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What is This?

Optical Origins of Opposing Facial Expression Actions

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Abstract

Darwin theorized that emotional expressions originated as opposing functional adaptations for the expresser, not as distinct categories of social signals. Given that two thirds of the eye's refractive power comes from the cornea, we examined whether opposing expressive behaviors that widen the eyes (e.g., fear) or narrow the eyes (e.g., disgust) may have served as an optical trade-off, enhancing either sensitivity or acuity, thereby promoting stimulus localization ("where") or stimulus discrimination ("what"), respectively. An optical model based on eye apertures of posed fear and disgust expressions supported this functional trade-off. We then tested the model using standardized optometric measures of sensitivity and acuity. We demonstrated that eye widening enhanced stimulus detection, whereas eye narrowing enhanced discrimination, each at the expense of the other. Opposing expressive actions around the eye may thus reflect origins in an optical principle, shaping visual encoding at its earliest stage—how light is cast onto the retina.

Emotional expressions can serve as external signals of internal mental states, and recent data lend support for their socially and culturally mutable adaptive role (Aviezer, Trope, & Todorov, 2012; Jack, Garrod, Yu, Caldara, & Schyns, 2012). However, a Darwinian perspective tethers this younger social utility of emotional expressions to an older sensory adaptation for the expresser (Darwin, 1872/1998; Susskind et al., 2008). Darwin suggested that expressions, rather than being a set of distinct basic emotions (Ekman, Sorenson, & Friesen, 1969), may originate from opposing actions and are thus best understood as varying along some dimensions (Oosterhof & Todorov, 2008; Russell & Barrett, 1999; Susskind et al., 2008). Here we examine one salient dimension spanning expression space—the widening and narrowing of the eyes (Lee, Susskind, & Anderson, 2013; Susskind et al., 2008)—and whether opposing expressive features that widen and narrow the eyes may have been selected to exploit a physical principle related to how light refracts.

Although facial muscles that reconfigure superficial eye features should have no direct influence on the pupil or the accommodative lens behind it, approximately two thirds of the eye's full refractive power comes from the cornea (Duke-Elder & Abrams, 1970). We therefore hypothesized that facial expressive behaviors that expose or conceal the cornea would have measurable consequences on the eye's optics and thereby perception. Specifically, we hypothesized that widening the eyes would increase the gathering of light to enhance sensitivity at the expense of acuity, thus prioritizing visual detection over discrimination. Conversely, we hypothesized that

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narrowing the eyes would better focus light to enhance visual acuity at the expense of sensitivity, thus prioritizing visual discrimination over detection.

The functional basis of this sensitivity-versus-acuity opposition is a familiar one, seen as a fundamental division throughout the visual system. Starting from retinal rods and cones, the magnocellular and parvocellular systems (Livingstone & Hubel, 1987) represent a fundamental trade-off between sensitivity and acuity carried on to the dorsal and ventral streams for the processing of "where" and "what" information, respectively (Ungerleider & Mishkin, 1982). Our thesis is that the expressive dimension of widening versus narrowing the eyes arose from a need to filter information toward one of these two channels, thus enhancing either the gathering or focusing of light to modulate the ability to detect or discriminate stimuli, respectively, in a situation-appropriate manner. After some initial coarse appraisal, an expression would serve to modify perceptual encoding toward one of two opposing needs—to increase sensitivity or discrimination.

We selected expressions of fear and disgust to test our hypothesis because they represent the largest and smallest eye apertures, respectively, consistent with their structural opponency (Susskind et al., 2008). Once triggered by a cue or context (e.g., faint movement, sounds, or odors; Öhman & Mineka, 2001), eye widening may improve detection and localization of a potential threat that requires enhanced vigilance, which would be consistent with the hypothesized function of fear (Whalen, 1998). Conversely, eye narrowing may improve perceptual discrimination (Sherman, Haidt, & Clore, 2012) to discern different kinds of threats, such as disease vectors and contaminated foods, avoidance of which is a hypothesized function of disgust (Chapman & Anderson, 2012, 2013; Rozin, Haidt, & McCauley, 2000). Rather than treat these as distinct emotions with distinct functions, however, we hypothesized that their functions are opposed along a single continuum, in accordance with Darwin's (1872/1998) principle of antithesis.

To examine our hypotheses, we first created a basic optical model of how sensitivity and acuity might be affected by facial expressions. We used eye aperture measurements of participants who posed expressions of fear and disgust. We then tested the model's predictions in a separate group of participants using standard measures of visual function—the Humphrey Field Analyzer (HFA; Carl Zeiss Meditec, Dublin, CA) for sensitivity and Bailey-Lovie eye charts (Bailey & Lovie, 1976) for acuity.

Optical Model

To create our models, we used posed fear and disgust expressions gathered from 19 participants in a prior study (Susskind et al., 2008). One image frame from each posed expression was submitted to appearance modeling (Cootes, Edwards, & Taylor, 2001). The image frame was then scaled, rotated, and aligned in MATLAB Version 7.04 (The MathWorks, Natick, MA). The left eye's aperture (distance from the top to the bottom of the eye) from each expression was extracted for use in our optical model. The apertures for each participant's fear and disgust expressions were averaged to calculate a theoretical neutral.

Sensitivity

Sensitivity can be defined as the amount of light gathered by the eye, because increased gathering enhances the likelihood of detecting the light source. The amount of light gathered is directly related to the area of the exposed eye by which light is collected and refracted through the cornea, eventually arriving on the retina. For simplicity, our model assumed a constant pupil size, sufficiently open that extra light refracted by greater exposure of the cornea would not be blocked by the pupil. The exposed eye area was the measure of sensitivity in our model. Because human eyes are horizontally elongated (Kobayashi & Kohshima, 1997) and they open vertically rather than concentrically, we approximated the area of eye opening through which light is collected as a simple rectangle with a constant width (w) and a height equal to the eye aperture (corneal diameter, d; Fig. 1a). This area was our model's index of sensitivity:

$$\text{sensitivity} = w \cdot d$$

Because width remained constant for each participant, sensitivity was solely a function of height. Sensitivity was thus predicted to increase as eye aperture increased from disgust to fear. To compute the model's predicted sensitivity values (Fig. 1c), we set each participant's eye width equal to his or her eye aperture height for fear.

Acuity

Acuity can be defined as the ability to discriminate two proximate points of light. If the points are imperfectly focused by the eye (e.g., because of nearsightedness), they arrive on the retina as blurs that overlap and hinder discriminability. Photographers call these blurs circles of confusion (CCs). We use the same term, although the blur is technically not a circle here because the eye opens vertically not concentrically. Because discriminability is impaired with larger CCs, we indexed acuity in our model as the negative size of the CC. Assuming constant pupil size as before, we approximated the eye as a single thin lens of focal power f_0. A cone of light rays from a point
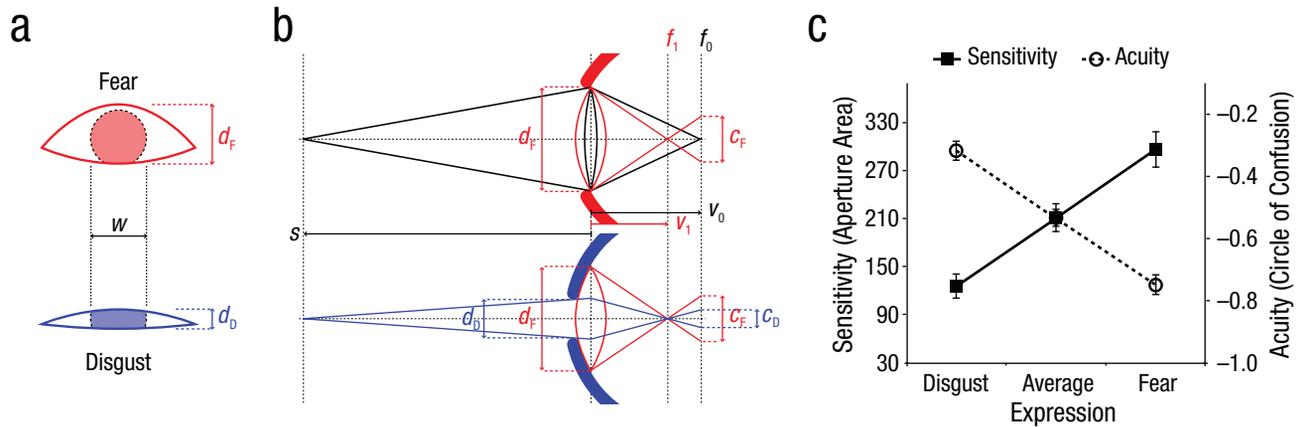
Fig. 1. Modeled optical effects of eye apertures for fear and disgust expressions. The area of eye aperture through which light is collected was approximated as a rectangle of constant width (w) and varying eye aperture diameter (d), as shown in (a). This diameter is larger for fear (d_F) than for disgust (d_D). In (b) the black lines show a cone of rays from a light source, s, correctly focused at the retina, v_0, by the lens of focal power f_0. When the light rays are correctly focused, no blur is created with eye widening or narrowing. But with an imperfect lens of focal power f_1, as in nearsightedness, the light is focused too close, v_1, and arrives on the retina as a blurred circle of confusion of size c_F (red lines). With a narrower aperture, d_D, light rays are focused at the same point (v_1) but create a smaller circle of confusion of size c_D (blue lines). The graph in (c) shows model predictions of mean sensitivity (left y-axis) and acuity (right y-axis) varying with facial expression. Sensitivity scores are indexed by exposed eye aperture area, as illustrated in (a). Acuity scores are indexed by negative size of the circle of confusion, as illustrated in (b). Higher scores indicate greater sensitivity or acuity. Error bars indicate ±1 *SEM*.

light stimulus in front of the lens, at distance s, travels through the eye aperture, d, and is correctly focused as a point at distance v_0, behind the lens, on the retina (Fig. 1b, black lines). When light rays are correctly focused, no blur is created with eye widening or narrowing. However, if focal power is imperfect (e.g., modeled as f_1 as a result of nearsightedness), the same light is incorrectly focused at point v_1 and falls on the retina instead as a CC of size c_F (Fig. 1b, red lines). From the thin-lens equation and similar triangles, we have the following:

$$\frac{1}{f_0} = \frac{1}{s} + \frac{1}{v_0}$$

$$\frac{1}{f_1} = \frac{1}{s} + \frac{1}{v_1}$$

$$\frac{v_0 - v_1}{v_1} = \frac{c_F}{d_F}$$

Algebraically combining these equalities, we get the CC size formula:

$$c_F = \frac{d_F \cdot s \cdot (f_0 - f_1)}{f_1 \cdot (s - f_0)}$$

Then, if we reduce the eye aperture to that for disgust, d_D, that reduces the CC size, c_D (Fig. 1b, blue lines), which affects only the numerator:

$$c_D = \frac{d_D \cdot s \cdot (f_0 - f_1)}{f_1 \cdot (s - f_0)}$$

That is, CC size is directly proportional to eye aperture, and because acuity is the opposite of CC size, we get:

$$\text{acuity} = -\frac{d \cdot s \cdot (f_0 - f_1)}{f_1 \cdot (s - f_0)}$$

Acuity was thus predicted to improve as eye aperture decreased from fear to disgust. To compute model values, we set the light stimulus at a constant distance, s, of 6 m. We used an approximate human-eye focal length, f_0, of 22 mm, and then modeled three nearsighted conditions of +1.0, +2.0, and +3.0 diopters (f_1 = 21.53, 21.07, and 20.64 mm, respectively), congruent with conditions in the acuity experiment described later. We then averaged acuity across the diopter conditions to compute the acuity that the model predicts (Fig. 1c).

General Method

All participants were undergraduate students from the University of Toronto. They provided a wide variety of eye anatomy (Blake, Lai, & Edward, 2003). Participants received course credit or $10 per session.

All experimental participants were trained to pose the expressions using only the upper face, because the lower face was stabilized by a chin rest. Participants were instructed on the expressions' Facial Action Coding

System action units (Ekman, Friesen, & Hager, 2002): for fear, raising the eyebrows and drawing them together and opening the eyelids; for disgust, wrinkling the nose; and for neutral, relaxing the face. The experimenter provided coaching and demonstrations, mirrors, and example images (Ekman et al., 2002) that highlighted the action units. This procedure has been demonstrated to produce reliable perceptual differences in expressers' visual-field size (Lee et al., 2013; Susskind et al., 2008) and independent observers' perception of fear and disgust in these eyes (Lee et al., 2013).

Sensitivity Experiment

Method

To test our model, we measured the left-eye sensitivity of 11 participants with normal or corrected-to-normal vision (contacts were allowed, but glasses were not because of visual-field occlusion). Each participant was tested in three sessions, each on a separate day. Each expression (fear, neutral, and disgust) was used once per session. For each run, we used the HFA's central 24-2 full-threshold test program, which recorded responses to detected light stimuli of varying luminance at 54 locations, arranged in a 6° grid on an equiluminant, equidistant visual-field hemisphere. The HFA ensured central fixation throughout. The stimulus was a white light subtending 0.43° of varying luminance shown for 200 ms on a white bowl surface (10 cd/m^2). The HFA reports sensitivity in decibels: 10 × log [maximum luminance ÷ detection threshold] dB.

After providing consent, participants were trained in a dimly lit room (ambient light, 14 lux). They were then adapted for 5 min in a dark room lit only by the HFA hemisphere. They remained in this room until the session ended. Participants responded to a detected light by pressing a button with their right hand. Expressions were posed and held for 20 s at a time, with 6- to 8-s breaks between poses. We measured pupil size during the HFA's automated gaze initialization at the start of each run, while posing the expression for that run.

Results

Eyes that express fear and disgust (Fig. 2a) influenced sensitivity throughout the visual field, most strongly in the periphery (Fig. 2b). This result is consistent with the altered occlusion associated with eye opening and closing (Lee et al., 2013; Susskind et al., 2008) and serves as a manipulation check for correct posing of fear and disgust expressions. However, for the primary analysis, we examined the data for only the most central locations (4.2° surrounding the fovea) to eliminate potentially confounding bias from occlusion effects in the periphery. The central-visual-field sensitivities were averaged for each run and submitted to a 3 (expression: fear, neutral, disgust) × 3 (session: 1, 2, 3) repeated measures analysis of variance (ANOVA). As the model predicted, there was a main effect of expression, $F(2, 20) = 6.4$, $p = .0072$, $\eta_p^2 = .39$; specifically, sensitivity was greater when participants posed a fear expression than when they posed a neutral expression, $F(1, 10) = 5.8$, $p = .036$, $\eta_p^2 = .37$, or
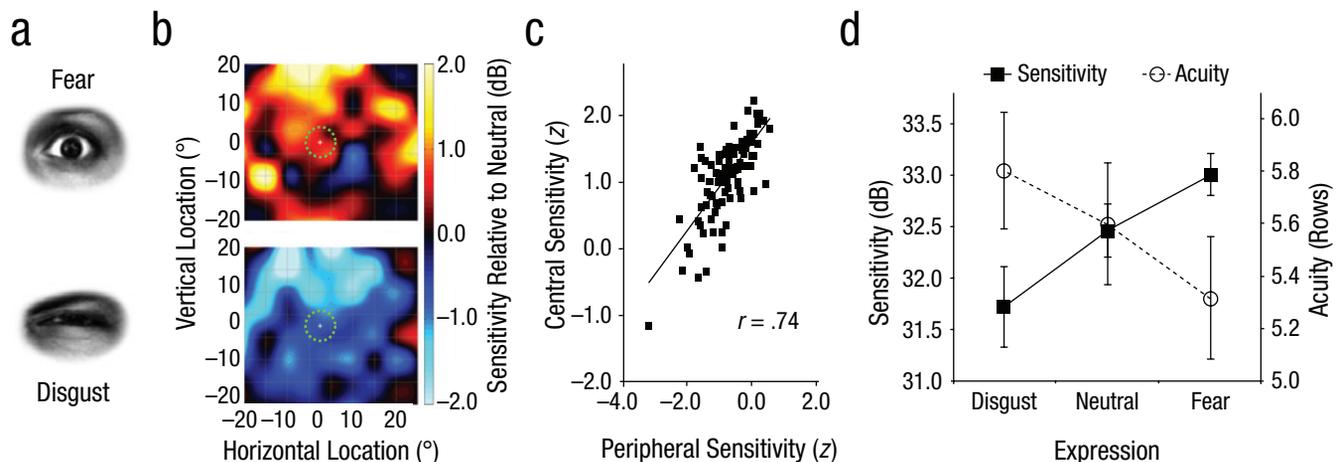

Fig. 2. Measured perceptual effects of eye apertures associated with fear and disgust expressions. Examples of fear and disgust expressions are shown in (a). Relative sensitivity maps (b) were created by averaging results at each point of the visual field and subtracting sensitivity associated with neutral expressions from sensitivity associated with fear expressions (top) and from sensitivity associated with disgust expressions (bottom). Hotter and cooler colors indicate greater positive and negative differences, respectively, relative to neutral. Fixation was at (0°, 0°). The dotted green circles indicate the centrally measured locations (4.2° visual angle from fovea). The graph in (c) shows central visual-field sensitivity as a function of peripheral visual-field sensitivity (mean visual angle from fovea = 20.6°, *SD* = 2.1°). Greater peripheral sensitivity is an index of eye opening. The graph in (d) shows mean sensitivity (left *y*-axis) and acuity (right *y*-axis) as a function of expression. Sensitivity scores are restricted to the central visual field. Acuity was measured as the number of correctly read rows of eye-chart letters; these scores were collapsed across contrast and diopter. Higher scores indicate greater sensitivity or acuity. Error bars represent ±1 *SEM*.

a disgust expression, $F(1, 10) = 8.3$, $p = .016$, $\eta_p^2 = .45$ (Fig. 2d).

These effects, rather than showing a categorical difference between expressions, appeared to reflect opposing ends of a continuum of structural variance—between which neutral resides—as illustrated by a strong linear positive correlation across all runs between peripheral-field ($20.6° ± 2.1$) sensitivity and central sensitivity, $r(97) = .739$, $p < .0001$ (Fig. 2c). That is, as eye aperture increased (indexed by increased peripheral sensitivity from reduced occlusion), parafoveal sensitivity increased, as the model predicted.

Experimental control measures reported by the HFA were analyzed in separate Expression × Session repeated measures ANOVAs. We found no pupil-size differences between expressions, $F(2, 20) = 0.13$, $p > .8$, which indicates a lack of autonomic feedback and suggests that the effect of expression was primarily optical rather than a secondary effect of emotional embodiment (e.g., Niedenthal, 2007). Because of occlusion, some gaze initializations for disgust-expression runs were performed while the participants posed neutral expressions; however, pupil size did not differ between fear and neutral expressions, $F(1, 10) = 1.0$, $p > .7$. Responses also did not differ with practice; there was no main effect of session on central sensitivity, $F(2, 20) = 1.2$, $p > .3$. Expression also did not have a significant effect on the number of fixation losses, $F(2, 20) = 0.03$, $p > .9$; false positive responses, $F(2, 20) = 2.1$, $p > .14$; or false negative responses, $F(2, 20) = 1.5$, $p > .23$. In conjunction, these data suggest that changes in the ocular adnexa (i.e., the structural envelope around the eye) are the primary factor responsible for the altered perceptual sensitivity associated with fear and disgust expressions.

Acuity Experiment

Method

To test our acuity model, we measured the visual acuity of 26 participants with normal or corrected-to-normal vision. We first gave them goggles (magnetic-resonance-compatible prescription glasses; Safevision, LLC, Webster Groves, MO) that myopically blurred their vision. The goggles were of different optical strengths (+1.0, +2.0, and +3.0 diopters). Given the additive nature of lens power, participants wore the goggles atop their usual correction glasses or contacts, if any. Participants were then tested on a set of Bailey-Lovie eye charts (Bailey & Lovie, 1976), nine with high contrast (black letters) and nine with low contrast (gray letters; 15% Michelson contrast).

The experiment was divided into blocks by contrast and then by diopter, and the block order was counterbalanced across participants. Expression order was counterbalanced within participants. Eye-chart order was randomized across participants. To help the participants stay on task, we instructed them to make the trained expressions to aid in reading the letters. Participants took breaks (i.e., they looked away from the chart) between holding expressions as needed. Acuity was measured as the number of rows of letters read.

Results

Two participants with outlying scores (> 2.5 *SD* from the mean) were removed from analysis, which left a final sample of 24. Eye chart acuity scores were submitted to a 3 (expression: fear, neutral, disgust) × 3 (diopter: +1.0, +2.0, +3.0) × 2 (contrast: high, low) repeated measures ANOVA. As predicted, there was a main effect of expression, $F(2, 46) = 4.7$, $p = .014$, $\eta_p^2 = .17$ (Fig. 2c). This effect was modified by an Expression × Diopter interaction, $F(4, 92) = 3.0$, $p = .022$, $\eta_p^2 = .12$, which revealed a more pronounced effect of expression with increasing need for acuity to overcome optical aberrations. Analysis of data for the higher diopters (+2.0 and +3.0) in a 3 × 2 × 2 repeated measures ANOVA revealed a larger effect of expression than in the previous analysis, $F(2, 46) = 7.8$, $p = .0012$, $\eta_p^2 = .25$, with participants exhibiting greater acuity when they posed disgust expressions than when they posed neutral expressions, $F(1, 23) = 6.9$, $p = .015$, $\eta_p^2 = .23$, or fear expressions, $F(1, 23) = 11.9$, $p = .0021$, $\eta_p^2 = .34$.

Sensitivity-Acuity Trade-off

Finally, we directly analyzed the trade-off between sensitivity and acuity by normalizing and submitting sensitivity and acuity scores to a 3 (expression: fear, neutral, disgust) × 2 (experiment: sensitivity, acuity) mixed-model ANOVA. As predicted by the optical model (Fig. 1c), there was a strong crossover interaction, $F(2, 66) = 13.7$, $p < .0001$, $\eta_p^2 = .29$, and sensitivity increased from disgust to neutral to fear expressions as acuity conversely increased from fear to neutral to disgust expressions, $F(1, 33) = 18.8$, $p = .0001$, $\eta_p^2 = .36$.

Discussion

Increasing evidence suggests that emotions influence the central nervous system at multiple levels to alter visual perception (e.g., Krusemark & Li, 2011; Sherman et al., 2012; Todd, Talmi, Schmitz, Susskind, & Anderson, 2012). The present findings show that emotional expressions can exert potent effects at the earliest stage of visual encoding by changing the eyes' capacity to gather and focus light. This evidence of early filtering is consistent with the functional origins of facial expressive actions. The opposing facial actions that widen or narrow the eyes and their associated optical consequences support

Darwin's (1872/1998) first and second principles of emotional expressive behavior. According to his first principle of function (i.e., serviceable associated habits), Darwin argued that expressions did not necessarily originate for communication and are therefore not arbitrary signals but shaped to provide some functional benefit for the expresser. The second principle of opposing form (i.e., antithesis) states that expressions can be understood as originating from opposing actions that support opposing functions (see also Susskind et al., 2008).

Although we found support for his theory of the origins of human expressions, Darwin (1872/1998) considered expressions largely vestigial. The sensory regulatory effects found in our experiments (and in Susskind et al., 2008; Lee et al., 2013) challenge this notion by suggesting that expressions' functional value coexists alongside their more modern social function (Allport, 1924; Barrett, 2011). For example, the enhanced sensitivity associated with eye widening may have been adaptive for its fast action relative to slower pupillary dilation. This egocentric function, then, would have been allocentrically co-opted for social communication (Andrew, 1963), the enhanced contrast of exposed eye whites (Kobayashi & Kohshima, 1997) serving as conspicuous physical signals (Lee et al., 2013).

Consistent with the distinct processing dynamics proposed for fear and disgust (Anderson, Christoff, Panitz, De Rosa, & Gabrieli, 2003), as well as their opposing effects on the autonomic nervous system (Levenson, 1992), the opposing perceptual effects revealed in the current experiments shed light on why these two negatively valenced and avoidance-action-related emotions are associated with opposing facial actions (Susskind et al., 2008). The expressive widening and narrowing of eye features may converge with the sympathetic dilation and parasympathetic constriction of the pupil (Beatty & Lucero-Wagoner, 2000; see also Brunton, 1938, regarding the sympathetically innervated Müller's muscle that further opens the eyes), potentially acting as the initial filters toward the magnocellular (dorsal) and parvocellular (ventral) visual streams (Ungerleider & Mishkin, 1982).

The selective enhancement of sensitivity or acuity, one at the expense of the other, suggests the differential need for "where" (magnocellular) and "what" (parvocellular) information. This selective enhancement is consistent with the distinct theorized functions of fear in promoting vigilance toward localizing an unknown, potentially moving threat (Öhman & Mineka, 2001; Whalen, 1998) and disgust in promoting discrimination (Sherman et al., 2012) of different kinds of threat, such as contaminated foods or disease vectors (Chapman & Anderson, 2012, 2013; Rozin et al., 2000). Social exaptation of the functional relationship between fear expressions and the magnocellular system is evidenced by their perceptual prioritization (West,

Anderson, Bedwell, & Pratt, 2010) and low-spatial-frequency tuning (Vuilleumier, Armony, Driver, & Dolan, 2003). In contrast, we predict that encoding of disgust expressions would be slower and more attentionally gated (Anderson et al., 2003), dependent on the ventral parvocellular system and high-spatial-frequency analysis.

In tempering our findings, we weigh considerations of ecological validity. First, from a functional standpoint, whereas the standardized optometric tests we used provide experimental precision, their capacity to allow us to infer utility in the case of real-world scenes is limited. When considering these expressions' modern utility, it is worth remembering that electricity and ophthalmology have essentially solved the problems of darkness and impaired acuity—and these solutions were not available until recently in human history.

Second, from a social-constructivist perspective (e.g., Barrett, 2006), widening and narrowing of the eyes may not universally characterize fear and disgust expressions, respectively, especially given the powerful influences of culture (Jack et al., 2012) and social and body context (Aviezer et al., 2008; Aviezer et al., 2012) on perception of facial expressions. However, if fear and disgust expressions were swapped, they would serve equally well as social signals of mental states but would have misaligned functional consequences (e.g., reducing acuity in disgust, as shown here, or making it harder to tell where someone is gazing during fear; Lee et al., 2013). From a comparative perspective, greater eye-white exposure related to eye widening is observed in dairy cows that have been separated from their young or that have been exposed to a sudden, unfamiliar stimulus (Sandem, Janczak, Salte, & Braastad, 2006). Thus, we argue that these functional benefits probably served as anchoring sources of invariance in expression perception across cultures and contexts. This conclusion is supported by the fact that powerful contextual effects do not cause narrow-eyed expressions to be judged similarly to wide-eyed ones, and vice versa (Aviezer et al., 2008).

The effects of eye widening and narrowing seen here are tied to a continuum of physical reconfigurations of eye aperture (Fig. 2c) rather than to discrete facial configurations. Thus, these opposing optical effects represent an underlying functional dimension of eye opening that may extend to other expressions (e.g., raising eyebrows in surprise or lowering them in anger; Susskind & Anderson, 2008). Furthermore, these opposing optical effects can occur in the absence of their discrete emotions such as fear and disgust and their associated autonomic expression. Therefore, such effects may provide a window (beyond basic emotions) into the intentions of the expresser and an optical basis for the ability to read complex mental states from the eyes (Baron-Cohen, Wheelwright, Hill, Raste, & Plumb, 2001).

If our expressions were arbitrary configurations, they would show little cross-cultural correspondence (Ekman et al., 1969; Izard, 1994). But rather than being a collection of discrete, independent categories (Ekman et al., 1969), our expressions probably adhere to some underlying universal functional principles (Darwin, 1872/1998; Lee et al., 2013; Susskind et al., 2008). Here we have provided such functional evidence, while embracing more modern dimensional approaches to facial expressions and their meaning (Oosterhof & Todorov, 2008; Russell & Barrett, 1999). Our findings suggest that one potential source of expressive invariance across cultures and contexts is rooted in opposing facial muscle actions around the eyes that arose to harness invariant principles of light.

Author Contributions

D. H. Lee and A. K. Anderson developed the model and experiments, assisted by J. G. Flanagan for the sensitivity experiment and by R. Mirza for the acuity experiment. R. Mirza conducted the acuity experiment. D. H. Lee performed the analyses for both experiments. D. H. Lee and A. K. Anderson wrote the manuscript together, assisted by J. G. Flanagan.

Acknowledgments

Declaration of Conflicting Interests

References

Allport, F. (1924). *Social psychology*. New York, NY: Houghton Mifflin.

Anderson, A. K., Christoff, K., Panitz, D. A., De Rosa, E., & Gabrieli, J. D. E. (2003). Neural correlates of the automatic processing of threat facial signals. *Journal of Neuroscience*, *23*, 5627–5633.

Andrew, R. J. (1963). Evolution of facial expression. *Science*, *142*, 1034–1041. doi:10.1126/science.142.3595.1034

Aviezer, H., Hassin, R. R., Ryan, J., Grady, C., Susskind, J. M., Anderson, A. K., . . . Bentin, S. (2008). Angry, disgusted, or afraid? Studies on the malleability of emotion perception. *Psychological Science*, *19*, 724–732. doi:10.1111/j.1467-9280.2008.02148.x

Aviezer, H., Trope, Y., & Todorov, A. (2012). Body cues, not facial expressions, discriminate between intense positive and negative emotions. *Science*, *338*, 1225–1229. doi:10.1126/science.1224313

Bailey, I. L., & Lovie, J. E. (1976). New design principles for visual acuity letter charts. *American Journal of Optometry and Physiological Optics*, *53*, 740–745.

Baron-Cohen, S., Wheelwright, S., Hill, J., Raste, Y., & Plumb, I. (2001). The "Reading the Mind in the Eyes" Test revised version: A study with normal adults, and adults with Asperger syndrome or high-functioning autism. *Journal of Child Psychology and Psychiatry*, *42*, 241–251. doi:10.1017/S0021963001006643

Barrett, L. F. (2006). Are emotions natural kinds? *Perspectives on Psychological Science*, *1*, 28–58. doi:10.1111/j.1745-6916.2006.00003.x

Barrett, L. F. (2011). Was Darwin wrong about emotional expressions? *Current Directions in Psychological Science*, *20*, 400–406. doi:10.1177/0963721411429125

Beatty, J., & Lucero-Wagoner, B. (2000). The pupillary system. In J. T. Cacioppo, G. Berntson, & L. G. Tassinary (Eds.), *Handbook of psychophysiology* (pp. 142–162). Cambridge, England: Cambridge University Press.

Blake, C., Lai, W., & Edward, D. (2003). Racial and ethnic differences in ocular anatomy. *International Ophthalmology Clinics*, *43*(4), 9–25.

Brunton, C. E. (1938). Smooth muscle of the periorbita and the mechanism of exophthalmos. *British Journal of Ophthalmology*, *22*, 257–268.

Chapman, H. A., & Anderson, A. K. (2012). Understanding disgust. *Annals of the New York Academy of Sciences*, *1251*, 62–76. doi:10.1111/j.1749-6632.2011.06369.x

Chapman, H. A., & Anderson, A. K. (2013). Things rank and gross in nature: A review and synthesis of moral disgust. *Psychological Bulletin*, *139*, 300–327. doi:10.1037/a0030964

Cootes, T., Edwards, G., & Taylor, C. (2001). Active appearance models. *IEEE Transactions on Pattern Analysis and Machine Intelligence*, *23*, 681–685. doi:10.1109/34.927467

Darwin, C. (1998). *The expression of the emotions in man and animals*. New York, NY: Oxford University Press. (Original work published 1872)

Duke-Elder, S., & Abrams, D. (1970). *System of ophthalmology: Vol. 5. Ophthalmic optics and refraction*. London, England: Henry Kimpton.

Ekman, P., Friesen, W. V., & Hager, J. C. (2002). *Facial Action Coding System*. Salt Lake City, UT: Research Nexus.

Ekman, P., Sorenson, E. R., & Friesen, W. V. (1969). Pan-cultural elements in facial displays of emotion. *Science*, *164*, 86–88. doi:10.1126/science.164.3875.86

Izard, C. E. (1994). Innate and universal facial expressions: Evidence from developmental and cross-cultural research. *Psychological Bulletin*, *115*, 288–299. doi:10.1037/0033-2909.115.2.288

Jack, R. E., Garrod, O. G. B., Yu, H., Caldara, R., & Schyns, P. (2012). Facial expressions of emotion are not culturally universal. *Proceedings of the National Academy of Sciences, USA*, *109*, 7241–7244. doi:10.1073/pnas.1211865110

Kobayashi, H., & Kohshima, S. (1997). Unique morphology of the human eye. *Nature*, *387*, 767–768.

Krusemark, E., & Li, W. (2011). Do all threats work the same way? Divergent effects of fear and disgust on sensory perception and attention. *Journal of Neuroscience*, *31*, 3429–3434. doi:10.1523/JNEUROSCI.4394-10.2011

Lee, D. H., Susskind, J. M., & Anderson, A. K. (2013). Social transmission of the sensory benefits of eye widening in

fear expressions. *Psychological Science*, *24*, 957–965. doi:10.1177/0956797612464500

Levenson, R. W. (1992). Autonomic nervous system differences among emotions. *Psychological Science*, *3*, 23–27. doi:10.1111/j.1467-9280.1992.tb00251.x

Livingstone, M. S., & Hubel, D. H. (1987). Psychophysical evidence for separate channels for the perception of form, color, movement, and depth. *Journal of Neuroscience*, *7*, 3416–3468.

Niedenthal, P. M. (2007). Embodying emotion. *Science*, *316*, 1002–1005. doi:10.1126/science.1136930

Öhman, A., & Mineka, S. (2001). Fears, phobias, and preparedness: Toward an evolved module of fear and fear learning. *Psychological Review*, *108*, 483–522. doi:10.1037/0033-295X.108.3.483

Oosterhof, N. N., & Todorov, A. (2008). The functional basis of face evaluation. *Proceedings of the National Academy of Sciences, USA, 105*, 11087–11092. doi:10.1073/pnas.0805664105

Rozin, P., Haidt, J., & McCauley, C. (2000). Disgust. In M. Lewis & J. M. Haviland-Jones (Eds.), *Handbook of emotions* (2nd ed., pp. 637–653). New York, NY: Guilford Press.

Russell, J. A., & Barrett, L. F. (1999). Core affect, prototypical emotional episodes, and other things called emotion: Dissecting the elephant. *Journal of Personality and Social Psychology*, *76*, 805–819. doi:10.1037/0022-3514.76.5.805

Sandem, A. I., Janczak, A. M., Salte, R., & Braastad, B. O. (2006). The use of diazepam as a pharmacological validation of eye white as an indicator of emotional state in dairy cows. *Applied Animal Behaviour Science*, *96*, 177–183.

Sherman, G. D., Haidt, J., & Clore, G. L. (2012). The faintest speck of dirt: Disgust enhances the detection of impurity. *Psychological Science*, *23*, 1506–1514. doi:10.1177/0956797612445318

Susskind, J. M., & Anderson, A. K. (2008). Facial expression form and function. *Communicative & Integrative Biology, 1*, 148–149. doi:10.4161/cib.1.2.6999

Susskind, J. M., Lee, D. H., Cusi, A., Feiman, R., Grabski, W., & Anderson, A. K. (2008). Expressing fear enhances sensory acquisition. *Nature Neuroscience*, *11*, 843–850. doi:10.1038/nn.2138

Todd, R. M., Talmi, D., Schmitz, T. W., Susskind, J. M., & Anderson, A. K. (2012). Psychophysical and neural evidence for emotion-enhanced perceptual vividness. *Journal of Neuroscience*, *32*, 11201–11212. doi:10.1523/JNEUROSCI.0155-12.2012

Ungerleider, L. G., & Mishkin, M. (1982). Two cortical visual systems. In D. J. Ingle, M. A. Goodale, & R. J. Mansfield (Eds.), *Analysis of visual behavior* (pp. 549–586). Cambridge, MA: MIT Press.

Vuilleumier, P., Armony, J. L., Driver, J., & Dolan, R. J. (2003). Distinct spatial frequency sensitivities for processing faces and emotional expressions. *Nature Neuroscience, 6*, 624–631. doi:10.1038/nn1057

West, G. L., Anderson, A. K., Bedwell, J. S., & Pratt, J. (2010). Red diffuse light suppresses the accelerated perception of fear. *Psychological Science*, *21*, 992–999. doi:10.1177/0956797610371966

Whalen, P. J. (1998). Fear, vigilance, and ambiguity: Initial neuroimaging studies of the human amygdala. *Current Directions in Psychological Science, 7*, 177–188. doi:10.1111/1467-8721.ep10836912