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Using a Contrast Illusion to Teach Principles of Neural Processing

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Neuroscience is a rapidly growing, multidisciplinary field that is advancing our understanding of the human condition. Therefore, studying key principles in neuroscience is critical for a well-rounded education across a wide range of disciplines. However, neuroscience concepts can be intimidating and challenging for undergraduate students to learn, especially when they lack active learning opportunities. To address this problem, we developed an interactive laboratory exercise to challenge students to use observational measurements of a visual contrast illusion to study neural activity. The goal of this study was to understand the effectiveness of this active learning exercise in increasing students' fundamental understanding of how perception is shaped by neural circuits in the retina. Students conducted simple psychophysical experiments to measure thresholds for detecting illusory spots under various conditions and described their results in a laboratory assignment. Assessment of students' confidence and practical understanding of neural processing, before and after engagement with the laboratory exercise, was used to improve curriculum and instruction.

Key words: lateral inhibition; receptive field; retinal ganglion theory (RGT); Hermann Grid; visual illusion; center-surround   antagonism

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Neuroscience discoveries are increasingly informing complex human problems. Hence, there is a growing need for a foundational neuroscience education across a range of disciplines in the undergraduate curriculum. However, teaching neuroscience-based concepts within non-natural science disciplines can have special challenges. Students in the social sciences often lack fundamental knowledge in the natural sciences (e.g., biology, chemistry, and physics), which is prerequisite for a solid understanding of many neuroscience principles. Also, classrooms dedicated for non-natural science departments are often ill-equipped for laboratory-based experiences where students may actively engage with and observe the brain at systems and cellular levels.

This is problematic in light of the growing literature demonstrating that teaching neuroscience is much more effective when active learning strategies and interactive pedagogies are utilized (Birkett, 2009; Keen-Rhinehard et al., 2009). Neuroscience research informs us that active learning has the advantage of stimulating multiple neural connections in the brain, which may promote memory and advance deeper understanding (Tokuhama-Espinosa, 2011). Thus, instructors of neuroscience-related curriculum are increasingly challenged to implement pedagogical strategies for active student engagement despite having limited resources to do so.

The principle of neural processing, or how neural circuits work to shape our mental experiences, is often taught in *Sensation and Perception* and *Biological Psychology* (aka *Physiological Psychology*, *Biopsychology*, *Brain and Behavior*) courses, which are part of the standard undergraduate Psychology/Neuroscience curriculum. However, learning how cells interact and encode information may be challenging for students who have limited prior exposure to basic concepts in cellular biology and neural circuit dynamics. Nevertheless, the visual system is an ideal model for introducing the principle of neural processing because visual processing begins with relatively small groups of interconnected neurons in the back of the eye (the retina), which respond to and process light in reproducible and tractable ways.

Visual illusions may shed light on the complex neural architecture and underlying mechanics of the visual system. Empirical studies of visual illusions have provided important insights into principles of neural interactions and their constraints (Eagleman, 2001). Because they are ubiquitous and interesting, visual illusions may serve as a powerful tool for helping students appreciate the dynamics and limits of the visual system when they learn about neural processing and how it shapes our visual experiences.

The Hermann Grid illusion (Herman, 1870) is the perception of gray spots at the intersection of black squares arranged in a grid against a white background (Figure 1a). These illusory gray spots manifest in the peripheral vision and disappear when fixating on the intersection. This powerful perceptual experience is easily reproducible via high contrast black and white grids created by superimposing intersecting vertical and horizontal white bars in evenly spaced patterns on a black background. The illusion can also be displayed in reverse contrast whereby white spots, instead of gray spots, would appear (Figure 1b).

This illusory percept is well suited for teaching principles of neural processing because one of the earliest known neural processes, called lateral inhibition, is widely used to explain the Hermann Grid illusion. Lateral inhibition arises from the horizontal transmission of inhibitory signals across neighboring nerve cells in the retina. It is thought to underlie the reduction of brightness (i.e., gray spots) seen at Hermann Grid intersections (Goldstein, 2010; Kalat, 2016).
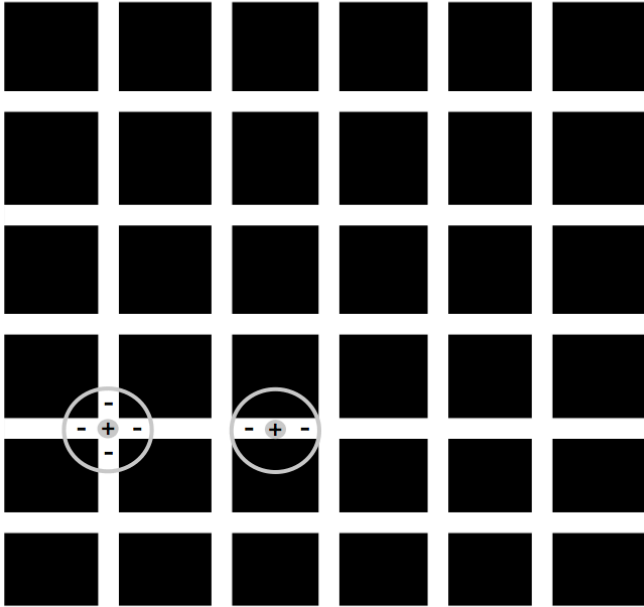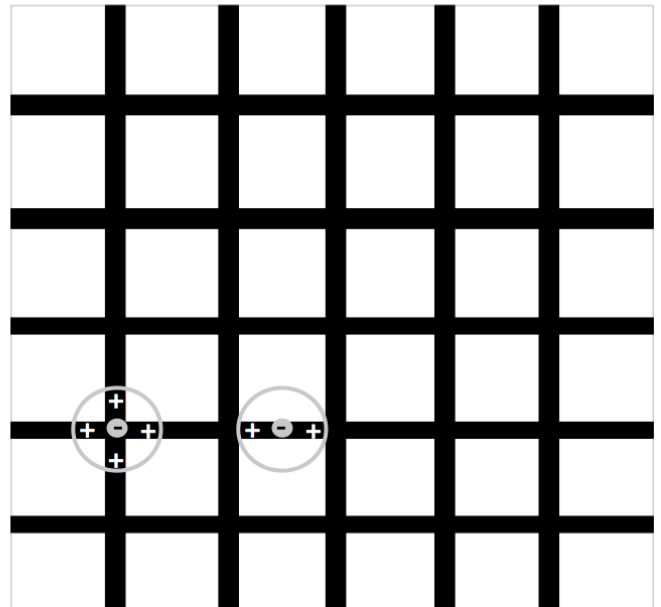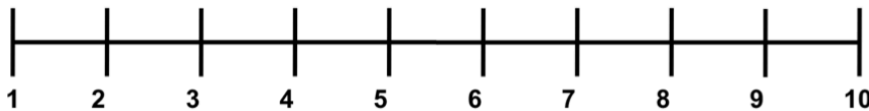
a. Classic Hermann grid with on-center receptive fields

b. Reversed contrast with off-center receptive fields

c. Intensity rating scale

Figure 1. *(a)* The standard Hermann Grid with concentric on-center superimposed at an intersection and corridor. The illusory dark spots can be seen in peripheral vision and disappears when fixating directly on the intersections. The on-center receptive fields receive more inhibition at the intersections than in the corridors. *(b)* The Hermann Grid is shown in reverse contrast with concentric off-center superimposed at an intersection and corridor. The illusory spots appear brighter due to the off-center receptive fields receiving less inhibition at the intersections compared to the corridors. *(c)* The ten-point intensity rating scale used in student experiments.

By studying retinal receptive fields, defined as the area on the retina in which a visual stimulus evokes a change in the firing activity of a cell (Goldstein, 2010; Kalat, 2016), neurophysiologists established that retinal ganglion cells are organized concentrically in an antagonistic fashion (Kuffler, 1953). Thus, due to lateral inhibition, some receptive fields have an excitatory-center-inhibitory-surround pattern (aka, on-center receptive fields) whereby stimulation of the center area (by a small spot of light) evokes excitatory neural activity, and stimulation of the surrounding area (by a larger spot of light) evokes lateral inhibitory response patterns. There are also inhibitory-center-excitatory-surround receptive fields (aka, off-center receptive fields), which have opposite response patterns. One of the most widely held explanations of the Hermann Grid illusion is the retinal ganglion theory (RGT), which is based on this antagonistic center-surround organization of the visual receptive field (Baumgartner, 1960). Thus, when a spot of light stimulates on-center cells at the intersection of a white grid on a black background, the receptive fields receive approximately twice as much lateral inhibition as it does when the receptive field cells fall in the corridors (Figure 1a). Thus, dark illusory spots are apparent.

Conversely, when darkness at the center of a black grid on a white background stimulates off-center cells at the intersection, the receptive field receives approximately half as much lateral inhibition than it does in the nonintersecting corridors (Figure 1b). Hence, the intersections appear brighter.

The explanatory power of the RGT is appealing, and thus, it is widely used in textbooks to explain the Hermann Grid illusion (i.e., Goldstein, 2010; Kalat, 2016). However, there is a growing literature that brings into question its tenability (e.g., Wolfe, 1984; Spillman, 1994; Schiller and Carvey, 2005). Notably, Schiller and Carvey (2005) offer a series of hypothesis driven visual demonstrations that show, very compellingly, that the retinal ganglion theory does not hold for the Hermann Grid illusion when tested under various experimental conditions. In providing readers the opportunity to serve as the experimental subject as they bear witness to the Hermann Grid's illusory percepts and its constraints, the Schiller and Carvey (2005) article serves as a unique teaching tool to engage undergraduates in the primary literature while they are learning about principles of neural processing. This is an ideal approach in light of previous research showing that

incorporating primary literature into lessons may improve students' ability to learn scientific content while helping to demystify the scientific process (Hoskins, 2008; Hoskins et al., 2011).

The current study examines the effectiveness of using the primary literature, combined with real time demonstrations, in improving students' fundamental understanding of how perception is shaped by neural circuits in the retina. To this end, selected components of the Schiller and Carvey (2005) article were integrated into an interactive laboratory exercise designed to expose students to alternative ideas about the neural underpinnings of the Hermann Grid illusion. Students conducted simple psychophysical experiments to measure their classmates' thresholds for detecting illusory gray spots in four experimental conditions. These conditions were intended to test various predictions based on the RGT.

The classic theory, as described by Baumgartner (1960), is based on local activity of receptors converging onto ganglion cells in the retina. Because the concentric on-center or off-center receptive fields have fixed sizes in the retina, it can be hypothesized that the size of the intersecting bar widths would bear some effect on the detection or intensity of the illusory gray spots in the Hermann Grid. By the same logic, viewing distance should also influence the illusory percept. On the other hand, manipulating the grid in manners that do not alter the center-surround antagonistic properties of the receptive fields should theoretically have no effect on the illusion (Schiller and Carvey, 2005).

Here we describe a Hermann Grid laboratory exercise designed for undergraduate students to test these predictions via psychophysiological experiments. Following the exercise, students were tasked with reporting and explaining their findings based on their understanding of concepts learned from their textbooks and/or the primary literature, as well as from their empirical interactions with the illusions. The effectiveness of this teaching approach in fostering a deeper understanding of key principles of neural processing was assessed via self-report measures obtained before and after the laboratory experience.

MATERIALS AND METHODS
Participants
Participants (*N* = 112, 99 females and 13 males) were undergraduate students enrolled in PSYC 4415 (Perception) at Kennesaw State University during the Spring 2017, Summer 2017, and Spring 2018 semesters. Participants ranged in age from 20 to 60, with a mean age of 22. Since this was an upper-level psychology course, the sample consisted mainly of young adult psychology majors. For this course, the only pre-requisite was passing a Research Methods course (PSYC 2300). Four classes, over the course of three semesters, were given the opportunity to participate in this study. Three of the classes were taught in a hybrid style 15-week course that met once a week for one hour and forty minutes. The other class was a 5-week summer course that met twice a week for three hours and forty-five minutes. Participation

was completely voluntary. However, the concepts addressed in this study (i.e., lateral inhibition, center-surround antagonism) were part of the course curriculum. All students in attendance on the day of the activity had the option to participate in the study. The Hermann Grid laboratory exercise counted as a grade in the course, regardless of whether they chose to participate in this study. This study was approved by the Kennesaw State University's Institutional Review Board prior to data collection.

Procedure
The study was introduced during regular class sessions aligned with the scheduled curriculum on relevant topics (i.e., neural convergence and lateral inhibition). Students were required to read the corresponding sections in the course textbook, *Sensation and Perception* (Goldstein, 2010), prior to their class arrival. After informed consent was obtained, demographic information was collected and participants took a Pre-lecture *Knowledge Probe* and *Confidence Survey* to assess their pre-existing understanding of the main concepts that would be examined in this study: lateral inhibition, antagonistic center-surround receptive fields, and the RGT. Next, they participated in a brief lecture and guided discussion (for approximate 45 minutes) about the classic theory along with alternative ideas proposed by Schiller and Carvey (2005) in their seminal paper, "The Hermann Grid Illusion Revisited". Based on these alternative ideas, students were challenged to critically examine and discuss a set of hypotheses related to the theory. Following the lecture/discussion, they completed a second Knowledge Probe and Confidence Survey (Post-lecture Survey).

They then participated in the Hermann Grid laboratory activity. Students were provided a paper packet that described the laboratory objectives: to (1) demonstrate a visually induced Hermann Grid illusion, (2) examine the retinal ganglion cell theory, (3) conduct simple psychophysical experiments to measure thresholds for detecting the phantom gray smudges under various conditions, (4) explore some alternative ideas about the Hermann Grid illusion. The packet also contained a brief explanation of the RGT, visual stimuli used for the experiment, and ten-point measurement scales from which to record their responses. Students were divided into self-selected groups where they worked together to measure each other's thresholds for seeing the illusion under four different viewing conditions. After data were gathered from all students, the instructor led another discussion about their observations relative to their predictions.

The lab included various manipulations of the standard Hermann Grid, across four experimental conditions, in order for students to investigate and test the principles behind the retinal ganglion theory. The conditions were (1) size of intersecting bars, consisting of three classic Hermann Grids of size dimensions, 42.3, 25, and 6.3 square inches, (2) viewing distance, where the participant viewed a large Hermann Grid (42.3 square inches) from a distance of 1.5, 3, or 4.5 feet from the grid (3) rotation of the standard grid (6.3 square inches), rotated at 10°, 25°,
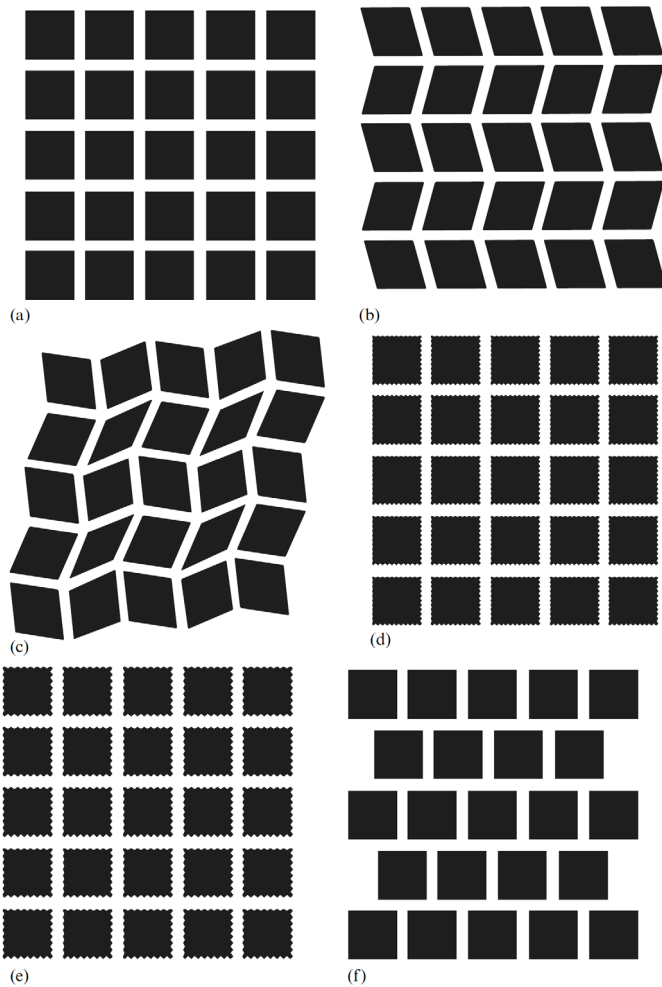
Figure 2. Adapted with permission from Schiller and Carvey (2005). *(a)* The classic illusion with straight, continuous bars. *(b)* Vertical bars are discontinuous. *(c)* Both vertical and horizontal bars are discontinuous. *(d)* and *(e)* Serrated bar edges shown for two spatial frequencies. Viewing *(d)* and *(e)* at a greater distance reinstates the illusion when the serrations can no longer be resolved. *(f)* Vertical bars are offset.

and 45º, and (4) manipulation of the standard grid characteristics that still maintained antagonistic center/surround properties, as demonstrated in Figure 2. In each condition, printed grids were held eye-level by the student experimenter at a distance of 1.5 feet from the participant, approximately one carpet square in the classroom. For the condition in which the size of the grid was manipulated, participants' visual angles were approximately 20.5º, 15.8º, and 7.9º at a distance of 1.5 feet from the experimenter.

For the condition in which the viewing distance was manipulated, the student experimenter initially stood one carpet square from the participant (1.5 feet). Then, they increased their distance by a second carpet square (totaling 3 feet) and a third carpet square (totaling 4.5 feet). Hence, the visual angle shifted from 20.5º to 10.3º and 6.9º respectively. The conditions and levels were presented to the participant in the exact order as listed above. For each condition, participants were instructed to fixate on the center of the grid, then asked to verbally indicate whether

or not they detected any gray smudges in their field of view. If they verbally responded, "yes", then they were instructed to rate the intensity level of the smudges from 1 (barely visible) to 10 (strong intensity/visibility) (Figure 1c). Each response was recorded on an integer scale provided by the student recorder (Figure 1c).

At the end of the experiment, the students who recorded the participants' responses were instructed to submit the experimental data online (via a *SurveyMonkey* link). For each condition, and each level in the conditions (total 15), the recorder had to report if the participant detected gray smudges (Yes/No). If smudges were detected, report the intensity level that was rated by the participant on the scale from 1 (barely visible) to 10 (definitely visible). From this, the instructor compiled the class responses and calculated the mean intensity rating for each condition level. Bar graphs were created in Excel for each condition to display the mean intensity ratings for the condition levels. The figures were sent out to the class and they were instructed to use that data to complete the laboratory assignment.

Laboratory Assignment

As part of a course grade, students were tasked to complete a lab assignment regarding the Hermann Grid laboratory activity. The Spring '17 course section was assigned a lab report. Instruction was provided on how to organize and write a lab report, which required the following sections written in APA format: title page, introduction, methods, results, discussion and references. Summer '17 and Spring '18 course sections were assigned a lab worksheet consisting of questions for assessing participation and content understanding. Both assignments covered the same objectives: discussing experiences/observations with the activity and its manipulations, interpreting findings in relation to the RGT, and applying what they learned to flexibly demonstrate critical-thinking.

Self-report surveys

To assess the participants' beliefs about their knowledge and understanding of concepts in neural processing and lateral inhibition, a *Knowledge Probe* and *Confidence Survey* was given at three separate stages in the study (Pre-lecture, Post-lecture, and Post-lab). The three-item *Knowledge Probe* asked them to indicate a statement that best describes their current knowledge of three main concepts: lateral inhibition, antagonistic center-surround receptive fields, and the retinal ganglion theory. There were five options to select: "1 = I've never heard of this", "2 = I've heard of it, but I don't really know what it means", "3 = I know what it is, but I can't confidently explain it in my own words", "4 = I know what it is and can confidently explain it in my own words", and "5 = I feel very confident in my ability to teach this concept to a peer". The three-item *Confidence Survey* asked how confident they feel in their ability to achieve the following: 1) Demonstrate mastery of conceptual understanding in the above concepts in an exam assessment; 2) Write a well-informed introduction section, detailing these concepts, for a lab report; and 3)

Clearly explain these concepts in their own words to a peer. The item choices were: "1 = Not at all", "2 = Not very", "3 = Somewhat", "4 = Very", "5 = Completely".

Final Survey

After completion of the lab assignment, a final survey (Post-Lab) was sent out, through Qualtrics, that reassessed their overall understanding of the concepts and their evaluation of the lab's effectiveness. The final survey included the same *Knowledge Probe* and *Confidence Survey* items, along with additional items to assess students' level of agreement on the lab activity's overall helpfulness. The questions were, "*The lab exercise helped me understand the lecture content*", "*The handout used in this lab was helpful when completing the experiment and lab assignment*", "*The instructions for lab exercise were clear and easy to follow*", "*The lab exercise gave me a practical understanding of the Retinal Ganglion Theory*", "*The lab exercise made the interpretation of the results easier*", and "*Writing the lab report or completing the lab assignment helped me to better grasp the lecture content*". The item choices were, "1 = Strongly disagree", "2 = Disagree", "3 = Somewhat disagree", "4 = Neither agree nor disagree", "5 = Somewhat agree", 6 = Agree, 7 = Strongly agree. Additional items assessed how well students believed that the lab exercise improved their knowledge of RGT, center-surround antagonism, and lateral inhibition. These were rated as: "1 = Not at all", "2 = A little bit", "3 = Some", "4 = A lot", and "5 = Definitely a lot". There was also an open-ended response probe seeking feedback about their overall impressions about the laboratory exercise and any suggestions for improvement.

RESULTS

Psychophysical experiments

Students conducted simple psychophysical experiments to measure the effects of various grid manipulations on the intensity ratings of illusory spots. Figure 3 shows the combined results of all students' responses across three academic semesters. It was hypothesized that the intensity ratings would be confined to a specific grid size, and the sizes of the corresponding intersections between bars. This prediction was based on the idea that retinal receptors, ganglion cells, and their receptive fields have fixed sizes. Thus, if the illusion is entirely dependent on their local antagonistic center-surround properties, then it should be restricted to certain intersection sizes.

Contrary to this hypothesis, students detected the illusion across the three different grid sizes (Figure 3a) and distances (Figure 3b). However, the results of a one-way repeated-measures ANOVA showed that the intensity ratings significantly decreased as the size of the grids decreased, $F(2,174) = 50.39$, $p < 0.0001$. Post hoc tests using the Bonferroni correction revealed that mean ratings for each size were significantly different from all other sizes. Intensity ratings also decreased significantly as the distance from the viewer increased, $F(2,170) = 20.42$, $p < 0.0001$. Post hoc tests revealed that the mean intensity ratings reported at a distance of 4.5 feet was significantly lower than the intensity ratings reported at 1.3 feet and 3
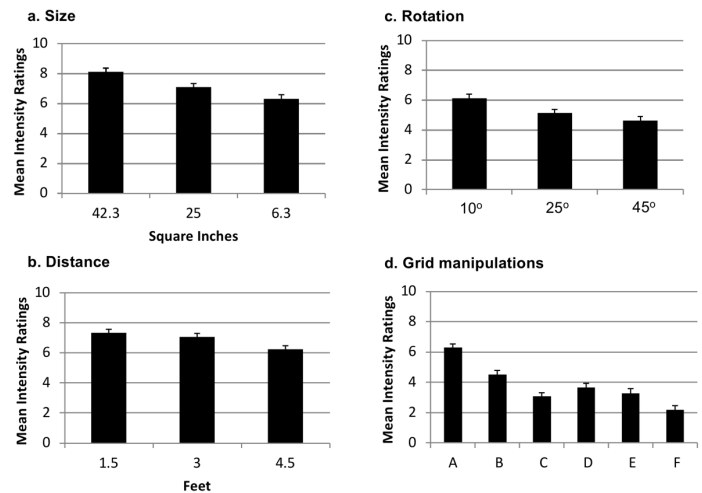

Figure 3. Mean (+SEM) intensity ratings for perception of illusory gray spots across the four experimental conditions. *(a)* Size of the grid measured in square inches, *(b)* Distance from observers measured in feet, *(c)* Rotation of the grid at increasing angles, (d) Manipulation of grid line characteristics (A = standard grid, B = discontinuous vertical bars, C = discontinuous vertical and horizontal bars, D = serrated edges, E = lower frequency serrated edges, F = vertical bars shifted.

feet. However, there was no significant difference between intensity rates reported at 1.3 and 3 feet. This suggests that the prediction may have some merit. While manipulating the size or distance of the intersection did not eliminate the illusion, it significantly diminished it.

It was also hypothesized that manipulating grid characteristics while maintaining the overall lightness contrast should not affect the illusion, given that the local antagonistic center-surround properties of the receptive fields are intact. To test this, a standard grid was rotated at 10°, 25°, and 45°. Although students detected the illusion across all rotations, the intensity ratings significantly decreased as the angle of rotation increased, $F(2,168) = 40.11$, $p < 0.0001$. (Figure 3c). Post hoc tests revealed a significant difference between each pairwise comparisons. In another test, the grid was manipulated five different ways. Figure 3d shows the intensity ratings for a standard grid (A) compared to a grid that has slanted, discontinuous vertical bars (B), or has slanted, discontinuous vertical and horizontal bars (C), or has high frequency serrated edges (D), or low frequency serrated edges (E), or has vertical bars that are shifted (F) (Figure 2). These manipulations resulted in dramatic reductions in intensity ratings, $F(5,195) = 36.6$, $p < 0.0001$. Post hoc tests revealed that the mean intensity ratings for the standard grid (A) were significantly higher than the ratings of all the other grids (B-F). Findings trended consistently across course semesters, as there were no interaction effects of course semester found in any of the above-stated statistics. Altogether, these findings suggest that factors other than local receptive field activity may be contributing to the Hermann Grid illusion.

Assessment of lab effectiveness

Pre-lecture, post-lecture, and post-lab Knowledge Probes were administered to assess changes in students'
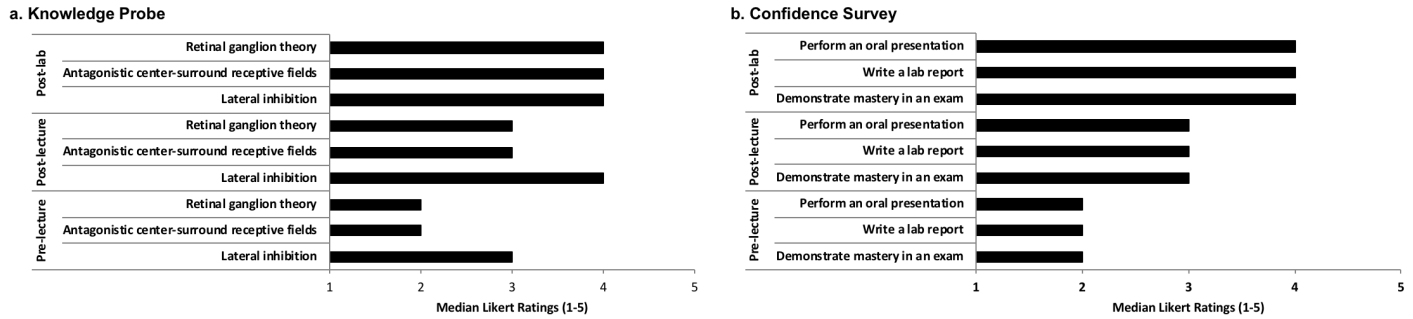
a. Knowledge Probe

b. Confidence Survey

Figure 4. Median response ratings for the Knowledge Probe *(a)* and Confidence Survey *(b)*. The *Knowledge Probe* asked them to indicate a statement that best described their current knowledge of the three main concepts: lateral inhibition, antagonistic center-surround receptive fields, and the retinal ganglion theory. There were five options to select from "1 = I've never heard of this" to "5 = I feel very confident in my ability to teach this concept to a peer". The *Confidence Survey* asked how confident they feel they can demonstrate understanding via various assessment items, with item choices from "1 = Not at all" to "5 = Completely".

conceptual understanding of lateral inhibition, antagonistic center-surround receptive fields, and the RGT. Confidence surveys were administered at the same time points to assess changes in students' overall confidence in demonstrating their understanding in an exam, a written report, or via oral communication.

Cronbach's alpha was calculated to measure internal consistency within both the Knowledge Probe and Confidence Survey. Nonparametric Friedman tests were conducted to evaluate differences among median Likert ratings (from 1-5) across the time points.

Across each time points, there was high internal consistency in ratings within the three content areas (lateral inhibition, center-surround antagonist, and retinal ganglion theory) addressed in the Knowledge Probe, (Pre-lecture, α = 0.78; Post-lecture, α = 0.76; Post-lab, α = 0.67). Hence, overall Knowledge Probe data were collapsed for comparisons across time points. There was a statistically significant difference among Pre-lecture, Post-lecture, and Post-lab Knowledge ratings with students reporting improvements in their content understanding over time, $\chi^2(2)$ = 100.39, p < 0.0001 (Figure 4a).

With high internal consistency across the three items (exam, written report, oral presentation) in the Confidence Survey (Pre-lecture, α = 0.91; Post-lecture, α = 0.80; Post-lab, α = 0.81), overall Confidence data were collapsed for repeated measures comparisons. There were significant improvements in students' confidence ratings across the time points, $\chi^2(2)$ = 81.69, p < 0.0001 (Figure 4b).

After completion of the lab exercise and assignment, students were asked to report how well they believed the lab activity improved their overall knowledge and understanding of the key concepts. The majority of students reported that the lab improved their overall knowledge "A lot" or "Definitely a lot" on lateral inhibition (combined 80.7%), center-surround antagonism (combined 66.3%), and retinal ganglion theory (combined 71.1%) (Table 1). They also rated the overall helpfulness of the lab activity on a range of outcomes. The majority of students either agreed or strongly agreed that the Hermann Grid laboratory exercise was overall helpful

(Table 1). Some students also provided feedback about their overall impressions about the laboratory exercise and suggestions for improvement. Comments about the lab were, "The lab activity was great! It really helped so much with understanding lateral inhibition", "The lab was very helpful", "The lab was clear and very helpful", "I believe this was one of the better labs", "It really helped me understand the concepts better", and "I thought that the lab was very useful and it gave me a lot of valuable knowledge about lateral inhibition and center-surround antagonism". The most common suggestion for improvement was to give more time to complete the activity. Several students reported feeling rushed to complete the experiment portion of the activity because most of the time was spent on discussion.

DISCUSSION

The overarching goal of this study was to use practical tools (i.e., primary literature and visual illusions) to engage undergraduate students in an interactive laboratory exercise designed to promote deeper understanding of principles of neural processing. The lab was conducted during a standard class session, after a brief lecture on content related to lateral inhibition, antagonistic center-surround receptive fields, and the RGT. Students' beliefs about their knowledge of these topics, their confidence in their ability to demonstrate understanding of these key concepts, and their attitudes about the overall helpfulness of the lab activity was assessed at various time points in the study. A central element of the Hermann Grid laboratory exercise was the empirical study of factors that might influence the Hermann Grid illusion. This involved an intensive review of a peer-reviewed paper in the primary visual science literature that criticized the prevailing retinal ganglion theory while offering testable demonstrations and alternative explanations (Schiller and Carvey, 2005). Thus, students had the opportunity to critically examine a classic theory that they read about in their assigned *Sensation and Perception* textbook and conduct psychophysical experiments to test the limits of the theory under various hypothesis-driven experimental conditions.

How well did this lab help improve your knowledge	Not at all	A little bit	Some	A lot	Definitely a lot
On lateral inhibition	0	1.2	18.1	53	27.7
On center-surround antagonism	0	4.8	28.9	45.8	20.5
On the retinal ganglion theory	1.2	3.6	24.1	53	18.1

Overall lab helpfulness	Strongly disagree	Disagree	Somewhat disagree	Neither agree nor disagree	Somewhat agree	Agree	Strongly agree
The lab exercise helped me understand the lecture content	1.2	1.2	0	1.2	20.5	39.8	36.1
The handout used in this lab was helpful when completing the experiment and lab assignment	1.2	1.2	1.2	2.4	14.5	39.8	39.8
The instructions for lab exercise were clear and easy to follow	1.2	1.2	3.7	0	18.3	42.7	32.9
The lab exercise gave me a practical understanding of the Retinal Ganglion Theory	1.2	2.4	4.8	0	30.1	44.6	20.5
The lab exercise made the interpretation of the results easier	1.2	1.2	1.2	1.2	22.9	39.8	32.5
Writing the lab report or completing the lab assignment helped me to better grasp the lecture content	1.2	1.2	2.4	4.8	19.3	41	30.1

Table 1. The percentage of students' responses to questions designed to assess overall understanding of the concepts and beliefs about the lab activity's helpfulness.

Altogether, the findings from this study suggest that this pedagogical approach was largely successful. Students reported significant improvements in their content knowledge as well as increased confidence in their ability to demonstrate their understanding after completion of the lab exercise and corresponding assignments (Figure 4). Overall, the majority of students believed that the lab exercise helped improve their content knowledge. In addition, the majority of students agreed that the lab exercise was clear and easy to understand, promoted a practical understanding of the retinal ganglion theory, and made the scientific data easy to interpret. Most students also agreed that completion of the lab assignment helped them better grasp the lecture content (Table 1).

Importantly, a culmination of results from students' experiments, spanning three academic semesters, provided new insight into the tenability of the RGT. Using a simple ten-point interval scale (Figure 1c), students rated the intensity level of the illusory spots from 1 (barely visible) to 10 (strong intensity/visibility) after four experimental manipulations (size, distance, rotation, and contrast characteristics). In testing the predictions made by Schiller and Carvey (2005), students served as experimental subjects as well as applied observers of the theory's validity.

Given that receptive fields have fixed sizes and known distribution across the retina, the illusory percept resulting from local center-surround antagonism should be confined to certain sized grid intersections. However, students consistently found across different semesters that the illusion persisted among varying grid sizes and distances (Figs. 3a and b). Also, there was remarkable consistency in the mean intensity ratings between the size and distance conditions (Figs. 3a and b). This is not surprising, given that students' visual angles during observations across the decreasing grid sizes (20.5°, 15.8°, and 7.9°, respectively)

were similar to the visual angles across increasing distances from the grid (20.5°, 10.3°, and 6.9°, respectively). Replication of this observation could make for an interesting class discussion about size-distance scaling, and the role of students' size perception on perceived illusory strength (see Murray et al., 2006 for a secondary literature on this concept).

These are important findings that are contrary to the predictions made from the RGT, which restricted the illusory effect to the inhibitory activity of receptors and ganglion cells within the retina. Nevertheless, students' results were not entirely inconsistent with this local model. When interpreting the results, students were quick to point out that the intensity ratings decreased as the grid size and distance decreased. Although other factors may be contributing to the persistence of the illusion, local receptive fields may in fact play a critical role in maintaining the strength of the illusory percept.

An alternative explanation posed by a growing body of vision scientists is that global factors beyond retinal ganglion cells play an important role in perception of the Hermann Grid illusion (Wolfe, 1984; Spillman, 1994; Schiller and Carvey, 2005). The output of retinal ganglion cells is modified by higher order cortical cells in area V1, which notably have larger receptive fields than retinal ganglion cells. This could explain why the illusion persists when the size and distance of the grid is varied. Students seemed to find this alternative explanation easy to understand since they were also learning about cortical organization and the increasing complexities of cortical receptive fields.

Further observations showing that the detection of illusory spots was significantly reduced when the grid was rotated posed another challenge for the local retinal ganglion cell model (Figure 3c). Also, there were dramatic reductions in the intensity rating when the grid's contrast

edges were manipulated in certain ways (Figure 3d). Since these manipulations only minimally altered the lightness contrast properties, thus maintaining underlying antagonistic center-surround cell activities, the diminished intensity ratings cannot be readily explained at the retinal level.   After reviewing the primary literature, students discussed alternative ideas to explain these findings. Previous studies have shown that people have lower acuity and contrast sensitivity to oblique lines compared to horizontal and vertical lines (Appelle, 1972; Westheimer, 2003).   This 'oblique effect' may be attributed to the orientation-selective receptive field properties of simple and complex cortical neurons (Mansfield, 1974), which make up the vast majority of cells in area V1 (Hubel and Wiesel, 1968). Based on this literature, and the ideas put forth in Schiller and Carvey (2005), it was concluded that the reductions in the illusion intensity from the grid manipulations is due to higher order neural circuit processing from orientation-selective cortical neurons which have reduced sensitivity to discontinuous and oblique bars.

The Hermann Grid laboratory activity is an effective experiential learning tool that promotes creative inquiry and deeper understanding of concepts related to neural processing.   The lab activity is low cost and highly reproducible, and can be flexibly utilized to test a range of predictions, either via a full laboratory experience or as a brief classroom demonstration. The Schiller and Carvey (2005) study offers additional grid manipulations, such as varying the contrast, color, and spatial arrangements of the grid. Although we did not test these manipulations, they could be easily implemented in a Hermann Grid laboratory exercise.

This exercise is amenable to a number of variations and approaches. For example, while we presented the RGT and reviewed the literature (Schiller and Carvey, 2005) before making predictions about the experiment, it might be a worthwhile challenge for students to come up with their own hypotheses, based on their current understanding of the RGT alone, before examining secondary literature. Also, an additional activity might be to challenge students to create their own grid manipulations and come up with their own predictions about how these manipulations might affect the detection and intensity of the illusory spots. Another exercise for students might be to have them calculate the visual angles themselves, across the different grid sizes and viewing distances, either by hand using standard equations, or via an online calculator. By shifting the learning environment from a passive, lecture-centered class session to an active, student-driven laboratory experience, the Hermann Grid laboratory may prove to be highly effective in facilitating undergraduate students' learning and increasing their confidence in their ability to flexibly apply their learning to various forms of knowledge assessments.

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