gobies, which obtain most of their food via cleaning. Some obligate cleaners, such as *L. bicolor* and *L. phthirophagus,* mostly eat fish mucus and so are not considered as cooperative as the rest. But even the supposedly very cooperative ones, like *L. dimidiatus,* will eat mucus when they can get it. Most cleaner fish, however, are facultative cleaners which means they do not rely solely on cleaning for food. Facultative cleaners tend to be juveniles, such as some butterfly and angel fishes and many wrasses. Some wrasse clean fish as juveniles but eat corals as adults.

What are the latest findings on cleaner fish? The evolutionary stability of cleaning mutualism has been recently examined. Cleaning interactions resemble the Prisoner's Dilemma: predators can cheat by eating the cleaner, while cleaners can cheat by eating mucus; hence both partners may cooperate or defect. But the solution is not a form of reciprocity, because the predator terminates the game if it cheats and so tit-for-tat-like strategies are not possible. Hence, *L. dimidiatus* are virtually unconditionally cooperative towards predators in the wild, though less so in the laboratory. *L. dimidiatus* also provide much tactile stimulation (rubbing with their pelvic fins) to predators, apparently to reduce conflicts from occurring. Non-predatory clients, however, use different control mechanisms: clients that can access only one cleaning station rely on aggression to control cheating cleaners, whereas those that can access more than one station flee and switch to another station. Oddly, the risk of aggression from predators toward nearby prey fish is greatly reduced as a by-product of cleaner fish presence and the tactile stimulation of predators by cleaner fish, suggesting cleaning stations act as safe havens from predator aggression.

Probably no surprise to most snorkelers, a recent study confirmed that cleaner fish have evolved some of the most conspicuous combinations of colors and patterns in the marine environment: they tend to be yellow or blue, aspects that are in stark contrast to their stripes and make them stand out from the reef background; blue in cleaners also attracts more clients to cleaning stations. Many new species of cleaner fishes have also been reported, even one of a shark apparently functioning as a 'cleaner' with a 'client' fish scraping its body against the shark's body; in this case there appears to be no benefit to the cleaner. Intriguingly, a recent molecular analysis suggests that cleaning in *Labroides* spp. evolved once, from a coral feeding lineage in the Miocene (~9.5 million years ago).

Any other oddities about cleaner fish? You bet! *L. dimiditus* become infected as a result of their cleaning behaviour when they feed on parasitic worms encysted in the skin of clients, a novel form of parasite transmission mediated by cleaning. And remarkably, *L. dimidiatus* cleans its mimic, the fangblenny *Aspidontus taeniatus.*

Should we keep cleaner fish in aquaria? Probably not. Surprisingly, *L. dimidiatus* are one of the top ten most exported fish to the US and UK. In Sri Lanka alone, an astonishing 20,000 were traded one year. The direct and indirect effects of the large-scale removal of this ecologically important species are unknown. To make matters worse, aquarium suitability information indicates *L. dimidiatus* is one of the two top species known not to acclimatize well to aquarium conditions. The other is mandarin fish. In Brazil, cleaner gobies were the sixth most exported marine ornamental fish species between 1999 and 2001. Unfortunately, only some cleaner gobies and temperate cleaner wrasse are bred in captivity.

Who cleans the cleaners? Everyone asks this question. They clean each other! Especially *L. dimidiatus.* Guppies in aquaria do too and you don't need to go snorkelling to see that!

Where can I find out more about cleaner fish?

Bshary, R., and Côté, I.M. (2008). New perspectives on marine cleaning mutualism. In Fish Behaviour, C. Magnhagen, V.A. Braithwaite, E. Forsgren, B.G. Kapoor, eds, (Enfield NH: Science Publishers), pp. 563–592.
Côté, I.M. (2000). Evolution and ecology of cleaning symbioses in the sea. Oceanog. Mar. Biol. *38*, 311–355.
Wabnitz, C., Taylor, M., Green, E., and Razak, T. (2003) From Ocean to Aquarium: The Global Trade in Marine Ornamental Species. (Cambridge, UK: UNEP World Conservation Monitoring Centre).

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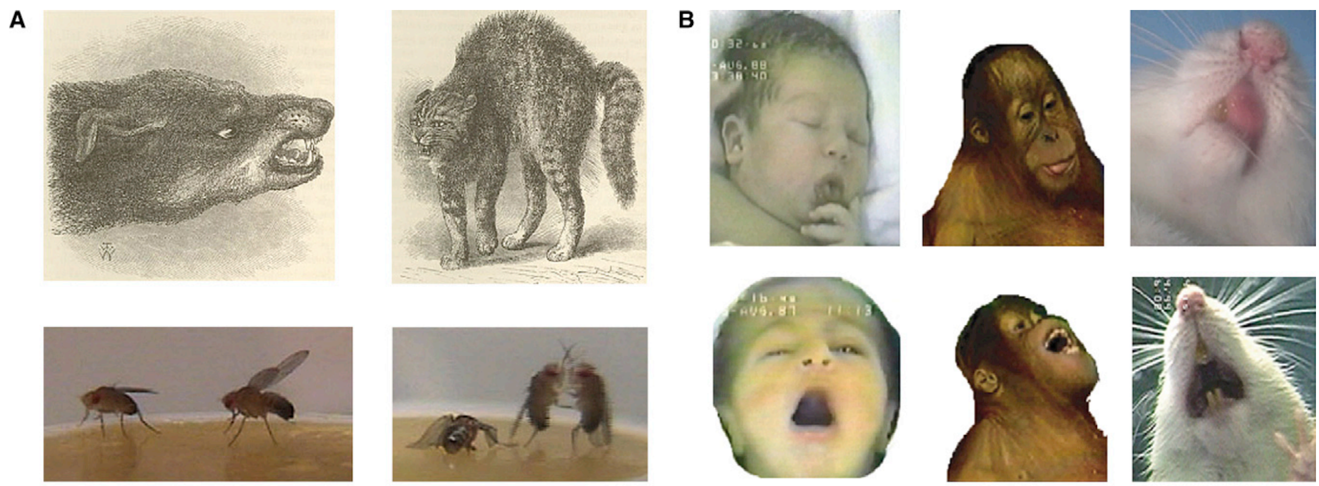
Primer

Emotion

Ralph Adolphs

When asked "what is an emotion?" most people answer in one of three ways. One answer is to list the most salient attributes of emotions. The psychologist and philosopher William James, in an 1884 essay with the eponymous title of our question, causally linked two commonsense attributes. According to James, certain stimuli can trigger emotional bodily reactions, and our perception of those changes constitutes our conscious experience of emotions, feelings. We see a bear: our heart rate accelerates, our blood pressure shoots up, and many other bodily changes transpire. Our perception of those changes in our body constitutes our fear of the bear. More recent accounts propose neurobiological substrates involved in causing emotional reactions and perceiving the feelings, laying the foundation for conceiving of emotions as neural states. Modern emotion theories typically try to account for the observations that emotions are triggered by events of some significance or relevance to an organism, that they encompass a coordinated set of changes in brain and body, and that they appear adaptive in the sense that they are directed towards coping with whatever challenge was posed by the triggering event. Emotions also have an onset, a dynamic timecourse, and an offset or resolution; their phasic nature is one feature that distinguishes them from moods. Additional layers of complexity are added, especially in humans, through our capacity to control and regulate our emotions (at least to some extent), and to vicariously experience the emotions of other people through empathy, both of which are current major themes in emotion research.

Emotions incorporate both sensory and motor features. Their sensory aspect derives from typically being induced by, and directed towards, some object as the stimulus: we are afraid *of* a bear, and angry *at* another person. Their motor aspect resides in the fact that emotions motivate behavior, an observation highlighted



Current Biology

Figure 1. Expressions of emotion across species.

(A) Defensive and aggressive behaviors in mammals and flies. Top: dog and cat behaviors of fear are shown from one of many illustrations in Charles Darwin's book, *The Expression of the Emotions in Man and Animals.* Bottom: aggressive behavior in male fruit flies. On the left a threatening raised-wing display is shown, on the right 'boxing' behavior (a decapitated female fly is lying next to the fighting males to help elicit the behavior). (Reproduced with permission from Chen *et al.* 2002; copyright National Academy of Sciences USA). (B) Facial gestures associated with palatable (top) and unpalatable tastants (bottom), the latter being the biologically most basic instance of disgust. These reactions of liking and disliking are seen in human infant, young orang-utan, and rat. (Reproduced from Berridge and Robinson 2003.)

in theories of emotion that describe them as action tendencies. Emotions have been called 'decoupled reflexes': like reflexes and fixed action patterns, emotional reactions are relatively stereotyped. We are not at liberty to invent a new emotional expression, nor to experience a novel emotion that is not in our biological repertoire to begin with. On the other hand, unlike with reflexes, we have some control over how emotions cause behavior, and the emotion and the behavior can be separated in time — my anger may not lead me to hit the person right now, but will predispose me to do so for some time.

A second answer to our initial question attempts to define emotion by contrast. Passions are contrasted with reason, a dichotomy with a long tradition from Aristotle through Hume. The modern version, exemplified in so-called 'dual-process' theories, contrasts emotion and cognition. Emotion is associated with implicit, rapid and automatic processing; cognition is associated with explicit, slow and deliberate processing. Feeling and thinking are the conscious experiences associated with emotion and cognition, and much attention has focused on how they interact. The relationship has typically been viewed asymmetrically: thinking corrects and controls feelings. Emotion regulation, noted above, would be one example; but quick reflection shows that this order of priority is apparent only in humans and only in adults, and even then only some of the time. More recently, the relationship has been turned on its head, in large part through the writings of Antonio Damasio. According to Damasio, reasoning requires emotion, and many of the complex decisions we make in everyday life become impossible without emotions to guide us. The role of emotion in decision-making is now a very prominent theme not only in cognitive neuroscience, but also in branches of economics.

A third way to answer our initial question is to begin listing some examples. Psychological investigations of emotion have a long history of attempting to demonstrate either that emotions fall along some dimensional continuum, or that they are discrete. The most common dimensional accounts propose two dimensions, typically arousal (or intensity) and 'valence' (pleasantness/unpleasantness), although other dimensions related to reward/punishment or approach/withdrawal are also possible. While appealing in their economy, dimensional accounts all suffer the same shortcoming: they cannot account for the patent diversity of behaviors and experiences associated with all the different emotions. Discrete accounts, by contrast, treat each emotion as a separate package that requires its own explanation at the level of experience, behavior, and neural instantiation. This raises the question of what precisely are all the discrete emotions.

What are the emotions?

Charles Darwin had some answers to this question. In 1872 he published *The Expression of the Emotions in Man and Animals*, just a year after *The Descent of Man* and originally intended as a chapter in the latter. Darwin applied his acute observations to the facial and bodily expressions of cats, dogs and infants, whose emotions we regularly divine from their nonverbal behavior (Figure 1). Building on Darwin's observations, the psychologist Paul Ekman studied emotions through one specific behavior: facial expression. This led to the idea of so-called 'basic emotions', expressed in faces and hypothesized to be in large part innately specified. Some commonly agreed upon basic emotions are happiness, surprise, fear, anger, disgust and sadness.

There is considerable phylogenetic continuity for some of these basic emotions, in particular for fear, anger and disgust. Even flies and lobsters exhibit behaviors that are aggressive, and rats make facial expressions of disgust. These emotions also show a range of elaboration within humans.

According to one line of thought, basic gustatory disgust forms the foundation on which moral disgust is also based: they are associated with similar facial expressions; they share similar feelings at their core; they are described by similar words; and they involve similar brain structures, notably the insula.

Some intermediate positions are also possible. Jaak Panksepp has articulated four basic emotional systems: fear, seeking, panic and rage. Each of these is associated with a particular set of neural structures and neurotransmitters, each can be elaborated to varying degrees, and each interacts with the other three. Such 'families' of emotions may map best onto the neurobiology. A major challenge is to provide a detailed account not only of the basic emotions, but also of the social or moral emotions, which evolved to regulate social behavior in groups. These include jealousy, pride, shame, guilt and embarrassment, as well as Schadenfreude, an emotion apparently in no need of a word in English.

The fact that German but not English speakers have Schadenfreude in their vocabulary, together with many other cross-cultural examples, suggests that the emotion categories depend in part on what concepts and words we have for them. An extreme line of thinking stimulated by this observation is that emotions are socially constructed, rather than basic features to be discovered in the biology. More plausible is the view that our current emotion categories will need to be modified in light of biological discoveries, but not that we will get rid of emotion altogether. For instance, the neurobiologically inspired emotion categories of Panksepp will likely carve nature at its joints better than do English words for emotions; and a mature theory of emotion will need to acknowledge that states such as thirst, hunger and pain have much in common with emotions proper.

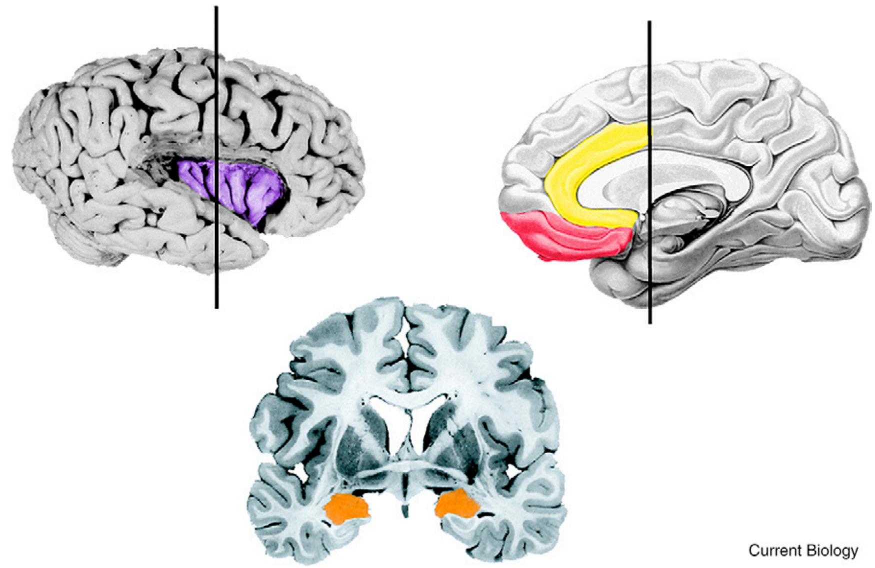


Figure 2. The emotional brain in humans.

Some of the many structures involved in emotion that are mentioned in the text: amygdala (orange), orbitofrontal cortex (red), anterior cingulate cortex (yellow), and insula (purple). Shown at the top are a lateral view of a human brain seen from the right (with a part of the frontal cortex carved away in order to reveal the insula underneath), and a sagittal view of the medial aspect of the right hemisphere; the vertical line in each indicates the approximate plane of the coronal section shown below.

Emotion and the brain

There is considerable consensus that the place to look for a theory of emotion is the brain. The general argument we already encountered above: brains cause emotional responses as well as feelings. More specifically, certain brain structures have been associated with certain features of emotion (Figure 2). Studies by Hess, Bard and Cannon in the early 1900s first showed that nuclei in the brainstem and hypothalamus orchestrate coordinated emotional responses. For instance, electrical stimulation of the hypothalamus in cats could elicit predatory aggressive behavior; and transection of the forebrain sparing the hypothalamus resulted in a phenomenon called 'sham rage', in which the animal exhibited rage-like aggression towards normally innocuous stimuli. These findings suggested that subcortical structures can directly trigger emotional behavior, but that the cortex is required for such behavior to be appropriate to the current context. A third set of structures was proposed to mediate between cortical appraisal and subcortical execution: the so-called limbic system, first coined by Paul Maclean in his theory of the triune brain.

Unsurprisingly, these earlier studies, while still useful in many respects as a framework, have given way to the realization that emotion processing is much more complicated, and more distributed. The literature offers something of a litany of piecemeal findings — with the hope that these will eventually be assembled into a coherent framework. A literature search quickly highlights some of the key pieces, at least in terms of citation counts: amygdala, prefrontal cortex and insula. Neurons in all these regions can respond to the emotional value of a stimulus independently of its sensory discriminative properties. The same touch, taste or smell will elicit different responses depending on whether it is judged to feel pleasant or unpleasant. A broad notion of emotion will include many other neural structures, such as the anterior cingulate cortex in motivating behavior, and the ventral striatum in reward learning.

Work on the amygdala's role in emotion has dual roots, one springing from Kluver and Bucy's seminal work in the 1930s on the emotional and social behavior of monkeys with amygdala lesions (although Kluver and Bucy did not localize their findings to the amygdala), the second springing from more recent work on reward learning in rodents. The first line of work led to modern studies in monkeys with selective pharmacological amygdala lesions which exhibit unusual placidity and tameness, as well as to a large corpus of work in humans demonstrating the amygdala's role in social judgments from facial expressions. The second line of work is reflected in current work on emotional memories and their pathologies, with direct applications to psychiatric illnesses in which the amygdala appears to be dysfunctional, including depression, anxiety, and post-traumatic stress disorder. A common thread running through all these varied studies has been some relation to processing threat or danger, leading to the idea that the amygdala is most important for fear.

Orbital and ventromedial sectors of the prefrontal cortex have been implicated in emotional aspects of social behavior by the famous accident of Phineas Gage in 1848 (although again no precise anatomical localization was made at the time). Gage suffered a gruesome accident in which an iron rod was blasted through his prefrontal cortex, resulting in severe alterations in his personality and social behavior. The modern-day study of patients with damage in these regions of prefrontal cortex formed the basis for Damasio's theory that decision-making requires emotion, and suggested that psychopaths might also have dysfunction of the prefrontal cortex. Aggression and anger have been most specifically associated with the prefrontal cortex, and regulation of these and other emotions fits with the known inhibitory projections from here to other brain structures such as the amygdala. A leading model of mood disorders argues that it is not pathology in the amygdala itself that can result in depression or anxiety, but rather a failure of normal inhibition of the amygdala by the prefrontal cortex, promising to take our phrenological and piecemeal understanding of the neurobiology of emotion to the systems level.

Emotion, interoception and empathy

William James' original hypothesis of feelings as the perception of bodily responses has been transposed into the brain by A.D. (Bud) Craig, who argues that the insula contains a neural representation of the state of our body and the substrate of how we feel. The insula is an interoceptive cortex that receives a wide bandwidth of signals from all over the body, with neuronal responses to pain, nausea and disgust. Just as the amygdala's suggested role in fear and the prefrontal cortex's in anger are now recognized to be descriptions that are too narrow, the emotional role of the insula is not limited to disgust. Instead, it may work together with regions of prefrontal cortex and anterior cingulate cortex in providing a continuously updated representation of the current state of our body, and hence of how we feel, encompassing both pleasant and unpleasant feelings.

In highly social species, emotions are contagious and serve important communicative roles. Empathy is one example of such contagion; it regulates social behavior as well as providing us with a mechanism for figuring out how others feel. According to one currently influential line of thinking, we do not need to figure out how others feel by elaborate deductions from their observed behavior. All we need to do is let empathy do its automatic work and look inside ourselves: if we know how we feel, we will know how the other person feels. Such 'simulation' accounts, first discovered as a possible mechanism for understanding goal-directed actions, are of course not the whole story, but they may account for a wide range of phenomena, from the contagion of smiles and babies' crying, to helping behaviors in primates, to deception and manipulation of others through fake emotional signals. The insula is activated not only by experiencing disgust directly, but also when viewing another person make a facial expression of disgust. Similarly, it is activated both when feeling pain oneself and when seeing somebody else in pain. Interestingly, the latter effect depends on how much we care for the other person: insula activation is greater when we see painful shock being given to our spouse than to a stranger we dislike.

How to investigate emotion, and why

Studies of human emotion typically measure autonomic responses, whereas those in nonhuman animals quantify overt behavior; yet neither of these provides a complete inventory of what we should measure. If emotions are thought of as neurobiological processes that coordinate a wide array of adaptive changes in neural information processing, somatic homeostasis, behavior and, in some cases, social communication, then we should attempt to measure all of these. In humans, we can add subjective verbal report to the list, assuming that this will eventually be anchored in the others.

Our measures of emotion at the level of the body are often considerably more impoverished than at the level of the brain. Neuroimaging studies in humans, for instance, typically collect long time series of changes in brain blood flow by concurrent measurements from up to 100,000 places in the brain every two to three seconds. Our somatic measures, by contrast, typically measure changes in the sweatiness of the hands upon the presentation of a stimulus, with some studies adding a few other measures such as heart beat, respiration, or pupil dilation. Subjective report is often measured only after the fact with simple questionnaires. Very few studies use dynamic stimuli to induce emotions, and almost none provides the subject the opportunity to act back on those stimuli.

There is no question that emotions depend on the brain, but this should not detract from the fact that they also depend on the body and the environment, and that a full understanding of their nature will require a functional explanation of how they evolved, how they develop, and how they are adaptive. It is perhaps especially the need for such a broader view that should stimulate the investigation of emotion in animal models, even invertebrate models, in order to gain insight into how it works in humans. As a prospective field of study, affective neuroscience (and affective biology more generally) excels in attracting funding, is portable to nearly any model species of animal, and is wide open with big questions to investigate.

Further reading

Berridge, K.C., and Robinson, T.E. (2003). Parsing reward. Trends Neurosci. *26*, 507–513.
Chen, S., Lee, A.Y., Bowens, N.M., Huber, R., and Kravitz, E.A. (2002). Fighting fruit flies: a model system for the study of aggression. Proc. Natl. Acad. Sci. USA *99*, 5664–5668.
Craig, A.D. (2002). How do you feel? Interoception: the sense of the physiological condition of the body. Nat. Rev. Neurosci. *3*, 655–666.
Dalgleish, T. (2004). The emotional brain. Nat. Rev. Neurosci. *5*, 582–589.
Damasio, A.R. (1994). Descartes' Error: Emotion, Reason and the Human Brain. (New York, NY: Gossett/Putnam).
Darwin, C. (1872/1998). The Expression of the Emotions in Man and Animals. 3rd Edition (P. Ekman, ed.) (London: Harper & Collins; New York: Oxford University Press).
Panksepp, J. (1998). Affective Neuroscience (New York: Oxford University Press).

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