

The shape of faces (to come)

Paul J Whalen & Robert E Kleck

Have facial expressions evolved randomly or do their different shapes support some adaptive purpose? New work offers evidence of a selection pressure that may have shaped fearful and disgusted expressions.

The human face is a canvas on which we can paint any number of different facial features to nonverbally communicate with those around us. These facial configurations need not be complicated. A simple raise of the eyebrow from a mother will halt an 11-year-old child right in his tracks.

But why do facial expressions look the way they do? Upturned corners of a mouth are seen as a good thing, whereas downturned corners are bad. Could it have gone the other way? Are the shapes of our facial expressions random or do these different configurations exist because they each support some specific adaptive purpose? In this issue, Susskind *et al.*¹ asked these questions of fearful and disgusted expressions.

In their study, subjects posed fearful and disgusted faces in various conditions. In one condition, subjects had to detect quick flashes of light on a wall that encompassed the entirety of their peripheral vision (much like a visit to the eye doctor). In another condition, the speed of subjects' eye movements to targets in their visual field was measured. And in yet another condition, the amount of air that subjects inspired through the nose was measured. Across all conditions, facilitated intake of sensory information was observed when subjects made fearful faces, whereas attenuated sensory intake was observed when subjects made disgusted faces.

To elaborate, when subjects posed fearful faces, they were able to detect more flashes of light in the upper extent of their peripheral visual field, they were faster to move their eyes to targets in their visual field and they took in more air through the nose. In contrast, when they posed disgusted expressions, they detected fewer flashes of light in the upper extent of their visual field, they were slower to move their eyes to visual targets and they took in less air through the nose. Thus, the converse movements of the brows, eyelids and nose enacted in the formation of these expressions had opposite effects on sensory intake (Fig. 1). This makes sense when one considers the situations where these expressions are encountered. Fearful expressions

a Disgust



Lowered brow
Narrowed eyes
Narrowed nostrils
Closed mouth

b Fear



Raised brow
Widened eyes
Flared nostrils
Open mouth

Figure 1 Fearful versus disgusted expressions. Note how the various parts of the face move in opposite directions in the two expressions, and therefore have opposite effects on sensory intake. Facial images from the NimStim set of facial expressions (MacArthur Foundation, <http://www.macbrain.org/resources.htm>).

are observed at times when you would do well to learn more about your surroundings and disgusted expressions are observed at times when you feel you have learned quite enough.

That eye widening should facilitate environmental monitoring is consistent with other data showing that the amygdala has a unique relationship with fearful facial expressions. Indeed, the amygdala uses the widened eyes in fearful expressions as a proxy for the presence of fearful faces², and lesions of the human amygdala result in an inability to properly scan the eye whites in fearful faces³. Further, electrical stimulation of the human amygdala results in eye widening and heightened visual scanning of the environment⁴ and produces nonspecific arousal responses such as pupil dilation⁴. Neuroimaging studies have shown that the amygdala is sensitive to the pupil size of others^{5,6}. Taken together, these findings support the hypothesized role of the amygdala in potentiating sensory information processing to facilitate learning about the predictive value of environmental events, a process referred to as associative orienting^{7,8}. More generally, these results suggest that your amygdala is sensitive to the very facial responses in others that it controls in you.

If the amygdala has shown an affinity for the facial expression of fear, then the analogous brain region for disgusted expressions would be the

insular cortex. Neuroimaging, as well as depth electrode recording studies, show that human insular cortex responds to disgusted faces^{9,10}, and damage to the insula produces deficits in the recognition of disgusted faces¹¹. Furthermore, insular pathology in Huntington's disorder is associated with a decreased disgust response and a similar recognition deficit of disgust¹². Although it is tempting to divide duties for the amygdala and insular cortex between fear and disgust and to suggest that they represent unique neural substrates for their processing, other work suggests that these reciprocally connected regions will interact along dimensions such as arousal, valence and/or attention, dimensions that cross the stark boundary between these two expression categories¹³.

One key point raised by Susskind *et al.*¹ is whether sensory intake is the only selection pressure that shaped fearful and disgusted expressions. It is probable that multiple selection pressures are involved. For example, it has been suggested¹⁴ that fearful faces look the way they do because such a facial configuration increases the apparent 'babyishness' of the expresser and, therefore, serves to elicit nurturing or protective responses from conspecifics. So, are different hypothesized selection pressures such as these mutually exclusive or can they peacefully coexist?

The authors are at the Department of Psychological and Brain Sciences, Dartmouth College, Hanover, New Hampshire 03755, USA.
e-mail: paul.j.whalen@dartmouth.edu

Darwin¹³ suggested that our facial expressions have been conserved throughout evolution; that is, if we look carefully, we will see similar expressions among nonhuman animal species. The study by Susskind *et al.*¹ suggests that it might be possible to find a biologically adaptive basis for all facial expressions. On the other hand, as long as a particular trait does not confer a disadvantage, it will also survive throughout evolution. It is therefore possible that the shape of some facial expressions confers a particular biological advantage, whereas others are either more random in their configuration or resulted from some nonbiological selection pressure.

For humans, even if a given facial expression originally evolved on the basis of one adaptive benefit, social evolution can assimilate it for its own purposes. It's fun to think about smiles in this context. How did baring a full mouth of teeth become the positive expression in our social world? Although Darwin thought he saw monkeys smiling¹⁵, if one looks carefully you eventually notice that there are no smiles between monkeys. There are playful faces, but no true smiles (S.E. Shelton, Wisconsin National Primate Research Center, personal communication). There is, however, a smile-like expression where the head tilts forward as the gaze is averted and the teeth are exposed by turning up the corners of the mouth. But, in the monkey world, this is no smile; this is a sign of fear, referred to as the fear grimace.

Ultimately, the fear grimace is a signal of submission. Subordinate monkeys offer it to dominant monkeys in appeasement. It's ironic that Darwin misinterpreted this expression as a true smile, as the fear grimace may well be the precursor of the human smile. For we often use smiles as a form of submission. As an example, imagine that you have a friend who thinks he's funnier than he actually is, but then his eleventh joke of the night is actually quite funny. You look down as you grin in a sort of, "Alright, you got me," gesture, a simple human form of submission.

What probably happened over time is that the originally submissive smile took on all kinds of newer meanings that were demanded by expanding social complexity. And now we find ourselves with an expression that indexes not only our own state of happiness, contentment, peace or even embarrassment, but also one that can embody what we want to say to others, in terms of acceptance, warmth or desire. The baring of teeth has socially evolved. More generally, this example demonstrates that the functional outcomes of biological and social evolution can coexist.

Facial expressions are powerful. They are succinct. And they are everywhere. Susskind *et al.*¹ have given us much to consider in terms of understanding why we look the way we do in certain situations. Future research can address

the relative biological versus social importance of various facial expressions. If there truly is ongoing social evolution of facial configurations, then we can only speculate about the future social pressures that will exist and of the new facial expressions to come, or of the ways in which existing expressions will be co-opted for new purposes. In the interim, your friends will make faces in situations that have relevance for the two of you. If you find yourself wondering if that face they just made was 'all about them' or 'all about you', know that it can simultaneously be about the both of you.

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Awake and asleep

Two-photon imaging *in vivo* has been used to monitor the activity of populations of cortical neurons. With some calcium dyes, these measurements have single-cell and single action-potential resolution. However, previous experiments looking at the spatiotemporal interactions of a large population of neurons have only been carried out in anesthetized animals. Until now, the relationship between population activity in the anesthetized animal and the awake animal has remained unclear. A new study on page 749 by Greenberg and colleagues now provides direct evidence to bridge this gap. Their findings suggest that the neuronal activity patterns of awake animals cannot be predicted from activity patterns seen under anesthesia.

The authors imaged calcium transients in layer 2/3 neurons in the visual cortex of awake, head-restrained rats, then anesthetized them and continued recording. In this way, they were able to measure the activity of the same neuronal population while the animals were awake and while they were anesthetized. The authors then used an algorithm that they had previously developed to identify action potential-evoked calcium transients based on the correspondence between the optical signal and the electrocorticogram. The algorithm was optimized using a separate set of data from simultaneous cell-attached electrophysiological and optical recordings in anesthetized animals.

Neuronal firing rates were much lower in anesthetized animals than in the awake animals, although the firing rates of individual neurons were correlated in the two states. During both anesthesia and awake periods, action potential firing in a single neuron temporarily increased action potential firing in the surrounding population; this effect was stronger for some neurons than for others and was stronger during anesthesia. Although neurons that were closer together were more likely to be influenced the same way by the onset of anesthesia, correlations between pairs of neurons in the awake state were independent of the correlations in the anesthetized state. There was a higher correlation between neurons in the anesthetized state, and population synchrony was also greater in the anesthetized condition.

These results represent the first direct comparison between neural population activity in awake and anesthetized animals. They suggest that the local patterns of activity in awake animals will probably provide stronger inputs to their targets in layer 5 than in anesthetized animals. More generally, these findings raise the important caveat that the spatiotemporal structure of action potential firing in a population of neurons recorded in an awake animal can not be directly inferred from recordings of the same neurons under the influence of anesthesia.

Hannah Bayer

