Jack, Rachael E., Garrod, Oliver G.B., and Schyns, Philippe G. (2014) *Dynamic facial expressions of emotion transmit an evolving hierarchy of signals over time.* Current Biology, 24 (2). pp. 187-192. ISSN 0960-9822

Report

Dynamic Facial Expressions of Emotion Transmit an Evolving Hierarchy of Signals over Time

Rachael E. Jack,[1,*] Oliver G.B. Garrod,[1] and Philippe G. Schyns[1]
[1]Institute of Neuroscience and Psychology, University of Glasgow, Glasgow, Scotland, G12 8QB, UK

Summary

Designed by biological [1, 2] and social [3] evolutionary pressures, facial expressions of emotion comprise specific facial movements [4–8] to support a near-optimal system of signaling and decoding [9, 10]. Although highly dynamical [11, 12], little is known about the form and function of facial expression temporal dynamics. Do facial expressions transmit diagnostic signals simultaneously to optimize categorization of the six classic emotions, or sequentially to support a more complex communication system of successive categorizations over time? Our data support the latter. Using a combination of perceptual expectation modeling [13–15], information theory [16, 17], and Bayesian classifiers, we show that dynamic facial expressions of emotion transmit an evolving hierarchy of "biologically basic to socially specific" information over time. Early in the signaling dynamics, facial expressions systematically transmit few, biologically rooted face signals [1] supporting the categorization of fewer elementary categories (e.g., approach/avoidance). Later transmissions comprise more complex signals that support categorization of a larger number of socially specific categories (i.e., the six classic emotions). Here, we show that dynamic facial expressions of emotion provide a sophisticated signaling system, questioning the widely accepted notion that emotion communication is comprised of six basic (i.e., psychologically irreducible) categories [18], and instead suggesting four.

Results

Knowledge of facial expressions of emotion and the information they transmit are deeply rooted in the perceptual expectations of observers (e.g., [4, 15]). Specifically, perceptual expectations are created from interacting with the external environment, whereby perceivable information (e.g., facial expression signals is extracted, consolidated, and retained as knowledge to later adaptively predict and interpret the world [21–24]. Thus, by probing the perceptual expectations of observers, we can model the facial expression signals transmitted and perceived in the social environment (see [10, 19, 20] for coevolutionary accounts of signal production and perception).

To analyze the perceptual expectations of dynamic facial expressions of emotion, we proceeded in three steps. First, to model the dynamic perceptual expectations of the six classic facial expressions of emotion, we combined a unique generative grammar of dynamic facial movements (the Generative Face Grammar [GFG]) [13] coupled with reverse correlation [14] in 60 Western white Caucasian observers (see the Supplemental Experimental Procedures, Observers, available online). Second, to quantify the signaling dynamics of the resulting facial expression models over time, we used information theory [16, 17]. Finally, to understand how the signaling dynamics supports emotion categorization over time, we used Bayesian classifiers.

Modeling Perceptual Expectations of Dynamic Facial Expressions of Emotion

Figure 1 illustrates the GFG and task procedure. On each trial, the computer graphics platform randomly selects a set of action units (AUs; i.e., specific facial movements performed by specific facial muscle[s] as described by the Facial Action Coding System [FACS] [8]) and values specifying six temporal parameters (represented as color-coded curves) to generate a random 3D facial animation (see Movie S1 for an example and the Supplemental Experimental Procedures, Stimuli). We asked each naive observer to categorize the random facial animations according to the six classic emotions ("happy," "surprise," "fear," "disgust," "anger," and "sad") or "don't know" (see the Supplemental Experimental Procedures, Task Procedure). Following the experiment, we reverse correlated each observer's categorical responses (see the Table S1) with the randomly chosen AUs and temporal parameters (see the Supplemental Experimental Procedures, Modeling Perceptual Expectations of Dynamic Facial Expressions of Emotion), producing a distribution of 720 dynamic facial expression models (60 observers $\times$ 6 facial expressions of emotion $\times$ male/female faces).

Quantifying the Signaling Dynamics of Facial Expressions of Emotion Models

To understand the signal form of the dynamic facial expression models, we first mapped the distribution of all AUs according to when they peaked in time (i.e., the peak latency of each AU). Figure 2 shows the AU peak latency distributions for all models pooled together (n = 720, All Facial Expression Models) and split by emotion (n = 120, Models Split by Emotion). In each panel, color-coded circles in each row represent the distribution of peak latencies (one circle per model) for each AU (see row labels), where brightness indicates proximity to the median time. As illustrated, dynamic facial expression models transmit certain AUs earlier in the signaling dynamics (e.g., Upper Lid Raiser) and some comparatively later (e.g., Lip Stretcher), reflecting expectations of an ordered, not uniform, transmission of face signals over time.

To objectively quantify AU signaling over time, we used Shannon entropy, which measures (in bits) the complexity (i.e., average uncertainty) of a signal. To compute signal complexity over time, we first divided the AU distributions into ten equally spaced time bins. For each time bin, we then computed the probability that each AU (n = 41) peaked within that bin, calculated across all 720 models (in Figure 2, All Facial Expression Models). We then split the models into the six emotion categories and repeated the same calculation for each emotion separately (in Figure 2, Models Split by Emotion). As shown by the white lines in each panel of Figure 2, signal complexity follows a common pattern over time: low

*Correspondence: rachael.jack@glasgow.ac.uk

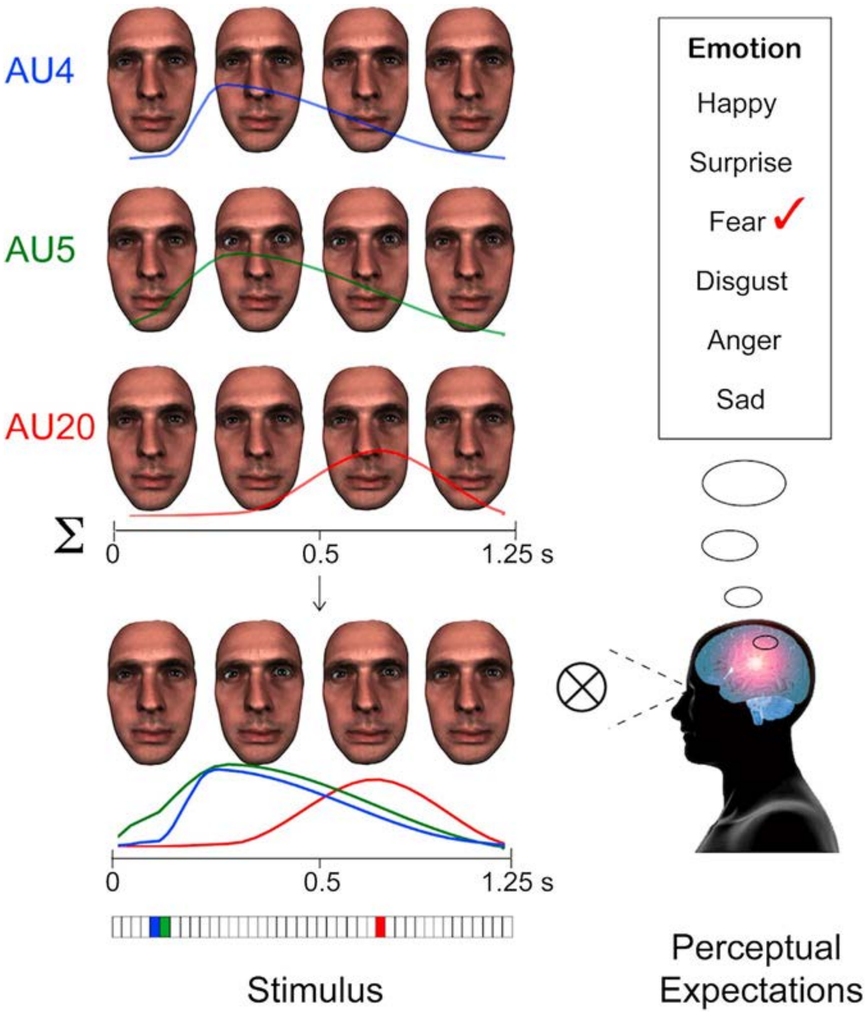

Figure 1. Generative Face Grammar to Reverse Correlate Dynamic Perceptual Expectations of Facial Expressions of Emotion

(Left) Stimulus. On each experimental trial, a computer graphics platform randomly selects from a total of 41 a subset of action units (AUs; here, AU4 in blue, AU5 in green, and AU20 in red) and values specifying their temporal parameters (represented as color-coded curves). The dynamic AUs are then combined to produce a 3D facial animation, illustrated here with four snapshots and corresponding color-coded temporal parameter curves. The color-coded vector below indicates the three randomly selected AUs comprising the stimulus.

(Right) Perceptual expectations. Naive observers categorize the random facial animation according to six emotions (plus don't know) if the movements correlate with their subjective perceptual expectations of that emotion (here, fear). Each observer categorized a total of 2,400 random facial animations displayed on same-race faces of both sexes.

See also Table S1 and Movie S1.

Together, these results show that dynamic facial expression models transmit an evolving hierarchy of signals over time, characterized by simpler, biologically rooted signals early in the signaling dynamics followed by more complex socially specific signals that finely discriminate the six facial expressions of emotion.

complexity (i.e., low entropy, high certainty) early in the signaling dynamics is followed by increasing complexity (i.e., high entropy, low certainty), before later decreasing.

Low entropy observed early and late in the signaling dynamics reflects the high probability (i.e., certainty) of the transmission of few AUs. To identify these AUs—i.e., those systematically transmitted earlier and later in the signaling dynamics—we calculated the Shannon information of each AU (measured in bits) across time. AUs with significantly low Shannon information ($p < 0.05$; see the Supplemental Experimental Procedures, Shannon Information) are highlighted in magenta (early AUs) and green (later AUs) in Figure 2. As shown in Figure 2, dynamic facial expression models transmit few AUs early in the signaling dynamics—i.e., Upper Lid Raiser, Nose Wrinkler, Lip Funneler, and Mouth Stretch (see magenta highlight). In contrast, different AUs are systematically transmitted later in the signaling dynamics—i.e., Brow Raiser, Brow Lowerer, Eyes Closed, Upper Lip Raisers, Lip Corner Puller + Cheek Raiser, and Lip Stretcher (see green highlight). (Table S2 shows peak latency differences between early and late AUs per emotion).

Notably, AUs systematically transmitted early in the signaling dynamics comprise those conferring a biological advantage to the expresser (i.e., Upper Lid Raiser, and Nose Wrinkler [1]), whereas AUs transmitted later comprise information diagnostic for categorizing the six classic emotions [25].

Classifying the Signaling Dynamics of Facial Expressions of Emotion

All signals, via evolutionary pressures, are designed to reliably transmit specific information to observers to support a near-optimal system of signaling and decoding [9, 26]. To understand the functional relevance of the hierarchical form of facial expression information transmission over time, we analyzed how this signaling supports emotion categorization for an idealized observer. To this aim, we constructed ten Bayesian classifiers (one per time point), where each classifier categorizes the face signals (i.e., AUs) transmitted up until that time point (e.g., at $t = 10$ the classifier categorizes the full signal) according to the six classic emotions (see the Supplemental Experimental Procedures, Bayesian Classifiers).

In Figure 3 (Bayesian Classifiers), each color-coded matrix shows the categorization performance of the Bayesian classifiers at each time interval, where lighter squares show higher posterior probability of an emotion and darker areas show lower posterior probability. As shown by the increasingly light squares across the diagonal, categorization performance increases over time with the progressive accumulation of signaled AUs. Squares outlined in magenta show the emotions systematically confused ($p < 0.01$) at each time point (e.g., at t3, surprise and fear confused, as are disgust and anger). Confusions between emotion categories occur early in the signaling dynamics, whereas accurate discrimination between emotions typically occurs later (indicated in Figure 3 with green squares for two examples—surprise/fear [t6] and disgust/anger [t7]).

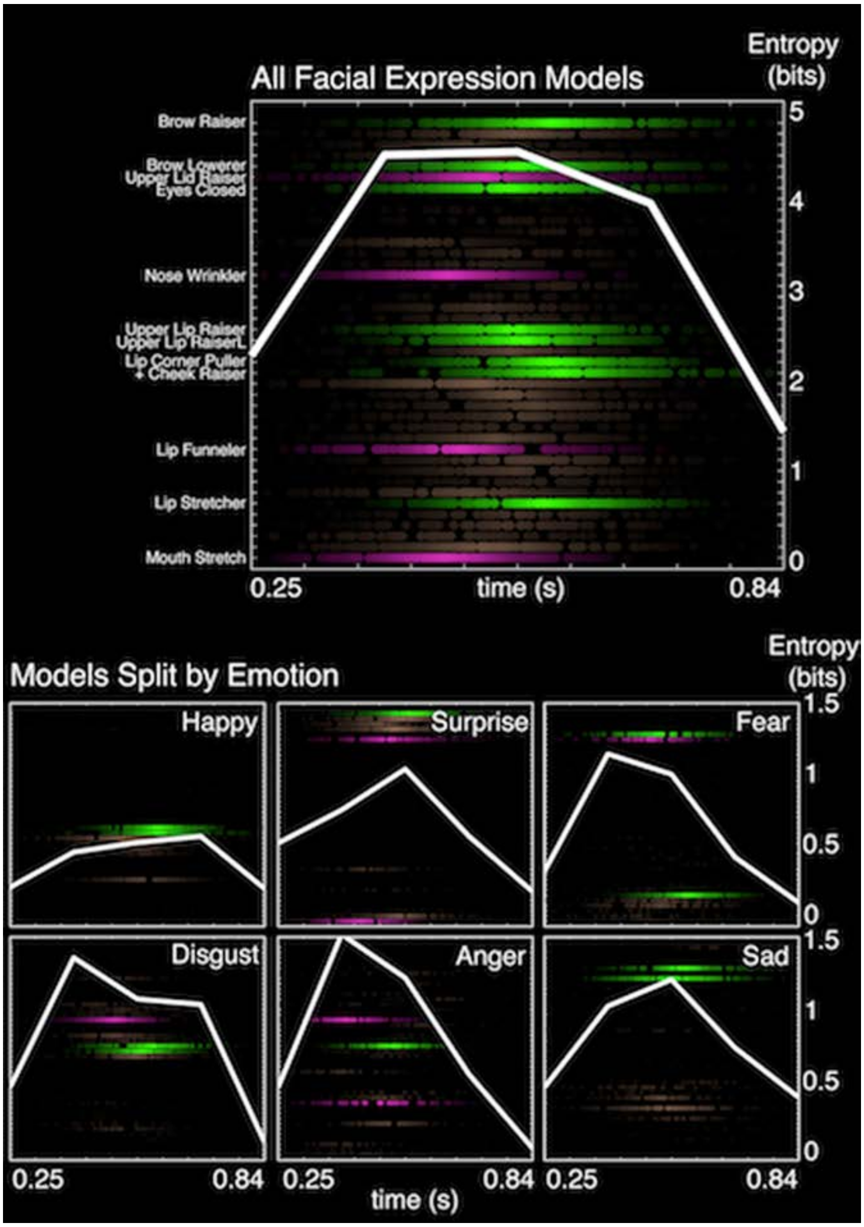

Figure 2. Expected Dynamic Signaling of Facial Expressions of Emotion over Time

To quantify the dynamic signaling of facial expression signals (i.e., AUs) expected over time, we mapped the distribution of expected times of all AUs comprising all models pooled (“All Facial Expression Models,” n = 720 models) and also split by emotion (“Models Split by Emotion,” n = 120 models).

(Top) All facial expression models. In each row, color-coded circles represent the distribution of expected times for each AU, where brightness indicates the median expected time and darkness indicates distance from the median, weighted by the proportion of models with that AU. As shown by the white line, signal complexity (measured by Shannon entropy, in bits) increases before later decreasing over the signaling dynamics, where low entropy reflects systematic signaling of few AUs. As represented by magenta circles, AUs systematically expected early in the signaling dynamics (e.g., Upper Lid Raiser, Nose Wrinker; $p < 0.05$) comprise biologically adaptive AUs [1]. As represented by green circles, AUs systematically expected later (e.g., Brow Raiser, Upper Lip Raiser; $p < 0.05$) comprise AUs diagnostic for categorizing the six classic emotions [25].

(Bottom) Models split by emotion. Note that observers expect Upper Lid Raiser to be transmitted early in both surprise and fear, and Nose Wrinkler to be transmitted early in disgust and anger. Together, these data show that dynamic facial expressions transmit signals that evolve over time from simpler, biologically rooted signals to socially specific signals.

See also Table S2.

To identify the AUs producing early confusions and those supporting later accurate discrimination, we used a leave-one-out method that removed each AU independently from all models and time points before recomputing the Bayesian classifier performance (see the Supplemental Experimental Procedures, Confusing and Diagnostic Face Signals). Figure 3 (Confusing and Diagnostic Face Signals) shows the AUs—presented as color-coded deviation maps—that produce early confusions (outlined in magenta) and support later discrimination between emotions (outlined in green) for two confusions (surprise/fear and disgust/anger).

As shown, early confusions between surprise and fear arise due to the common transmission of Upper Lid Raiser and Jaw Drop, (t2) then Upper Lid Raiser (t3–t5), with accurate discrimination arising due to the later availability of Eyebrow Raiser (t6). Similarly, disgust and anger are confused early in the signaling dynamics due to the common transmission of Nose Wrinkler (t2–t5), then Lip Funneler (t6), with accurate discrimination occurring due to the later transmission of Upper Lip Raiser Left (t7). Based on systematic early confusions between specific emotion categories, these results reflect that expected early face signals enable discrimination of only four emotion categories – i.e., (1) happy, (2) sad, (3) fear/surprise, and (4) disgust/anger—whereas the later availability of diagnostic information supports discrimination of all six emotion categories.

Discussion

Using perceptual expectation modeling, we derived the dynamic signaling of the six classic facial expressions of emotion—happy, surprise, fear, disgust, anger, and sad—in 60 Western white Caucasian observers. Information-theoretic analysis showed that the dynamics transmit information evolving from simpler, biologically rooted signals (e.g., Upper Lid Raiser and Nose Wrinkler) to more-complex signals. Using Bayesian classifiers, we show that early signaling is characterized by the common transmission of specific AUs (e.g., Upper Lid Raiser) between emotion categories (e.g., surprise and fear), thereby giving rise to systematic confusions. In contrast, later signaling comprises the availability of diagnostic information (e.g., Eyebrow Raiser), supporting the accurate

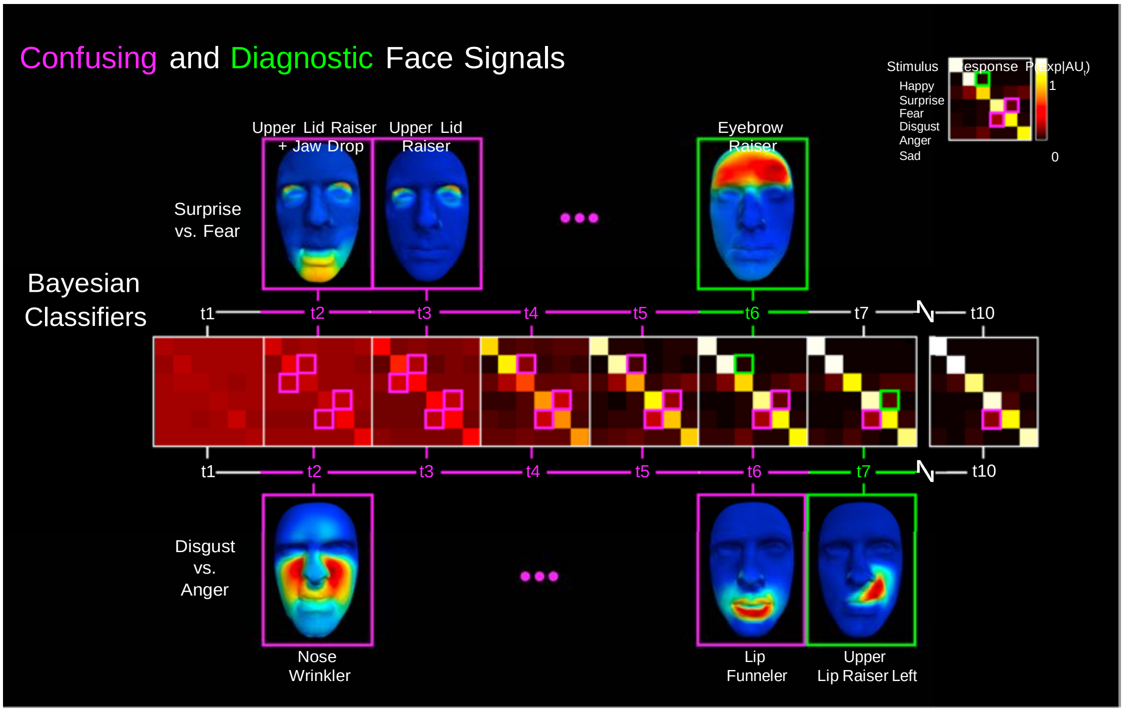

Figure 3. Categorization of Expected Dynamic Facial Expressions of Emotion over Time

Bayesian classifiers. At each time point (t), color-coded confusion matrices show the posterior probability of each expression (see key in top right for emotion labels), given the face signals (i.e., AUs) expected up until that time point [expressed as $P(Exp|AU_t)$]. Lighter squares indicate higher probability; darker squares indicate lower probability (see color bar in key). Squares outlined in magenta show that significant confusions ($p < 0.01$) between surprise and fear, and disgust and anger occur early in the expected signaling dynamics, which later largely disappear (indicated with green squares for two examples). Confusing and diagnostic face signals. Using a leave-one out method, we identified the AUs (represented as deviation maps) eliciting confusion (outlined in magenta) and supporting discrimination (outlined in green) between emotions. Surprise versus fear: early confusion arises from the expected common transmission of Upper Lid Raiser and Jaw Drop (t2), then Upper Lid Raiser (t3–t5). Discrimination of surprise is achieved later due to the availability of Eyebrow Raiser (t6). Disgust versus anger: here, early confusion arises on the basis of Nose Wrinkler (t2–t5) then Lip Funneler (t6). Discrimination of disgust is later achieved due to the availability of Upper Lip Raiser Left (t7). Our data show that fewer emotion categories are discriminated early in the signaling dynamics, followed by discrimination of all six categories later in the signaling dynamics. See the Supplemental Experimental Procedures, Bayesian Classifiers, for full details of the analyses and results.

discrimination of all six emotion categories. We conclude that observers expect dynamic facial expressions of emotion to transmit specific sequences of signals over time, which supports the successive categorization of different emotion signals.

Dynamic Facial Expression Models Show Evolutionary Adaptive Signaling Patterns

As predicted by biological signaling accounts of enhanced signal function by design [27], our dynamic facial expression models show adaptive signaling patterns. For example, observers expect regularities in the timing of signal transmission, which could confer an adaptive advantage of prediction by facilitating detection and recognition, thereby releasing resources for other adaptive actions (e.g., fight, flight). Such patterns are mirrored by the sequential decoding of static images of facial expressions in the brain [9, 28, 29], which could provide additional predictive advantages. Relatedly, face signals expected early comprise those modulating sensory exposure (e.g., Nose Wrinkler and Upper Lid Raiser; [1, 30, 31]), which, by virtue of their evolutionary and biological origins [32, 33], probably evolved as rapid behaviors to enhance their sensory advantages (e.g., rapid muscle contractions protecting the eyes, nose and mouth would provide an effective strategy for rejecting noxious contaminants). Early signals also comprise information characteristic of detectability (e.g., sudden movement, high contrast typical of danger signals [34]), which could act as salient “attention grabbers” [35, 36].

Thus, our models adhere to biological signaling accounts, where features of signal design such as predictability, detectability, and speed confer an adaptive advantage to both the expresser and receiver (see also [32, 37]).

Dynamic Facial Expression Models Transmit an Evolving Hierarchy of Information over Time

Although widely considered to communicate the six basic human emotions, it is surprising that dynamic facial expression signaling design underoptimizes their accurate categorization. Specifically, expected dynamic facial expressions initially elicit systematic confusions—i.e., fear/surprise and disgust/anger—before later supporting accurate categorization of six emotion categories. Our data raise several key questions. First, why would facial expressions, evolved for near-optimal emotion communication, systematically give rise to confusion? Indeed, biological signaling accounts predict the extinction of ambiguous (i.e., unreliable) signals [38]. Second, why should diagnostic information appear later, not earlier, in the signaling dynamics? Rather, the reported “confusing” face signals—i.e., Upper Lid Raiser and Nose Wrinkler—could reliably signal broader, context-relevant information prior to more complex categorizations. For example, the Upper Lid Raiser (i.e., eye whites common to fear and surprise)—a high-contrast, visually salient signal [39] associated with rapid deep-brain activity (e.g., amygdala [40]; see also [41] for a discussion])—could indicate "fast-approaching danger" requiring immediate response (e.g., fight/flight). Similarly, the nose wrinkle (common to disgust and anger)—a fine-scale, short distance signal [42]—could indicate "stationary danger" of proximal threats (e.g., pathogens). Thus, early face signaling could comprise rapid and unambiguous (i.e., diagnostic) signals of danger (i.e., a high-cost condition) that provide information about the relative proximity and speed of the threat [30].

Basic Emotion Communication Comprises Fewer Than Six Categories

Correspondingly, our data also question the notion that human emotion communication comprises six basic, psychologically irreducible categories ([18]; see [43 for a review). Rather, our perceptual expectation models show "basic" facial expression signals are perceptually segmented across time [44–46] and follow a "biologically basic to socially specific" hierarchical signal evolution. Specifically, early facial expression signaling supports the discrimination of four categories, namely happy, sad, fear/surprise (i.e., fast-approaching danger) and disgust/anger (i.e., stationary danger), which are only later more finely discriminated as six emotion categories. Our data reflect that the six basic facial expressions of emotion, like languages [47], are likely to represent a more complex set of modern signals and categories evolved from a simpler system of communication in early man developed to subserve developing social interaction needs [48–50]. Similarly, after early human migration, increasing socioecological diversity probably further specialized once common facial expressions, altering the number, variety, and form of signals to support adaptive social interaction within a given culture [51–54]. Knowledge of precisely how facial expression signals vary across groups and their influence on cross-group communication remains fundamental to understanding the complexities of human social interaction (see [55] for a review).

Here, we show that observers expect dynamic facial expressions of emotion to transmit an evolving hierarchy of information over time, thereby questioning the notion of hardwired recognition of a limited and prescribed set of six discrete emotion categories. Our data instead suggest that basic emotion communication comprises fewer categories.

Supplemental Information

Supplemental Information includes Supplemental Experimental Procedures, two tables, and one movie and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2013.11.064.

Acknowledgments

The Economic and Social Research Council (ES/K001973/1 and ES/K00607X/1), British Academy (SG113332), and John Robertson Bequest awarded by the University of Glasgow supported this work.

Received: August 25, 2013
Revised: November 28, 2013
Accepted: November 29, 2013
Published: January 2, 2014

References

1. Susskind, J.M., Lee, D.H., Cusi, A., Feiman, R., Grabski, W., and Anderson, A.K. (2008). Expressing fear enhances sensory acquisition. Nat. Neurosci. 11, 843–850.
2. Andrew, R.J. (1963). Evolution of Facial Expression. Science 142, 1034–1041.
3. Darwin, C. (1999). The Expression of the Emotions in Man and Animals, Third Edition (London: Fontana Press).
4. Jack, R.E., Garrod, O.G.B., Yu, H., Caldara, R., and Schyns, P.G. (2012). Facial expressions of emotion are not culturally universal. Proc. Natl. Acad. Sci. USA 109, 7241–7244.
5. Ekman, P., Sorenson, E.R., and Friesen, W.V. (1969). Pan-cultural elements in facial displays of emotion. Science 164, 86–88.
6. Tomkins, S.S. (1962). Affect Imagery Consciousness, Volume 1 (New York: Springer).
7. Tomkins, S.S. (1963). Affect Imagery Consciousness, Volume 2 (New York: Springer).
8. Ekman, P., Friesen, W., and Hagar, J.C., eds. (1978). Facial Action Coding System Investigators Guide (Salt Lake City: Research Nexus).
9. Schyns, P.G., Petro, L.S., and Smith, M.L. (2009). Transmission of facial expressions of emotion co-evolved with their efficient decoding in the brain: behavioral and brain evidence. PLoS ONE 4, e5625.
10. Smith, J.M. (1993). Evolution and the Theory of Games (Cambridge: Cambridge University Press).
11. Jiang, B., Valstar, M., Martinez, B., and Pantic, M. (2013). A dynamic appearance descriptor approach to facial actions temporal modeling. IEEE Trans Cybern. Published online April 19, 2013. http://dx.doi.org/10.1109/TCYB.2013.2249063.
12. Krumhuber, E.G., Kappas, A., and Manstead, A.S. (2013). Effects of dynamic aspects of facial expressions: a review. Emot. Rev. 5, 41–46.
13. Yu, H., Garrod, O.G.B., and Schyns, P.G. (2012). Perception-driven facial expression synthesis. Comput. Graph. 36, 152–162.
14. Ahumada, A., and Lovell, J. (1971). Stimulus features in signal detection. J. Acoust. Soc. Am. 49, 1751–1756.
15. Dotsch, R., Wigboldus, D.H.J., Langner, O., and van Knippenberg, A. (2008). Ethnic out-group faces are biased in the prejudiced mind. Psychol. Sci. 19, 978–980.
16. Shannon, C.E. (2001). A mathematical theory of communication. SIGMOBILE Mob. Comput. Commun. Rev. 5, 3–55.
17. Magri, C., Whittingstall, K., Singh, V., Logothetis, N.K., and Panzeri, S. (2009). A toolbox for the fast information analysis of multiple-site LFP, EEG and spike train recordings. BMC Neurosci. 10, 81.
18. Ekman, P., Friesen, W., and Ellsworth, P. (1982). What emotion categories or dimensions can observers judge from facial behavior? In Emotion in the Human Face, P. Ekman, ed. (New York: Cambridge University Press), pp. 39–55.
19. Arak, A., and Enquist, M. (1993). Hidden preferences and the evolution of signals. Philos. Trans. R. Soc. Lond. B Biol. Sci. 340, 207–213.
20. Guilford, T., and Dawkins, M.S. (1991). Receiver psychology and the evolution of animal signals. Anim. Behav. 42, 1–14.
21. Murphy, G.L. (2004). The Big Book of Concepts (Cambridge: MIT Press).
22. von Helmholtz, H. (2005). Treatise on Physiological Optics, Volume 3 (New York: Dover Publications).
23. Inhelder, B., and Piaget, J. (1958). The Growth of Logical Thinking from Childhood to Adolescence (New York: Basic Books).
24. Yuille, A., and Kersten, D. (2006). Vision as Bayesian inference: analysis by synthesis? Trends Cogn. Sci. 10, 301–308.
25. Smith, M.L., Cottrell, G.W., Gosselin, F., and Schyns, P.G. (2005). Transmitting and decoding facial expressions. Psychol. Sci. 16, 184–189.
26. Hasson, O. (1997). Towards a general theory of biological signaling. J. Theor. Biol. 185, 139–156.
27. Dukas, R. (1998). Cognitive Ecology: The Evolutionary Ecology of Information Processing and Decision Making (Chicago: University of Chicago Press).
28. Schyns, P.G., Petro, L.S., and Smith, M.L. (2007). Dynamics of visual information integration in the brain for categorizing facial expressions. Curr. Biol. 17, 1580–1585.
29. van Rijsbergen, N.J., and Schyns, P.G. (2009). Dynamics of trimming the content of face representations for categorization in the brain. PLoS Comput. Biol. 5, e1000561.
30. Rozin, P., and Fallon, A.E. (1987). A perspective on disgust. Psychol. Rev. 94, 23–41.

31. Rozin, P., Lowery, L., and Ebert, R. (1994). Varieties of disgust faces and the structure of disgust. J. Pers. Soc. Psychol. 66, 870–881.
32. Lee, D.H., Susskind, J.M., and Anderson, A.K. (2013). Social transmission of the sensory benefits of eye widening in fear expressions. Psychol. Sci. 24, 957–965.
33. Chapman, H.A., Kim, D.A., Susskind, J.M., and Anderson, A.K. (2009). In bad taste: evidence for the oral origins of moral disgust. Science 323, 1222–1226.
34. Cott, H.B. (1940). Adaptive Coloration in Animals (New York: Oxford University Press).
35. Senju, A., and Johnson, M.H. (2010). Is eye contact the key to the social brain? Behav. Brain Sci. 33, 458–459.
36. Niedenthal, P.M., Mermillod, M., Maringer, M., and Hess, U. (2010). The Simulation of Smiles (SIMS) model: Embodied simulation and the meaning of facial expression. Behav. Brain Sci. 33, 417–433, discussion 433–480.
37. Lee, D.H., Susskind, J.M., and Anderson, A.K. (2010). Fear expressions enhance eye gaze discrimination. J. Vis. 10, 630.
38. Zahavi, A. (1987). The theory of signal selection and some of its implications. In International Symposium of Biological Evolution (Bari: Adriatica Editrice), p. 305.
39. Blakemore, C., and Campbell, F.W. (1969). On the existence of neurones in the human visual system selectively sensitive to the orientation and size of retinal images. J. Physiol. 203, 237–260.
40. Whalen, P.J., Kagan, J., Cook, R.G., Davis, F.C., Kim, H., Polis, S., McLaren, D.G., Somerville, L.H., McLean, A.A., Maxwell, J.S., and Johnstone, T. (2004). Human amygdala responsivity to masked fearful eye whites. Science 306, 2061.
41. Pessoa, L., and Adolphs, R. (2010). Emotion processing and the amygdala: from a 'low road' to 'many roads' of evaluating biological significance. Nat. Rev. Neurosci. 11, 773–783.
42. Smith, F.W., and Schyns, P.G. (2009). Smile through your fear and sadness: transmitting and identifying facial expression signals over a range of viewing distances. Psychol. Sci. 20, 1202–1208.
43. Ortony, A., and Turner, T.J. (1990). What's basic about basic emotions? Psychol. Rev. 97, 315–331.
44. Davidoff, J., Davies, I., and Roberson, D. (1999). Colour categories in a stone-age tribe. Nature 398, 203–204.
45. Goldstone, R.L. (1994). Influences of categorization on perceptual discrimination. J. Exp. Psychol. Gen. 123, 178–200.
46. Schyns, P.G., Goldstone, R.L., and Thibaut, J.P. (1998). The development of features in object concepts. Behav. Brain Sci. 21, 1–17.
47. Fay, N., Garrod, S., Roberts, L., and Swoboda, N. (2010). The interactive evolution of human communication systems. Cogn. Sci. 34, 351–386.
48. Dunbar, R.I. (1998). The social brain hypothesis. Brain 9, 10.
49. Enquist, M., and Arak, A. (1993). Selection of exaggerated male traits by female aesthetic senses. Nature 361, 446–448.
50. Huxley, J. (1966). A discussion on ritualization of behaviour in animals and man. Philos Trans R Soc Lond B Biol Sci. 251, 249–271.
51. Gerhardt, H. (1983). Communication and the environment. Anim. Behav. 2, 82–113.
52. Mesoudi, A., Whiten, A., and Laland, K.N. (2006). Towards a unified science of cultural evolution. Behav Brain Sci. 29, 329–383.
53. Oishi, S., Hahn, J., Schimmack, U., Radhakrishan, P., Dzokoto, V., and Ahadi, S. (2005). The measurement of values across cultures: A pairwise comparison approach. J. Res. Pers. 39, 299–305.
54. Elfenbein, H.A. (2013). Nonverbal Dialects and Accents in Facial Expressions of Emotion. Emot. Rev. 5, 90–96.
55. Jack, R.E. (2013). Culture and facial expressions of emotion. Vis. Cogn. Published online September 18, 2013. http://dx.doi.org/10.1080/13506285.2013.835367.