Uncertainty reveals surround modulation of shape

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Noisy estimations of shape can be partially resolved by incorporating relevant information from the context. The effect of surround stimuli on shape perception becomes clear in illusions of shape contrast and assimilation. In this study, we answer the question how a surround-induced bias depends on the reliability of shape signals. This way, we assess the processes by which an observer incorporates relevant data from the context into the shape estimate. We selectively added visual noise to the center and surround and compared a bias in shape perception with a control condition where no noise was added. In the conditions where shape and surround stimuli were well defined, we found a shape-contrast bias. When the surround stimuli were degraded, this contrast bias decreased. Most interestingly, when the central shape was degraded, an assimilation bias was observed. This bias was larger when the entire stimulus was degraded compared to when only the central shape was degraded. This suggests that shape contrast is the result of inference processes relying on local representations in early visual areas whereas assimilation is related to inference processes by global representations in higher visual areas.

Keywords: 3D shape, noise, Bayes, contrast, assimilation, visual, perception

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Introduction

We rarely question the veridicality of our perception of the visual world but the inference processes involved occur under conditions of uncertainty. Three-dimensional (3D) shape, for example, has to be inferred from two-dimensional (2D) retinal projections where the mappings are not only one-to-many but also many-to-one. In such cases, noisy estimations can be partially resolved by incorporating relevant data from the context (Schwartz, Hsu, & Dayan, 2007). The influence of surround stimuli on perception becomes clear in biases of shape contrast, where perception is biased in the direction opposite to a neighboring stimulus. Such biases have been found in various geometric properties such as slant, curvature, and depth and in stimuli that are defined by different depth cues, such as binocular disparity, motion, and shading-and-texture (Anstis, 1975; Cornsweet, 1970; Curran & Johnston, 1996; Gibson, 1933; Graham & Rogers, 1982; te Pas & Kappers, 2001; te Pas, Rogers, & Ledgeway, 2000). Assimilation, where shape perception is biased in the direction of the surround, also occurs but has been reported less frequently (Poom, Olsson, & Borjesson, 2007; van der Kooij & te Pas, 2009; van Ee, Banks, & Backus, 1999). Here we address the issue how surround stimuli influence the estimate of 3D shape.

Bayesian frameworks have been successfully applied to describe the perception of 3D shape from a combination of depth cues. In such an approach, an estimate of 3D shape is derived from weighted linear combination of shape estimates by depth cues such as binocular disparity, motion, and perspective (Landy, Maloney, Johnston, & Young, 1995). Inherent in this kind of model is the idea that there are both cue-dependent (shape by cue x) and cue-invariant (shape from cue combination) representations of shape. This idea is supported by functional imaging data, which show that BOLD responses in early visual areas are related to the shape signal from individual depth cues whereas activity in higher visual areas, such as LOC and MT+, is related to the combined shape estimate (Welchman, Deubelius, Conrad, Bülthoff, & Kourtzi, 2005). These representations might differ in more than cue invariance; receptive field sizes in the monkey visual cortex are much larger in these higher visual areas compared to striate cortex (Zeki, 1978). In a previous study (van der Kooij & te Pas, 2009) we have shown that both types of representation are involved in the integration of shape and surround, causing qualitatively different surround-induced biases. When shape and surround were defined by the same depth cue and integration could occur by cue-dependent representations, a contrast bias was observed. But when they did not share depth cue information and integration had to occur through cue-invariant

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representations, an assimilation bias was found. In the latter case integration most likely had to occur through cue-invariant representations. Similar findings were reported by Poom et al. (2007) and van Ee et al. (1999). Thus, an observer can integrate shape and surround by information from different types of representation and assign different weights to the information. The information carried by the representations might be constrained by the neural properties of different cortical areas. Furthermore, the idea of weighted combination is supported by the findings that the percept depends on the reliability of information in the stimulus (Ernst & Banks, 2002).

But surround stimuli also provide different types of information to the observer. They provide relative shape cues (i.e., the difference between surround and central shape) that have to be weighted (van Ee et al., 1999). If a high weight is given to this difference, perception might become biased in the direction opposite to neighboring stimuli. In line with such reasoning, a reduced contrast bias in slant perception has been found with an increased gap between shape and surround, which reduces the reliability and consequently the weight of relative shape cues (Poom et al., 2007). For these relative shape cues to be effective, shape and surround have to fall on different receptive fields. On the other hand, there are substantial correlations between image points that are spatially near to each other or that are close in time. This means that the temporal and spatial context will induce expectations about the value in a certain image point (Howe & Purves, 2005). Observer's knowledge of such correlations is evident in their ability to replace missing pixels in digital images based only on neighborhood information (Kersten, 1987).

In conclusion, an observer can rely on different types of shape representation and has different types of information at hand when incorporating information from surround stimuli into the shape estimate, which may lead to biases of shape contrast or assimilation. Recent findings (Poom et al., 2007; van der Kooij & te Pas, 2009) suggest that a contrast bias is the result of integration by cue-dependent representations whereas an assimilation bias is related to integration by cue-invariant representations, but the issue *how* surround stimuli influence the perception of 3D shape can only be further resolved after it has been clarified what causes the shift in bias direction (contrast or assimilation).

Because the outcome of Bayesian inference depends strongly on the reliability of shape signals, external noise methods have successfully been used as a tool for system identification (Ernst & Banks, 2002; Tjan, Lestou, & Kourtzi, 2006). From this given, we develop a simple paradigm to show how surround-induced bias direction depends on the reliability of shape signals. Thereby we illuminate the inference processes by which information from surround stimuli is incorporated in the 3D shape estimate. Relative shape cues become less reliable and lose influence on perception when surround information is degraded. Therefore, a contrast bias will be decreased. But when the shape signal of the central stimulus is degraded, local information might be impoverished to the extent where the observer comes to rely on more global shape representations. Integration by these representations might cause averaging of the shape signal from the central shape and surround and an assimilation bias in shape perception. Also, an observer might come to rely on a different type of information when integrating information from the surround in the shape estimate.

In summary, we expect illusions of shape contrast to decrease when shape stimuli are degraded whereas we expect assimilation biases to become visible when the shape stimuli are degraded. Although the dependency of shape–surround interactions on the reliability of shape signals is relatively unexplored, studies on center–surround interactions in motion provide results that are in line with our predictions for shape (Hanada, 2004).

We reduce the reliability of shape signals by adding local noise to the shape stimuli (Ernst & Banks, 2002; Tjan et al., 2006). Noise is selectively added to the center and surround stimuli and surround-induced shape biases are compared to a control condition where no noise is added. In this control condition, we expect to replicate the findings of a slant contrast effect. In the condition where the surround is degraded, we expect relative shape cues to receive less weight and a decrease in bias. But of greatest interest are the conditions where the central shape is degraded by added noise. In this case we expect an assimilation bias in shape perception.

Methods

Stimuli

Random dot stereograms depicted a hinged plane receding in depth, flanked by two larger hinged planes (Figure 1). Random dots were back-projected from the screen onto the 3D structures in such a way that texture and perspective cues to shape would signal a flat surface. All shapes were 21.6° visual angle high, the central shape was 5.9° wide, and flankers measured 12.9° of visual angle in width. Central shape and surround stimuli were separated by a gap of 1° visual angle. Pixel density was 2.7 pixels per degree of visual angle and one pixel subtended 0.001 degrees of visual angle. Observers made dihedral angle comparisons of a range (60° to 140°) with a constant reference of 100° dihedral angle (method of constant stimuli).

To measure a surround bias, we varied the dihedral angle of the surround between the reference and test interval. The dihedral angle of the surround stimuli was either 50° or 150° and there were two surround conditions: one where the dihedral angle of test surround was smaller compared to the reference surround and one where it was

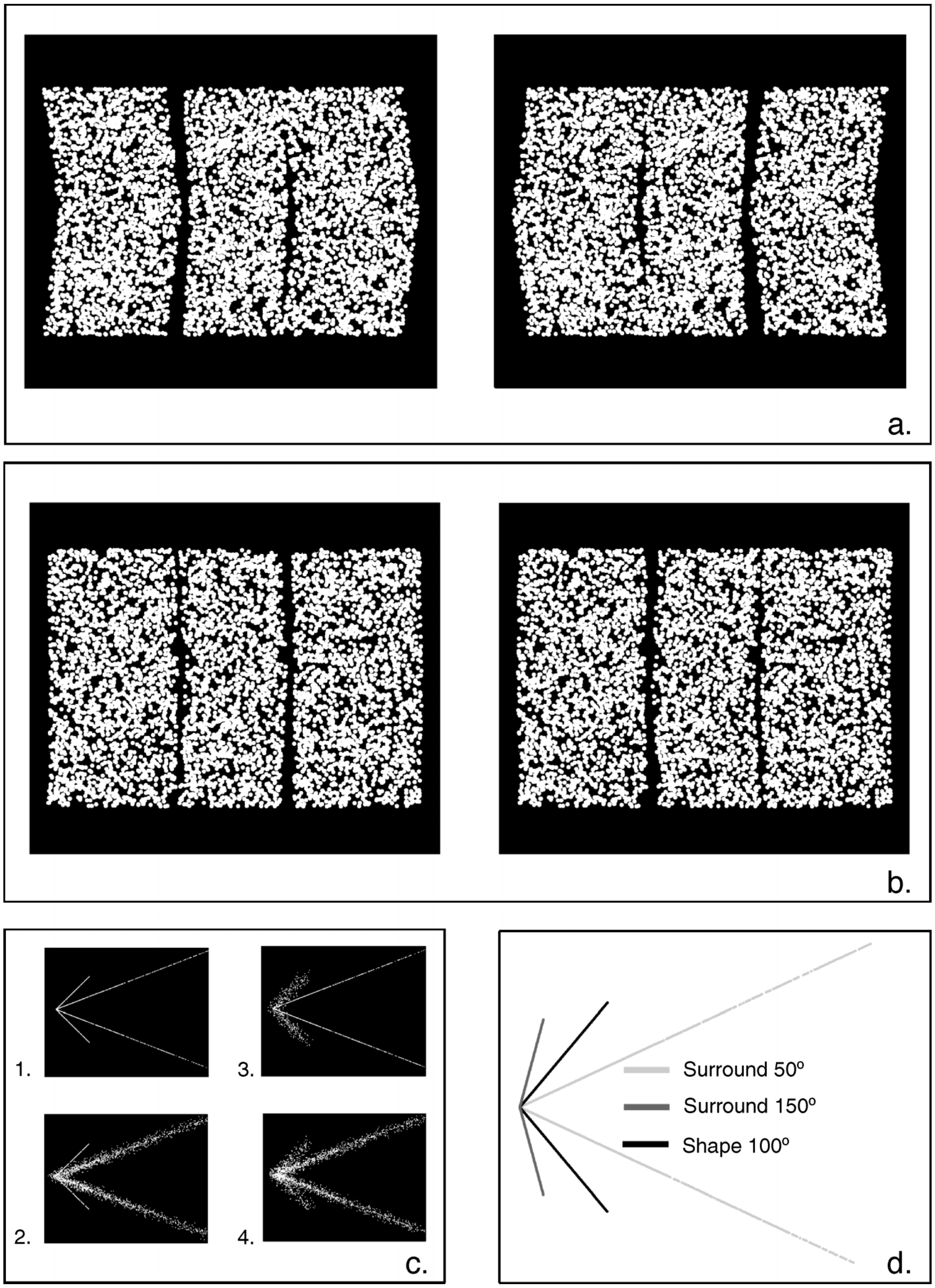

Figure 1. Stimulus setup. (a) Stereogram of the condition where the dihedral angle of the surround was 50°. (b) Stereogram of the condition where the dihedral angle of the surround was 150°. Both prepared for fusion. (c) Noise conditions: (1) "no noise," (2) "surround noise," (3) "target noise," and (4) "stimulus noise" conditions for the situation where the surround had a dihedral angle of 150°. (d) Side-view cartoon of the shape stimuli (the separation of the *x*-axis is not visible in this side view).

larger. Shape reliability was varied by selectively adding local shape noise to the stimuli. Local shape noise was created by displacing dots on the shape surface in a random direction in three-dimensional space, resulting in a maximal displacement of 3.6 centimeters orthogonal to the hinged plane. In a "surround noise" condition, noise was selectively added to the surround shape stimuli, in a "target noise" condition noise was added to the central target, in a "stimulus noise" condition the entire stimulus was degraded, and in a control condition no noise was added (Figure 1c).

Procedure

The two surround conditions ("larger" or "smaller") × 4 noise conditions ("no noise," "surround noise," "center noise," or "stimulus noise") × 16 test dihedral angles resulted in 128 different trial types, of which subjects performed 10 replications. A trial started with a 750-ms presentation of a central shape and surround, followed by a 750-ms gray fixation cross and the presentation of a second shape and surround for 750 ms. Next, the fixation cross reappeared and the observer decided whether the first or second central shape had the smallest dihedral angle. After the observer responded the fixation cross turned blue to indicate that a key press had been given and stayed on the screen for an inter-trial interval of 1 s. As noise is estimated over a period of several trials (Hanada, 2004), these trials were blocked by noise condition, and each block took about 30 minutes to measure. All subjects started with the "no noise" condition, followed by the "surround noise" condition and continued with the "stimulus noise" and "target noise" conditions. This way, lower discrimination thresholds in the conditions where no noise was added to the central shape could not be attributed to a learning effect. To assess subjects' stereo vision and to further minimize effects of learning during the experimental conditions, subjects first trained angle discrimination from binocular disparity with 10 replications of each test dihedral angle on stimuli where only the central shape was presented. Feedback was given by a change of fixation-cross color (green for correct and red for incorrect). In total, the training phase took 20 minutes. Five subjects whose stereo vision was too poor to perform the task and for whom the psychometric curve could not be fitted in either of the conditions were excluded from further participation. Two of the authors and four subjects that were naive as to the purposes of the experiment participated. All subjects had normal or corrected-to-normal vision.

Analyses

The PSE and discrimination threshold were calculated by fitting the proportion of "smaller dihedral angle" responses at each test stimulus angle with a cumulative Gaussian (the psychometric function, see Figure 2). The angle discrimination threshold, which we define as the 84% correct threshold that we obtain from the psychometric function, results in a measure of shape reliability (1/discrimination threshold). In the absence of the surround, the PSE should be equal to the angle of the central reference. Thus, the interesting parameter in this experiment is the difference between the PSE and the central

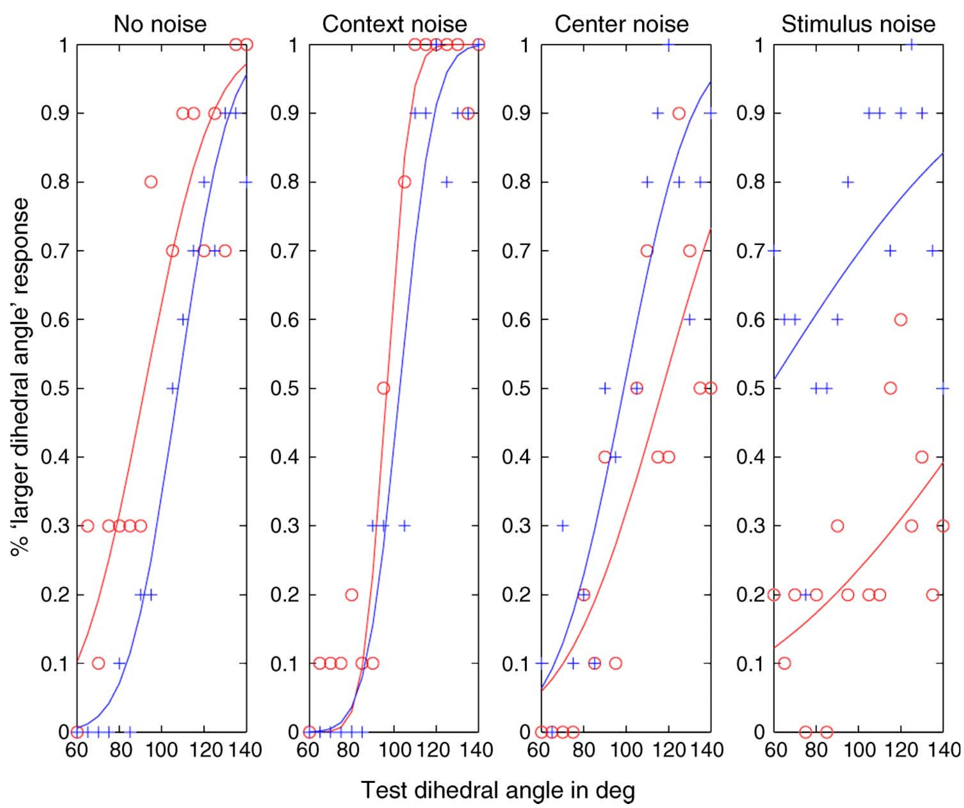

Figure 2. The fitted psychometric curves for the different surround and noise conditions on the data from a sample subject (HN). Red circles represent data from the condition where the dihedral angle of the test surround was larger compared to the reference surround and blue plusses represent data from the condition where the dihedral angle of the test surround was smaller compared to the reference surround.

reference angle: the bias. We define the bias in such a way that negative values represent a shift away from the surround dihedral angle (contrast) and positive values represent a shift towards the surround dihedral angle (assimilation).

Results

To test how a surround bias in shape perception depends on visual noise, we compared the biases and discrimination thresholds from the individual subjects (Table 1) between noise conditions with a repeated measures ANOVA (Figure 3). We first checked for differences between the conditions where the dihedral angle of the test surround was smaller or larger compared to the reference surround dihedral angle. A repeated measures ANOVA with the factors Surround ("larger dihedral angle" or "smaller dihedral angle") and Noise ("no noise," "surround noise," "target noise," or "stimulus noise") on the bias and discrimination threshold data from the 6 subjects revealed no difference in bias ($F(1,5) = 0.06$, $p = 0.82$) or discrimination threshold ($F(1,5) = 0.12$, $p = 0.74$) between the two surround conditions and we combined data from these conditions. Veridicality of shape perception without surroundings was assessed by an analysis of the training data where no surround stimuli were present. In both cases average biases did not differ significantly from zero.

Next, we compared bias size between noise conditions. There was a significant effect of Noise condition ($F(5) = 4.36$, $p = 0.02$). We further looked into this effect with a series of one-tailed paired sample *t*-tests. Whereas we found an contrast bias in the "no noise" condition, an assimilation bias was observed in the "stimulus noise" condition ($t(5) = -3.74$, $p = 0.03$). Furthermore, bias size was smaller in the "surround noise" condition compared to the "no noise" condition ($t(5) = -2.44$, $p < 0.01$). There seemed to be a similar decrease in bias size between the Target Noise and Stimulus Noise conditions, although this did not reach significance. One subject, SP, deviated from this pattern and showed a contrast bias in both the "no noise and stimulus" noise conditions. We attribute this to the fact that she was a highly experienced psychophysical observer and might have developed different strategies in estimating shape.

As the discrimination threshold is inversely related to shape reliability, we next compared discrimination thresholds between noise conditions with a repeated measures ANOVA with the factor Noise ("no noise," "surround noise," "target noise," "stimulus noise"). There was a main effect of the factor Noise ($F(5) = 9.57$, $p = 0.001$). Further investigation of this effect with a series of one-tailed paired sample *t*-tests showed that whereas discrimination thresholds were much higher in the conditions where noise was added to the central target compared to the conditions where no noise was added to the target, there was no significant difference between the noise conditions within these two situations ("no noise" vs. "surround noise" ($t(5) = 1.71$, $p = 0.43$) and "target noise" vs. "stimulus noise" ($t(5) = -1.73$, $p = 0.07$); Figure 2).

Discussion

Unreliable estimates of shape can be partially resolved by incorporating relevant information from the surround in the shape estimate. This could occur through different types of shape representation. Also, an observer could use different strategies. In this paper, we address the issue on how information from surround stimuli is integrated in the estimate of 3D shape. As external noise methods have proved a powerful tool for system identification (Ernst & Banks, 2002), we answer the question on how a surround-induced perceptual bias depends on the reliability of shape signals. To this end, we selectively added correlated shape noise to the central shape or surround and compared a surround bias with a control condition where no noise was added to the stimuli. Overall, a reliable central shape was associated with a contrast bias whereas an unreliable central shape was associated with assimilation biases. In the control condition, we replicated findings of a contrast bias in shape perception (Poom et al., 2007; te Pas & Kappers, 2001; van Ee et al., 1999). When only the surround was degraded, the contrast bias was diminished and when only the central shape was degraded, the

	No noise		Surround noise		Target noise		Stimulus noise	
Subject	Bias	*T*	Bias	*T*	Bias	*T*	Bias	*T*
SM	−10.80	19.56	−11.57	22.75	12.12	68.13	13.30	70.30
HN	−7.89	22.03	−3.19	10.70	9.16	31.08	53.54	86.06
SP	−13.23	17.30	−9.13	19.74	−27.02	41.18	−19.90	38.53
TG	−4.37	8.90	−0.78	7.26	7.49	15.02	1.72	20.14
KK	−3.04	12.29	−0.42	18.62	15.63	25.87	30.23	37.38
JV	−6.67	12.21	−2.53	10.66	1.08	19.53	1.08	37.16

Table 1. Bias and discrimination threshold (*T*) for each of the subjects in degrees of angle observed in the different noise conditions.

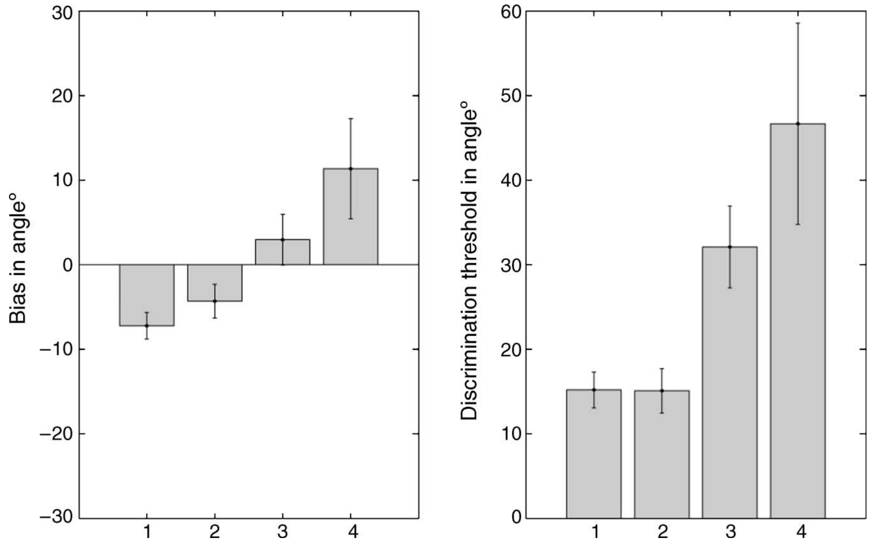

Figure 3. Average bias and discrimination threshold, derived from the psychometric curve, in degrees of angle as a function of noise condition (1 = "no noise," 2 = "surround noise," 3 = "target noise," 4 = "stimulus noise." Negative biases mean contrast and positive biases mean assimilation. Error bars represent standard errors of the mean (N = 6).

assimilation bias tended to diminish, although this did not reach significance. This suggests that the reliability of the central shape determined bias *direction,* whereas the reliability of the difference between the central shape and surround determined bias *size*. Yet, it is important to note that low reliability of the central shape is not a necessary condition for assimilation. Several reports exist of assimilation biases between hinged planes when the central shape and surround were defined by a different depth cue (Poom et al., 2007; van der Kooij & te Pas, 2009; van Ee et al., 1999). In all studies discrimination thresholds for the central shape were much below the discrimination thresholds for the noisy surfaces in this study.

The way in which a surround-induced bias depends on the reliability of shape signals could clarify whether biases of shape contrast and assimilation are caused by a single mechanism or whether they are the result of complementary processes. Whereas a contrast bias can be explained with relative shape cues, which are combined with direct shape cues (van Ee et al., 1999), Bayesian models of shape contrast cannot explain the shift in bias direction with added noise. We will first show how two highly intuitive hypotheses, which explain contrast and assimilation effects from a single mechanism, cannot account for the full set of our results. We show how the evidence presented here relates to the neural architecture involved in the perception of three-dimensional shape and make a case for the position that biases of shape contrast and assimilation are the result of complementary processes. First, one might attribute the shift in bias direction to the fact that adding shape noise to the central shape or surround diminished the reliability of the difference between the central shape and surround up to an extent where the difference between shape and surround is below threshold. Contrast would be the result of the perception of two Gestalten whereas assimilation results from the perception of one Gestalt (van Lier & Wagemans, 1997). But this explanation cannot account for the full set of our results. The area between the central shape and surround surface can be taken as a measure of the reliability of the difference between shape and surround. Using this measure, the reliability of the difference between shape and surround is about equal when only the central shape is degraded or when only the surround is degraded. But perceptual biases are very different between the two conditions: when the surround is degraded, contrast occurs, but when the central shape is degraded, assimilation is observed. Alternatively, one could propose that the surfaces to which noise was added appeared to have less depth and, therefore, larger dihedral angles. When the surround has a smaller dihedral angle compared to the central shape, this would have indeed decreased the difference between the central shape and surround. But when in the situation where the surround has a larger dihedral angle, the difference between central shape and surround would be *enhanced*. As we tested both situations, these shifts in bias would have averaged out. To summarize, the shift in bias direction cannot be explained from low reliability of the difference between shape and surround, nor can it be explained by "flattening" of dihedral angles with added noise.

Instead, we make a case for the position that contrast and assimilation biases are the result of complementary processes that rely on shape representations in different cortical areas. Both cue-dependent and cue-invariant representations are involved in the perception of 3D shape and surround stimuli can influence the shape estimate through both types of representation (van der Kooij & te Pas, 2009). Cue-dependent representations have been linked to activity in early, striate, visual areas whereas cue-invariant representations have been linked to fMRI activity in higher visual areas such as the lateral and temporal occipital cortices (Welchman et al., 2005). Furthermore, studies in cats and monkeys have shown that receptive field sizes are smallest in the central primary visual cortex (V1) and increase gradually in both higher and more peripheral parts of visual areas (Felleman & Van Essen, 1991; Maunsell & Newsome, 1987; Van Essen, Newsome, & Maunsell, 1984; Zeki, 1978). Estimates range from less than 1 degree in V1 to more than 8.5 degrees in LOC. This means that our central shape is much larger than receptive field sizes in early visual areas where information from individual depth cues is processed whereas the *entire* stimulus, encompassing the central shape and its surround, falls into the receptive fields of higher visual areas. We attribute biases of shape contrast to relative shape cues. For such relative cues to be effective the central shape and surround must fall on different receptive fields, so that local information can be compared. For this task, the relatively small receptive fields in early visual areas would especially be effective. Assimilation, on the other hand, might have been caused by shape and surround falling on a single receptive field in higher visual areas such as LOC and the temporal occipital cortex. If neurons in this area are unable to differentiate between shape and surround they would average the depth signal over the entire receptive field, causing an assimilation bias. Besides being physiologically plausible, this explanation of contrast versus assimilation biases is also in accordance with reports that assimilation biases are associated with integration by cue-invariant representations (in higher visual areas) whereas contrast biases are associated with integration by cue-dependent representations, typically found in early visual areas. The switch from contrast to assimilation with added noise might be caused by the fact that our noise methods especially degraded local information, shape could only be perceived after averaging depth information over the shape surface. Therefore the observers might have come to disrespect local information in favor of global information, probably represented in higher visual areas with large receptive fields. Additionally, when shape information is unreliable, the observer might also take into account the correlations that exist between image points that are spatially near to each other. Observers' knowledge of such correlations is evident in their ability to replace missing pixels in digital images based only on neighborhood information (Kersten, 1987). If observers fill in unreliable shape information with information from the surround by averaging or spatial smoothing, biases of assimilation would easily occur.

To summarize, we hypothesize that biases of shape contrast are caused by weighting of relative local shape cues, represented in early visual areas where receptive visual fields are small, whereas assimilation biases are caused by the low spatial resolution of receptive fields in higher visual areas where 3D shape from cue combination is encoded. When perceptual information in the central target is poor, subjects might come to rely more on the global shape signal in these higher areas.

Conclusions

We have shown that bias direction in shape–surround interactions depends on the reliability of shape signals. When shape information is relatively reliable, the surround invokes a contrast bias in shape perception. But when noise is added to the entire stimulus assimilation of shape and surround occurs. These findings suggest that shape and surround are integrated at different levels of the neural architecture involved in the perception of 3D shape. Relative information might be represented in lower visual areas whereas global shape information might be represented in higher visual areas such as the lateral and temporal occipital cortices.

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