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Abstract

A critical step in visual perceptual processing is integrating local visual elements into contours so that shapes can be derived from them. It is often assumed that contour integration may reflect hardwired coding of low-level visual features. In this study, we present novel evidence indicating that integration of local elements into contours can be learned subliminally, despite being irrelevant to the training task and despite the local properties of the display varying randomly during training. Learning occurred only when contours were consistently paired with task-relevant targets—echoing the findings of previous studies on subliminal learning of low-level features. Our data indicate that task-irrelevant, exposure-based learning extends beyond local low-level visual features and may play a critical role at multiple levels of visual perceptual organization.

Keywords

learning, visual perception, attention, cognitive development

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Scene perception depends on perceptual organization processes that group local visual elements into global structures and segment them from the scene's background. A typical example of this is contour integration, in which separate but aligned local elements are grouped and segmented from a background texture of similar elements. The processing of global contours maintains the Gestalt rule of good continuation, which is also common in natural scenes (Geisler, Perry, Super, & Gallogly, 2001; Sigman, Cecchi, Gilbert, & Magnasco, 2001). Although some basic characteristics of contour integration are consistent with the "hardwired" neural connectivity in the primary visual cortex (e.g., Field, Hayes, & Hess, 1993; Li & Gilbert, 2002), recent studies have demonstrated that longitudinal development and learning of contour detection continue into adulthood. This evidence supports the notion that perceptual organization can be adapted to different visual contexts (e.g., Kovacs, Kozma, Feher, & Benedek, 1999; Li, Piech, & Gilbert, 2008; Schwarzkopf, Zhang, & Kourtzi, 2009).

Recently, Li et al. (2008) used extracellular recording in monkeys to show that contour-detection training enhanced neuronal responses in the primary visual cortex to aligned local segments, and these enhanced responses were associated with improved perceptual contour detection. However, this training effect was eliminated by anesthesia and was limited to late phases of the neural response; hence, it may be permeated

by top-down processes (e.g., Lamme, 1995). These findings indicate that contour integration reflects the adaptability of visual processes in perceptual organization.

What factors may be critical for learning contour representations? There are two major possibilities: (a) repeated exposure to aligned local elements and (b) enhanced response to features relevant to a target contour. The latter has been suggested by Li et al. (2008), who found significant contourrelated response modulation in the primary visual cortex after training with contour detection, but not after exposure to taskirrelevant contours. However, in that study, exposures to taskirrelevant contours always preceded exposures to task-relevant contours, so the lack of learning for task-irrelevant stimuli could have been due to insufficient exposure. There have been several recent studies showing that under certain conditions, consistent exposure to task-irrelevant features can improve detection (e.g., Chun & Jiang, 2003; Deroost & Soetens, 2006; Frenkel et al., 2006; Godde, Stauffenberg, Spengler, & Dinse, 2000), even when the features are presented subliminally during learning (Nishina, Seitz, Kawato, & Watanabe, 2007;

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Watanabe et al., 2002; Watanabe, Nanez, & Sasaki, 2001; for a review, see Seitz & Watanabe, 2009). In the present study, we applied the method of subliminal learning to investigate the possibility of task-irrelevant contour learning.

It has been demonstrated that subliminal learning—that is, decreases in the threshold of detection of an irrelevant background feature after exposures to unresolved levels of the feature requires consistent exposures to a perceptible target along with the unresolved background feature (Seitz & Watanabe, 2003). This learning is typically highly specific to the feature presented during training. To date, subliminal learning has been shown only for low-level features that are spatially local, such as local dot motion (Watanabe et al., 2001, 2002) or static Gabor patches (Nishina et al., 2007). In our study, we assessed whether subliminal learning extends to a level at which local elements are integrated into global contours. Providing evidence of subliminal learning would indicate that contour integration is facilitated even by task-irrelevant contour exposure. It is critical to note that we took steps to ensure that local (background) properties of the displays varied randomly during learning; hence, learning should reflect grouping abstracted from the local elements present on each learning trial.

In our study, exposure to subliminal task-irrelevant global contours took place as participants trained on a task that required the identification of a slow rotation in one of two sequentially displayed, suprathreshold foreground shapes. A subliminal global contour was always presented in the background of one of the two displays (randomly selected). This contour was composed of local, oriented elements and was embedded within a random array of similar local elements. The other background display included only randomly distributed oriented elements. Subliminal learning was tested in two groups of participants differing only in whether they were shown subliminal contours that were paired consistently or randomly with a foreground target.

Method

Participants

Nineteen University of Birmingham undergraduate students with normal or corrected-to-normal vision were recruited. One participant was excluded because of high variability in preliminary tests. Nine participants (7 females and 2 males; mean age = 20.7 ± 3.0 years) were included in the consistent-pairing training group. The other 9 participants (6 females and 3 males; mean age = 21.3 ± 3.6 years) were included in the random-pairing training group.

Stimuli and apparatus

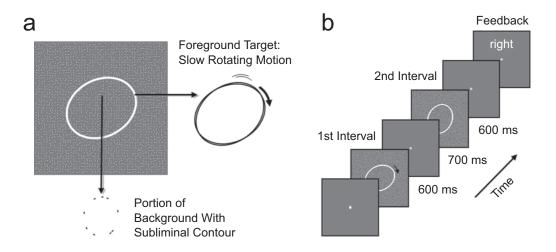
Stimuli were displayed on a 21-in. Samsung (Ridgefield Park, NJ) SyncMaster monitor (with Asus X1300 video card; ATI Radeon, Sunnyvale, CA; 1,280 × 1,024; 60-Hz refresh rate) driven by an Intel Core 2 computer. Stimuli were generated in

real time using a MATLAB-based PsychToolBox environment (Brainard, 1997). Luminance was linearized by an 8-bit lookup table. The stimuli were viewed in a dark room at a distance of 57 cm, using a chin rest.

Training stimuli. The training stimuli subtended an area of 21° × 21° and consisted of a central foreground shape (a single white line that formed an ellipse, with an average size of 9.2° × 11.5°) displayed against a background array of local elements (see Fig. 1a). The aspect ratio (ranging between 0.76 and 0.84) and orientation of the shape varied randomly. There were two kinds of foreground shapes: target and nontarget. A target foreground shape rotated slowly around its center (0.72 deg/s on the first trial; rotation speed was adjusted in the following trials). Rotation direction varied randomly across trials. A nontarget foreground shape was displayed statically. The background of all training displays included approximately 2,166 local, elongated, pseudorandomly positioned Gabor elements of the same size (envelope $SD = 0.09^{\circ}$ along the carrier axis and 0.11° along the orthogonal axes), spatial frequency (5.1 cycles/deg), and phase (90°). These background elements were randomly oriented and irrelevant to the task.

In half of the stimuli, several local elements were arranged to form a global contour drawn from the general class of elliptic contour (average size of 5.3° × 6.3°; the element capacity was always 40). These were the trained contours (see Fig. 1c; left image). The number of contour elements was set individually so that, for each participant, the global-contour-detection level was one staircase step below his or her detection threshold (see the Procedure section); this level was maintained throughout. Random background elements that overlapped a contour were excluded. This procedure reduced element density locally, but the effect was small and spatially random, given the small numbers of contour elements and the random variation in the distribution of local elements. The subliminal contour was presented at the center of the display, always within the area bounded by the foreground shape. To minimize the contributions of local features to contour learning (see the appendix), we varied randomly and independently the aspect ratio (between 0.78 and 0.9) and the global orientation of the contour, as well as the positions of the local elements making up the contour, across trials. Also, the global contours and the foreground shapes varied independently of each other in their size and global orientation. Consequently, the likelihood of pairing locally the foreground target with a specific local orientation was minimal.

Testing stimuli. The testing stimuli subtended an area of $11^{\circ} \times 11^{\circ}$ and consisted of a random array of local elements similar to the training background stimuli (there was no foreground shape). Half of the displays also included a global contour, and half did not. The global shape of the contour was drawn pseudorandomly from one of two shape types: elliptic (trained) and angular, triangle-like (not trained; Fig. 1c). The overall display



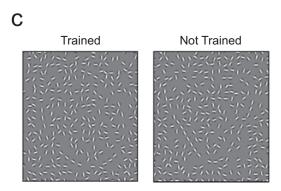


Fig. 1. Stimuli and trial design. Target training stimuli (a) featured a foreground elliptical shape that rotated slowly at a rate that was above the participant's detection threshold. Nontarget stimuli included a similar foreground shape that was displayed statically. The stimulus background always included a random array of local Gabor elements, either with or without an embedded subliminal global contour. In the training trials (b), two training stimuli were presented sequentially, each for 600 ms, with an interstimulus interval of 700 ms. One stimulus included the target (i.e., rotating foreground shape), and the other stimulus included the nontarget static shape. The task was to report the stimulus interval containing the rotating foreground shape. Participants received feedback about their response accuracy at the end of each trial (the word "right" in white or the word "wrong" in black; approximately 7° above the fixation point). The background of only one of the stimuli included an embedded subliminal contour among the random elements. Examples of trained and not-trained contour shapes used in threshold and constant-level testing blocks (see Fig. 2) are shown in (c). For the purpose of illustration, the contours in this figure include more elements than were typically used in the actual tests.

area for the test stimuli (but not the contour area) was smaller than the display area for the training stimuli in order to minimize the effects of spatial attention on contour detection. The number of contour elements depended on the type of testing block (i.e., whether it was a threshold or a constant-level test; see the Procedure section).

Procedure

The two participant groups went through an identical experimental procedure during the training blocks and were exposed to similar numbers of foreground and background stimuli. However, for the consistent-pairing group, foreground targets were consistently paired with subliminal background contours, and nontarget foreground shapes were paired with random background arrays. For the random-pairing group, the

presentations of targets and the subliminal contours were not correlated. All testing blocks were run in the same manner for the two groups.

Each participant completed six experimental sessions comprising training blocks and testing blocks (Fig. 2; sessions usually took about 1.5 hr to complete). Across 20 training blocks throughout the six sessions, participants were exposed to the task-irrelevant subliminal contours while they attempted to identify the foreground target. Contour detection capability was assessed during the experiment in two types of testing blocks: threshold and constant-level testing. Threshold testing blocks assessed each participant's contour-detection thresholds before and after the training period (at the beginning of Session 1 and at the end of Session 6, respectively). The difference between contour-detection thresholds at these time points indexed the level of contour-detection learning. Pretraining threshold data

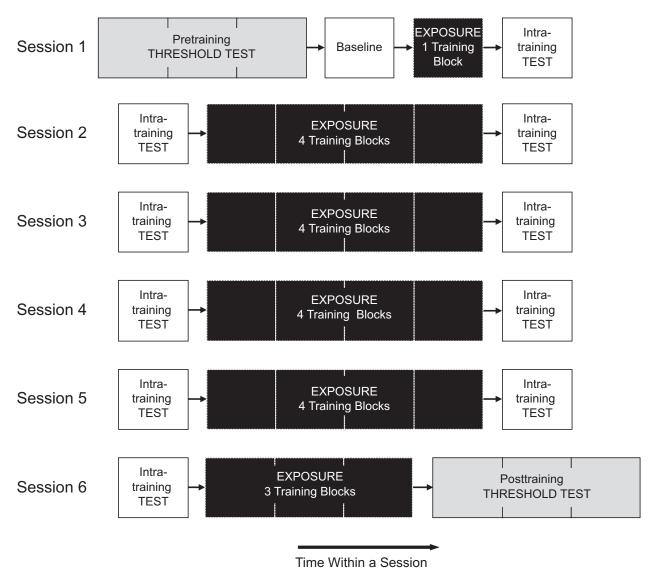


Fig. 2. Design of the experiment. Each participant took part in six experimental sessions. Exposure to subliminal contours took place during training blocks. Contour-detection thresholds were evaluated for each participant at the beginning of Session I and at the end of Session 6. The number of contour elements selected to be exposed during the training as below-threshold (subliminal) contours was verified in a constant-level testing block before training, and the data of that block also served as baseline data for subsequent intratraining constant-level testing blocks.

were also used to set a subliminal contour level for each participant during training. We avoided further assessments of contour-detection thresholds during the training period to minimize exposures to suprathreshold contours; such exposures could potentially facilitate learning (e.g., Ahissar & Hochstein, 1997). Instead, in intratraining testing blocks during the training period, a constant-level testing approach was applied to trace the accuracy of detecting subliminal contours across sessions. The intratraining testing blocks were run before and after each training session (except posttraining at the last session). One initial constant-level testing block followed the pretraining threshold testing blocks and served both to validate that the contour level selected to be exposed during training was below the participant's contour-detection threshold and to provide a baseline for the intratraining testing blocks.

In threshold testing blocks, the number of contour elements on each trial (starting with four-element contours) depended on performance on the previous trial, whereas in constant-level testing blocks, the number of contour elements corresponded to the individual's subliminal contour-detection level and was held constant across the trials. The number of threshold testing trials in a block varied, depending on the trial-by-trial performance. There were 100 trials per constant-level testing block.

Although stimuli and the tasks in the training and the testing blocks differed, the trials in all blocks had a sequential two-interval, two-alternative, forced-choice design (Fig. 1b). Each trial started with a small, bright central fixation point. Approximately 1.5 s later, the fixation point vanished, and the first of the two stimuli appeared for 600 ms. After this, the

display went blank (except for a dim fixation point) for an interstimulus interval of 700 ms. The second stimulus then appeared for 600 ms. Participants responded by pressing one of the two mouse buttons to indicate in which stimulus the foreground shape rotated. Response time was unlimited. After every two blocks, there was a short break.

Training blocks. In training trials, one stimulus included a rotating foreground shape (target) and the other stimulus included a static foreground shape (nontarget). The task was to identify which stimulus interval contained the rotating target. Neither the background array nor the embedded subliminal contour were mentioned in the instructions for the task. Each participant's responses were followed by feedback text indicating whether the participant correctly identified the target (for 500 ms); then a new trial began. Task difficulty was maintained at 84% correct responses by increasing or decreasing the target's rotation speed (using a staircase algorithm). Participants were also informed about their overall performance level following each block to facilitate their task engagement. It took 90 trials on average to complete a training block.

Testing blocks. In both threshold and constant-level testing blocks, the stimuli comprised random background elements, and one of the two displays per trial included a global contour. The task was to identify which interval included a contour. No feedback was provided, and participants were informed about neither the contour types nor the different types of testing blocks. The participants were informed that the contour shape might vary across trials and that it could subtend a wide area of aperture. Trials with trained contours were pseudorandomly interleaved with the trials with not-trained contours. The data for the not-trained contours were used to evaluate the transfer of learning across different classes of contours.

Threshold testing blocks evaluated contour-detection thresholds (allowing 70.1% correct detection) using a one-up, twodown staircase algorithm (Wetherill & Levitt, 1965; the staircase step was 117.5%, rounded to the nearest integer for actual element number). To minimize learning transfer from suprathreshold contours, we used upward staircases (the initial level consisted of four-element contours). There were two randomly interleaving staircases per block to evaluate thresholds for trained and not-trained contour types. Each staircase was terminated after nine reversal trials. The last six reversal trials were then considered for calculation of the threshold (in log units). The testing block was ended after both staircases were terminated. For each contour type, the number of contour elements corresponding to the average across three threshold evaluations was considered to be the actual threshold. Subliminal contour level was defined as the number of elements corresponding to one staircase step below threshold (rounded to the closest integer). This level was always validated in the following constant-level testing block (which was used also for determining the baseline detection level for this contour). Constant-level testing blocks included only subliminal

contours (half trained and half not trained). For each contour type, accuracy was evaluated across 50 trials.

Results

The results of the pretraining constant-level baseline test validated, for each participant, a below-threshold detection level for the subliminal contours the participant would be exposed to during the training (see the Method section and baseline results in Fig. 3). Before training, the two participant groups showed similar contour-detection thresholds for the trained and not-trained contour types (Fig. 4, upper left graph). However, subsequent to training, the consistent-pairing group had a lower detection threshold for the trained contour type relative to the pretraining threshold (p = .01, paired two-tailed t test; Fig. 4, results for trained contours in the upper right graph). This demonstrates a large learning effect (Cohen's d =1.75; about 25% threshold change on average; Fig. 4, lower graph). In contrast, the random-pairing group showed only a small, nonsignificant improvement (approximately 6% threshold change; p = .52). Note that the dependence of learning on the consistent pairing of stimulus' background and foreground rules out effects based on task familiarity or on mere exposure (which was matched in the consistent-pairing and randompairing groups). Instead, it indicates that subliminal learning depended on the correlated co-occurrence of the background and foreground stimuli.

It is interesting to note that learning was confined to contours of the trained shape type. With the not-trained contour shapes, posttraining detection thresholds remained comparable

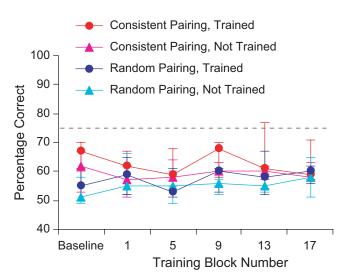


Fig. 3. Median percentage of correct detection of (initially) subliminal contours during the pretraining and intratraining constant-level testing blocks. The data from the pretraining block provide a baseline level of contour detection. Results are shown for the performance of the consistent-pairing and random-pairing groups for the trained and not-trained contours. The dashed line corresponds to the accuracy level considered to be the just-noticeable contour detection (75% correct). Lower and upper error bars indicate the first and third quartiles, respectively.

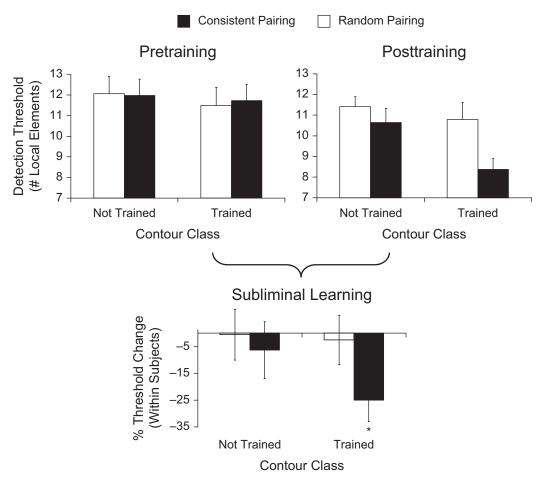


Fig. 4. Overall learning effect. The upper panels show pretraining (left) and posttraining (right) contour-detection thresholds across trained and not-trained stimuli, for each training group. The lower panel shows the within-subjects difference between the pretraining and posttraining threshold for the trained and not-trained stimuli, for each participant group. Negative change indicates improvement. Error bars represent standard errors of the mean. The asterisk indicates a significant change (p < .05).

to the pretraining thresholds in both the consistent-pairing and the random-pairing groups (ps=.33 and .5, respectively; Fig. 4). Note, also, that although exposure to subliminal contours was effective for inducing contour learning, the subliminal contours remained subliminal throughout regardless of the training condition or the contour type (Fig. 3). Similarly, there was no clear correlation between the initial contour-detection accuracy (i.e., during the pretraining constant-level baseline test) and the degree of learning (the percentage of threshold change; r=-.015 for the trained contour in the consistent-pairing group). This contradicts the idea that—although low—the initial detectability level of the subliminal contour accounts for learning.

Discussion

The results provide the first evidence that global, perceptual organization can be improved by repeated subliminal exposures to task-irrelevant global features. As with the subliminal learning of local visual features found in previous studies

(Watanabe et al., 2001, 2002), consistent co-occurrence of the subliminal background contours and relevant foreground targets was necessary for learning. However, in contrast to previous demonstrations, the learning we found is unlikely to reflect modification of local, low-level processes because the local features, as well as overall orientation and extent of the contours, varied randomly across trials. As with low-level subliminal learning, learning in our study was specific to the trained feature (i.e., the type of global contour shape). This suggests improved processing of a particular form of grouping relationship. This improvement generalizes across local components and global orientations of the particular shape type, but it does not extend to other nontrained grouping relationships.

Our findings demonstrate that a contour-related task is not essential for contour learning to occur. The findings also contradict an account suggesting that contour learning reflects learning to attend to the trained contour, given that in our study the contour was always subliminal. At the same time, learning depended on particular patterns of exposure. Mere exposure to subliminal contours did not suffice for learning.

 $0.84^{\circ} \times 0.84^{\circ}$

Trials with a local contour Trials with any local element Pixel size segment in a pixel (%) in a pixel (%) Circular variance per pixel $0.21^{\circ} \times 0.21^{\circ}$ $\leq 5 (1.1)$ < 25 (20.2) \geq 0.74 (0.92) $0.42^{\circ} \times 0.42^{\circ}$

 \leq 88 (80.8)

~100

Table A1. Cross-Trial Distribution of Gabor Elements in Simulated Contour Stimuli

 \leq 15 (3.9)

 \leq 36 (7.5)

Note: The simulated subliminal contour included 10 elements—approximately the mean subliminal contour level across participants. Only simulated displays with a contour were included in this analysis. Median values across contour-related pixels are shown in parentheses. Circular variance (S) is a number between 0 and 1, in which 0 indicates full bias to a specific orientation, and I indicates even likelihood of any orientation (Fisher, 1995). The closer the circular variance is to I, the higher the orientation variability. Here, $S_{x,y}$ at location x,y across trials $t = 1 \dots N$, is calculated as $S_{x,y} = 1 - r_{x,y}$.

in which
$$\overline{r}_{x,y} = \frac{1}{N} \sqrt{\sum_{t=1}^{N} \left[R_{x,y,t} \sin 2\theta(x,y)_{t} \right]^{2} + \sum_{t=1}^{N} \left[R_{x,y,t} \cos 2\theta(x,y)_{t} \right]^{2}}$$
. $R_{x,y,t}$ is the vector summation magnitude across

the orientations of all elements within pixel x,y in trial t (transformed from 180° to 360° scaling), and $\theta(x,y)$, is local orientation at pixel x,y in trial t (i.e., the angle of the vector summation; transformed to 180° scaling). The factor 2 in the sum reflects a transformation from 180° to 360° circular scaling (see Fisher, 1995). Pixel sizes of 0.21° × 0.21°, 0.42° × 0.42° , and $0.84^{\circ} \times 0.84^{\circ}$ correspond to 100×100 , 50×50 , and 25×25 grids, respectively.

Instead, learning was exposure dependent, as it required consistent co-occurrence of contours and other detectable and relevant signals.

The similarity between our results and previous findings for low-level, local, subliminal (thus, implicit) learning effects, together with the reliance of that learning on consistent pairing of the subliminal contour and the foreground target, supports the idea that subliminal learning involves a common, Hebbian-like, neuronal plasticity mechanism (Seitz & Dinse, 2007), which can operate at different levels of cortical processing. This basic learning mechanism could be beneficial for its "low-cost" coding of co-occurring descriptors of the environment.

Appendix

Table A1 summarizes the cross-trial distribution of local background elements in contour-related pixels (i.e., with at least one event of contour element) across 1,836 simulated training trials. At a fine scale corresponding to small receptive fields (e.g., a pixel size of $0.21^{\circ} \times 0.21^{\circ}$), the occurrence of any contour element within any local pixel was rare ($\leq 5\%$), and the local orientation of the element within the pixel was highly variable across trials (circular variance > 0.74; Fisher, 1995). (We are using *pixel* to refer to the graining level of the analysis—reflecting receptive field size in the eye—not of the monitor.) The likelihood of a local element falling in a given pixel increased as the pixel grain became coarser, but this held both for oriented elements falling on a contour and for those that were merely background. The cross-trial variability in local orientation in coarser pixels became even higher.

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Declaration of Conflicting Interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

 \geq 0.81 (0.95)

 \geq 0.84 (0.97)

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References

Ahissar, M., & Hochstein, S. (1997). Task difficulty and the specificity of perceptual learning. Nature, 387, 401–406.

Brainard, D.H. (1997). The Psychophysics Toolbox. Spatial Vision, 10, 433-436.

Chun, M.M., & Jiang, Y. (2003). Implicit, long-term spatial contextual memory. Journal of Experimental Psychology: Learning, Memory, and Cognition, 29, 224-234.

Deroost, N., & Soetens, E. (2006). Perceptual or motor learning in SRT tasks with complex sequence structures. Psychological Research, 70, 88-102.

Field, D.J., Hayes, A., & Hess, R.F. (1993). Contour integration by the human visual system: Evidence for a local "association field." Vision Research, 33, 173–193.

Fisher, N.I. (1995). Statistical analysis of circular data. New York, NY: Cambridge University Press.

Frenkel, M.Y., Sawtell, N.B., Diogo, A.C., Yoon, B., Neve, R.L., & Bear, M.F. (2006). Instructive effect of visual experience in mouse visual cortex. *Neuron*, 51, 339–349.

Geisler, W.S., Perry, J.S., Super, B.J., & Gallogly, D.P. (2001). Edge co-occurrence in natural images predicts contour grouping performance. Vision Research, 41, 711-724.

Godde, B., Stauffenberg, B., Spengler, F., & Dinse, H.R. (2000). Tactile coactivation-induced changes in spatial discrimination performance. Journal of Neuroscience, 20, 1597-1604.

Kovacs, I., Kozma, P., Feher, A., & Benedek, G. (1999). Late maturation of visual spatial integration in humans. Proceedings of the National Academy of Sciences, USA, 96, 12204–12209.

Lamme, V.A. (1995). The neurophysiology of figure-ground segregation in primary visual cortex. *Journal of Neuroscience*, 15, 1605–1615.

- Li, W., & Gilbert, C.D. (2002). Global contour saliency and local colinear interactions. *Journal of Neurophysiology*, 88, 2846–2856.
- Li, W., Piech, V., & Gilbert, C.D. (2008). Learning to link visual contours. *Neuron*, *57*, 442–451.
- Nishina, S., Seitz, A.R., Kawato, M., & Watanabe, T. (2007). Effect of spatial distance to the task stimulus on task-irrelevant perceptual learning of static Gabors. *Journal of Vision*, 7(13), Article 2. Retrieved September 30, 2010, from http://www.journalofvision.org/content/7/13/2
- Schwarzkopf, D.S., Zhang, J., & Kourtzi, Z. (2009). Flexible learning of natural statistics in the human brain. *Journal of Neurophysiol*ogy, 102, 1854–1867.
- Seitz, A.R., & Dinse, H.R. (2007). A common framework for perceptual learning. *Current Opinion in Neurobiology*, 17, 148–153.

- Seitz, A.R., & Watanabe, T. (2003). Psychophysics: Is subliminal learning really passive? *Nature*, 422, 36.
- Seitz, A.R., & Watanabe, T. (2009). The phenomenon of task-irrelevant perceptual learning. Vision Research, 49, 2604–2610.
- Sigman, M., Cecchi, G.A., Gilbert, C.D., & Magnasco, M.O. (2001).
 On a common circle: Natural scenes and Gestalt rules. *Proceedings of the National Academy of Sciences*, USA, 98, 1935–1940.
- Watanabe, T., Nanez, J.E., Sr., Koyama, S., Mukai, I., Liederman, J., & Sasaki, Y. (2002). Greater plasticity in lower-level than higherlevel visual motion processing in a passive perceptual learning task. *Nature Neuroscience*, 5, 1003–1009.
- Watanabe, T., Nanez, J.E., & Sasaki, Y. (2001). Perceptual learning without perception. *Nature*, 413, 844–848.
- Wetherill, G.B., & Levitt, H. (1965). Sequential estimation of points on a psychometric function. *British Journal of Mathematical and Statistical Psychology*, 18, 1–10.