed to be the parameter of a stationary binomial distribution, so finding flanker-caused performance changes amounts to detecting differences in binomial parameters. When computing confidence intervals for differences of binomial parameters, we use the Agresti–Caffo method, in which one modifies a Wald interval by adding two successes and two failures to each estimated proportion (Agresti & Caffo, 2000). Like the Wald interval, the Agresti–Caffo confidence interval uses the Gaussian approximation for binomials, which is not valid if p is near 0 or 1, or n is too small. In our data, $0.55 < p < 0.85$, and $n > 5000$ for all conditions. We verified that alternative statistics agreed with the significance conclusions of Agresti–Caffo for representative test cases (specifically a permutation test and a Bayesian MCMC method, not shown). The Agresti–Caffo intervals graphed for each subject may exclude the point of zero difference; this can be used to test a hypothesis at $p > 0.05$.

To determine if performance differences between conditions were significant at the population level, we used a 2-way ANOVA (anovan in Matlab, linear model, type 3 sum squared error). We tested for reliable changes across conditions accounting for the expected variability for each subject. For each subject and condition, we obtained multiple estimates of the performance based on a non-overlapping sample of N trials selected randomly from the testing phase. We used $N = 200$ trials per estimate. For interleaved trials without flankers ($F-$ mix in Supplementary Figure S3), the number of estimates ranged from 3 to 13, compared with 78–253 estimates of $F+$. For comparing flanker conditions (Figures 4 and 5), the number of independent

estimates per flanker condition and subject ranged from 19 to 62. The resulting distributions were approximately Gaussian (e.g., when comparing flanker conditions typically 26/28 passed Lilliefors' test, close to the 5% failure rate expected on chance). Nevertheless, because distributions cannot be guaranteed to be Gaussian, we also report Friedman's test (friedman in Matlab), which has lower power but does not assume normality.

Whenever we made multiple comparisons, we used Tukey's honestly significant difference criterion (multcompare in Matlab) with a criterion of $p < 0.01$. For example, we tested all pairwise differences between the four stimulus conditions. Tukey's criterion for significance is more stringent, to adjust for the fact that making more comparisons increases the probability that one of them will cross significance by chance. A graph showing the critical values for hypothesis testing is shown in Supplementary Figure S5, where all six pairwise comparisons are reported. Results were not different with $p < 0.05$ criterion. All tests that were significant with the 2-way ANOVA were also significant for Friedman's test except for one comparison (Supplementary Figure S5e), as discussed there.

The 95% confidence intervals for differences in d' or criterion within individual subjects (Figures 5e and 5f) were determined using a Monte Carlo Markov Chain. For each subject and stimulus condition, we sampled the posterior distributions of d' constrained by the number of observed hits, misses, correct rejects, and false alarms. The model assumes that the hit and false alarm counts are independent binomial distributions and uses a uniform prior over hit and false alarm rates. The d' or criterion posterior was estimated using WinBUGS and software written by Michael Lee (Lee, 2008). The distribution of d' difference or criterion difference is sampled by taking the difference between independent random draws of two performance conditions. The confidence interval is the range of these data after removing the 2.5% highest and 2.5% lowest samples.

Acknowledgments

*PMM and EDF contributed equally to this work. Each made essential contributions to the conception, design, and implementation of the general method and technology for high-throughput automated training and testing of rats in 2AFC visual tasks, with help and critical discussion from PR. PMM was responsible for the conception of the flanker experiment, design and implementation of the task, training and data collection, data analysis, interpretation of the results, and writing of the manuscript, with help and critical discussion from EDF and PR.

We thank Lung-hao Tai, Tony Zador, Carlos Brody, Zach Mainen, and Tim Gentner for generously sharing their behavioral training methods and hardware, on which our methods and apparatus are based. We thank Fan Li and Dan Parks for assistance with software engineering and Ginger Beriones and Nareg Kalajian for assistance in constructing training equipment. We thank Sarah Meder, Danielle Dickson, Alee Bowden, Marv Zech, Liz Murphy, Yuli Wang, Holly Vo, Aria Jafari, and Duc Nguyen for running daily behavioral sessions.

This work was supported by a Hellman Foundation Fellowship, an Innovative Research Grant from the Kavli Institute for Brain and Mind, a Scholar Award from the J. S. McDonnell Foundation, and NIH R01 Grant EY016856. PMM and EDF were both supported by NSF IGERT Grant DGE9987614; PMM was also supported by NSF IGERT Grant DGE-0333451 to GW Cottrell/VR de Sa and by an NSF Graduate Research Fellowship.

Commercial relationships: none.
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