

Article Addendum

Facial expression form and function

Joshua M. Susskind* and Adam K. Anderson

Department of Psychology; University of Toronto; Toronto, Ontario Canada

Key words: adaptation, cross-species, emotion, evolution, facial expression, nonverbal displays, sensory function

From an evolutionary perspective, facial expressions would serve adaptive functions that promote genetic fitness. While many ideas have been proposed,¹ the specific adaptive functions of expressing emotion on the face have largely remained untested since Darwin proposed a set of expressive functional principles over 130 years ago.² Recently, we showed that expressions of fear and disgust alter the biomechanical properties of the face, such that fear increases while disgust decreases sensory exposure.³ Additional vector flow analyses presented here reveal that anger and surprise expressions may similarly be shaped by sensory contraction and expansion action tendencies. An examination of the temporal dynamics of sensory modulation may reveal a general principle shaping expressive form rather than a specific adaptation shaping fear and disgust. Furthermore, if sensory modulation is a general principle, this function should be present across species rather than only in humans. Although facial morphology differs across species, detailed examination of sensory intake in different species may reveal the origins of facial expressions inherited by humans.

Facial Expression Form and Function

While facial expressions convey highly recognizable emotional signals,⁴ their specific forms may have originated not for communication, but as functional adaptations of more direct benefit to the expresser.⁵⁻⁷ The idea that expressions are evolutionary adaptations has a long history originating in the work of Charles Darwin,² but until recently no studies have conducted a direct test of the adaptive value of displaying a particular expression configuration. Our research demonstrated that fear and disgust expressions alter the sensory organs on the face to increase versus decrease sensory exposure to the environment.³ The increase in exposure measured while posing fear expressions is consistent with the proposed role of fear in promoting sensory vigilance during an emotional episode where it may be important to detect and elude threats.^{8,9} Likewise, the

decrease in exposure of the sensory surfaces measured while posing disgust expressions is consistent with sensory rejection of potential contaminants.^{10,11} However, the role of sensory regulation in shaping emotional expressions is likely not limited to fear and disgust expressions but instead may represent a general principle shaping the physical appearance of a range of different commonly recognized expressions in humans as well as in other animals. Previously we focused on facial action patterns characterizing fear and disgust, revealing opposing action tendencies shaping the appearance of these expressions.³ We conducted additional vector flow analyses using the same appearance model³ that indicate these underlying action patterns contribute to other commonly recognized facial expressions (Fig. 1). While the compressing vector flow pattern appears more holistic for disgust (Fig. 1A) than for anger (Fig. 1B), anger shares the brow lowering flow component with disgust. Moreover, the anger vector flow pattern highlights a lip pressing action that causes the lower jaw to rise and the mouth to shut, suggesting sensory closure. Like the fear expression (Fig. 1C), surprise reveals an expanding vector flow pattern, resulting in raised eyebrows, an elongated nasal passage, and an open mouth (Fig. 1D). In addition to shaping static facial displays of commonly recognized emotions in humans, we further suggest that sensory regulating components may underlie the temporal dynamics of expressions as well as the continuity of these facial actions across species.

Temporal Dynamics and an Underlying Sensory Dimension Shaping Expressive Form

We have focused solely on static configurations without examining the role of dynamics. Sensory regulation may be even more evident in the temporal dynamics of spontaneous facial expression sequences. For instance, slow-motion video of a typical startle response in humans following a loud noise reveals an initial protective posture resembling wincing in which the eyes close and the muscles around the eyes tighten.^{12,13} This sensory protective facial configuration is often followed by a wide-eyed posture resembling surprise or fear.¹⁴ One explanation for this patterned response to an intense and unexpected environmental change is that it is foremost important to protect the sensory organs from harm and secondarily important to locate the source of the unseen startling event. Thus, the startle pattern involves both aspects of sensory regulation that may have been the precursors of prototypical of fear and disgust expressions and that have come to signal more complex emotional states.

*Correspondence to: Joshua M. Susskind; Department of Psychology; University of Toronto; 100 St. George Street; Toronto, Ontario M5S 3G3 Canada; Tel.: 416.978.1540; Fax: 416.978.4811; Email: josh@aclab.ca

Submitted: 09/08/08; Accepted: 09/17/08

Previously published online as a *Communicative & Integrative Biology* E-publication: <http://www.landesbioscience.com/journals/cib/article/6999>

Addendum to: Susskind JM, Lee DH, Cusi A, Feiman R, Grabski W, Anderson AK. Expressing fear enhances sensory acquisition. *Nat Neurosci* 2008; 11:843-50.

Continuity Across Species in Facial Expression Form and Function

Homologues to the human facial startle response are present in non-human primates¹⁵ indicating that sensory regulating facial action tendencies are not unique to humans. Significant continuity of facial actions across species would be strong evidence for the origin of facial expression form in adaptive sensory function. A source of evidence for the continuity of the sensory expanding tendency of fear facial expressions comes from a study examining bovine eye whites. The authors found that a high percentage of eye whites indicated frustration and fear, which were postulated to enhance sensory vigilance.¹⁶ Documenting cross-species correlates of facial expressions is difficult due to the varied morphology of the face. However, the recent development of methods for facial action coding in chimpanzees allow for cross-species comparisons.¹⁷ Although the outward appearance of the face differs, chimpanzees have many of the same facial muscles as humans and can exhibit fine control over the mimetic musculature of their faces.¹⁸ The varied expressive repertoire of chimpanzees includes brow raising/lowering and upper lip raising,¹⁷ suggesting that their facial actions may serve to regulate sensory intake. Future field research examining the cross-species effects of facial actions on sensory regulation would thus be a promising avenue to extend our understanding of the evolutionary origins of facial expressions, perhaps revealing that expressive tendencies are largely rooted in the need to actively sample and respond to events in an uncertain world.

Acknowledgements

This work was supported by the Canada Research Chairs program and a Natural Sciences and Engineering Research Council grant to Adam K. Anderson

References

- Schmidt K, Cohn JF. Human facial expressions as adaptations: Evolutionary questions in facial expression research. *Am J Phys Anthropol* 2001; 116:3-24.
- Darwin C. *The Expression of the Emotions in Man and Animals*. London: John Murray, 1872.
- Susskind JM, Lee DH, Cusi A, Feiman R, Grabski W, Anderson AK. Expressing fear enhances sensory acquisition. *Nat Neurosci* 2008; 11:843-50.
- Ekman P. Basic Emotions. In: Dalglish T, Power T, eds. *The Handbook of Cognition and Emotion*. Sussex: John Wiley and Sons, Ltd., 1999: 45-60.
- Gratiolet P. *De la Physionomie et des Mouvements d'Expression*. Paris: Hetzel, 1865.
- Piderit T. *Mimik und Physiognomik*, 3rd Ed. Detmold, 1867.
- Pieper A. *Cerebral Function in Infancy and Childhood*. New York: Consultants Bureau, 1963.
- Davis M, Whalen PJ. The amygdala: vigilance and emotion. *Mol Psychiatry* 2001; 6:13-34.
- Gray JA. *The Neuropsychology of Anxiety*. New York: Oxford University Press, 1982.
- Rozin P, Fallon AE. A perspective on disgust. *Psychol Rev* 1987; 94:23-41.
- Vrana SR. The psychophysiology of disgust: differentiating negative emotional contexts with facial EMG. *Psychophysiology* 1993; 30:279-86.
- Ekman P, Friesen WV, Simons RC. Is the startle reaction an emotion? *J Personal Soc Psychol* 1985; 49:1416-26.
- Landis C, Hunt WA. *The Startle Pattern*. New York: Farrar and Rinehart, 1939.
- Tomkins SS. *Affect, Imagery, Consciousness*, Vol. 1. New York: Springer, 1962.
- Winslow JT, Parr LA, Davis M. Acoustic startle, prepulse inhibition, and fear-potentiated startle measured in rhesus monkeys. *Biol Psychiatry* 2002; 51:859-66.

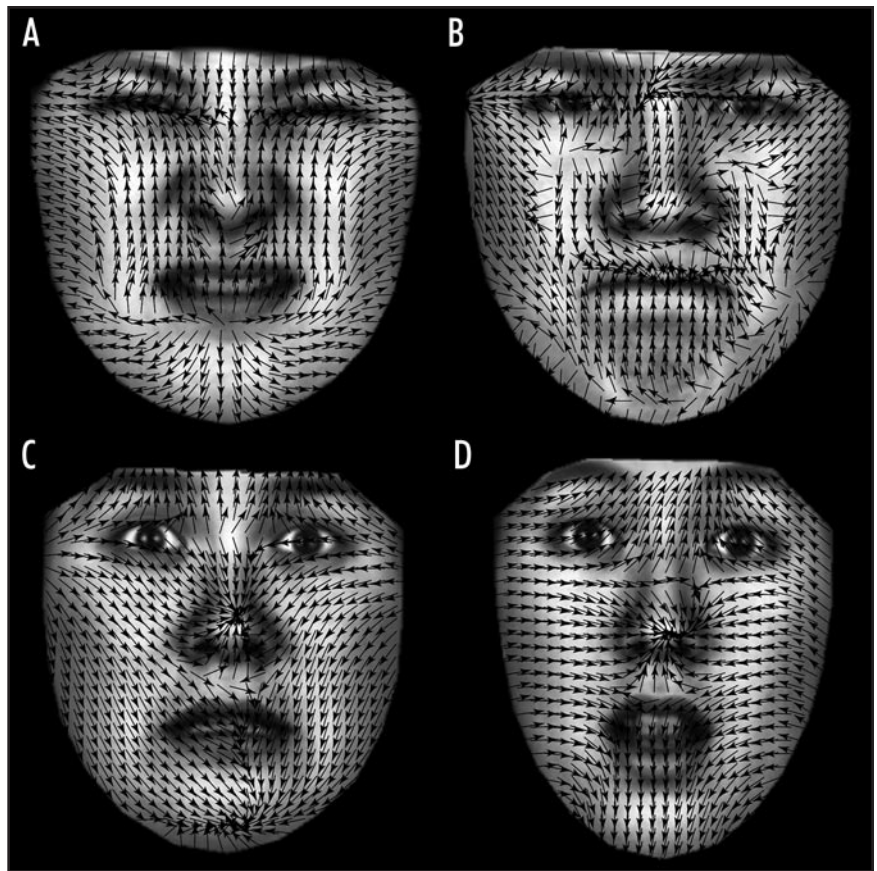


Figure 1. (A) Disgust, (B) anger, (C) fear and (D) surprise facial expression prototypes. Arrows depict vector flow fields of skin surface deformations stemming from the mean face defined in computational appearance space³ to the corresponding expression prototype, allowing visualization of the underlying facial action patterns.

- Sandem A, Janczak A, Salte R, Braastad B. The use of diazepam as a pharmacological validation of eye white as an indicator of emotional state in dairy cows. *Appl Anim Behav Sci* 2006; 96:177-83.
- Vick SJ, Waller B, Parr L, Smith Pasqualini M, Bard K. A cross-species comparison of facial morphology and movement in humans and chimpanzees using the facial action coding system (FACS). *J Nonverb Behav* 2007; 31:1-20.
- Burrows AM, Waller BM, Parr LA, Bonar CJ. Muscles of facial expression in the chimpanzee (*Pan troglodytes*): descriptive, comparative and phylogenetic contexts. *J Anat* 2006; 208:153-67.