Human Emotional Expression and the Peripersonal Margin of Safety

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Abstract: The brain evolved to give special representation to the space immediately around the body. One of the most obvious adaptive uses of that peripersonal space is self-protection. It is a safety buffer zone, and intrusions can trigger a suite of protective behaviors. Perhaps less obvious is the possible relationship between that complex protective mechanism and social signaling. Standing tall, cringing, power poses and hand shakes, even coquettish tilts of the head that expose the neck, may all relate in some manner to that safety buffer, signaling to others that one's protective mechanisms are heightened (when anxious) or reduced (when confident). Here I propose that some of our most fundamental human emotional expressions such as smiling, laughing, and crying may also have a specific evolutionary relationship to the buffer zone around the body, deriving ultimately from the reflexive actions that protect us.

Key words: Evolution; emotional expression; smile; laughter; peripersonal space; startle reflex

Introduction

The present article describes how smiling, laughing, and crying may have evolved. It does not try to explain the origin of the underlying emotional states such as happiness, humor, or sadness. Instead, the hypothesis focuses on the possible evolutionary origin of the overt, motoric components, the body and face movements that are used by humans during the expression of these emotions. Why do we make such bizarre, quirky gestures to convey specific internal states? Why should leaking lubricant from the eyes become a means of soliciting psychological support? Even supposing we could understand what humor is and how it emerged in humans, why should it be expressed by baring the teeth and crinkling the skin around the eyes?

The hypothesis arose from previous work on a network of neurons in the primate brain that processes the space around the body, the so-called peripersonal space, and that may be related to defending a margin of safety (Cooke and Graziano, 2004; de Vignemont and Iannetti, 2015; di Pellegrino and Ladavas, 2015; Duhamel at al., 1998; Graziano, 2018; Graziano et al., 1994; Rizzolatti et al., 1981). Each peripersonal neuron responds to tactile stimuli within a specific, receptive field on the body, and to visual stimuli in the space near that tactile receptive field. Some neurons also respond to auditory stimuli, and are sensitive to sound sources in the space near the body. Given these properties, each neuron appears to monitor a multisensory region of space anchored to the body surface. In aggregate, the population of neurons could act almost like an air-traffic radar system, monitoring the location and movement of nearby objects relative to different parts of the body. In studying these neurons in two specific regions of the primate cerebral cortex, the ventral intraparietal area in the parietal lobe and a polysensory zone in the frontal lobe, my colleagues and I discovered that artificial electrical stimulation of the neurons typically evoked a consistent suite of movements (Cooke and Graziano, 2004; Cooke et al., 2003; Graziano et al., 2002). The stimulation-evoked movements closely mimicked defensive or protective actions.

For example, if a site in cortex – a cluster of neurons about half a millimeter in diameter – responded to a touch on the right hand and to the sight of objects looming toward the hand, then electrical stimulation of that site, artificially activating the local neurons with a train of pulses for half a second, would evoke a characteristic, fast withdrawal of the arm behind the back into a guarding posture. If a site in cortex responded to a touch on the right cheek and to the sight of objects in the space near the right cheek, then stimulation would evoke an even richer, characteristic set of movements. Both eyes would squint, with stronger muscular contraction on the right. The facial skin would fold in a manner that appeared to protect the eyes. The upper lip would lift, caused by a contraction of muscles in the face that mobilized the skin on the cheek upward toward the eye. The ears would fold back against the head. The head would duck down and turn toward the left. The shoulders would pull up. The torso would turn and the right arm would lift, the hand moving rapidly into the space beside the head, as if blocking an impending impact toward the right side of the face. Stimulating other sites in cortex evoked many other defensive movement sets, each one specific to the region of the body monitored by the multisensory neurons that had been stimulated.

My colleagues and I conducted a series of studies on these multisensory neurons, not just using electrical stimulation, but also chemical stimulation and single neuron recording, to examine their relationship to defensive actions (Cooke and Graziano, 2004; Cooke et al., 2003; Graziano et al., 2002). We also studied protective movements evoked by natural stimuli such as an air puff or a ping pong ball fired from an air gun (Cooke and Graziano, 2003). These studies suggested that the peripersonal neurons were part of a sophisticated input-output system that could transform sensory information about the space near the body into coordinated protective actions.

In the course of these studies, I spent years watching protective actions unfold in real time and in slow motion on recorded media, dissecting them into types and components. It was during these many observations that I began to notice the similarity between defensive actions and emotional expressions. The similarity suggested a possible evolutionary path, in which some human emotional expressions were mimics of a set of behaviors originally evolved for the protection of the body surface.

Evolutionary hypotheses can be highly speculative, and I acknowledge that the present proposal is no exception. It is extremely difficult to design a decisive experiment to test how a specific trait evolved. Nonetheless, over the past decade I have written about the hypothesis, explaining the rationale behind it and how it fits with relevant data (Graziano, 2008; 2015; 2018). In this article I summarize the case for the hypothesis. I argue that the similarity between defensive actions and emotional expressions is not a superficial one. It is not simply that human emotional expressions involve contraction of the facial muscles, and defensive actions do too. Instead, the relationship may be more specific. I describe how protective actions may have been coopted by evolution and turned into social displays, and then further shaped and modified into human smiles, laughter, and crying. In this hypothesis, the brain mechanisms of peripersonal space are the origin of at least some of our most characteristic human emotional expressions.

Defensive actions

The pioneering studies of Strauss (1929) first showed that an unexpected loud sound (a gunshot behind the head, in Strauss' experiments) causes an extremely fast, consistent reflex in people. The reflex has been studied extensively since then (Davis, 1984; Koch, 1999; Landis and Hunt, 1939). Figure 1 illustrates some of the components in humans from classic studies by Landis and Hunt (1939). The startle response includes the following components:

The torso curves forward and the knees and hips bend, reducing the person's height.

The arms are drawn forward and pulled close around the stomach or chest.

The shoulders are lifted and the head pulled down and forward, in effect blocking external access to the neck.

The eyes blink, and the musculature around the eyes contracts to cause a squint.

The muscles in the cheeks contract, pulling the facial skin up toward the eyes and increasing the folds of skin that pucker around and potentially protect the eyes. A consequence of this upward mobilization of facial skin is that the teeth are exposed – especially the upper teeth, and especially the "eye teeth" or the cuspids located laterally in the mouth.

Although Straus never observed it, another characteristic component of the startle reaction is a centering of the eyes. In studies from my own lab (Cooke and Graziano, 2003), we found that these eye movements are not the normal saccades a person might make to look at objects. They are slower and have a distinctive curved trajectory. They are probably caused by the co-contraction of all six extra-ocular muscles, a reflex that pulls the eyeball back into the head by a millimeter or two.

The acoustic startle reflex could be described as a generalized defensive stance. It is not tuned to the specifics of the stimulus. Whether the stimulus comes from the left or right, or has a specific timbre or meaning, the initial startle reaction is essentially the same. Crouching down reduces the exposure of the body to predators. Pulling the arms over the torso protects both the soft abdomen and the hands. Raising the shoulders and ducking the head protects the neck, one of the most vulnerable body parts to predation. The facial muscle movements conspire to protect the eyes.

The protection of the eyes is the strongest part of the reaction. As the startle response becomes weaker, perhaps in reaction to lower amplitude sounds, or perhaps due to habituation during repeated stimulus presentation, the components from the neck down begin to drop out, while the facial components are the last to remain. The final reaction to drop out involves only a blink and some tension in the cheek muscles. Moreover, the contraction of the orbicularis muscle around the eyes has the fastest reaction time of any startle component, as fast as twelve milliseconds from the onset of the sound to the initial rise in muscle activity (Cooke and Graziano, 2003). When a video of a startle reaction is slowed and shown frame by frame, the most obvious components, the ones that jump out visually, are the closure of the eyes and the flashing of teeth as the upper lip pulls up.

This flashing of the teeth during a generalized defensive stance can easily be misinterpreted. It is easy to imagine the action as readying the teeth to bite, or perhaps to warn off an attacker. But that interpretation is incorrect. The muscles involved are different from the biting, attacking, or snarling muscles that ring the mouth, and consequently the shape of the mouth is different. Instead, the muscle contraction is mainly in the cheeks, bunching the flesh of the cheeks upward in a manner that helps protect the eyes. Imagine walking from a dark indoor space into an ultra bright, sun-saturated summer day. Your whole face contracts into a kind of sun smile, or maybe a sun grimace, exposing your upper teeth, bunching your cheeks upward, wrinkling the skin around your eyes and protecting them from the excess light. You are not preparing to bite anything. That pseudo-smile is a byproduct of protecting the eyes.

A defensive reaction to a loud sound or to a looming object can be broken down into two phases. The first is the generalized protective stance, which I have just described. It is fast, preliminary, and takes into account essentially none of the specifics of the threatening stimulus. The second is a more stimulus-specific response. In our own studies of defensive reactions to air puff on the cheek (Cooke and Graziano, 2003), we saw an initial phase that began in the facial muscle activity at about ten to twenty milliseconds. The face and body shaped into a generalized protective stance. Then by about fifty milliseconds, the stance began to evolve into a spatially directed one, stronger on the side of the air puff, the head turning away, the arm and hand on that side rising up in a blocking movement. Figure 2 shows some of the facial components of a standard defensive movement in a species of monkey, *Macaca fascicularis,* illustrating especially the muscle tension around the eyes and the lifting of the upper lip, in this case on the side of the face relevant to the threat.

This second, spatially specific phase can be extremely complicated, as we saw in our studies. A looming object or air puff threatening the top of the head causes the head to pull down and both hands to rise. A threat to the side of the face causes the head to turn aside and the hand and arm to shoot out laterally, as if thrusting away or blocking the potential threat. A threat to the side of the torso causes the elbow to move rapidly to a blocking position near the waist, and the body to shift away. A threat to the forearm causes the arm to pull rapidly in toward the abdomen and the upper body to hunch protectively over the arm. A threat to the hand causes the arm to whip behind the back. All of these reactions are slower than the initial startle phase, and yet so fast that they preclude any cognitive component. Within fifty milliseconds, the spatial computations are evidently in progress and the body can react in a directed manner.

In our studies of cortical mechanisms, we found evidence that this second phase, the spatially specific phase, is controlled by and depends on the peripersonal neurons that we studied in the cortex (Cooke and Graziano, 2004). The initial phase, the generalized protective stance, may involve other brain mechanisms. Work on the acoustic startle reflex suggests that it is coordinated at least partly by the pontine reticular formation (Davis, 1984; Koch, 1999). Other aspects of a defensive reaction, such as computing which objects should be recognized as safe and which are intrinsically suspicious or threatening, may involve many structures and networks, notably the amygdala and other systems involved in emotional valence (e.g. LeDoux, 2007).

How defensive movements might evolve into social signals

A defensive reaction, as fast as it may be, is not a simple, unvarying reflex. It changes depending on context, and those changes can reveal a great deal about the inner state of a person. For example, if a person is put on edge through a series of weak electrical shocks, and then hears an unexpected, loud sound, that person's defensive startle reaction will be greatly exaggerated (Grillon et al., 1991). Irritants like unpleasant pictures or odors can cause the same exaggeration of the startle reaction (Ehrlichman et al., 1995; Lang et al., 1990; Patrick et al., 1996). People who suffer from anxiety disorders have measurably enhanced defensive reactions (Grillon, 2008; Grillon et al., 1996; McTeague and Lang, 2012). If your child suddenly lunges at you, you'll react one way – maybe putting out your hands to catch him. If a large dog that you have only just met suddenly lunges, you are already nervous and suspicious, probably already partly in a protective stance with respect to the animal, and your defensive reaction to the lunge will be exaggerated. Mood, thought, attention, emotion, and expectation sift through cortical and subcortical circuitry, and modulate the mechanisms that govern the defensive reaction. The defensive reaction is in turn visible to anyone else watching.

If an antagonist is watching you, and you wish to avoid broadcasting clues about your internal state, you can suppress or delay a great deal of behavior, but a defensive response is urgent. It cannot safely be suppressed. You have no good option except to make the movement, protect yourself from the threat of the moment, and very possibly reveal something of your internal state to your watchful antagonist. This obligatory throughput from internal state to visible display is what makes defensive movements a good starting point for evolution to shape social signals. Defensive movements are, in effect, a data breach. They are a conduit through which information about your internal states, especially your emotional vulnerabilities, leak out to anyone watching. The information can be used to predict your behavior in the near future. Evolution can go to work on this situation, shaping the brains of animals to automatically perceive and take advantage of the streams of information leaking out of other nearby animals.

For example, we all intuitively recognize the body language of confidence. A person stands tall, his back straight. His shoulders are down and his head is up. His arms are at his sides, or even spread out expansively. He is showing a kind of negative image, an exaggerated opposite to the defensive stance shown in Figure 1. We also intuitively recognize the body language of timidity. The person has a slight hunch, the head is ducked down, the shoulders slightly raised, and the arms tend to be pulled in across the front, perhaps clasped together over the chest or stomach. We can read something of a person's internal state from the extent to which a generalized defensive stance is active or absent in that person.

My contention here is not that peripersonal space and defensive movements shaped the evolution of emotion. Much has been written about the evolution of emotions and the commonalities in the emotional mechanisms of human and many non-human animals (e.g. de Waal, 2011; Panksepp, 2007). The evolution of emotion, however, is not at issue here. My contention is that the specific, quirky, physical actions by which we communicate internal emotional states has been profoundly influenced by peripersonal space and defensive movements.

The origin of smiling

The evolution of a social signal is easily misunderstood. The reason is that it is easy to pay too much scientific attention to the sending of the signal. One is tempted to pose the evolutionary question: how did the sender evolve to use that specific signal as a means of expressing itself? For example, how did people evolve to use a smile to express happiness? However, it is now widely accepted that with respect to social signals, evolution shapes the receiver first, then the sender (Dawkins and Krebs, 1978; Fridlund, 1994; Godfray and Johnstone, 2000; Grafen and Johnstone, 1993; Schmidt and Cohn, 2001). The receiver evolves to react in a specific way when it observes a specific stimulus. As a result of that first evolutionary step, the sender has been given a lever by which to manipulate the behavior of the receiver. The sender then evolves to control or exaggerate that triggering stimulus in a strategic way. To help illustrate that hypothesized process, in the following paragraphs I will tell a story, a hypothetical step-by-step account of how a defensive movement might turn into a smile, starting with the originating stimulus, then progressing to the evolution of the receiver, and finally moving to the evolution of the sender. This account is a fiction meant to clarify the concepts. In reality, the components probably co-evolved in a highly interactive manner.

Although my account of the origin of smiling emphasizes protective movements more than some other accounts, it is nonetheless close to the current, widely accepted explanation of the evolutionary origin of the smile, or the affiliative gesture called the 'silent bared teeth display' (Beisner and McCowan, 2014; De Marco and Visalberghi, 2007; Preuschoft, 1992; Thierry et al., 1989; Von Hooff, 1962). In subsequent sections, I will extend the argument and propose an analogous account for laughing and of crying.

The original stimulus

To explain how a smile might have evolved from a defensive gesture, imagine a scenario in which you and I are primates, perhaps as much as fifty million years ago, before the evolution of the smile but after the evolution of the standard defensive stance against a looming threat. Suppose I am a large, aggressive monkey and you are smaller. I stride past you.

Since I am a looming object with high negative valence, your peripersonal neurons respond to me, monitoring my trajectory, coordinating signals that adjust your posture. You lean away from me. Your torso hunches. Your arms pull in to protect your hands and your abdomen. Your head lowers and your shoulders lift to protect your neck, more so on the side that faces me. The muscles around your eyes contract. It is useful to keep your eyes open and your face turned partly toward me, so that you can maintain a close watch. But even though your eyes are open, the surrounding muscles in the brow and on the side of the snout contract to form a protective puckering of the skin toward the eyes. As a consequence of this facial contraction, your upper lip is pulled up, exposing your upper teeth. The baring of teeth is not a prelude to biting. The shape of the mouth is associated with the mobilization of the nasolabialis muscle, wrinkling the skin on the side of the face upward toward the eyes.

Your reaction inadvertently broadcasts information about you – information about how you perceive me. I could, in principle, infer that you are non-aggressive toward me and a hierarchical underling. I could guide my own behavior toward you partly on the basis of that information. At this early moment in primate evolution, however, I lack the specialized neural pathways to process that information and use it to my advantage. Your defensive stance is simply a matter of pragmatic self-protection, and not yet acting as a social signal.

The receiver

Suppose, again, that you and I are monkeys, but evolution has further shaped the brain, giving me the tools to take advantage of the available visual cues. I now have a set of reactions wired into me. The reactions do not stem from explicit cognition. I cannot look at you and logically deduce the relevant information. I have something more like a cortical reflex or an instinct, like a rabbit reacting instinctively to a shadow passing overhead. When I see your stance, your hunched posture, raised upper lip, and squinted eyes, that stimulus acts as an automatic trigger. It makes me treat you as a non-threatening conspecific, and therefore makes me less aggressive toward you. The brain has evolved to take advantage of useful, available information. The receiver has evolved.

The sender

Now that we have a stimulus (the defensive reaction) and a receiver whose behavior is affected by that stimulus, evolution can go to work shaping the sender to manipulate that signal. Suppose a brain system evolves that can *mimic* the defensive stance. Even when I am not directly looming into your personal space, even when your peripersonal neurons are not triggered and your defensive mechanisms are not recruited, you now have a capacity to flash a mimic defensive stance in my direction, thereby altering my behavior. By tapping into preexisting wiring in me, the stimulus makes me less likely to attack you. Your behavior is, again, not the result of explicit cognition. You do not cleverly reason out that if you generate a pretend cringe, it will make me think you are non-threatening, thereby altering my behavior toward you. The interaction between us lies deep beneath the level of explicit cognition. Evolution has given us these behaviors and reactions because they confer a survival advantage. In a similar way, a stick insect does not know that it is mimicking a stick or that the mimicry has the useful effect of camouflaging it from predators.

Just as the stick insect is a mimic, your socially generated defensive stance is a mimic. It is not a real defensive reaction. I do not know what specific mechanisms in the brain might generate this social signal, though there has been some speculation. There is no reason to think that the peripersonal networks are responsible. The two behaviors are quite different. A true defensive stance protects you from a potentially dangerous object looming into personal space. It is fast and exquisitely tuned to protect the most vulnerable parts of your body, especially the eyes. In contrast, the mimic defensive stance is a way to manipulate another monkey even at a distance. It is much slower and tuned to be easily visible. It probably involves turning your face directly toward the other monkey and exaggerating the facial components of the action, while at the same time keeping your eyes open. It is a separate, modified behavior that evolved on the back of an older, defensive behavior.

Here we finally have a true social signal. You produce it and I receive it. The signal is known as the 'silent bared teeth display' and has been documented in many species of primate (Beisner and McCowan, 2014; De Marco and Visalberghi, 2007; Preuschoft, 1992; Thierry et al., 1989; Von Hooff, 1962). They cringe down, duck the head, and raise the shoulders. The skin puckers and crinkles around the eyes but the eyes remain open. The upper lip pulls up and the upper teeth show. The display is a signal of nonaggression and is believed to be the origin of the human smile.

The term 'silent bared teeth display' is misleading because it refers only to the teeth and in that way misses the connection to a standard defensive stance. The epicenter of the action is the face, and in a passing, quick example of the display, one sees the upper lip pull up, flashing the upper teeth. But a full gesture of non-aggression can recruit a larger set of muscles. In humans, the epicenter of the smile is not the teeth but the contraction of musculature around the eyes, as the nineteenth century neurologist Duchenne pointed out (Duchenne, 1990). Although a human smile is usually limited to the face, other components around the body can also appear. Think of the new intern, with low status in the company, smiling at a vice president far up in the hierarchy. He grins, teeth on display, face crinkled painfully around the eyes, body slightly hunched, knees slightly bent, shoulders slightly raised, hands pulled inward and curled over the abdomen or chest. At least in its more extreme manifestations, a smile retains the echo of the defensive cringe.

I am not suggesting that the human smile *is* a defensive cringe. A smile does not protect the eyes or express fear. I am suggesting that the evolutionary *precursor* of a smile is a defensive cringe that protects the eyes in folds of skin. In this proposal, a smile is an evolutionary mimic that has lifted free of its original context.

The evolutionary origin of smiling is different from its psychological origin. Most people assume that we smile because we feel happy. Many scientists have studied the origin of emotional states and the commonality of emotional mechanisms in humans and non-human animals (e.g. de Waal, 2011; Panksepp, 2007). Here, however, the question is much more specific: not why do we have certain emotional states, but why do we produce a specific motoric action? Why, when making an affiliative gesture, do we bare the upper teeth and crinkle the eyes? Ultimately, the survival advantage of a smile is the same as the advantage of any social signal: it manipulates the behavior of the receiver.

The origin of laughter

Ethologists have described a gesture called the open-mouth play face (Cordoni et al., 2016; Darwin, 1872; Henry and Herrero, 1974; Jolly, 1966; Palagi, 2008, 2009; Preuschoft, 1992; Ross et al., 2010; von Hooff, 1962). It is common among many mammals. Anyone with a pet dog knows it well. When playing, the dog opens its mouth slightly in a characteristic way. When mammals play, they gently bite, and that mouth action may have evolved into a communicative gesture to help regulate the play. The great apes, like most primates, have an open-mouth play face (Darwin, 1872; Ross et al., 2010; von Hooff, 1962). In addition to the visual display, the great apes add a sound. For example, when a chimpanzee is tickled, it opens its mouth and makes a series of huffing sounds. Bonobos, Gorillas, and orangutans do the same. Darwin (1872) discussed this remarkable ape huffing sound, and it has been studied systematically more recently by Ross et al. (2010). They find similarities in the sound spectrum between the huffing in apes and human laughter. The more genetically related a species of ape is to humans, the more similar the sound spectrum. By implication, at least part of human laughter may have evolved first in the common ancestor to apes and humans. Other scientists have argued that an analogue of play laughter can even be found in rats, who emit high frequency sounds as a part of their social interactions (Panksepp, 2007).

In my view, the human version of play huffing goes beyond the open mouth and the "ha ha" sound. Consider what extreme laughter looks like. The skin wrinkles and puckers around the eyes. The muscles in the cheeks mobilize the skin upward, further protecting the eyes in puckered folds. As the cheeks bunch upward, the upper lip is pulled up, exposing the teeth. Tears are secreted. The shoulders lift and pull forward, the torso curls forward, and the arms pull in, curling around the abdomen. In humans, laughter includes what appears to be a mimic defensive reaction. In other great apes, during the play display, the components of a defensive stance are not obviously displayed. The eyes are not closed or puckered. Something may have happened in evolution, after our separation from the great apes, that shaped our uniquely human style of laughter.

In 2008 I suggested a possible explanation (Graziano, 2008). Just like the commonly accepted evolutionary explanation for the smile, my suggested explanation for laughter depends on the reflexive actions that protect us when peripersonal space is invaded. The speculation begins with tickle-evoked laughter, a reaction to an intrusion into personal space.

Consider a time five or six million years ago, after the human split with chimpanzees. Our ancestors have already evolved the open mouthed play face and the huffing sound seen in all great apes, but have not yet evolved our specific human variety that includes a defensive stance. Suppose you and I are Australopithecines and we are play fighting. Many animals play fight with their mouths, trying to land gentle bites. As primates, we also play fight with our hands. Suppose you are an adult and I am a child. Your goal in the play fight is to penetrate my defenses and make contact with a vulnerable body part. My goal is to block you and protect myself.

When your hands intrude into the defended buffer of space around me, my peripersonal neurons become active and trigger a defensive reaction. My body curls, my arms move into blocking postures, my shoulders lift to protect my neck, my facial muscles contract to protect my eyes. As your attacking hand looms farther into my peripersonal space, my defensive reaction becomes stronger. If you make contact with my skin, my peripersonal neurons fire at peak activity and my defensive reactions become frantic. If you land a blow or a scratch near my eyes, even a gentle one, my tear ducts leak lubricant to protect my eyes.

In the context of the play fight, this reflexive, defensive behavior inadvertently broadcasts information about me. It demonstrates that you have won that moment in the fight. You have scored a point, so to speak. The defensive set broadcasts information content that could be roughly translated as, "touché." At this point, however, we do not yet have a social signal. We have only a normal defensive reaction. There is, so far, no reason for you to interpret my behavior in any specific way, or for me to deploy that behavior strategically as a communicative signal.

Imagine we fast-forward, perhaps a million years. Evolution has had time to further shape systems in the brain to take better advantage of the available information. Suppose again we are human ancestors engaged in a play fight. I produce a defensive set as your hand penetrates my protected spaces. You now have pathways wired into your brain to react to that defensive set. Your reaction is not the result of any explicit cognition. An instinctive behavior has evolved, and you react automatically. My defensive set demonstrates that your hand action has just been successful, and therefore it reinforces your behavior, shaping your ability to win the play fight. My defensive set becomes a specific reward to you. But my defensive squirm also has the effect of causing you to pause. In a play fight, it is counterproductive to push too far or scratch too deep. In these ways my defensive set provides useful information to regulate your behavior in the play fight. At this point, we *still* do not have a true social signal. I am merely defending my body, and you are adjusting your behavior based on your observations of my defensive actions.

Fast-forward once again, another million or so years. The brain has evolved, not only to receive the signal, but to send it strategically. By deploying a mimic defensive set, I can manipulate your behavior. Although I can still generate a normal defensive set when your hand looms in, I can now also generate a mimic behavior. The mimic behavior is not a real defensive reaction because

I can produce it even when the defense is not urgent. Even if you lightly touch my skin, the touch can trigger an exaggerated reaction from me. I'm sending out a touché signal. I'm saying, "You got me! I'm dispensing your reward! Now give it a moment's rest and don't go too far!" The behavior I emit has lifted free of the original behavior and turned into a true social signal.

And so we have tickle-evoked laughter, a social signal that evolved to regulate a particular kind of human interaction. It acts as a social reward and as a mediating signal.

The explanation I have offered here is quite narrow. It does not explain where the huffing sound comes from, or the open-mouthed play face. It does not explain how tickle-evoked laughter might have branched into the many kinds of human laughter used in a vast range of social contexts. It narrowly focuses on how some of the motoric components of human laughter mimic a natural defensive set typical of an intrusion into personal space. Laughter may have evolved originally from play fighting in which one player attacks the defended spaces of the other player. It is now a social reward that one person can give to another person as part of playful interaction, and it retains some physical characteristics of a defensive set.

The origin of crying

Crying is a difficult behavior to study from an evolutionary perspective because only humans do it. Other animals make distress cries. We may call it crying when a puppy whimpers, but generating a distress sound differs from human crying. Most attempts to explain the origin of human crying focus on the tears, but the tears are only one out of a large set of components.

Human crying in its most intense form includes a secretion of tears, a pursing of skin around the eyes, a bunching upward of the cheeks, a lifting of the upper lip, a lowering of the head, a raising of the shoulders, a hunching of the torso, a pulling of the arms into a blocking posture around the abdomen or chest or face, and a repeated aspiration that is sometimes voiced. Many of these components match a normal defensive set.

Other animals solicit comfort by making noise. No other animal, as far as I know, solicits comfort by partially mimicking the actions that normally protect the face from a collision. Why do humans cry like this?

Darwin's explanation (Darwin, 1872) begins with babies screaming in order to express negative emotion. In his speculation, the extreme forcing of air through the windpipe excites blood flow to the face. That extra blood flow risks rupturing the blood vessels in the eyes. To protect the eyes, the facial muscles contract, packing the eyeballs in a tight, protective cushion. The squeezing of muscles around the eyes, along with the air pressure from the screaming, forces fluid out of the tear ducts.

Another influential account of crying was proposed nearly a hundred years later by Andrew (1963). He argued that crying mimics a case of contaminants in the eyes. It evolved as a way to express distress.

These previous accounts focus on the sender of the signal – on why the physical act of crying would be used to express sadness or distress. As I noted above, it is now generally accepted that social signals evolve because of the impact they have on the receiver (Dawkins and Krebs, 1978; Fridlund, 1994; Godfray and Johnstone, 2000; Grafen and Johnstone, 1993; Schmidt and Cohn, 2001). There may be many reasons why we evolved the emotional state of sadness, but the specific external signal is a different matter. Crying, like any other social signal, is likely to be a display for others. It is a means of manipulating a receiver. Crying solicits comfort from others. To understand the evolutionary origin of crying, we must start with its specific impact on the receiver.

Although other animals do not cry in the human sense, they do provide comfort to each other. Most commonly across animal species, adults comfort infants. Infants therefore have a range of distress calls that can solicit help from their parents. But my own proposed account begins with circumstances in which adults comfort adults. Suppose you and I are both chimpanzees and we belong to the same family group. One day you badly beat me in a dispute over food. After the fight, you comfort me. Other chimps from the same group might also comfort me by grooming or touching me. In bonobos, the comforting sometimes takes the form of makeup sex (Clay and de Waal, 2013; Furuichi, 2011). Underlying these instances of adult-on-adult comforting is an initial burst of aggression that threatens social amity. The social amity is crucial in a highly cooperative species. Because fights are inevitable, it is adaptive to have a mechanism for comforting the victim afterward.

Given this social dynamic, here is my proposed evolutionary account of the quirky motoric components of crying.

Sometime after hominins split from the chimpanzee lineage, when our ancestors were Australopithecines three or four million years ago, we lived in cooperative social groups. But we were prone to fighting. An analysis of the bone structure of Australopithecines (Morgan and Carrier, 2013; Carrier and Morgan, 2014) suggests how our ancestors might have fought. In one interpretation, the facial bones of hominins, from Australopithecus to modern humans, are buttressed to withstand the stress of a blow, much like the facial bones of a bighorn sheep are buttressed to withstand the stress of a head collision. Moreover, according to the same authors, the bones of the Australopithecus hand are shaped to optimize curling the fingers into a fist and delivering a forceful punch. The implication is that Australopithecines engaged in ritual fighting by making fists and punching each other in the face. Many species have unique methods of fighting. Dear lock antlers. Giraffes swing and bang their necks together. Hippopotamus fight with wide-open mouths. Many species of monkey bite and also scratch each other with their fingernails. Humans, evidently, ball their hands into a boney club and hit each other in the face, and may have been doing so for millions of years, predating our modern species. It is a species-typical behavior. I know of no other species that engages in that specific mode of fighting. Perhaps it is one of the many evolutionary factors in flattening our snouts into vertical faces.

Suppose you and I are Australopithecines in a fight and I win. I punch you hard in the nose. I've penetrated your peripersonal space and made violent contact with your face. All your usual defensive reflexes are deployed. Your eyes water in a rapid autonomic response, protecting your eyeballs from potential scratch or contaminants. (If you have ever accidentally struck yourself in the nose, note how much your eyes water.) The skin purses around your eyes and your upper lip pulls up hard, further wrinkling the skin protectively around your eyes. Your head ducks down, your shoulders rise, your arms pull across your torso or into a blocking posture across your face.

As the aggressor, I need a mechanism for recognizing when I have won the fight, and especially when I have gone too far and hurt you. That mechanism should automatically trigger me to reduce my aggression and offer comfort. In that way, I can repair the social amity after the fight. Others in the family group also need a mechanism for recognizing when to offer comfort to you, if you are in distress after the fight.

Your extreme defensive reaction offers the most obvious signal. In this hypothesis, the brain evolved to receive that particular signal. When I see you enact an extreme defensive set, the kind normally triggered by a violent punch to the nose, it triggers an instinctive reaction in me. I reduce aggression and give comfort. The adaptation is a simple, effective way to help preserve social amity after a fight.

Now we reach the Machiavellian part of the story. Given that I have evolved that reaction, you can take advantage of my wiring. If you mimic that particular type of defensive reaction, especially if you exaggerate it and extend it in time over seconds or minutes, you should be able to extract comfort from me. Maybe I never fought you, and have shown no aggression toward you. Maybe nobody has hurt you. Your peripersonal neurons are not involved and you are not making an actual defensive movement. Nonetheless, if you approach me and display that particular kind of behavior, it will press my built-in buttons and extract comfort from me. I'm wired to dispense comfort, or least to cease any aggression toward you, when I see you produce that signal.

Once again, the process is not an explicit, cognitive one. You have no need to figure out the causes and effects intellectually, in order to deploy the behavior. Evolution has built the behavior into the brain. When you need comfort, that behavior is triggered in you instinctively.

In this hypothesis, crying is not a facial protective action. It is a mimic. The mimic roughly resembles, but is not exactly the same as the original. In my lab, I have watched hours of video of people and other primates hit in the face with ping pong balls and air puffs and the reaction is brief, efficient, and not nearly as dramatic as crying. In contrast, the mimic behavior is exaggerated, extended in time, and noisy. Perhaps the noise helps attract attention. The mimic behavior is tuned not to protect the body, but to evoke a reaction in the receiver. Crying, in this proposal, is a distortion and exaggeration of a defensive set, deployed strategically to elicit a comfort reaction, or at least a rapid de-escalation of aggression, in others.

Summary

I acknowledge that the hypotheses proposed in this article are speculative. My argument is that a standard defensive stance, typically triggered by intrusions into peripersonal space, was coopted by evolution and modified to become a set of situation-specific social signals. The argument rests on the point-by-point similarity among smiling, laughing, and crying. All three expressions resemble a standard defensive behavioral set. They share the contraction of the obicularis muscle around the eyes; the bunching of the cheek muscles upward toward the eyes, causing the upper lip to pull up, exposing the upper teeth; and in extreme forms, the ducking of the head, lifting of the shoulders, hunching of the torso, and pulling of the arms over the front of the torso. This behavioral set is different from other emotional expressions (Ekman and Friesen, 1972). For example, in human anger, the musculature around the eyes is not contracted, but instead the eyes are opened wide; the cheeks are not mobilized upward; the teeth are exposed by a retraction of local muscles in the lips rather than in the cheeks; and the shoulders do not lift protectively around the neck. Only some human expressions mimic the defensive stance.

Protective peripersonal space is easily overlooked. It invisibly surrounds the body and the mechanism for it lies mainly beneath the surface of consciousness. Yet it coordinates some of the most important interactions between self and world. It clears a margin of safety and protects the body. As research into peripersonal space expands, one emerging lesson is that the mechanism has an outsized impact on almost all aspects of life, well beyond the narrow scope of space within a meter or so of the skin. Peripersonal space has an unexpected relevance to tool use, social spacing, and perhaps even self awareness (e.g. Graziano, 2018; Ladavas and Serino, 2008; Pellencin et al., 2018; Salomon et al., 2017). Here I suggest that peripersonal space, through evolutionary time, has even shaped our most characteristic human facial expressions – a thought that makes this peripersonal-space researcher smile.

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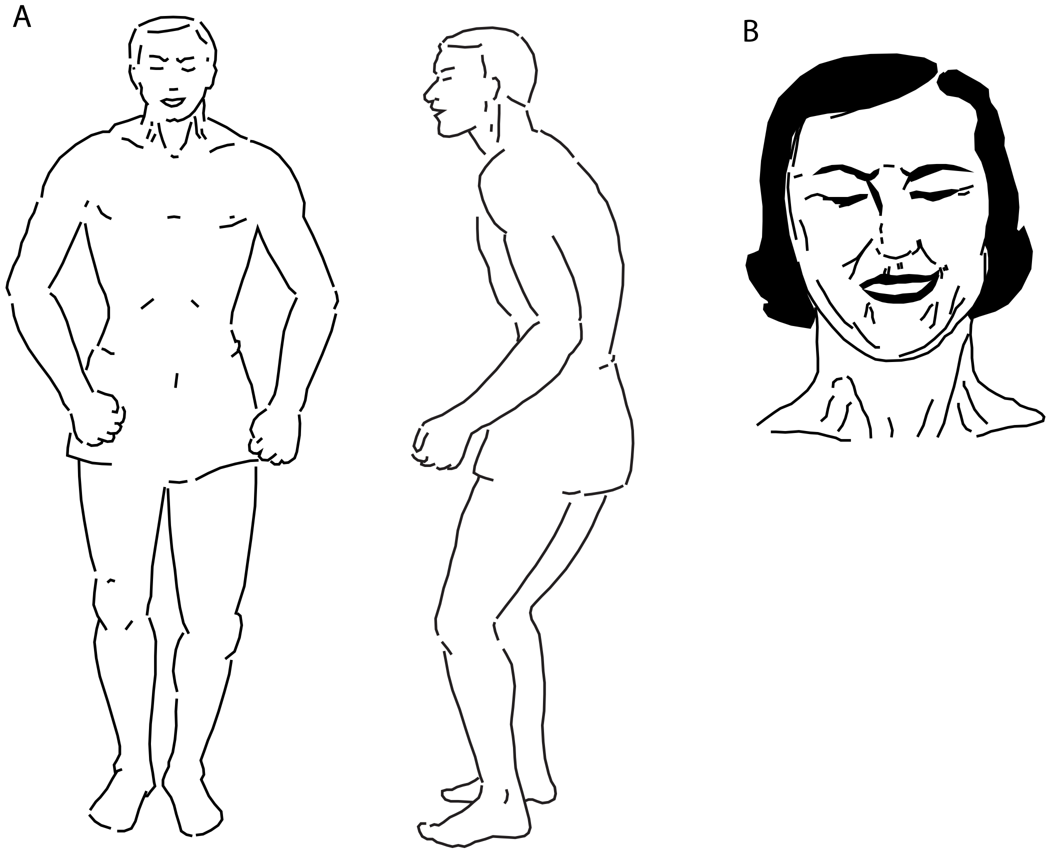

Figure 1: Startle response, adapted from classic illustrations in Landis and Hunt (1939). A. Body components. B. Facial components. In the startle response to a loud sound, the torso curves forward and the knees and hips bend, reducing the person's height. The arms are drawn forward and pulled close around the stomach or chest. The shoulders are lifted and the head pulled down and forward, reducing external access to the neck. The eyes blink, and the musculature around the eyes contracts to cause a squint. The muscles in the cheeks contract, pulling the facial skin up toward the eyes and increasing the folds of skin that pucker around and potentially protect the eyes. A consequence of this upward mobilization of facial skin is that the teeth are exposed – especially the upper teeth. The strongest, most consistent part of the action is the facial component. The action resembles the human smile.

Figure 2. Defensive response in a monkey (*Macaca fascicularis*) to an activation of peripersonal mechanisms monitoring the left side of the face (from Cooke and Graziano, 2004). A. Resting state. B. State approximately 100 ms into the defensive reaction. The musculature around the eye and in the upper face contract, drawing skin protectively toward the eye. A consequence of this upward mobilization of facial skin is that the upper teeth are exposed. Again, the defensive reaction resembles a normal affiliative gesture (such as a human smile), at least on one side of the face where the protective action occurs. It differs in that, in an affiliative gesture, though the muscles around the eyes contract, the eyes usually do not close entirely.