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Distinct effects of contour smoothness and observer bias on visual persistence

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Abstract

Stable object perception relies on persistent yet temporary neural representations under constantly fluctuating stimulus conditions. The mechanisms by which such representations are formed and maintained are not fully understood but presumably involve interplay between early and higher-tier visual cortical mechanisms. Here we show that the visual persistence of highly camouflaged contours is based on the persistent operation of mechanisms sensitive to contour smoothness, which we dissociate from individual differences in response bias. Our results are consistent with existing models of visual cortical processing that predict persistent contour perception, which until now has not been studied systematically in relation to contour integration. We argue that the surprisingly long duration of contour persistence is in part due to response bias but that the strong modulatory effects of contour smoothness on persistence indicate sustained reverberation of a contour binding mechanism in visual cortex, a unique type of short-term visual memory that supports perceptual continuity.

Keywords: visual persistence, contour integration, camouflage, hysteresis, memory, reverberation, visual cortex

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Introduction

Contours are powerful indicators of object shape and surface boundaries. Visual sensitivity to the physical properties of contours is consistent with the statistical properties of contours in natural images (Geisler & Perry, 2009; Geisler, Perry, Super, & Gallogly, 2001), and this is often reflected in neurally plausible models of contour integration. The *association field* model of contour integration binds discrete edge information into perceptually continuous contours through mutual facilitation between visual cortical neurons with similarly oriented classical receptive fields (Field, Hayes, & Hess, 1993). The existence of an association field and other qualitatively similar contour integration mechanisms is consistent with patterns of long-range horizontal connections in visual cortex (Sigman, Cecchi, Gilbert, & Magnasco, 2001), as well as an abundance of corroborative psychophysical data. Here we are interested in the possibility that the association field supports the *persistence* of contour integration, and thus perceptual continuity in both space and time.

Stable perception relies on the capacity of neural circuits to temporarily maintain perceptual representations under constantly changing sensory input. The neural basis of this ability is not fully understood, but it may be partly due to intrinsic memory properties of early visual cortical mechanisms. For example, O'Herron & von der Heydt (2009, 2011) reported persistent figure-ground border ownership signals in single neurons in visual cortex, which they interpreted as the basis for stable figure-ground segmentation under fluctuating stimulus conditions. The existence of this type of persistent neural activity in visual cortex may be indicative of positive feedback loops within visual cortex (Grossberg, 2015). Accordingly, some have proposed that excitatory feedback circuits bind contour features (Francis, 1996; Francis, Grossberg, & Mingolla, 1994), but whether or not contour integration mechanisms like the association field exhibit persistence is uncertain. If so, this would mean that contour integration mechanisms play an essential foundational role in stable object perception.

Positive feedback models of contour processing in visual cortex predict that persistent contour binding should occur in the absence of an inhibitory reset signal, such as stimulus offset (Francis, 1999). Perceptual effects consistent with these predictions are evident in a demonstration (https://sites.google.com/site/visualformpersists/) adapted from Regan (1986). In the demonstration, a contour-defined bird becomes visible by virtue of structure-from-motion and, critically, it persists perceptually even after it stops moving (left demo), but only when the contour segments remain embedded in the camouflaging background (right demo). The duration of this type of *contour persistence* is typically 1-3 s, and contour visibility ends instantaneously when contour elements are physically removed (Ferber, Humphrey, & Vilis, 2003, 2005; Large, Aldcroft, & Vilis, 2005; Strother, Lavell, & Vilis, 2012; Strother et al., 2011), consistent with offset-initiated reset and the prevention of contour "hallucination" in the absence of supporting visual input (Li, 1998). The duration contour persistence is considerably longer than the neural persistence reported by O'Herron & von der Heydt (2009, 2011) for figure-ground border ownership signals in visual cortex (0-1.3 s), and it is also longer than any other type of shape-related visual persistence we are aware of (e.g., Bruchmann, Thaler, & Vorberg, 2015; Landman, Spekreijse, & Lamme, 2003; O'Herron & von der Heydt, 2011; Shioiri & Cavanagh, 1992; Supèr, Spekreijse, & Lamme, 2001; Wallis, Williams, & Arnold, 2009; Wutz, Weisz, Braun, & Melcher, 2014). The relatively long duration of contour persistence is remarkable in its own right, and may reflect the size of the underlying neural network (Compte, Brunel, Goldman-Rakic, & Wang, 2000; Toyoizumi, 2012).

The first published study of contour persistence focused on the maintenance of motion-defined groupings in object-selective lateral occipital cortex (Ferber et al., 2003), well beyond the cortical locus of an association field in V1. Unlike V1 neurons, neurons in lateral occipital cortex (LOC) represent a shape independent of the physical properties of its defining contour (Altmann, Bülthoff, & Kourtzi, 2003; Kourtzi & Kanwisher, 2001). Thus, visual persistence of contour-defined form limited to LOC would suggest that V1 merely sends feedforward signals to LOC, in contrast to evidence that V1 and LOC are part of a recurrent contour processing circuit (Drewes, Goren, Zhu, & Elder, 2016; Shpaner, Molholm, Forde, & Foxe, 2013; Wokke, Vandenbroucke, Scholte, & Lamme, 2013). A study by Strother et al. (2012) showed that persistent neural activity could be traced to the retinotopically-defined representation of a contour in primary visual cortex, which supports the possibility that contour persistence is rooted in the sustained activation of low-level (e.g., V1) contour integration mechanisms.

In support of this possibility, previous studies showed that scrambling contour elements and increasing inter-element distance can decrease the duration of contour persistence (Ferber & Emrich, 2007; Ferber et al., 2005; Strother & Alferov, 2014), but none of these studies systematically manipulated inter-element orientation, as in more traditional psychophysical studies of contour integration. We performed our first experiment to measure the effect of parametric manipulations of contour smoothness on contour persistence, which has never been done, and is necessary to entertain the possible involvement of the association field mechanism of contour integration. This experiment, and two others, also allowed us to differentiate effects of contour smoothness on persistent contour integration from individual differences in observer bias to perceive a contour as having disappeared into a camouflaging background.

Methods

Subjects

Eighteen volunteers (20-36 years of age, 6 female; all were naïve except for one of the authors) participated in all three experiments. All observers were right-handed, with normal or corrected-to-normal vision. Informed consents were collected and the study was approval by the Institutional Review Board of University of Nevada, Reno.

Apparatus

All experiments were conducted using a 20-inch Dell Trinitron P991 monitor (1024 × 768 resolution) with an 85-Hz refresh rate. The stimulus computer was a 2.4-GHz Mac Mini with an NVIDA GeForce 320M graphics processor (256 MB of DDR2 SDRAM). Stimuli were created and presented using Psychtoolbox-3 (Kleiner et al., 2007) for MATLAB (Mathworks Inc., Natick, MA). Participants viewed stimuli binocularly from a distance of 60 cm in all three experiments.

Experiment 1: Contour Persistence

Stimuli and Procedure

In a dim room, participants viewed arrays of short black line segments (0.3º × 0.03º) against a white background upon which additional line segments forming a circular contour were superimposed after a brief delay (Figure 1). Observers were instructed to fixate a blue cross (0.3º × 0.3º) at the center of the screen and press a button when contour circle was no longer visible. On each trial, the background array was presented first, and after 2 s, a contour circle appeared with abrupt onset against the background array, always centered within the aperture (https://sites.google.com/site/experimentdemos/). Background line segment arrays consisted of 3250 line segments displayed across the entire screen (36.9º × 28.1º), with a density of ~3.13 segments/deg^2. Circle contour segments covered 40% of the of the contour circle's circumference. Both the background and embedded circle remained on the screen for 6 s, during which time observers responded with a button-press indicating that they could no longer see the circle. It is important to note that, although the circle and background did not change physically during this time, circles appeared to fade into the background. After the 6 s response period, the screen went blank for 1 s, and the next trial began. This cycle repeated until the end of the experiment.

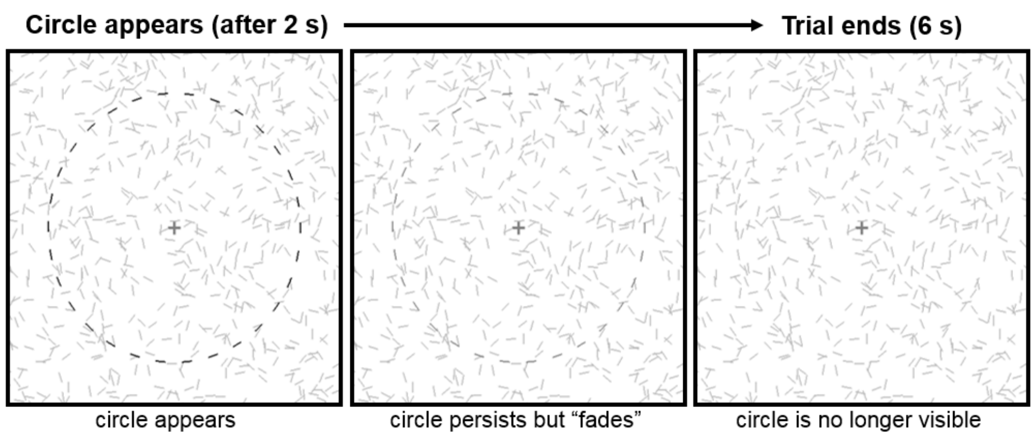

Figure 1. Illustration of contour persistence during a trial. Once a contour circle appeared against a camouflaging background it was perceived to fade even though its comprising elements remained superimposed on the background. The task of observers was to indicate when the circle was no longer visible. Although the color of line segments belonging to circle and background differs here for purpose of illustration, all line segments were black in the experiment.

The radii of contour circles were either 1.5º, 3º or 4.5º to create uncertainty with respect to contour location in visual field. The smoothness of the circular contour was manipulated by changing range of the angle (α) between line segments and corresponding tangents to the circular path (Figure 2a), which varied from 0º (smooth and co-circular) to 60º (jagged circles comprised of line segments with randomly varying α between 0º and 60º). Contour smoothness was restricted between 0º to 60º (in 10º increments) because results of a pilot study indicated no change in visibility between 60º and 90º; Figure 2b shows examples. Contour circle radii were changed trial by trial in order to reduce predictability and to avoid potential adaptation effects. All combinations of jitter and circle size were implemented randomly within the cycle of experimental trials. Observers completed 20 practice trials, and then 20 to 30 trials for each of the seven levels of contour smoothness (for a minimum total of 140 and a maximum total of 210 experiment trials over the course of ~35 minutes, with three opportunities to rest).

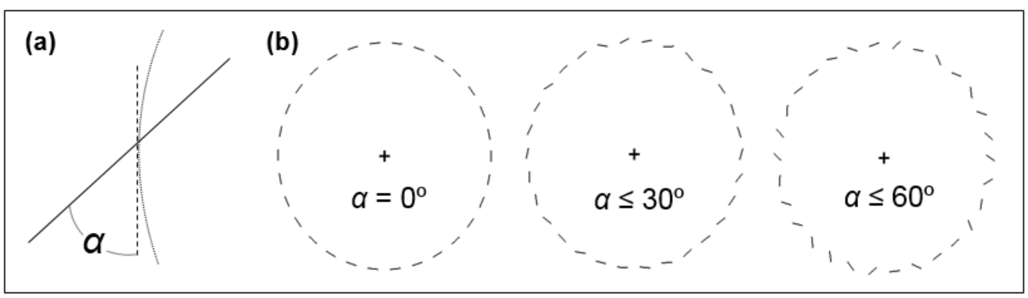

Figure 2. The smoothness of contour circles was allowed to vary as a function of α, the angle between a contour element and a tangent to the circle, as shown in (a). Three examples are shown in (b); as α increases circle contours become less smooth. Note that α is not fixed, and the value of α is the maximum deviation of the orientation of a contour element from the tangent to the circle at the location of the element.

Results and discussion

We measured observers' response times (RTs) indicating that a previously visible contour had disappeared. All analyses were performed on the relationship between α and RT. Although circle size was allowed to vary randomly, we did not include it in our analyses due to the limited number of trials per condition per observer (and Strother & Alferov, 2014, reported some degree of scale-invariance). RTs were longest for α = 0º (mean = 2.92 s) and shortest for α = 60º (mean = 2.16 s), indicating an overall difference of .76 s between the two most extreme contour smoothness conditions. The leftmost graph in Figure 3 is a scatterplot of individual observers' mean RTs at each level of α fit with a regression line. A group-level linear regression analysis of the effect of α on RT was highly significant, $R^2 = 0.39$, $F(1, 124) = 22.04$, $p < 0.001$, meaning that contour smoothness predicted the duration of contour persistence such that the duration of persistence decreased as the contour became less aligned. We also performed a one-way repeated-measures analysis of variance (ANOVA) to identify which levels of α had the greatest effect on RT because, as is evident in Figure 3, RTs were similar for α=0° and α=10°, and also for α= 40°, α= 50° and α=60°. As expected this ANOVA revealed a significant main effect of α on RT ($F(6, 102) = 47.34$, $p < 0.001$), and importantly, Bonferroni corrected pairwise comparisons showed that RTs for α=0° and α=10° were longer that RTs for α > 10° (but not different from each other), and RTs for α= 40°, α= 50° and α=60° did not differ from each other but were significantly shorter than α < 40° (all p-values < 0.05). This means that, at a group level, the greatest effects of α on RT occurred between 10°

and 40°, with an overall difference in RTs between min and max α was ~.75 s.

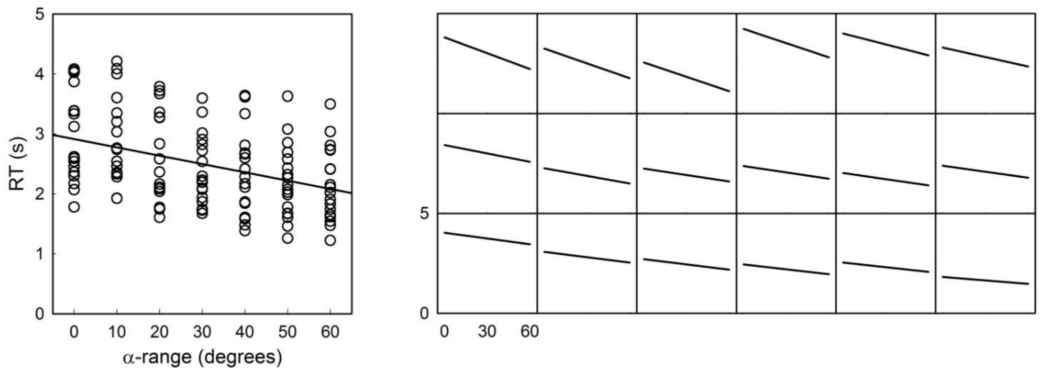

Figure 3. Results from Experiment 1. The left graph is a scatterplot of individual observers' mean RTs indicating duration of contour persistence at each level of α. The negative slope of the regression line indicates decreasing persistence with decreases in contour smoothness. The right graphs show regression lines for individual observers (plotted on the same scale as the group results) sorted by steepness of slope.

In addition to our group-level analyses, we performed linear regression analyses on individual observers' data in order to obtain operationally-defined measures of *sensitivity* to α (regression coefficients) and also individual observer *bias*, measured as mean RT (averaged across all α levels), to be used in subsequent correlation analyses. The matrix of graphs in Figure 3 shows regression lines for individual observers. In agreement with our group level analyses, linear regression analyses for all except one observer (whose slope was nevertheless negative) were statistically significant (p always < 0.05). The range of α sensitivities was -0.006 to -0.026 s/deg, and the range of bias was between 1.65 to 3.75 s. When we performed a Pearson correlation on sensitivity and bias we found that the two measures were not correlated, $r(16) = -0.35$, $p = 0.15$. This is important because it suggests that α sensitivity and bias to report contour disappearance are independent.

Experiment 2: Background *accretion* and contour hysteresis

Stimuli and Procedure

In this experiment we used a novel paradigm to investigate the hysteresis of contour visibility as a function of contour smoothness in the context of *increasing* background density. On each trial, a contour circle was presented in the absence of a background, and 30 ms after its onset, background line segments were added at a rate of 15 line segments per 30 ms (Figure 4); this processes looped and 15 background line segments were added simultaneously during each iteration (https://sites.google.com/site/experimentdemos/). Observers were instructed to press a button as soon the contour circle became fully camouflaged by the accreting background (number of background elements present at time of button-press was the dependent measure). Properties of the contour circle (radii, line segment size, orientations and spacing within the circular contour) were identical to those of the contour circles used in Experiment 1, as were the fixation instructions, number of trials, 1 s inter-trial interval and opportunities for breaks.

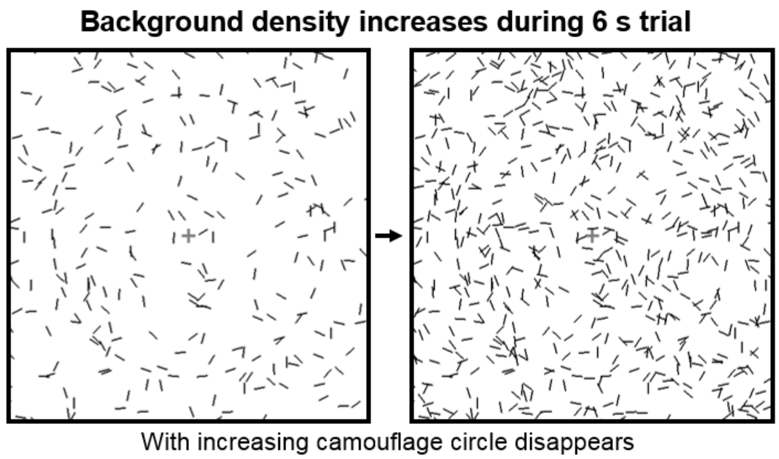

Figure 4. Illustration of trial in which a circular contour becomes increasingly camouflaged as the density of the background is increased. Background changes were always incremental and observers indicated when they could no longer see the circle.

Results and discussion

To measure the effect of contour smoothness on hysteresis, we recorded the density of dynamic increasingly camouflaging background at the point when observers indicated that a previously visible contour had disappeared. The leftmost graph in Figure 5 is a scatterplot of individual observers' data at each level of α fit with a regression line. A group linear regression analysis of the effect of α on hysteresis was highly significant, $R^2 = 0.84$, $F(1, 124) = 304.29$, $p < 0.001$. We also performed a repeated measures ANOVA, which showed results similar to those reported for Experiment 1: a significant main effect of α ($F(6, 102) = 76.09$, $p < 0.001$), such that background density at time of contour disappearance was greatest for α=0º (Mean = 2.47 segments/deg^2) and least for α=60º (Mean = 1.55 segments/deg^2); and Bonferroni corrected pairwise comparisons showed that effects of contour smoothness were greatest between α=10º and α=50º. Contours with α=0° and α=10° required denser backgrounds to become fully camouflaged as compared to contours with α > 10° (but α=0° and α=10° did not different from each other, as in Experiment 1). Background densities for α= 50° and α=60° did not differ from each other but were significantly shorter than α < 50° (p always < 0.05). This means that, at a group level, the greatest effects of α on background density required for full camouflage occurred between 10° and 50°, with an overall difference in background density between min and max α of .92 segments/deg^2.

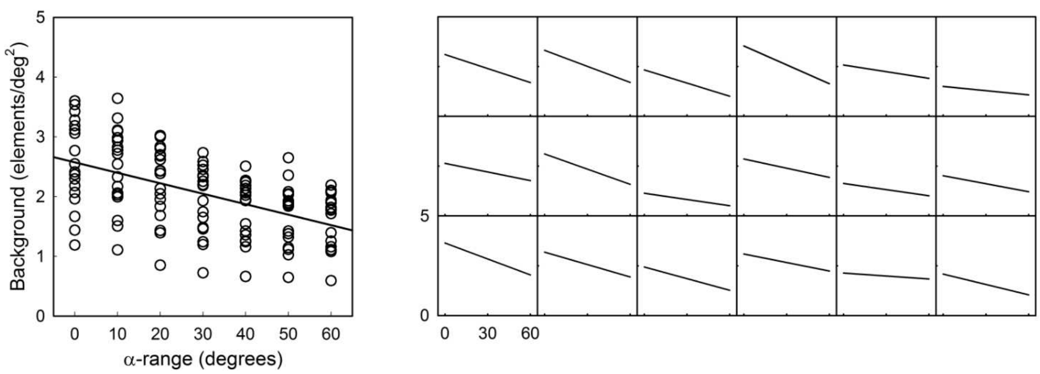

Figure 5. Results from Experiment 2. The left graph is a scatterplot of background densities, for each level of α, at which observers reported the contour circle to disappear. The negative slope of the regression line means that with decreases in contour smoothness, a progressively less dense background was required for full camouflage. The right graphs show regression lines for individual observers (plotted on the same scale as the group results) in the same order as Figure 3.

As in Experiment 1, we performed linear regression analyses on individual observers' data in order to obtain measures of sensitivity and bias. The matrix of graphs in Figure 5 shows regression lines for individual observers. Linear regression analyses were statistically significant for all observers (p always < 0.05). The range of regression coefficients (sensitivities) was -0.030 to -0.005 segments/deg^2 per jitter degree, and the range of background densities averaged across α (bias) was between 0.80 to 2.73 segments/deg^2. Pearson correlation showed that the slope and mean were correlated (unlike in Experiment 1) such that steeper slopes were correlated with greater degrees of bias, $r(16) = -0.60$, $p < 0.01$.

Experiment 3: Background *deletion* and contour detection

Stimuli and Procedure

In this experiment we investigated the detectability of contours embedded within a background of *decreasing* density as a function of contour smoothness. On each trial, a contour circle fully camouflaged by a dense array of background line segments and gradually became visible as background line segments were removed (Figure 6). As in Experiment 2, the process of changing the background began 30 ms into the trial, after which the 5000 background line segments were gradually reduced to zero by the end of the trial (https://sites.google.com/site/experimentdemos/). Line segments were removed at a rate of 15 line segments per 30 ms for the first 3000 line segments and 10 line segments per loop iteration for the remaining 2000 line segments. Pilot results showed that high line segment deletion rates late in the trial resulted in an inability of observers to respond prior to the complete disappearance of the background (as in Experiment 2, the dependent measure was number of background elements at the time of button-press).

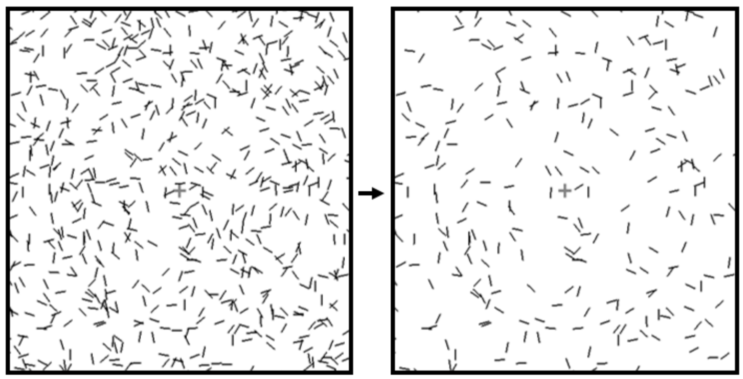

Figure 6. Illustration of trial in which a circular contour becomes increasingly visible as the density of the background is decreased. Background changes were always incremental and observers indicated when a camouflaged circle became visible.

Results and discussion

To measure the effect of contour smoothness on contour detection, we recorded the density of dynamic increasingly camouflaging background at the point when observers indicated that a completely camouflaged contour became visible. The leftmost graph in Figure 7 is a scatterplot of individual observers' data at each level of α fit with a regression line. As expected, a group linear regression analysis of the effect of α on detectability was highly significant, $R^2 = 0.71$, $F(1, 124) = 304.29$, $p < 0.001$, which means that the necessary density of the background to maintain full camouflage decreased as the contour became less smooth. We also performed a repeated measures ANOVA, which showed results similar to those reported for

Experiment 1: a significant main effect of α , $F(6, 102) = 164.71$, $p < 0.001$, such that background density at time of contour detection was greatest for α=0º (Mean = 1.95 segments/deg^2) and least for α=60º (Mean = 0.55 segments/deg^2); and Bonferroni corrected pairwise comparisons (p always < 0.05) showed that effects of contour smoothness were greatest between α=10º and α=60º. Contours with α=0° and α=10° required denser backgrounds to become fully camouflaged as compared to contours with α > 10° but did not different from each other (as in Experiments 1 and 2). In short, the greatest effects of α on background density required for detection occurred between 10° and 60°, with an overall difference in background density between min and max α of 1.4 segments/deg^2. This indicates a greater effect of α on visibility as compared to Experiment 2, and the overall difference in bias (mean background density required for full camouflage), which was less for this experiment as compared to Experiment 2, is consistent with effects of perceptual hysteresis of "visibility" versus "invisibility" in detection tasks in general.

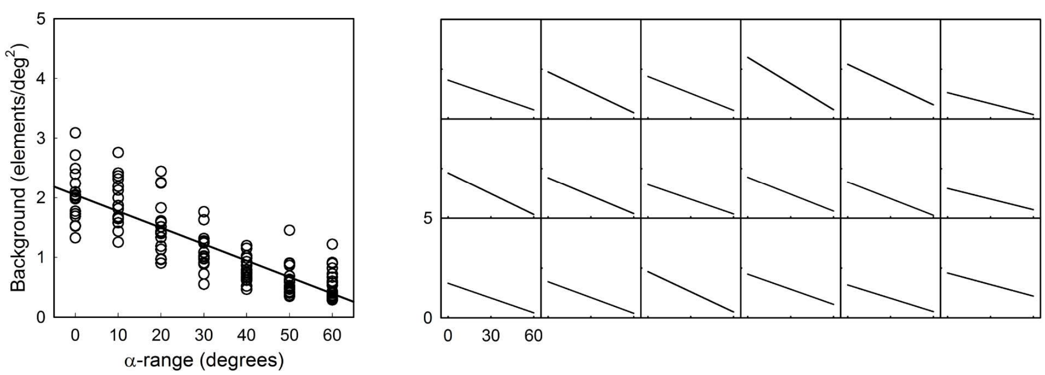

Figure 7. Results from Experiment 3. The left graph is a scatterplot of background densities (plotted on same scale as Experiment 2, Figure 5), for each level of α, at

which observers reported a contour circle to become visible. The negative slope of the regression line means that with decreases in contour smoothness, a progressively less dense background was required for contour visibility. The right graphs show regression lines for individual observers (plotted on the same scale as the group results) in the same order as Figures 3 and 5.

As in the previous experiments, we performed linear regression analyses on individual observers' data in order to obtain measures of sensitivity and bias. The matrix of graphs in Figure 7 shows regression lines for individual observers. Linear regression analyses were statistically significant for all observers (p always < 0.05). The range of regression coefficients was -0.042 to -0.017 segments/deg^2 per jitter degree, and the range of mean was between 0.76 to 1.82 segments/deg^2. Pearson correlation showed that the slope and mean were correlated, $r(16) = -0.61$, $p < 0.01$ (as in Experiment 2, but unlike in Experiment 1).

Inter-experiment correlations

In addition to conducting correlation analyses on the sensitivity and bias measures within each experiment, we assessed correlations between these measures between the three experiments (Figure 8). We found that sensitivity to changes in α were correlated across all three experiments: Pearson correlation of sensitivity in Experiment 1 (contour persistence) and Experiment 2 (contour hysteresis) was $r(16) = 0.48$, $p = 0.043$; Pearson correlation of sensitivity in Experiment 1 (contour persistence) and Experiment 3 (contour detection) was $r(16) = 0.47$, $p = 0.048$; and Pearson correlation sensitivity in Experiment 2 (contour hysteresis) and Experiment 3 (contour detection) was r(16) = 0.52, p = 0.026.

We also performed correlation analyses on individual observer bias: Pearson correlation of sensitivity in Experiment 1 (contour persistence) and Experiment 2 (contour hysteresis) was , r(16) = 0.56, p = 0.015; Pearson correlation of sensitivity in Experiment 1 (contour persistence) and Experiment 3 (contour detection) was r(16) = 0.22, p = 0.39; and Pearson correlation sensitivity in Experiment 2 (contour hysteresis) and Experiment 3 (contour detection) was r(16) = 0.34, p = 0.17.

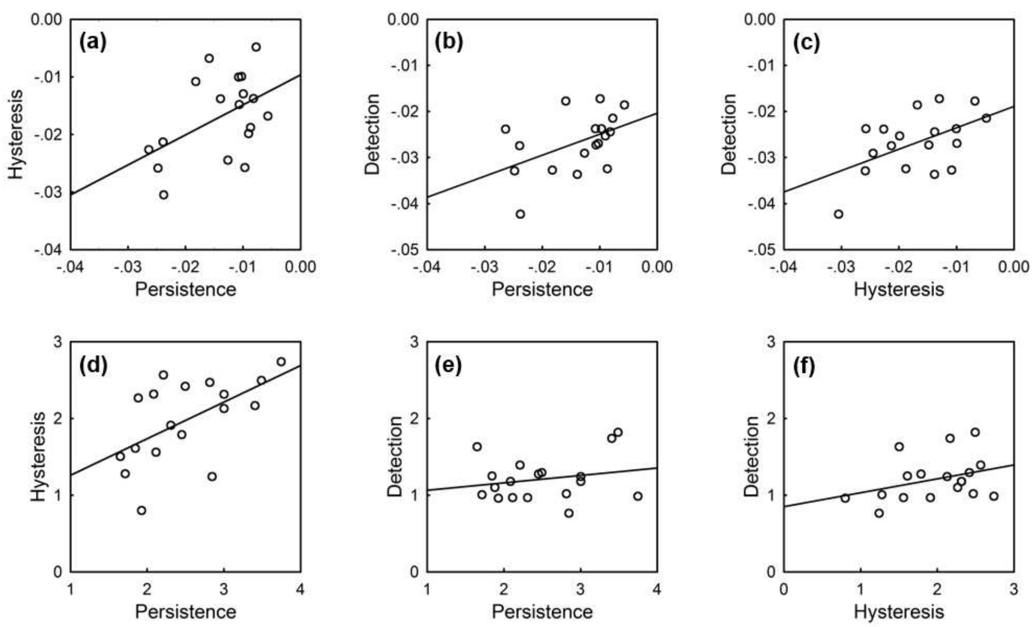

Figure 8. Inter-experiment correlation analyses showed that whereas observers' sensitivities were correlated between experiments, bias was not, except for Experiments 1 (contour persistence) and 2 (contour hysteresis). The top row of scatterplots shows significant correlations of observers' sensitivities to α (regression coefficients) across all three experiments: (a) Experiments 1 and 2; (b) Experiments 1 and 3; and (c) Experiments 2 and 3. The bottom row of scatterplots show a significant correlation of observer bias (overall means) between Experiments 1 and 2 (d), but no

significant correlations were found for bias between Experiments 1 and 3 (e), or between Experiments 2 and 3 (f).

General Discussion

The main goal of our study was to show that contour persistence is founded upon the sustained operation of a smoothness-sensitive contour integration mechanism. In Experiment 1 we showed that increasing contour smoothness resulted in increasing persistence durations. The effect of contour smoothness on the duration contour persistence parallels the effects of contour smoothness on detectability in psychophysical studies of contour integration (for reviews see R. Hess & Field, 1999; R. F. Hess, Hayes, & Field, 2003). This finding alone suggests that intrinsic reverberation of the association field is the basis of contour persistence, possibly in combination with top-down feedback, which plays an important role in contour integration more generally (Gilbert & Li, 2013). Crucially, however, we also showed that the influence of contour smoothness can be dissociated from individual differences in response bias. This means that contour persistence reflects a confluence of bottom-up and top-down influences rather than a mere delay in reporting that a camouflaged contour is no longer visible. Because both factors were expected to contribute to the duration of contour persistence, to different degrees in different individuals, we performed our analyses on operationally defined measures of *sensitivity* to contour smoothness and response *bias.*

We defined sensitivity as the slope (regression coefficient) of a regression line fit to persistence durations as a function of α for individual observers, and we defined bias as the mean value of the dependent measure used in each experiment, for individual observers, averaged across the different levels of α. As expected, we also observed considerable variability in each measure across individuals in all three experiments. By testing more subjects than is typical in psychophysical studies of contour integration, we were able to show that smoothness sensitivity and response bias were uncorrelated in Experiment 1, although this was not the case for Experiments 2 and 3. We interpret this relative de-coupling (but not necessarily independence) of individuals' sensitivities to α and response bias as indicative of distinct contributions of stimulus and observer to the duration of contour persistence. That is, even if it is the case that the notably long duration of contour persistence—approximately 2.5 s on average—is in part due to observer bias, roughly 40% (~1 s) of this, on average, is explained by the effect of contour smoothness. This means that, not only is the overall duration of persistence relatively long as compared to other types of visual persistence (e.g., Bruchmann et al., 2015; Landman et al., 2003; O'Herron & von der Heydt, 2011; Shioiri & Cavanagh, 1992; Supèr et al., 2001; Wallis et al., 2009; Wutz et al., 2014), the time scale over which it is modulated by contour smoothness is also quite long.

If we attribute the modulation of contour persistence as being due to an association field or similar contour integration mechanism, then this mechanism itself exhibits persistence. One could argue that a smoothness-sensitive contour integration mechanism (e.g., in V1) merely passes on a stronger input to a higher-tier shape representation (e.g., in LOC, Altmann et al., 2003; Fang, Kersten, & Murray, 2008; Kourtzi, Tolias, Altmann, Augath, & Logothetis, 2003), which serves as the locus of persistence, as proposed in the first study of contour persistence (Ferber et al., 2003). If so, then the longer duration of persistence for smooth contours would be due to the effect of contour smoothness on the initial input to this representation, with stronger input for smoother contours. However, if this were the case, then early visual cortex (e.g., V1) would not need to participate after relaying its inputs to higher-tier areas like LOC. Two fMRI studies by Strother and colleagues showed that this is not the case, and that contour-specific neural activity in V1 was correlated with the duration of contour persistence (Strother et al., 2012; Strother et al., 2011). Their findings were consistent with the idea that, rather than passively inheriting input from early visual cortex, a V1-LOC loop entails recurrent input verification (i.e., checking whether or not contour edges have been physically removed) to sustain a persistent contour representation. This behavior of the V1-LOC circuit during contour persistence is consistent with recent neurophysiological findings (Drewes et al., 2016), and may be related to "input filtering" (Patten et al., 2015).

In addition to our analysis of smoothness sensitivity and observer bias in Experiment 1, we also performed within-experiment correlation analyses within Experiments 2 and 3. In contrast to Experiment 1, sensitivity and bias were significantly correlated within Experiments 2 and 3. The negative correlations for Experiments 2 and 3 indicate that observers who were more sensitive to contour smoothness tended to show less of a contribution of bias (i.e., sensitive observers are more "objective" in the sense that their performance is better predicted by stimulus properties than by idiosyncratic bias). This means, that whereas sensitivity to contours smoothness in Experiments 1 and 2 can be diluted by observer bias (for reasons that are unclear), this was not the case for Experiment 1, further evidence in favor of the relative independence of sensitivity and bias in persistence, even though we cannot say that the two are fully independent. This is important because we are claiming that even though some portion of the duration of contour persistence is due to observer bias, a substantial portion reflects the sustained operation of a smoothness-sensitive contour integration mechanism.

In addition to performing correlations between sensitivity and bias within experiments, we also performed between-experiment correlations. We found that individuals' sensitivities to contour smoothness were positively correlated across all three experiments (Figure 8), such that observers with steep slopes relative to other observers tended to exhibit this across the different experiments. This is reassuring given the difference in dependent measures, and means that individuals' smoothness sensitivities in contour persistence predict their smoothness sensitivities in other contexts and tasks, including detection, which is routinely employed to study contour integration. This correlation was not guaranteed given the variable influences of task, stimulus context and top-down influences on contour (Gilbert & Li, 2013; Qiu, Burton, Kersten, & Olman, 2016; Robol, Casco, & Dakin, 2012), and the fact that individuals' slopes were not identical across experiments (albeit highly similar). In short, consistency of contour smoothness sensitivity further reinforces our view that contour persistence reflects the persistent operation of a smoothness-sensitive contour integration mechanism.

In contrast to inter-experiment correlations of contour smoothness sensitivity, the only significant correlation in bias was between Experiments 1 and 2. This implication of this is that while individual differences in bias to report contour disappearance in Experiments 1 and 2 are mutually predictive, and reflect similarity of task (to maintain contour representation in the face of impending camouflage), irrespective of context (static versus increasing background density). This finding was somewhat surprising given the lack of correlation in bias between Experiments 2 and 3. Taken together, these results suggest that the correlation in bias for Experiments 1 and 2 reflects an "I no longer see it" criterion that is distinct from an "I see it" criterion, either as the result of task and/or context. This is interesting in its own right, and it further highlights the dissociation between sensitivity and bias, which were correlated in Experiments 2 and 3 (but not Experiment 1), but nevertheless show different patterns of inter-experiment correlation.

In conclusion, the distinct effects of smoothness sensitivity and bias on contour persistence shown here are consistent with the persistent reverberation of contour integration circuits in visual cortex. We previously speculated about the involvement of an association field mechanism in contour persistence (Strother & Alferov, 2014; Strother et al., 2012), in addition to top-down effects related the recognition of a contour-defined object (Emrich, Ruppel, & Ferber, 2008; Strother et al., 2011). Persistent contour representation is explicitly predicted by some models of visual cortical processing, especially in the absence of positive feedback loop re-setting (e.g., Francis et al., 1994; Grossberg, 2015). Taken together with our findings, we conclude that the association field of contour integration, or similar visual cortical mechanism, is a likely neural basis of perceptual continuity in both space and time.

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