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A Visually-Induced Eyelid Droop Illusion as a Classroom Demonstration of Cross-Modality

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Cross-modality, or the interaction between the different senses, has emerged as a fundamental concept in perceptual neuroscience and psychology. The traditional idea of five separate senses with independent neural substrates has been invalidated by both psychophysical findings of sensory integration and neurophysiological discoveries of multi-modal neurons in many areas of the brain. Even areas previously thought to be unimodal have been shown to be influenced by other senses, thus establishing multisensory integration as a key principle of perceptual neuroscience.

There are several obstacles to students' understanding of the concept. First, everyday subjective experience is modal: one sees, hears, smells the world and is rarely aware that these seemingly separate impressions are in reality fully integrated with each other. Second, standard content in undergraduate classes and textbooks still emphasizes the modal model of the senses and their corresponding brain areas and rarely mentions cross-modal phenomena. Third, feasible classroom demonstrations of cross-modality are few, making it difficult to provide students with first-hand experience that would aid their understanding of the principle.

This article describes an accessible and effective classroom demonstration of cross-modality between low-level vision, touch and proprioception. It consists in the illusion of eyelid droop in one eye when the other eye has been dark-adapted and when both eyes are exposed to the dark. The perceptual effect is dramatic and reliable. It illustrates cross-modality at a fundamental level of perception and might provide a means to help integrate the teaching of the concept into the standard content of undergraduate classes.

Key words: multisensory integration, cross-modality, illusions, class demonstrations

Cross-modality, or multisensory integration, has emerged as an important principle in the field of cognitive neuroscience and sensory perception. The traditional idea that we have five independent senses processed in thoroughly distinct brain modules has been overturned by findings of multi-modal neurons in both subcortical and cortical brain areas (e.g., Graziano, Yap & Gross, 1994; Graziano & Gross, 1995; Duhamel, Colby, & Goldberg, 1998; Meredith, 2002). Even areas previously thought to be unimodal show cross-modal interactions, even in the early stages of the neural response (Bulkin and Groh, 2006; Mishra et al., 2007) indicating that multisensory integration is a fundamental property of neural processing. Accordingly, on the perceptual level, many examples of multisensory perceptions have been found that illustrate the impossibility of clearly separating one sense from the other in subjective experience. Some well known examples include: Feeling an object by hand while simultaneously viewing its distorted shape through prism glasses leads to a distorted perception of the felt shape (Hay et al., 1965); viewing a speaker's lip movements will influence what the speaker is perceived to be saying (McGurk and McDonald, 1976); viewing a rubber hand being tapped in a random sequence but in synchrony with one's own hidden hand will lead to the eerie sensation that the rubber hand is one's own (Botvinick and Cohen, 1998).

Despite the wide acceptance of cross-modality by the research community, undergraduate students of neuroscience and sensory perception have little exposure to the concept for several reasons. First, students have little awareness of multisensory interaction based on their own life since, subjectively speaking, our everyday perceptual experience is modal: our sensory impressions seem to fall into categories such as smell, vision, audition and rarely are we aware that these seemingly separate sensations in fact deeply influence each other and that a unimodal impression often arises from the unification of different sensory inputs into one perceptual whole. (The exception here might be the interaction of smell and taste which students might have experienced when a cold impaired both their sense of smell and of taste). Second, the large amount of important material on each of the individual senses that generally needs to be covered in an undergraduate class leaves little space for an in-depth discussion of multisensory integration. Similarly, textbooks (for example, Wolfe et al., 2006; Gazzaniga et al., 2008) focus on the individual modalities in separate chapters with little focus on cross-modality. Third, there are few demonstrations of cross-modal perception that would be feasible in a mid- to large-size class and that could provide each student with a memorable, poignant experience of the principle. Such demonstrations seem crucial precisely because students cannot rely on their normal, everyday experience for any familiarity with the concept. The best-known demonstrations of cross-modality between vision and touch would require materials (such as prism glasses, rubber hands) and carefully controlled conditions not generally available in a classroom. The rubber hand illusion (Botvinick and Cohen, 1998), for example, would be hard to administer in a class of 30 students since it would require a rubber hand for each student and the precise timing of touches to both the rubber hand and the student's real hand. Thus, demonstrations that allow a large group of students to actually experience cross-modal perception are usually restricted to audio-visual interaction. Of these, the McGurk effect (for which several versions are now available on www.youtube.com) is by far the most impressive. Much more subtle effects include the double-flash illusion (where a single light flash accompanied by two quick beeps is perceived as a double-flash; see http://shamslab.psych.ucla.edu/demos/), and Shimojo and Shams (2001) for a review), and the motion-bounce illusion in which addition of a sound will make two objects on an ambiguous motion path seem as though they are bouncing off, rather than moving past, each other (Sekuler et al., 1997; for a demonstration, see http://www.michaelbach.de/ot/mot_bounce/index.html).

The following describes how a strong visually-induced proprioceptive illusion (Wolfe et al., 2007) can be used for a compelling and easily conducted class demonstration of a fundamental interaction between vision, touch and proprioception. The demonstration consists in an illusion of eyelid droop triggered by asymmetric dark adaptation, as we previously described elsewhere (Wolfe et al., 2007): When only one eye is dark-adapted and both eyes are exposed to a dim environment, only the dark-adapted eye can see while the light-adapted eye cannot. Under these conditions, observers report a strong illusion of the light-adapted, 'blind' eye's lid as sagging or drooping. We hypothesized that this illusion is a result of the brain 'explaining' the asymmetry in vision by creating an illusory proprioception of the eyelid that could account for this asymmetry: "The eye that cannot see is closed." Consistent with this hypothesis, the illusion disappears or decreases when covering the eye by hand, i.e., when introducing sensory information that is congruent with the interocular difference in vision. These observations illustrate a three-way cross-modal interaction: proprioception (eyelid position sense) is influenced by both vision (light-dark difference in the two eyes) and touch (feeling the hand covering the eye).

The illusion and its modulation by somatosensory input also illustrate the important concept of the probabilistic nature of perception and neural processing (often described in a Bayesian framework; see, for example, Kersten et al., 2004; Ma et al., 2006). The cross-modal effect appears to result from the brain's previous experience with normal combinations of visual and somatosensory information: usually any asymmetry in the two eyes' ability to see is caused by one eye being closed. Thus, based on previous, normal experience, a very likely explanation for visual asymmetry is that one eye is closed. The brain thus appears to 'create' the illusion of one eyelid as drooping as it is trying to unify the conflicting visual and somatosensory input based on what is a probable state of the world according to previous experience. When unambiguous, real somatosensory input is available that in itself can provide a perfectly probable explanation for the visual asymmetry, the illusion becomes unnecessary and disappears; it is "explained away" by the information that the eye is covered. (For an in-depth discussion of "perceptual explaining away" in the Bayesian framework, please see Kersten and colleagues, 2004). The illusion is thus reversible and students can make it disappear and reappear by covering and uncovering the eye.

While the neural mechanism for the illusion is not known, it might involve subcortical areas like the superior colliculus which receives information from both 'luminance detectors' and primary eyelid afferents (see Wolfe et al., 2007) and/or cortical, face-centered visuo-tactile neurons which have been revealed in non-human primates (Graziano et al., 1994; Graziano and Gross, 1995) and whose existence in humans is suggested by observations on neurological patients with neglect symptoms (Làdavas et al., 1998). The perceptual demonstration could thus also be tied to a discussion of both neural mechanisms and clinical applications (also see Wolfe and Carpinella, 2008).

The demonstration uses minimal resources and can be easily administered in large classes: it requires only one eyepatch per participant and a classroom that can be darkened. Furthermore, the effect is particularly convincing as an illustration of how fundamental cross-modality is in perceptual processing: unlike the cross-modal perceptions described above which mainly rely on higher level, spatial vision (such as vision of lip movements or limb location), the present illusion demonstrates the interaction of basic light-dark (or low-level) vision with other senses. While illusions relying on higher-level vision might invite speculation that they result from cognitive processes, rather than from basic sensory interactions, it would be difficult to make this point about the present phenomenon which results from basic light-dark information.

In conclusion: this demonstration, using very few resources, can provide even larger undergraduate classes a memorable experience of cross-modality at an elementary level of perception. The present paper shows that the demonstration is easily administered in classes as large as 30 students, that 95% of students experience the illusion, that the effect is reversible, and that students find it compelling and interesting. While not a focus of this paper, possible ways to integrate demonstrations of two other important principles in perceptual neuroscience (spectral sensitivity and luminance threshold) are also described, so that interested readers can find suggestions and materials for maximizing the use of the demonstration by combining it with other teaching activities, where appropriate for class content.

MATERIALS AND METHODS

Students (n=91) in four psychology and neuroscience courses (sizes ranging from 11 to 31) over four different semesters participated in the class demonstration. All were naïve to the cross-modal illusion.

The activity had three main components: *Part 1:* Monocular dark-adaptation, 18-25 minutes. This period always took place in the regular classroom and consisted in one eye being dark-adapted behind an eyepatch while class proceeded under normal (photopic) light conditions so that the other eye stayed light-adapted. *Part 2:* Dark conditions, 5-10 minutes. During this part, both eyes were exposed to the dark so that the effects of asymmetric dark adaptation could be observed. This second part was conducted in a darkened, windowless room, which in some cases was the regular classroom itself and in others a lab room located across the hallway from the regular classroom. *Part 3*: Gathering of results and discussion as a whole class, 10-20 minutes.

While the present paper focuses on the demonstration of the cross-modal illusion, the monocular dark adaptation induced in Part 1 also lends itself to a demonstration of the effects of dark adaptation on luminance threshold and on spectral sensitivity (Purkinje shift) during Part 2, should this content be appropriate for a given course. While the exact description of these methods goes beyond the purpose of this paper, interested readers will find links to materials and information below, as well as a brief description of the procedure and the results from one class of 31 students.

Parts 1 and 2:

Cross-modality: For Part 1, each student was given an eyepatch (black, with elastic headband) and 2-3 facial tissues. They were asked to fold up the tissues to a square of about 2x2 inches that would cover the entire orbit of the eye and that was slightly larger than the eyepatch itself. They were then asked to cover one eye with the tissue square, to put the eyepatch on top of it, and to secure the patch around the head with the elastic strap. The tissues were used to create a better seal to the face than what the patch alone would provide so that the light block would be more complete. Students were asked to close the other eye and to adjust the tissues and patch so as to minimize the light they could see with the patched eye. (Students wearing glasses were asked to put the tissues and patch behind the glasses on one eye.)

They were then asked to keep the patch undisturbed for the next 18-25 minutes so that the eye behind the patch would dark-adapt during this time, while class proceeded in normal light conditions that were in the photopic range. (The illuminance was between approximately 700 lux and 2000 lux, depending on the lighting fixtures and on whether or not the classroom had windows. For an approximation of illuminance values under different conditions, see http://en.wikipedia.org/wiki/Lux). Depending on the focus of the class, this period of time was used to discuss the phenomenon of cross-modal interaction (however, without mentioning the specific illusion to be demonstrated), and/or the mechanisms of dark-adaptation and different spectral sensitivity in photopic and scotopic vision.

Part 2: After 18-25 minutes, student were asked to put one hand over the eyepatch and cover it tightly and to look right into the overhead light for about 30 seconds, so as to strongly light-adapt the unpatched eye and to thus maximize the difference between the two eyes' states of adaptation. Following this, all room lights were turned off but light was allowed to enter from a door that was left ajar by about one inch. (Illuminance was approximately 0.05 lux). Students were asked to remove the eyepatch and tissues and to keep both eyes open. They were asked to make a mental note of any sensations they felt in the eyelids and the skin surrounding each eye. They were then asked to cover the light-adapted eye by hand and to make a mental note of whether the sensation surrounding the eye changed when the eye was thus covered.

Luminance Thresholds and Purkinje Shift: An in-depth outline of the Purkinje shift and its demonstration can be found at http://www.yorku.ca/eye/toc-sub.htm (under 'Purkinje shift'). During Part 1 (i.e., under photopic conditions), students were given a sheet of paper (8x3.5 inches) displaying an approximately equiluminant red and blue square (see http://www.yorku.ca/eye/purkink1.htm) and asked to mark the square that looked lighter to them under these photopic conditions. They were also given a paper (8x2 inches; see supplementary materials) with a grayscale composed of 20 rectangles (ranging in luminance from black to white) displayed on a black background that would be used to estimate their luminance threshold in the dark-adapted and light-adapted eye when in the dark. Then, during Part 2, students were asked to take their luminance threshold with each eye separately while closing the other eye by marking the darkest rectangle they could distinguish against the black background. (Alternatively, students can simply use any sheet of paper with text on it, and they can try to read the text with their dark-adapted and their light-adapted eye. Students will generally find that it is impossible to read anything with their light-adapted eye but that they can make out some text with the dark-adapted one). To illustrate the Purkinje shift, students were asked to look at the sheet with the red and blue square using the dark-adapted eye, and to mark the square that looked lighter to them when in the dark.

Part 3:

Students were asked to indicate their answers to a number of questions with a show of hands and to give open-ended comments on the open-ended questions.

1. When in the dark, did it feel as though the eyelid of the light-adapted ('blind') eye was sagging or drooping?
2. Did you notice any other sensations in the eye or face? If so, what were they?
3. Did the sensation change when you covered the eye by hand? How so?

Students were then asked what they thought causes the illusion of eyelid sag under the conditions that were induced by asymmetric dark adaptation.

For an exploration of luminance threshold and Purkinje shift, the following questions were added:

4. Was there a difference in luminance threshold between the two eyes? Which eye could detect darker areas on the grayscale, the light- or dark-adapted eye?
5. Which square looked brighter to you in the light, the red or the blue?
6. Which square looked brighter in the dark (to the dark-adapted eye)?

RESULTS

As illustrated in Figure 1, 86 of the 91 students (95%) reported the cross-modal illusion of eyelid sagging in response to Question 1. Some students offered other descriptions of the sensation in response to Question 2, such as: blind, numb, tingly, swollen, puffy, 'like someone punched me', 'like having had Novocaine', eyelid is paralyzed, eye is closed, cannot tell if the eye is open or closed. In response to Question 3, all 86 students experiencing the illusion reported that the sensations decreased or disappeared when the eye was covered by hand.

To make some informal observations about students' response to the effect: Students react with great surprise to their experience of the illusion. Many shout out in surprise, laugh, or express how strange a sensation it is. Similar reactions occur when the sensation magically disappears (or at least decreases) when the eye is covered by hand. Several students commented informally or on course evaluations that this demonstration was one of their favorites in the course. A few students even commented that they went on to tell their friends about it and tried it out again at home. Given the compelling nature of the demonstration, it is thus not surprising that students were easily led into speculations and discussions of the causes of the illusion, including a discussion of its possible neural substrate. Such discussion can simply be sparked by asking students what they believe could be the reason for this effect. Where appropriate for the level and content of the class, the conversation can then lead to advanced topics such as probabilistic perceptual processing and brain areas with multimodal neurons.

Readers interested in integrating a time-efficient demonstration of dark-adaptation and spectral sensitivity into this class activity on cross-modality might find it helpful to know that in the class for which this was tested, all 31 students (100%) reported the expected effect of dark-adaptation on luminance thresholds as measured on the grayscale, in that the dark-adapted eye could detect far darker rectangles than the light-adapted eye. Twenty-nine students (94%) reported the Purkinje shift in that the red square looked brighter in the light and the blue square looked brighter in the dark. One student thought that the two squares looked equally bright under both conditions, and one student thought the red square looked brighter under both conditions.

DISCUSSION

As the numerical data and the informal observations above illustrate, the eyelid droop illusion is an effective teaching tool. It is experienced by nearly all students and is a dramatic demonstration of cross-modal integration and the probabilistic nature of neural and perceptual processing. It can be reversed by a simple manipulation so that it can be made to disappear and reappear at will. It requires few resources, is feasible for a large audience, can be adjusted to take anywhere between about 30 and 60 minutes (including discussion), and can be combined with a demonstration of other important neuroscience or perceptual principles such as the duplex nature of the retina, dark-adaptation, threshold measurements, and spectral sensitivity.

Some limitations of the demonstration, or issues arising in its discussion, might include:

Using informal 'raise your hand' questioning might influence students to answer in conformity with others and might thus have distorted the numbers presented in the results. While this is a possibility, the proportion of students reporting the illusion (95%) here is identical to the percentage of observers reporting it in carefully controlled experiments where participants recorded their responses privately and were asked several control questions (Wolfe et al., 2007; 20 out of 21 participants) making it unlikely that the present results were due to normative influences. If class time allows, and where appropriate for the level of the course, one can either use the carefully controlled questioning used by Wolfe and colleagues (2007) for the demonstration or introduce a class discussion of good experimental design in this context.

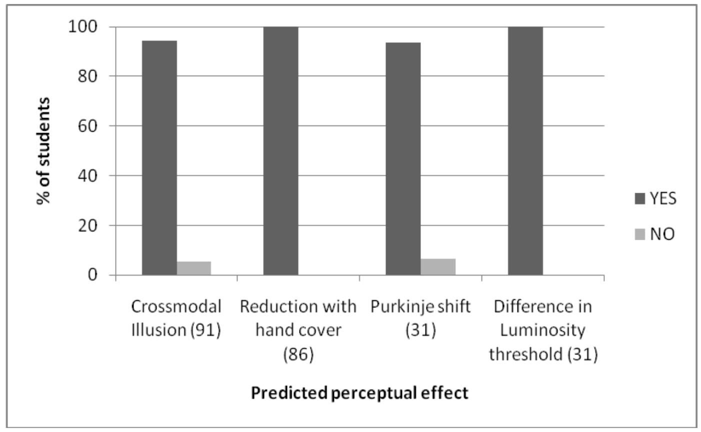

Figure 1. Percentage of students experiencing ('Yes"; dark bars) or not experiencing ('No'; light bars) each of the predicted effects. (Number in parentheses indicates number of students tested for each effect).

Some students actually have a hard time believing that the eyelid droop is illusory because the effect is so strong. It is thus important to emphasize that the effect is indeed an illusion and that the eye is actually open, as was confirmed in the original study of the illusion. The suggestion that the eye is actually closed could also be a starting point for discussion of why the eye would return to normal when covered by hand. This effect would be difficult to explain unless the lid droop was illusory. Discussing this reversibility of the illusion will not only convince students that this is an illusion, not a real lid droop, it can also provide a good example of the probabilistic nature of perception, or of the phenomenon of "perceptual explaining away" discussed in the introduction.

Because asymmetric dark-adaptation was accomplished with prolonged wearing of a patch that exerts slight pressure to the area of the eye, some students wondered if the strange sensation in the eyelid and skin around the eye might have been caused by the prolonged asymmetry in tactile input to the two sides of the face rather than the asymmetry in dark adaptation. Again, this could lead into a discussion of why the illusion would disappear when the eye is covered by hand. Tactile asymmetry would not provide a parsimonious explanation of this change in the illusion, especially since the original study (Wolfe et al., 2007) demonstrated that the illusion disappears/decreases when either eye is covered or actively closed. Similarly, in the original study asymmetric dark-adaptation was induced while all but eliminating any tactile asymmetry: First, both eyes were dark-adapted and then one eye was briefly light-adapted (<1 min) while the other eye was held closed and covered by hand. Finally, in more recent studies (Wolfe and Carpinella, 2008), we induced the illusory lid droop by inserting an occluder contact lens into one eye thus inducing visual asymmetry in the absence of any tactile asymmetry.

While the demonstration is clearly effective in terms of the number of students experiencing the illusion and of generating interest in the phenomenon, there is no evidence yet that the activity leads to better learning of the concepts involved. It is tempting to speculate that first-hand experience of the illusion would lead to better understanding and retention of concepts such as cross-modality, dark adaptation, and probabilistic nature of perception, but it is impossible to make this assertion without first gathering data on indicators of student long-term and short-term learning.

Despite these possible limitations, the demonstration outlined here can serve as a valuable and accessible teaching tool. It provides a compelling experience that students react to with interest and engagement. It can be used in the context of teaching several different and important perceptual and neuroscience concepts, and it may help integrate the concept of cross-modality into the standard content of undergraduate neuroscience and perception courses.

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