



Emotion Researcher

The Official Newsletter of the International Society for Research on Emotion

- [Home](#)
- [Interviews](#)
- [Articles](#)
- [Spotlight](#)
- [Conferences](#)
- [ISRE](#)
- [In Memoriam](#)
- [Contact](#)

[Editor's Column](#)

There is much to enjoy in this issue! Click on the post title to get a quick overview of what's inside.

[ISRE Matters](#)



Check out Arvid Kappas' first column. ISRE's new President welcomes all to the new online edition of the *Emotion Researcher*

[Young Researcher Spotlight](#)



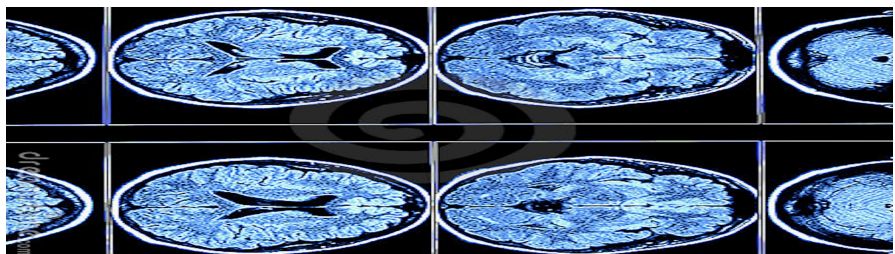
Come inside to discover who is this issue's featured young researcher!



[Traffic Count](#)

- Total reads:

[EMOTIONAL BRAIN – December 2013](#)



How does the brain implement emotions? Four leading emotion researchers discuss the matter from a variety of theoretical perspectives

[An Interview With Joe LeDoux](#)



Read a wide-ranging interview with Joe LeDoux, one of the world's leading affective neuroscientists. Joe tells us about his latest views on the emotional brain, on the relation between emotion and cognition, and on the future of affective science

Editor's Column – Emotional Brain Issue

Andrea Scarantino, Department of Philosophy & Neuroscience Institute, Georgia State University

I am very pleased to welcome you to the first online edition of the *Emotion Researcher*. I am hopeful that you will appreciate the new possibilities offered by the online platform. Most importantly, you will now be able to comment on the articles being published, email them, share them on Facebook, Twitter and other social media, explore further work by the author through hyperlinks, access and search past issues of *Emotion Researcher*, link to the newsletter from your own website, and keep track in real time of emotion conferences and other news relevant to our field.



The success of the online version will largely depend on what we do with it as a community. I am just as curious as you are to see how things will go! I encourage you to participate, and to contact me with ideas for future issues and comments on how to continue improving the *Emotion Researcher*. I am convinced that the public nature of an online platform will greatly benefit ISRE in the long run, solidifying its position as the premier international society for the study of emotions.

I want to thank [Jerry Parrott](#) for having chosen me as the new ER editor, [Arvid Kappas](#) for having been a strong supporter of the online format, and Christine Harris for having done such a great job as the previous editor. A shout out also goes to Nathan Consedine, who edited the *Emotion Researcher* jointly with Christine at the beginning of her tenure, and to all past editors of the newsletter.

You will notice a couple of changes in addition to the online format. The first is a new *Interviews* section, in which I plan to collect interviews with prominent emotion theorists about their life and research. I could not be happier with how the interview with [Joe LeDoux](#) went. Joe was incredibly generous with his time and shared lots of personal information, pictures and even videos of his life as the front man of the Amygdaloids, New York's most famous band named for a part of the brain. Most importantly, Joe released a truly substantive interview on the evolving nature of his cutting-edge research, which I hope you will enjoy as much as I did.

The second change is a new *Young Researcher Spotlight* section, in which a young emotion researcher offers a self-presentation of his or her work. I am hoping that over time this section will allow our community to get to know some of the best work being done by young researchers around the world in a variety of disciplines. The first featured researcher is psychologist [Iris Mauss](#), whose work covers the degree of coherence among different components of emotional responses, people's ability to regulate emotions, and individual and cultural differences in what people believe about emotions. Check out her intriguing work in the Spotlight section.

This issue is entitled *The Emotional Brain*. I chose this as the inaugural topic of the online edition because of the importance the study of the brain basis of emotions has acquired in recent emotion research. I thought it was time to take stock of what we have learned over the past few years about how the brain implements emotions. As it turns out, we have learned a lot, even though we are far from having reached an age of consensus about which framework and techniques to adopt for our exploration.

Four leading specialists in affective neuroscience and psychology are going to give us a fascinating tour of some of the main live options. [Jaak Panskepp](#) summarizes his influential position on the existence of seven primary process emotional systems in the brain, which he refers to as SEEKING, LUST, CARE, PLAY, RAGE, FEAR, and PANIC. These systems combine with learning and higher cognition to generate the rich panoply of human emotions. One of the Panskepp's distinctive proposals is that the activation of primary process neural

systems generates feelings in both human and non-human animals. In his contribution, he explores the payoffs that his framework can offer for developing animal behavioral models of psychiatric disorders, reporting in particular on new possible interventions for human depression.

[Kristen Lindquist](#) presents an alternative psychological constructionist view, according to which emotions are built in the brain from more primitive building blocks that are not themselves specific to emotion. One of the key constructionist proposals is that a person experiences an emotion when he or she makes a “situated conceptualization” of an underlying core affective state. This approach connects emotional experience and conceptual knowledge in a tight embrace. Lindquist argues that the constructionist model offers the best explanation of the neuroimaging data, accounting for instance for the lack of one-to-one correspondence between discrete emotions and specific brain areas.

[Luiz Pessoa](#) explores how a network perspective can help us understand the interaction between emotion and cognition. On his view, the mapping between structure and function in the brain is both pluripotent (one-to-many) and degenerate (many-to-one). His central suggestion is that the unit of analysis in affective neuroscience should be *networks* of co-activated brain regions. One of the implications of his analysis is that the age-old distinction between emotion and cognition collapses. Brain regions are neither “cognitive” nor “emotional”, because the same brain region can contribute to traditionally cognitive or traditionally emotional processes depending on the network in which it is recruited.

[Stephan Hamann](#) emphasizes how assessing the neuroimaging evidence becomes complicated in the presence of theoretical models as diverse as basic emotion theory, psychological constructionism, and LeDoux’s recent survival circuits idea (more details on the latter in LeDoux’s interview in this issue). Hamann argues that a major outstanding challenge for affective neuroscience is to reconcile these models in light of the evidence that functional neuroimaging and other neuroscience methods provide, and he offers some suggestions towards integration.

All in all, these four articles offer a compelling view that the study of the emotional brain is alive and well. Cumulatively, they serve as a warning to researchers in other fields that reverse inferences from the activation of an isolated brain region to the involvement of folk psychological emotions like *fear, anger, disgust, happiness, sadness* etc. – let alone *emotion* writ large – are to be drawn very cautiously.

ISRE Matters – Emotional Brain Issue

Arvid Kappas, Psychology, University of Bremen, ISRE's President

Dear ISRE members and Friends of ISRE,

I am truly excited to know that you are reading the first newsletter under the stewardship of Andrea Scarantino. He has a clear vision regarding the content and function of the ISRE newsletter. The way I see it, an important theme Andrea wants to pursue is *connection*. It will connect different branches of emotion research, specialists in a field with those just curious, the well-established researcher with the PhD student. However, one of the most exciting aspects is that for the first time the newsletter will be available not only to ISRE members but also others who share an interest in emotion research. Indeed, at this point the newsletter is a link to the outside. If you are not an ISRE member yet, why don't you consider coming in – join us!



ISRE is the natural home for academics who believe that the study of emotions is a truly *trans disciplinary* topic that benefits from multi-level approaches, from the view of different disciplines and their methods. Transdisciplinary here means that the topic itself is not by default located within a particular field – and this has an impact on how, as a society, we want to foster progress in understanding affective processes. For example, we believe that there is a mutual benefit of natural, behavioral, and social sciences to engage with the humanities because emotions are such an integral part of arts, literature, music, theatre and the likes. Because of the way that emotions are shaped by social experiences in cultural contexts and within biological constraints the aspect of cross-culturality is a key aspect of the topic and how it is studied. One of the most exciting developments in emotion research in recent years must be the addition of affective neuroscience to the “family”. While I try to make sense of what this brings to the table in my research and teaching (I have been teaching a Social Neuroscience seminar since 2006), I am baffled by how some believe that unveiling brain mechanisms can offer a straightforward solution to the many puzzles of our discipline.

For example, the puzzles of how to define what emotions are, how many emotions there are, what role cultural concepts play in shaping them, and how we can or not control them, or how they control us – all of these do not go away by the discovery of the neural networks that are involved in emotions. Because we as researchers still need to define what people are doing in a scanner, what they are looking at, which questions they answer in their mind. If the meaning of basic concepts, such as joy [English], joie [French], or Freude [German] do not map to 100% this will also affect what happens in the brain of participants who grew up here or there. In other words, moving from one language to another does not mean that even words which seem like straight translations have the same meaning and use. Sensitivity to these issues is provided by researchers from different cultural contexts, just as from different disciplines. 30 years of ISRE experience show that this is not just an idea – this is real!

One of the central themes of my presidency will be to make sure that issues such as interdisciplinarity, internationality, gender, seniority of researchers are not just abstract concepts but issues we discuss, reflect upon and turn to a strength in our collective endeavor to understand affective phenomena, whether we call them emotions, affects, moods – I mean the whole family. I have set into motion some activities in this direction and in the next issues of The Emotion Researcher I will talk more about these. You know, ISRE matters!

P.S. did you “like” our [ISREorg](#) Facebook page yet?

Roll The Credits – Emotional Brain Issue

W. Gerrod Parrott, Department of Psychology, Georgetown University, ISRE President Emeritus



I like to read the credits at the end of movies. I sit in the dark theater long after most other audience members have left, watching an enormous list of jobs and people scroll upwards. It's interesting to see the many jobs and locations, but I don't entirely know why I do this. I don't even understand many of the job titles—what is a Key Grip, a Gaffer, or a Foley Artist anyway? I think part of my motivation is the awe I feel at the sheer number of highly specialized and talented people who must work together to produce the film I just saw. My own job usually isn't like this—scholarship is a solitary activity much of the time, and I find the idea of working with others toward a common goal to be very appealing.

Being President of ISRE for the past four years was a chance to work on something more like a movie. I joined a team of people who treasure our Society and who want to continue to develop its tradition of promoting in terdisciplinary and international study of emotions and moods. During my years in office many people volunteered their time and skills toward that cause. Now that my term is finished, I would like to “roll the credits.”

The first credits go to the three ISRE officers who worked most closely with me to ensure that ISRE's daily operations went smoothly. Our Membership Secretary, Diana Montague, screened membership applications and provided the warm welcome that was many current members' first introduction to ISRE. Our Website Coordinator, Ursula Hess, worked wonders in getting a very rudimentary web platform to perform a variety of new functions at very minimal cost. Jeanne Tsai served as Treasurer at the beginning of my term, and maintained and passed along a well-organized set of records. The Treasurer for most of my term was Yochi Cohen-Charash, who frugally kept the books and significantly built up ISRE's reserves. All three performed services for which a larger organization might hire assistants, and they deserve our gratitude because they made it possible for ISRE to operate efficiently on modest revenue.

A second set of credits goes to six ISRE officers who oversaw the operation of our Society's intellectual products. These would be the Conference Program Chairs, journal editors, and newsletter editors. The Program Chair for the Kyoto meeting was Brian Parkinson, and for the Berkeley meeting was Joe Campos—both supervised stimulating and innovative conferences. The Editors of *Emotion Review* when I became President were Jim Russell and Lisa Feldman Barrett, and when I stepped down were Jim Russell and Christine Harris, and in the middle was Jim Russell alone. All three editors did superb service by making *Emotion Review* an outstanding academic publication. Finally, the editors of our newsletter *The Emotion Researcher* were Christine Harris and Nathan Consedine when I began, with Christine handling the job alone subsequently. They produced a series of attractively laid-out issues that have enduring scholarly value in addition to the news and announcements of a typical newsletter.

Finally, the credits should list the elected board of directors, whose judgment and guidance have been so helpful as ISRE continues to evolve. I worked with two elected boards. Between the Leuven and Kyoto meetings the directors were Louis Charland, Ann Kring, Makoto Nakamura, and Dawn Robinson. Between Kyoto and Berkeley they were Hideki Ohira, Mikko Salmela, David Sander, and Jan Stets. I am grateful to them all for their service.

This list of credits is limited, perhaps artificially, to those whose positions are named as officers in ISRE's Bylaws. There are of course many others: local organizers for the conferences, members of the Program Committees for those conferences, members of *Emotion Review's* editorial board, and countless other ISRE memb

ers who have contributed to ISRE's operation and evolution over the past four years. With this rolling of the credits we acknowledge all their contributions and welcome those of the people who have stepped forward to continue ISRE's activities in the years ahead.

Joe LeDoux: The Emotional Brain, Gumbo and the Amygdaloids

An Interview with Andrea Scarantino

Joe LeDoux is the Henry and Lucy Moses Professor of Science at New York University in the Center for Neural Science, and he directs the [Emotional Brain Institute](#) at NYU and the Nathan Kline Institute. His work is focused on the brain mechanisms of memory and emotion and he is the author of [The Emotional Brain](#) and [Synaptic Self](#). LeDoux has received a number of awards, including the Karl Spencer Lashley Award from the American Philosophical Society, the Fyssen International Prize in Cognitive Science, Jean Louis Signoret Prize of the IPSEN Foundation, the Santiago Grisolia Prize, the American Psychological Association Distinguished Scientific Contributions Award, the American Psychological Association Donald O. Hebb Award. LeDoux is a Fellow of the American Academy of Arts and Sciences, the New York Academy of Sciences, and the American Association for the Advancement of Science, and a member of the National Academy of Sciences. He is also the lead singer and songwriter in the rock band, [The Amygdaloids](#).



Joe LeDoux

Check out Joe's twitter and Facebook accounts:

- Twitter: <https://twitter.com/LeDouxScience>
- Twitter: [@theamygdaloid](#)
- Facebook: <https://www.facebook.com/joseph.ledoux>
- Lab Facebook Page: <https://www.facebook.com/ledoux.lab>
- New Lab Website: www.cns.nyu.edu/ledoux
- Lab Blog "An Emotional Brain Is a Hard Thing to Tame": <http://ledouxlab.tumblr.com/>

You grew up in rural Louisiana. As a child, were you interested in the brain, in science, in animals, or in anything remotely connected to what you do now?

I was the son of a butcher and one of my jobs in the market was to "clean the brains," which meant get them in an edible state. To do this, I basically had to strip off the meninges (the layers of protective covering) and then find and remove the lead bullet (the animals were stunned by a .22 caliber shot between the eyes, which meant the bullet usually ended up in the brain). So I indirectly learned quite a lot about the physical features of the brain, its texture and shape, especially how some parts are more easily separated than others. On several occasions I also watched cows being shot.

I was taught by Nuns at the time, and had been indoctrinated with a lot of religious ideas, like the notion that people have immortal souls but that when animals die they simply cease to exist. As the bullet penetrated the skull and the cow dropped to the floor, I couldn't help wondering whether animals might also have souls. Later, I flipped my view and concluded that the whole idea was wrong—that neither people nor animals have immortal souls.

What was your major in college?

I went to college at LSU and majored in marketing, and then got a Masters in marketing as well. But I was enamored with psychology and took classes in that area. I got really into psychology, and especially behaviorism. At one point I wrote to BF Skinner at Harvard, and his response about my interest in the intersection of psychology and marketing made me realize I wanted to do psychology. A pivotal class for me was "The Psychology of Learning and Motivation". It was taught by Robert (Bob) Thompson, a physiological psychologist who had worked briefly with Karl Lashley, the father of the field concerned with studies of brain and behavior. Bob Thompson was trying to do what Lashley couldn't—localize learning and memory in the brain.

He had a great idea—study lots of different learning and memory tasks with different behavioral requirements and make lesions in lots of brain areas. Areas implicated in all tasks would constitute the core of the brain's learning and memory system. I worked in his lab in my spare time while completing my Master's Thesis on consumer protection issues, and decided that physiological psychology was the area of psychology I wanted to pursue. With Bob's help, I was accepted into grad school at SUNY Stony Brook.

At SUNY Stony Brook in the 1970s, you did your PhD work on split-brain patients with Mike Gazzaniga. Has this early work had an influence on your future research and if so how?

My work with Gazzaniga was extremely influential in many ways. Mike and I spent a lot of time on the road together. The patients we were testing were mostly in Vermont and New Hampshire, as the surgeon doing the split-brain operations was at Dartmouth. So once a month we'd travel up there for a 3 or 4 night stay. After the day's work was done, we'd end up discussing the findings in a bar. By the second drink we were talking about philosophy of science.

He believed in the big questions. When I suggested I wanted to learn to do some biochemistry, he said, "Why would you do that? You can hire a biochemist if you have a good question you want to answer with that kind of methodology." By the third drink we were into philosophy of life. It was a great time.

How did you come to study emotion in the brain at a time in which the emotions were not really at the forefront of neurobiological research?

The big question Gazzaniga and I were pursuing at the time was the idea of consciousness as a means of making



Young Joe, probably 3 years old, roughly 1952



The Countdowns. This was Joe's high school band in 1964 (Joe is the second from the left)



Joe with his mother, Pris LeDoux. Graduation day, June 1971, LSU

ing sense of one's life. This came out of an observation that Gazzaniga made while I was testing one of the patients. We showed the separated hemispheres different pictures and then put out a bunch of cards with additional pictures on them and the task was to point to the card that was somehow related to what was seen. In the key study, the left hemisphere saw a chicken and the right a snow scene. The right hand then pointed to a chicken claw and the left hand to a shovel. When asked to explain his choices, the patient (actually his left hemisphere) said, "I saw a chicken so I picked the chicken claw and you need a shovel to clean out the chicken shed." The shovel part was a total confabulation that was filled in by the left hemisphere to make sense of why the left hand (right hemisphere) had chosen the shovel. Gazzaniga speculated that we all do this all the time.

Behaviors come out of our brains for reasons that we are not consciously privy to and we interpret those in such a way as to create a coherent story about our life in the here and now that makes sense in terms of our past and future. Mike went on to focus on the nature of consciousness and I turned instead to how the emotions work unconsciously. From Bob Thompson, I had gotten interested in emotion and motivation in relation to memory and found a way to explore this in the split-brain setting. This interested Mike as well since he had also developed an interest in emotion and motivation, in part through his friendship with the social psychologists, Leon Festinger, "Mr. Cognitive Dissonance," and Stanley Schachter, who brought emotion into cognitive psychology. I designed a study where we put emotional stimuli in the right hemisphere of a split-brain patient. The left hemisphere couldn't say what the stimulus was but could rate its emotional valence on a 5-point scale from good to bad. Somehow emotional meaning of the stimulus was processed separately from perceptual object in the brain.

Over drinks, Mike said, "You know, there's not much work on emotion these days". A light went off in my head and I said that's going to be my topic, the place where I get my big question. And the question I started with was, "How does emotion get processed separately from cognition in the brain?" In retrospect it was a naïve question but it got me into emotion. I decided to return to rats since there were no good ways to study the human brain in much detail at the time. I spent 12 years working at Cornell Medical School in Don Reis' neurobiology lab, where I had the opportunity to learn lots of different techniques. This helped me enormously as I began to ask questions about how emotional stimuli are processed in the rat brain.

In 1996, your book *The Emotional Brain* (Simon and Schuster) was published to wide acclaim. One of its central themes is that emotions and feelings should be distinguished. I know your views have changed to some extent since then, but why did you think at the time that brain science required emotion and feeling to be distinguished?

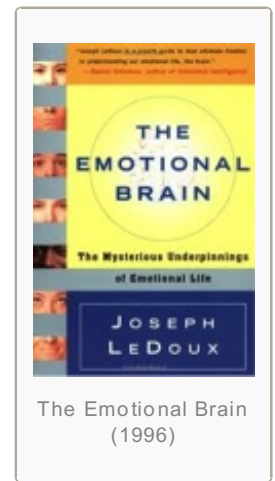


Joe in the first mobile split-brain testing lab; a camper trailer outfitted with a tachistoscope. Probably 1975 somewhere in Vermont



Joe and Nancy Princenthal on their wedding day, February 26, 1982

I was steeped in the ideas of cognitive science when I was doing the split-brain work. And one thing I was really impressed with was the fact that cognitive science had found a way to study the mind without having to solve the mind-body problem, the consciousness problem that the behaviorists had eschewed and gotten rid of. The cognitive mind was not a place where experiences occur so much as a place where information is processed. That processing might lead to conscious experience, but the processing was where the action was. As Lashley had pointed out, we are never consciously aware of processing; we are only aware of the content created by that processing. When I turned to emotion I was surprised at how little this logic was being used in psychology or neuroscience.



The neuroscience of perception had smoothly transitioned from the behaviorist to the cognitive approach. Great progress was being made in understanding how the brain processes the color red in the act of seeing without having to first understand how the brain experiences the color red in a sunset. Emotions, though, continued to be thought of as the content of subjective states—conscious feelings. For example, animal researchers studying circuits that controlled behavioral and autonomic responses often claimed to be locating where feelings of fear, anger, pleasure, and so forth occur in the brain.

I felt there were logical and conceptual problems with the subjective approach to emotions in animals that could be overcome by applying the ideas of cognitive science to emotion. We could study the way the brain detects and responds to threats, for example, without having to address the problem of how the brain creates subjective content—the feeling of fear. Threat detection and conscious feelings seemed like different things. I thought that surely they interacted, but that maybe more progress could be made by studying them separately. I laid this all out in a book chapter in 1984 and then proceeded to apply this logic to the study of Pavlovian fear conditioning in the brains of rats.

By the time I started writing *The Emotional Brain* in the mid 1990s, research that I and others were doing had made quite a lot of progress in understanding how the brain learns about, stores, and then later detects and responds to conditioned stimuli—tones that had acquired threat value by paired with shocks. I saw no need to bring the feeling of fear into this process, especially since I was particularly interested in how the brain rapidly detects and responds to threats before one can consciously know the threat exists.

At the same time, I did continue to have a lingering interest in consciousness from my split-brain days, and did want to know how we might become consciously aware that our brain was responding unconsciously to an emotional stimulus and might also feel the emotion. I believed that the way to go was to assume that we become conscious of emotional stimuli the same way we become conscious of anything else. Mounting evidence indicated that conscious awareness of sensory stimuli occurs when attention directs information about a stimulus and retrieves long-term memories into the temporary mental workspace called working memory. So it seemed to me that feelings might come about when the unconscious consequences of emotional arousal come together with sensory and memory information in working memory, thus creating a conscious emotional experience.



This is a long answer to why I felt we needed to distinguish between unconscious processes that detect and respond to emotional stimuli, and conscious feelings that are cognitively assembled via working memory. The terms emotion and feeling seemed like they could capture that difference. But I no longer believe that these terms should be used that way.

To understand how your thoughts on the matter have evolved, a useful starting point is your recent

processes uncovered in animals apply to the human brain. My colleague Liz Phelps has done a tremendous service to the field by painstakingly pursuing this. But the other is that it allows studies of the unique capacities of the human brain. Is fMRI as precise as we would like it to be? No. But it is still valuable, and for those who recognize its limits and work within these, and interpret their results accordingly, it is a terrific tool.

The emotion that you have studied the most is fear, or what you now call the *defense survival system*. Why did you pick fear? And what is your current understanding of what fear is?

Fear is a conscious experience that occurs when one is in danger. But there is no one thing that the word fear refers to. Fear of a snake at your feet is different from fear of public speaking or taking a test, or of sexual failure, of falling in love, or of starving or freezing to death, of the eventuality of death, or of fear itself. I like to think of emotions like fear as emerging the way the flavor of a soup emerges from its ingredients.

Salt, pepper, garlic, and water are common ingredients that go into a chicken soup. The amount of salt and pepper can intensify the taste without radically changing the nature of the soup. You can add other ingredients, like celery, carrots and/or tomatoes, and still have variant of a chicken soup. Add roux and it becomes gumbo, while curry paste pushes it in a different direction. Substitute shrimp for chicken in any variant and the character again changes. None of these are soup ingredients per se. They are things that exist independent of soup, and that would exist if a soup had never been made. Emotional feelings are like this. They emerge from non-emotional ingredients. Specifically, they emerge from the coalescing of non-emotional neural ingredients in consciousness. The particular ingredients, and the amount of each, define the character of the feeling. Many of the non-emotional neural ingredients that contribute to the feeling of fear are amygdala-triggered consequences that occur as part of the unconscious defensive motivational state: body responses and brain arousal, direct input from the amygdala to cortical areas, feedback from body responses to the brain (including to the amygdala, cortical areas and arousal systems), initiation of goal-directed behaviors that produce additional feedback, and so on.

When information about these various activities coalesces in consciousness with information about the external stimulus and long-term memories about what that stimulus means, then the resulting feeling that emerges is some variant of fear. Whether we feel concerned, scared, terrified, alarmed, or panicked depends on the particular characteristics of the internal factors aroused in the brain and factors from the body, and information about the stimulus and its context. In the presence of these neural ingredients, feelings occur automatically in consciousness, similar to the way the essence of a soup emerges from its ingredients. But “automatic” does not mean “without cognition”. Unconscious cognitive factors involved in attention, monitoring, information integration, and so on contribute to the conscious state that emerges. Motive states are created from general-purpose mechanisms but the resulting state is specific to the motivational demands of the moment. A defensive motive state is different from a reproductive (sexual) motive state. And even within a category, the nature of the motive state can vary considerably (scared vs. panicked) depending on the circumstances. It is important to point out that some feelings do not depend on unconscious motive state ingredients. Many human feelings are like this—for example, compassion, pride and shame. These so-called social emotions are primarily based on cognitive assessment of one’s circumstances. While emotions resulting from motive states emerge in consciousness in a bottom-up fashion, social emotions are built from cognitive processes in top-down fashion.

While fear is a prototypical bottom-up emotion, it can also arise from top-down influences. We can think our way into fear, and activate a defensive motives state this way. But in addition we can have intellectual fears, such as the fear of our eventual



death, that depend on top-down processes rather than simply emerging bottom-up from motive states. The enormous complexity in the various conscious manifestations of fear suggests that there is no one thing that the term fear refers to, and certainly there is no fear module in the brain that is responsible for all of the states to which we apply the label fear. Psychologists like Lisa Barrett and Jim Russell have made this point as well, emphasizing that emotions are psychological constructions built from non-emotional processes. Fear, the conscious feeling of being afraid, is what happens when we are aware that certain ingredients have come together to compel a certain interpretation of the state we are in. Anxiety, that worry or apprehension one has when dwelling on the past and/or anticipating the future, is a variation on this theme. The same holds of other emotions as well. In order to understand emotions we thus need to understand consciousness.

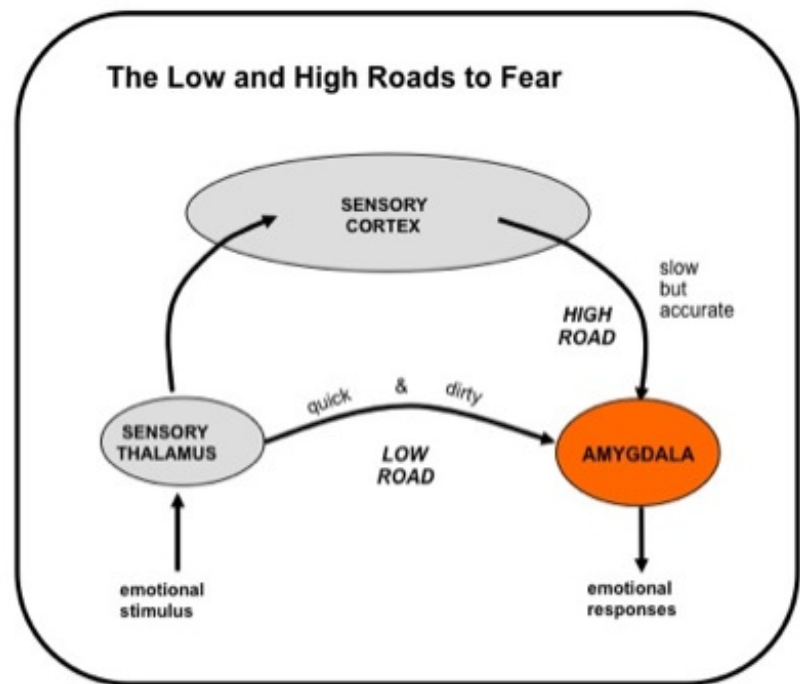


You famously described a “low” road to fear that projects along a subcortical pathway directly to the amygdala, and a “high” road to fear that projects to the amygdala indirectly through the sensory cortex. Do you think this dual pathway idea captures a deep truth about what emotions are, or is it likely to only be found in fear?

The fact is, triggering events for emotions often involve unconscious detection processes, whether we are talking about fear, joy, sadness, pride, or whatever. The emotion is a conscious experience, a feeling, but it is jump-started unconsciously. The low road/high road idea made that easy to understand. But it also led to what I now see as an inaccurate view of the high road. It now seems clear that both thalamic and cortical inputs to the amygdala are unconscious processing channels. Just because the visual cortical areas that project to the amygdala (via the high road) can be part of visual conscious experience by virtue of connections with prefrontal and parietal circuits that contribute to attention, working memory, and consciousness, does not mean that the high road consciously activates the amygdala.

More generally, do you think the neural basis of fear is a good model for understanding the neural basis of other emotions such as, say, shame and embarrassment? And do you think all emotions have a dedicated neural basis?

I do not think fear has a dedicated neural basis, a module, that gives rise to the feeling of fear. As I said above, fear, in my view, is a conscious experience that comes about like any other conscious experience—by representation of unconscious ingredients in working memory circuits (broadly defined to include multiple lateral and medial prefrontal regions parietal attention networks). It just has ingredients that non-emotional experiences don't have. And different forms of fear, as discussed above, will themselves have different ingredients. If this view of fear is right, it would probably be useful in understanding other emotions, but not because the feeling of fear or any other emotion has a dedicated neural system.



The low and high sensory roads to the amygdala. Sensory information reaches the amygdala from the sensory thalamus (low road) and sensory cortex (high road). Both are probably non-conscious inputs the amygdala. However, the information in the high road is potentially the same or similar to information that is projected to cortical areas that allow for conscious perceptual experience (e.g. frontal and parietal areas). The low road is a quick and dirty route, as it provides only crude stimulus information

Lots of mental disorders are disorders of the fear response. How is your neurobiological understanding of fear affecting the way you think of therapy for fear disorders? Are we getting any closer to finding a cure for phobias or PTSDs or social anxiety or panic disorders?

Research on the neural basis of “fear” has been really successful because of the availability of simple paradigms that are amenable to neural circuit analysis. For example in so-called fear conditioning, a specific stimulus comes to elicit an innate defense response. One can thus connect the dots in the brain between stimulus and response and identify the circuit. But studies of anxiety, depression, and other disorders typically do not have this kind of stimulus-response luxury, making them much harder to pin down. So we’ve learned a lot about threat pathways. But this leads to two problems.

One problem is that fear conditioning has sometimes been thought of as *the* way to study all things fear (and sometimes, all things related to emotion) in the brain. This is partly my fault since *The Emotional Brain* was mostly about “fear” research. Fear conditioning is good for exploring stimulus driven aspects of “fear,” and thus is useful for studying the underlying states that occur when a phobic patient encounters their phobic stimulus, or when a PTSD patient is exposed to trauma-related cues. It is less useful for conditions like generalized anxiety where there is no specific stimulus involved.

The other problem is one that I’ve been hinting at throughout the interview. The circuits that detect and respond to conditioned threats are not the circuits that themselves give rise to a feeling of fear elicited by such stimuli. Problems arise when these two things are confused. For example, there was much surprise in the press when a patient with amygdala damage was found to be able to experience panic induced by breathing CO2. The

only reason you would be surprised is if you believe that feelings of fear (and panic) flow out of the amygdala.

In a landmark experiment in rats, you showed that it's possible to erase the memory of a specific traumatic event without affecting other memories. How did you do that and what do you take to be the implications of this discovery for humans? Do you think we will ever be able to remove memories of specific traumatic events?

In 2000, Karim Nader, Glenn Schafe, and I published a paper that re-ignited interest in a topic that had been fairly dormant for a while. This was reconsolidation, the idea that memories become subject to change during retrieval, allowing the memory to be updated. Because it is a new memory, it has to be re-stored or reconsolidated. Much work has been done on this since. Jacek Debiec, Valerie Doyere and others in the lab showed that very specific memories could be deleted. And much has been learned about the molecular mechanisms as well. Reconsolidation has important implications for the therapy of anxiety disorders since unlike exposure (extinction) therapy the threat memory does not readily recover over time or in the presence of triggers. But Marie Monfils and I later found that extinction could be made more permanent if it was done after a single retrieval trial. The details are too complicated to explain, but in brief the idea is that if you retrieve the threat memory and then wait 10-60 min before starting a series of extinction trials then extinction is more enduring. Daniela Schiller, Liz Phelps and I then showed it works in humans in the lab. The big question is whether it will work in the clinic.

Your interest in memory is on full display in another one of your bestselling books – *Synaptic Self* (Viking, 2002) – where you argue that memory plays a central role in making us who we are. What exactly is the *Synaptic Self*, and why do you think that the Self and memory are so intimately related?

A key way that behavioral information and other kinds of information are encoded in the brain is by way of synaptic connections within and between networks.

Some behavioral tendencies are encoded innately (genetically and epigenetically) and others through experience. These are both memories. In one case they are species memories, and in the other they are individual memories. In both cases, the memory is stored via synaptic connections. From the point of view of mind and behavior, then, nature and nurture are not two different things, but two ways of doing the same thing: wiring synapses.

This is relevant to the self because in order to be the same person from moment to moment, day to day and year to year, our brain has to remember who we are. I am not just referring to memory in the conscious sense of explicit, declarative memory, but also to the many forms of implicit or unconscious memory that we have. There is much more to the self than meets the mind's eye. Much of the self is stored in systems that operate unconsciously. All your traits and habits, for example– tendencies to act in a certain way in a certain situation.



When we are self-aware, this comes about in one of two ways. We can access those aspects of our self that are stored in conscious or explicit memory. But we can also monitor the behavioral and bodily manifestations of implicit processes and learn about ourselves this way. As I described above, this was one of the main conclusions that came out of my PhD thesis work with Mike Gazzaniga, and it became the basis of Gazzaniga's own *interpreter theory* of consciousness.

What do you consider to be your most significant contributions to the study of emotion?

One important contribution was to help get emotion back into the limelight in neuroscience. At the time, cognition was the rage and emotion was on the back burner. When I submitted my first grant on emotion, it was rejected.

ted. The review said one can't study emotion in the brain; emotion is too subjective. But that's just what I had been saying. I had a way to study emotion without wrestling with the subjective part. Just study the unconscious processing of the stimulus as it controls the response. The reviewer didn't get it. But I retitled the grant to be about the neural basis of conditioning rather than the neural basis of emotion, added some conditioning control groups, and got funded.

The review was wrong-headed but it had an important consequence. It got me funded to do what I wanted to do. And it led me to see my work in terms of emotional learning and memory. The idea of implicit (unconscious memory) was just taking off in cognitive science, and my ideas helped make emotional memory one of the key unconscious memory processes. There were many researchers studying learning and memory using various shock paradigms, but they tended to be more into the memory than the emotion part. The idea of emotional memory was a good branding strategy (maybe those two marketing degrees paid off). While this strategy certainly helped my career, it also helped get the field going.

One could say that I sold out—that I should have stuck with emotion as emotion. But I don't view it this way. Learning plays an important role in what drives emotional feelings. So by studying how threats are learned about and stored is very important. I have no regrets with the way I ended up pursuing things. I am happy with the approach I took and the progress I made using it.

I guess another contribution was to provide an anatomical framework for understanding how emotion could be thought of in terms of unconscious brain processes. Some initially thought this meant the Freudian dynamic unconscious (a storehouse of repressed conscious information). But I was thinking of it the way cognitive science was—as information processing that is unconscious by virtue of wiring. This framework paved the way for me to trace the pathways that allow unconscious processing from stimulus to response in the brain, and, as just mentioned, to study unconscious learning and memory.

I've also had two crusades in my career that I am happy I pursued. One was the attempt to take down the limbic system theory of emotion. I've been trying to do this since the late 1980s. The limbic system idea is a compelling idea that lacks empirical support. I'm not sure I've gotten very far in this crusade but I think it's important because scientists use this idea in an explanatory way. But it's a house of cards. I've summarized the arguments in numerous places, including *The Emotional Brain* and *Synaptic Self*. The other crusade, which we already discussed, is about the imprecise ways we use emotion terms like fear. This too, I think, is important to pursue. Scientists have an obligation to be precise in their thinking and terminology. Otherwise, data are interpreted in confusing ways and the field does not progress. And lay people and journalists get the wrong idea. Scientists then start using the lay meaning, closing the circle of confusion. The limbic system theory and the way we talk about emotions are both examples of imprecise interpretations that lead to confusion that could be avoided by being a little more careful. I know that both crusades are uphill battles. But I'm committed.

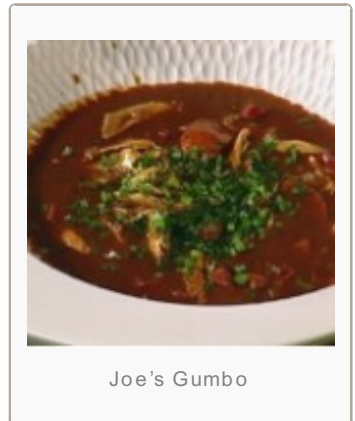
You are from Eunice, deep in Cajun country. What are your favorite dishes from there? Do you have a family recipe to share?

When the air turns chilly from a north wind, I get a craving for gumbo and usually time the fall gumbo with a big LSU football game. This takes lots of planning since it requires that I first order a shipment of Louisiana smoked sausage and tasso from CajunGrocer.com. The smoked meats are not as good as the ones my father used to make in his meat market (Boo's Market) but they are essential (in a pinch, I sometimes bicycle from my apartment in Williamsburg to Greenpoint and pick up some double smoked kielbasa from the Driggs Avenue Polish market, but I prefer the Louisiana stuff). I also order some hot boudin for an appetizer (pork is the best, but sometimes I get the pork/alligator combo). A few days before the game, I start the process, since gumbo (like a lot of other food) is better after it consolidates its flavor. First thing is you have to make a roux. I used to



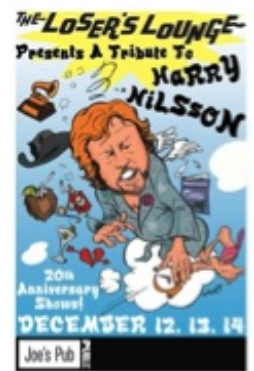
do this the old fashion stove top way, which takes forever. Then I found a micro wave version that does the trick in 30 min. Mix one cup of flour and one cup of vegetable oil. Put in microwave. Cook for 3 min. Stir. Repeat until the roux starts to turn brown. Stir more often once it is brown. Continue until it has the dark brown color of a Hershey's chocolate bar (closer to dark than milk chocolate though). Stir, stir, stir. Do not let it burn. If you have little black flecks in it, you've burned it. Start over. Once you have a roux, fill a gumbo pot (a big soup pot) half way with water and bring to a boil. Put in the roux and stir. When dissolved, boil for 30 min. In the meantime, chop a large onion, bell pepper, and lots of garlic. Throw them in at 30 min. Lots of salt, black and red pepper. Add cut up chicken, 2 sticks of sausage, and 1 stick of tasso (not essential). Cook until the chicken is tender.

Let cool. Put in the fridge for a day or two. On the day of the game, remove from fridge and simmer until hot. Eat some boudin with a cold beer during the first half. Add scallion tops (the green part) and parsley. At half-time, serve over white rice with Tabasco sauce on the table. More beer to wash it down. Having 2 servings is unavoidable. But going for the third is probably a mistake, unless the game is going poorly and you are feeling sorry for yourself. The next morning, be sure to have some boudin with an ice-cold beer (but Coca Cola will also do just fine since it is breakfast). You should still have some gumbo left for lunch. And if you have more of the sauce left, but find the chicken to be depleted, pick up a pound of Gulf shrimp and throw them in for dinner. Oh, be sure to have some Alka Selzer on hand.



You now live in New York City, where you are a member of the Center for Neural Science at New York University. What are some of your favorite things do to in the city? And are you willing to share the names of your three favorite restaurants in New York?

New York is a great place to live and work. I love going out to hear music. One of my favs is something called Losers Lounge. It happens once every few months at Joe's Pub, which is near NYU (no, I'm not that Joe). The head honcho of Loser's Lounge is Joe McGinty (he's not the Joe of Joe's pub either). He picks a theme (Neil Young, Supremes, Pince, John Lennon) and his band does the songs note for note. Each song is sung by a different New York singer. It sounds corny but it is a fabulous event. You get to learn a lot about different musicians around town by watching these shows. It's also fun going to various small, dark, dank clubs that have the aroma of years old stale beer infused in the floor and walls. My wife is in the art world, so we do a lot of stuff connected to that as well. In terms of favorite restaurants, it's hard to pin that down. In Williamsburg, where we live, Aurora is terrific. For a pretty simple but really tasty Mediterranean meal, we like Café Mogador. In Manhattan, there are of course endless choices in all price ranges. We used to live in Chelsea, and Suenos was our go to place for a Yucatan dining experience.



I know you are working on a new book. What is its title, when will it be out and what is it going to be about?

It's going to be called "Anxious." Not surprisingly, it will be about fear and anxiety, viewed from my new perspective on emotion. I hope to be done by May 2014, and have it in print, winter 2015.

Please list a handful of articles or books that have had a deep influence on your thinking.

Skinner BF (1938) The behavior of organisms: An experimental analysis. New York: Appleton-Century-Crofts.
Geschwind N (1965) The disconnection syndromes in animals and man. Part I. Brain 88:237-294.
Kandel ER, Spencer WA (1968) Cellular neurophysiological approaches to the study of learning. Physiological Reviews 48:65-134

MacLean PD (1949) Psychosomatic disease and the “visceral brain”: Recent developments Bearing on the Papez theory of emotion. *Psychosomatic Medicine* 11: 338-353.

Nauta WJH, Karten HJ (1970) A general profile of the vertebrate brain, with sidelights on the ancestry of cerebral cortex. In: *The Neurosciences: Second Study Program* (Schmitt FO, ed), pp 7-26. New York: The Rockefeller University Press.

Jackendoff R (1987) *Consciousness and the Computational Mind*. Cambridge: Bradford Books, MIT Press.

You were recently elected to the National Academy of Sciences, a very exclusive club of highly distinguished scientists. If you were to give some (free!) career advice to young scientists, what would that be?

If you don't love what you are doing, do something else. It's usually a long road from grad school to a successful career. And you are more likely to get there if you're doing something you want to do. But I guess the other thing that needs saying is that it's important to remember that you are more than your career. Don't completely ignore the other aspects of your life to get ahead at work.

You are the front man of New York's most famous band named for a part of the brain: [The Amygdaloids](#). Are the Amygdaloids part of a master plan to make neuroscience popular or do you just like music? Where can we listen to some of Amygdaloids' songs?

Well I guess it's good to be the most famous anything in NY. I have always been strongly drawn to music. I love making it and playing it, and hearing it. It's an amazing experience when several people get together and start playing a song and then it magically transcends the individuals and becomes an entity on its own.

There's really nothing quite like it. That doesn't happen all the time, but when it does, it's wonderful. So ultimately that's why I do it. But at some point I figured out I could mesh my love of music with my passion for understanding the brain. So I started writing songs about mind and brain and mental disorders. We call our music Heavy Mental, which the title of our first CD. We've recorded 3 CDs, with some new recording in progress now. Our second CD, *Theory of My Mind*, feature Rosanne Cash on backing vocals on two songs. Our music can be heard at through our website: www.amygdaloids.com. Below are a couple of music videos:



The Amygdaloids, circa 2013. From left, Amanda Thorpe, Joe LeDoux, Daniela Schiller, and Tyler Volk

Note: if you are interested in listening to [The Amygdaloids'](#) new songs, please send an email to amygdaloids.freesongs@gmail.com to obtain a download code.

Also, I've been involved in a video series called “My Mind's Eye” that blends music with scientific interviews. Each interview is themed around an Amygdaloid's song about mind and brain. These are being hosted by Scientific American. The first one was with Ned Block and can be seen below:

<http://blogs.scientificamerican.com/observations/2013/01/28/what-is-consciousness-go-to-the-video/>

Since you compose music, I wonder if you have any views on how the creative process of a musician compares with the creative process of a neuroscientist. Is writing music with someone else a bit like co-authoring a paper?

I find the creative process of composing music to be pretty different from science. It takes so long for ideas in science to be materialized in experiments. But when things go well I can sit down and crank out a song in a few hours. But you have to figure in that I am hardly a pro when it comes to music and song writing. But col

laborative writing of a song is not that different from collaborating on a scientific paper.

What do you think is the main question that future affective neuroscience should be focusing on?

I'm not a fan of the term affective science. I think we should throw out terms like affective and cognitive science. It was useful to have the designation cognitive science to help launch an approach that differed from behaviorism. Cognitive science then become so dominant that affective science was needed to carve out a research area. But ultimately what we care about is how mind and behavior come out of the brain. I think we are ready to do away with these artificial distinctions and just study mind, brain and behavior without putting research or researchers in tracks that limit what they do and how they do it.

Subcortical Sources of our Cross-Species Emotional Feelings and Psychiatric Implications

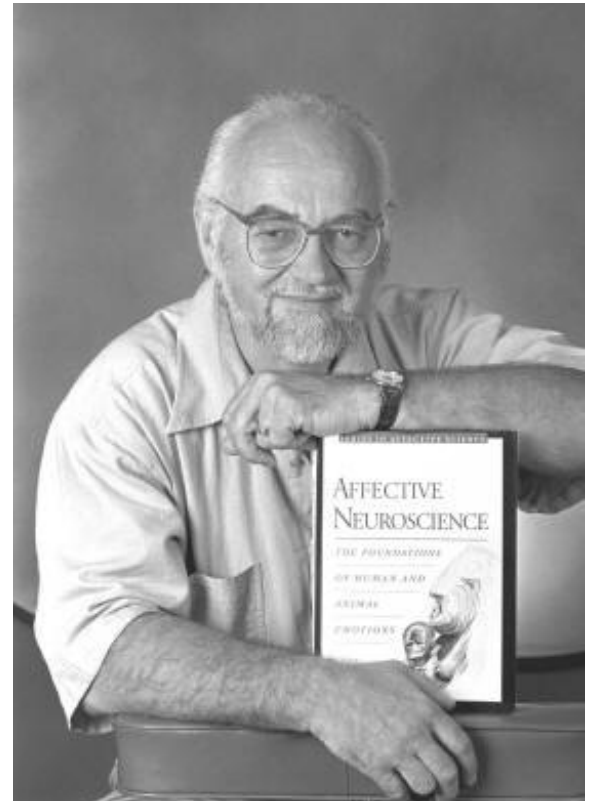
Jaak Panksepp, Department of Integrative Physiology and Neuroscience, College of Veterinary Medicine, Washington State University

How affective feelings evolved in human and animal brains remains one of the central scientific mysteries of our field. To illuminate such deeply psychological question, we have few strategic options but to seek relevant neuroscientific evidence from other animals. There remain barriers to this. It is still commonly believed that “We will never know what an animal feels” (LeDoux 2012, 666), a bias that closely aligns with classical behaviorist and ethological traditions (e.g., consider Nobel Laureate Nico Tinbergen’s assertion in his *Study of Instinct* (1951, 4) that “[b]ecause subjective phenomena cannot be observed objectively in animals, it is idle to claim or deny their existence.”).

Such skepticism was scientifically “reasonable” before the advent of modern neuroscience, but continuing skepticism in the current era overlooks abundant affective neuroscience data for animal emotional feelings—namely, that animals find artificial activation of what I call *primary-process* subcortical emotional systems to be rewarding and punishing. Clearly, these effects do not arise from neocortical read-out processes such as working memory, but rather directly from deep subcortical networks which generate instinctual emotional behaviors (e.g., self-stimulation of the SEEKING system survives radical neo-decortication at birth—Huston & Borbély, 1973). Thus, the affective neuroscience perspective is that animal research provides abundant evidence for the subcortical sources of emotional feelings in all mammals (Panksepp, 1982, 1985, 1998).

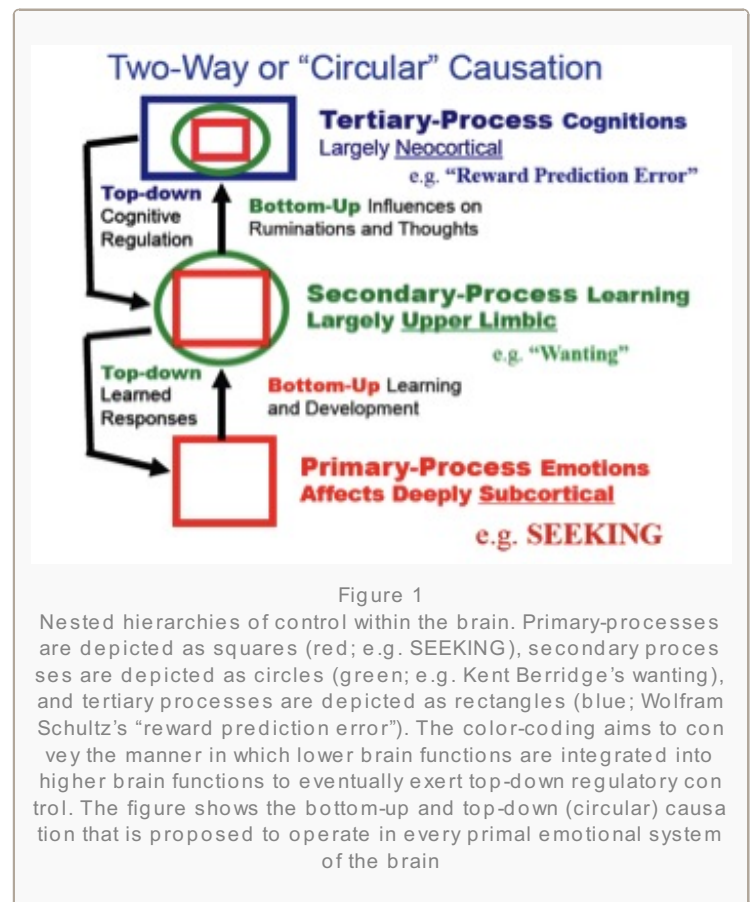
This argument has been laid out simplest in Panksepp (2011). We can evoke at least 7 emotional patterns with subcortical Deep Brain Stimulation (DBS), each associated with distinct forms of arousal that are either *rewarding* (SEEKING, LUST, CARE and PLAY, all of which are evoked along the trajectory of the Medial Forebrain Bundle (MFB)) or *punishing* (RAGE, FEAR, and PANIC) (see Panksepp & Biven, 2012 for a recent review).

It is important to note that the capitalizations are meant to highlight that what is being referred to are primary-process affective systems of the brain, which are next to impossible to study incisively in humans. Indeed, to sustain conceptual clarity, I divide the evolved brain mechanisms critical for understanding affective phenomena into a tripartite level of analysis—primary (raw instinctual-affective), secondary (unconscious learning and memory related processing) and tertiary (higher cognitive manifestations) levels.



As highlighted in Figure 1, each of these levels needs distinct nomenclatures for clear discourse to emerge, which remains especially difficult in areas such as emotion research where few scientifically agreed upon definitions exist. Abundant evidence for SEEKING, RAGE, FEAR, LUST, CARE, PANIC and PLAY systems are detailed elsewhere (Panksepp, 1998). Human PET-based brain imaging (more appropriate for envisioning affective states than fMRI) has seen such systems in human brains (see Figure 2, based on work by Damasio, et al., 2000).

Work on these, and other affective systems (e.g. sensory and homeostatic), should help us understand how “reinforcements” are engendered in the brain, promoting learning and memory. The resulting secondary-process levels of behavioral complexities, especially well detailed in studies of fear conditioning (LeDoux, 2012) may arise from neural “Laws of Affect” whereby fluctuating primary-process affective feeling circuits control learning and solidification of memories—as in the transformation of “silent-synapses” in dynamic changes in glutamatergic transmission (see Chapter 6 Panksepp & Biven, 2012). Claims that primary-process emotional arousals are not experienced in animals need to be cashed out with demonstrations that rewards and punishments can work effectively in humans without any associated experienced affective changes.



The fact that the primary-process level of analysis can only be well pursued in animal models makes the need for clear functional neuronal-circuit based discourse essential. There are many reasons to believe that the higher mental apparatus depends critically on the foundation of primary and secondary brain-mind processes that are best illuminated through cross-species brain research. It is understandable why human psychology has remained unenthused by discussions of primary-process emotional systems—it has little direct access to such brain mechanisms. Conversely, animal investigators have no access to tertiary-process higher mental processes. Such conundrums make any discourse between different levels of analysis difficult (e.g., see Zachar & Ellis, 2012), and a coherent synthesis essential.

My own work has explicitly sought to clarify cross-species, primary-process emotional systems and the feelings they generate. The critical fact that has permitted this is our ability to evoke coherent emotional response patterns with Deep Brain Stimulation. The affective evaluation of those evoked states is achieved with traditional operant learning procedures (conditioned approach and escape), which can at the very least tell us whether

the feelings are positive or negative, with the possibility of discriminating different rewarding feelings (Stutz, et al., 1974) and relating such data to human affective experiences (Panksepp, 1985).

In my estimation, the continuing neglect, indeed denial, of affective processes in animal brain research has prevented us from envisioning how the mind was constructed in brain evolution, where subcortical functions are foundational for all the rest (Solms & Panksepp, 2013). It also explains the failure of animal research to yield new psychiatric medicines, all of which, since the initial breakthrough starting 60 years ago, have been discovered by chance. The subsequent widespread use of animal behavioral models of psychiatric disorders has yet to yield any new psychiatric medicines. I predict we can do better when we begin to scientifically understand our own primal emotional feelings through cross-species research.

Indeed, that was my main reason for investing in primary-process affective neuroscience strategies. Based on this understanding, we are currently evaluating three new interventions for human depression: i) the discovery of new antidepressants that can facilitate social-joy as studied through ancestral PLAY processes of the brain (Burgdorf, et al., 2011), ii) the treatment of depression by stimulating brain SEEKING (“enthusiasm” in the vernacular) urges, through deep brain stimulation (DBS) of the human medial forebrain bundle (MFB) (Coenen, et al., 2012), and iii) the use of safe opioids such as buprenorphine for anti-depressant and anti-suicidal effects, by reducing psychological pain arising from brain PANIC arousal (Yovell, Panksepp, et al., in progress). With an understanding of the opioid neurochemistries of separation-distress and social-bonding, some progress has also been made in treating autism (Bouvard, et al., 1995), and through the study of PLAY, new psychosocial treatments for ADHD are being envisioned (Panksepp, 2007)

Affective neuroscience also offers a vision of how consciousness evolved: At the beginning there emerged raw affects, whose function was to anticipate survival issues: All positive affects inform organisms, uncon-

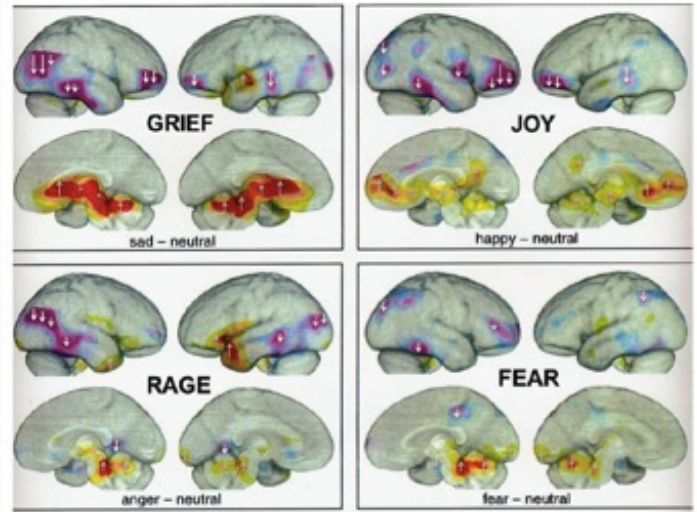


Figure 2

An overview of brain arousals (reds and yellows) and inhibitions (purples) depicted on lateral surfaces of the right and left hemispheres (top of each panel) and medial surfaces of the corresponding hemispheres (bottom of each panel), while humans experience various basic emotions evoked by autobiographical reminiscing. Upper left: sadness/GRIEF; upper right: happiness/JOY; lower left: anger/RAGE; lower right: anxiety/FEAR (data from Damasio, et al. 2000; overall patterns of activation and inhibition (this figure graciously provided by Antonio Damasio). To highlight the directionality of changes, as monitored by changes in blood flow, inhibitions are indicated by downward arrows (predominating in neocortical regions), while arousals are depicted by upward arrows (predominantly in subcortical regions where emotional behaviors can be evoked by brain stimulation in animals)

ditionally, that they are proceeding on paths of survival. All negative feelings inform organisms, also unconditionally, about probable paths of destruction. These affective “intuitions” are cashed out—extended in time—through learning and memory, becoming mental appraisals as they mix with abundant *tertiary-process* higher cortical processes, which emerge via culturally guided developmental learning and epigenetic processes. This vision can diminish disagreements among people working on different levels of analysis of psychological processes of common interest.

A cross-species affective neuroscience allows us to integrate findings from basic animal brain research and constructivist views of the human mind, by recognizing how investigators are working on common interests at different levels of brain-mind organization. That these views are often at odds reflects a failure of our educational enterprises to integrate scientifically meaningful images of bottom-up developmental processes with maturation of top-down, thought-laden regulatory processes. One of the finest, and least appreciated, pieces of good news is that the neocortex at birth resembles a *tabula rasa* more than a conglomerate of evolutionarily specialized modules. All neocortical specializations, even our capacity for vision, arise through early sensory experiences and epigenetic moldings of higher brain functions. Constructivism works best in our understanding of higher mental functions, and hence what makes humans unique; evolutionary perspectives work best in understanding the subcortical specializations that all mammals share. Such disparate views can be integrated (see Zachar & Ellis, 2012 for relevant discussions).

It may be wise for emotion-science to wholeheartedly welcome the good news: We can finally comprehend the general neural principles that undergird our emotional affects by studying homologous processes in other animals. This knowledge has allowed us to develop new biological ways to understand and treat psychiatric disorders. One of our lead antidepressant molecules, GLYX-13, discovered by taking the social-joy (PLAY arousal) of other animals seriously, in the form of “rat laughter” (Burgdorf, et al., 2011), is currently in FDA approved Phase 2b human testing, with promising results from the Phase 2a “proof of concept” studies already completed: http://www.drugs.com/clinical_trials/naurex-s-novel-antidepressant-glyx-13-recognized-one-windhover-s-top-10-neuroscience-projects-watch-10010.html. If that mind medicine, which may facilitate the progression of psychotherapy, by facilitating learning (i.e., GLYX-13 facilitates neuronal long-term potentiation, an electrophysiological marker of learning), ever comes to market, it may be the first time neuroscientific research into brain emotional processes, as opposed to mere serendipity, has yielded an effective way to treat any human psychiatric disorder. This was facilitated by the first validated psychoassay for positive social affect—namely systematic tickling of rats to generate an ancestral form of laughter.

For a general introduction to Jaak’s life and career, take a look at the following two recent interviews:

- [Discover Magazine: The Man Who Makes Rats Laugh: Jaak Panksepp](#)
- [Washington State Magazine: The Animal Mind Reader](#)

You can also check out Jaak’s foreword to his wife’s Anesa Miller’s new book, entitled [To Boldy Go](#).

References

Bouvard, M.P., Leboyer, M., launay, J.-M., Recasens, C., Plumet, M.-H., Waller-Perotte, D., Tabuteau, F., Bondoux, D., Dugas, M., Lensing, P., and Panksepp, J. (1995) Low-dose naltrexone effects on plasma chemistries and clinical symptoms in autism: A double-blind, placebo-controlled study. *Psychiatry Research*, 58, 191-201

Burgdorf, J., Panksepp, J., & Moskal, J. R. (2011). Frequency-modulated 50kHz ultrasonic vocalizations: a tool for uncovering the molecular substrates of positive affect. *Neuroscience & Biobehavioral Reviews*, 35(9), 1831-1836.

Coenen, V.A., Panksepp, J., Hurwitz, T.A., Urbach, H., & Mädlér, B. (2012) Human medial forebrain bundle (MFB) and anterior thalamic radiation (ATR): Diffusion tensor imaging of two major subcortical pathways that may pro

mote a dynamic balance of opposite affects relevant for understanding depression. *The Journal of Neuropsychiatry and Clinical Neurosciences*, 24, 223-236.

Davis, K. L. & Panksepp, J. (2011). The brain's emotional foundations of human personality and the Affective Neuroscience Personality Scales. *Neuroscience & Biobehavioral Reviews*, 35(9), 1946-1958.

Huston, J.P. & Borbély, A.A. (1973). Operant conditioning in forebrain ablated rats by use of rewarding hypothalamic stimulation. *Brain Research*, 50, 467-72.

LeDoux, J. (2012). Rethinking the emotional brain. *Neuron*, 73(4), 653-676.

Panksepp, J. (1982) Toward a general psychobiological theory of emotions. *The Behavioral and Brain Sciences*, 5, 407-467.

Panksepp, J., (1985) Mood changes: In P.J. Vinken, G.W. Bruyn, & H.L. Klawans (Eds). *Handbook of Clinical Neurology* (Revised Series). Vol. 1. (45): *Clinical Neuropsychology*. Amsterdam: Elsevier Science Publishers, pp. 271-285.

Panksepp, J. (1998). *Affective Neuroscience: The Foundations of Human and Animal Emotions*. New York: Oxford University Press.

Panksepp, J. (2005). Affective consciousness: Core emotional feelings in animals and humans. *Consciousness & Cognition*, 14, 19-69.

Panksepp, J., (2007). Can PLAY diminish ADHD and facilitate the construction of the social brain. *Journal of the Canadian Academy of Child and Adolescent Psychiatry*, 10: 57-66.

Panksepp, J. (2011). Cross-species affective neuroscience decoding of the primal affective experiences of humans and related animals. *PLoS One*, 6(8): e21236.

Panksepp, J. & Biven, L. (2012). *Archaeology of Mind: The Neuroevolutionary Origins of Human Emotions*. New York: Norton.

Solms, M. & Panksepp, J. (2012). The “Id” knows more than the “Ego” admits: Neuropsychanalytic and primal consciousness perspectives on the interface between affective and cognitive neuroscience. *Brain Science*, 2, 147-175.

Stutz, R.M., Rossi, R.R., Hastings, L., & Brunner, R.L. (1974). Discriminability of intracranial stimuli: The role of anatomical connectedness. *Physiology & Behavior*, 12, 69-73.

Zachar, P., & Ellis, R. (Eds.). (2012). *Categorical versus dimensional models of affect: A seminar on the theories of Panksepp and Russell* (Consciousness and Emotion book series). Amsterdam, the Netherlands: John Benjamins

What can the brain tell us about emotion? A constructionist approach to emotion-brain correspondence

Kristen A. Lindquist, Department of Psychology, University of North Carolina, Chapel Hill

It goes without saying that the brain produces emotions—in this day and age, you'd have to be a pretty staunch dualist to argue otherwise. The big question that remains concerns *how* the brain creates emotions. Historically, it was assumed that each emotion had a discrete biological core responsible for its creation, such as a certain brain area (e.g., the amygdala) or a network of areas in the evolutionarily “old” portion of the brain (e.g., a network in the brainstem and other subcortical regions). This idea is known as *faculty psychology* (Lindquist & Barrett, 2012)—it is the commonsense notion that specific experiences (anger, disgust, fear, thinking, remembering, acting) each correspond to a specific, evolved, and anatomically defined neural mechanism.



In contrast to this faculty psychology approach, recent research suggests that emotions are instead *constructed* out of more fundamental psychological processes that are not themselves specific to emotion (for reviews see Barrett, 2006; Barrett, 2009; Cunningham et al., 2013; Lindquist, 2013; Lindquist & Gendron, 2013; Lindquist, Wager, Kober, Bliss-Moreau & Barrett, 2012). In this view, instances of emotion (e.g., an experience of anger at a friend) emerge from basic, interacting psychological ‘ingredients’ that each perform a domain-general psychological function that contributes to a variety of emotions, cognitions, perceptions, and actions.

In the constructionist approach my colleagues and I take to understanding the nature of emotion (Barrett & Satpute, 2013; Lindquist, 2013; Lindquist & Barrett, 2012; Oosterwijk et al., 2012; Wilson-Mendenhall et al., 2011), we hypothesize that these basic ingredients involve representations of the body (called “interoceptive sensations” or “core affect”), representations of prior experiences (called “concept knowledge”), representations of the external world (“exteroceptive sensations”) and attention (“executive control”). According to our approach, the brain is a predictive system (see Friston & Kiebel, 2009), always using prior experiences to disambiguate and make meaning of sensations from the body and world. A person experiences an emotion (e.g., anger at a friend) when he makes a “situated conceptualization” of his core affective state in a given context using concept knowledge about emotion (e.g., knowledge about the concept of anger, prior experiences of anger in a similar context)."

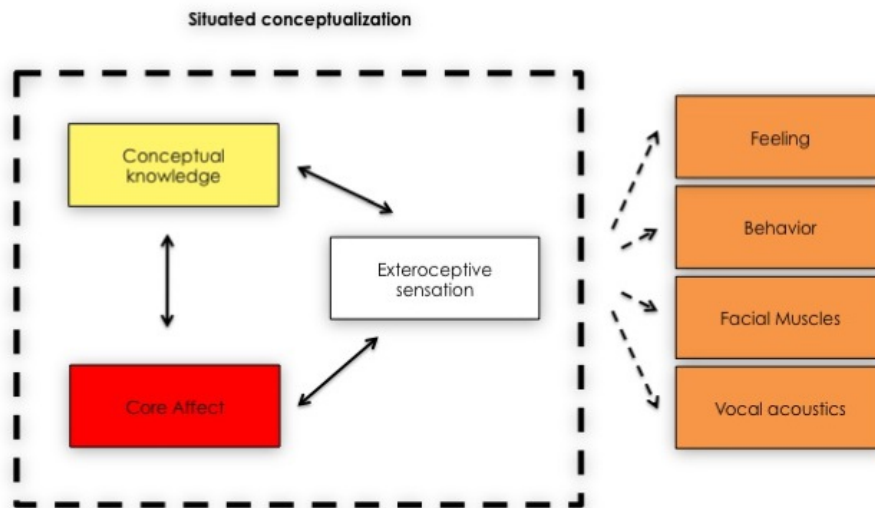


Figure adapted from Lindquist, Wager, Bliss-Moreau, Kober & Barrett (2012). Our constructionist model hypothesizes that information from the body (core affect; red), sensory input from the world (exteroceptive sensation; white) and representations of prior experiences that are supported in part by language (conceptual knowledge; yellow) mutually constrain one another to produce an emergent emotion that can be measured as a series of causal indicators (orange). In a given instance of emotion (e.g., *anger at a spouse*), the causal indicators will form one pattern, and in another instance (e.g., *anger at an injustice*), they will form a different pattern.

Growing neuroscientific evidence from human lesion studies, neuroimaging, and studies of non-human animals supports such a constructionist view of the mind; emotions appear to involve the interaction of neural networks that serve domain-general functions that are not specific to emotions. Contrary to a faculty psychology view, the empirical evidence suggests that certain brain regions are not specific to certain emotions. For instance, although once heralded as the brain basis of fear in mammals, research shows that the human amygdala has neither consistent nor specific increases in activation during instances of fear. Individuals with amygdala lesions can still perceive fear on others' faces when they are specifically directed to look at the diagnostic features of fearful faces (i.e., the eyes; Adolphs et al., 2005). Individuals with amygdala lesions can even experience intense fear when deprived of oxygen (Feinstein et al., 2013). Nor is the human amygdala specific to fear. During neuroimaging experiments of healthy individuals, it shows increased activity during the experience and perception of many different emotions (Lindquist et al., 2012; Vytal & Hamann, 2010).

Another important source of evidence in favor of a constructionist view of the mind is the finding that human emotions involve networks that are not themselves specific to emotion. Brain regions demonstrating increased activity during emotion experiences and perceptions appear to play core affective, conceptual, sensory, and executive control roles across other psychological domains such as moral judgments, empathy, autobiographical memory, and even visual perception (Lindquist & Barrett, 2012).

These networks interact with one another when a person experiences an emotion, consistent with the idea that emotions emerge from the combination of domain-general networks, rather than from a single emotion-specific network. For instance, a brain network supporting *core affect* shows increased interaction with a network supporting *conceptualization* as the intensity of sadness increases over the course of a movie (Raz et al., 2012). Complex patterns of activity within these interacting domain-general networks are also associated with experiences of different emotion categories (e.g., anger, disgust, fear, lust, etc.) (Kassam et al., 2013).

Although it is tempting to assume that evidence for such patterns across brain networks involved in core affect, conceptualization, attention and sensory perception is evidence for the evolutionarily given circuit for an emotion category, it is problematic to interpret neuroscientific data in this manner. First, the pattern observed for a certain emotion category (e.g., anger) differs based on the *context* in which it is experienced (e.g., a physical v. a social situation; Wilson-Mendenhall et al., 2011), suggesting there is no single network for that emotion

category. Second, scientists also observe patterns of brain activity that correspond to experiences of nominal kind categories that are human constructions learned through experience such as cars, bottles, and athletes (Huth et al., 2012). But we would never assume that a neural pattern associated with perceiving a car gives evidence for the evolutionarily-endowed “car network”. Consequently, it’s not clear why similar data would provide evidence for an evolutionarily-endowed “fear network.” The evidence is thus more consistent with the idea that emotions emerge from the combination of more basic neural parts that perform domain-general functions.

A further piece of evidence in favor of a constructionist perspective is that the domain-general networks that support basic psychological functions such as core affect, conceptualization, exteroceptive sensation and executive attention appear to be “intrinsic” networks that are constrained by anatomical connections between brain areas (e.g., Yeo et al., 2011). Many of these networks exist in non-human animals (Rilling et al., 2007; Vincent et al., 2007) and develop in humans across early life (Gao et al., 2011). We thus suggest that they comprise a set of basic functional building blocks of the mind.

In contrast to these domain-general intrinsic networks, neural networks that support adaptive mammalian behaviors (e.g., freezing, attack, maternal behavior; Panksepp, 2004) are sometimes cited as emotion-specific networks. Many of these largely subcortical networks are indeed preserved across species and are certainly relevant to human emotions. Yet neither human nor non-human emotions seem reducible to the specific behaviors supported by such networks—a network for freezing, for instance, cannot logically be considered the network for a complex category such as fear since both humans and non-human animals engage in many behaviors beyond freezing in the face of a threat (Barrett et al., 2007; LeDoux, 2012).

If we reduce the category of fear to the network for freezing, we cannot say that a human or even a rat is fearful when it attacks a threatening intruder, flees, or engages in other defensive behaviors. Instead, networks supporting these adaptive mammalian behaviors can be considered additional ‘ingredients’ of the mind that contribute to some, but not all instances of emotion. For example, a network for freezing might contribute to an instance of fear when a person sees a snake in the garden, but not when she strikes a mugger in a dark alley.

To sum up, growing evidence demonstrates that a constructionist approach is a useful avenue to understanding emotion-brain correspondence. What remains to be seen is whether the ingredients hypothesized at present (e.g., Lindquist & Barrett, 2012) are the best candidates for the basic ‘ingredients’ of the mind more generally. As network-based neuroscientific approaches progress, we might find that alternative, more specific formulations of intrinsic networks are in fact the best candidates for the brain’s functional building blocks. This process of discovery will rely not just on advanced technology, but also on precise and well-validated psychological models of emotion that can constrain the interpretation of neuroscientific results.

References

- Adolphs, R., Gosselin, F., Buchanan, T. W., Tranel, D., Schyns, P., & Damasio, A. R. (2005). A mechanism for impaired fear recognition after amygdala damage. *Nature*, 433, 68-72.
- Barrett, L. F. (2006). Are emotions natural kinds? *Perspectives on Psychological Science*, 1, 28-58.
- Barrett, L. F. (2009). The future of psychology: Connecting mind to brain. *Perspectives on Psychological Science*, 4, 326-339.
- Barrett, L. F., Lindquist, K. A., Bliss-Moreau, E., Duncan, S., Gendron, M., Mize, J., et al. (2007). Of mice and men: Natural kinds of emotions in the mammalian brain? A response to Panksepp and Izard. *Perspectives on Psychological Science: a journal of the Association for Psychological Science*, 2, 297-297.
- Barrett, L. F., & Satpute, A. B. (2013). Large-scale brain networks in affective and social neuroscience: Towards an integrative functional architecture of the brain. *Current Opinion in Neurobiology*.

- Cunningham, W. A., Dunfield, K. A., & Stillman, P. E. (2013). Emotional states from affective dynamics. *Emotion Review*, 5, 344-355.
- Feinstein, J. S., Buzza, C., Hurlemann, R., Follmer, R. L., Dahdaleh, N. S., Coryell, W. H., et al. (2013). Fear and panic in humans with bilateral amygdala damage. *Nature Neuroscience*, 16, 270-272.
- Friston, K., & Kiebel, S. (2009). Predictive coding under the free-energy principle. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 364, 1211-1221.
- Gao, W., Gilmore, J. H., Giovanello, K. S., Smith, J. K., Shen, D., Zhu, H., et al. (2011). Temporal and spatial evolution of brain network topology during the first two years of life. *PLOS One*, 6, e25278.
- Huth, A. G., Nishimoto, S., Vu, A. T., & Gallant, J. L. (2012). A continuous semantic space describes the representation of thousands of object and action categories across the human brain. *Neuron*, 76, 1210-1224.
- Kassam, K. S., Markey, A. R., Cherkassky, V. L., Loewenstein, G., & Just, M. A. (2013). Identifying emotions on the basis of neural activation. *PLOS One*, 8, e66032.
- LeDoux, J. (2012). Rethinking the emotional brain. *Neuron*, 73, 653-676.
- Lindquist, K. A. (2013). Emotions emerge from more basic psychological ingredients: A modern psychological constructionist model. *Emotion Review*, 5, 356-368.
- Lindquist, K. A., & Barrett, L. F. (2012). A functional architecture of the human brain: Insights from emotion. *Trends in Cognitive Sciences*, 16, 533-554.
- Lindquist, K. A., & Gendron, M. (2013). What's in a word: Language constructs emotion perception. *Emotion Review*, 5, 66-71.
- Lindquist, K. A., Wager, T. D., Kober, H., Bliss-Moreau, E., & Barrett, L. F. (2012). The brain basis of emotion: A meta-analytic review. *Behavioral and Brain Sciences*, 35, 121-143.
- Oosterwijk, S., Lindquist, K. A., Anderson, E. C., Dautoff, R., Moriguchi, Y., & Barrett, L. F. (2012). States of mind: Emotions, body feelings, and thoughts share distributed neural networks. *NeuroImage*, 2110-2128.
- Panksepp, J. (2004). *Affective neuroscience: The foundations of human and animal emotions*: Oxford University Press, USA.
- Raz, G., Winetraub, Y., Jacob, Y., Kinreich, S., Maron-Katz, A., Shaham, G., et al. (2012). Portraying emotions at their unfolding: A multilayered approach for probing dynamics of neural networks. *Neuroimage*, 60, 1448-1461.
- Rilling, J. K., Barks, S. K., Parr, L. A., Preuss, T. M., Faber, T. L., Pagnoni, G., et al. (2007). A comparison of resting-state brain activity in humans and chimpanzees. *Proceedings of the National Academy of Sciences of the United States of America*, 104, 17146-17151.
- Vincent, J. L., Patel, G. H., Fox, M. D., Snyder, A. Z., Baker, J. T., Van Essen, D. C., et al. (2007). Intrinsic functional architecture in the anaesthetized monkey brain. *Nature*, 447, 83-86.
- Vytal, K., & Hamann, S. (2010). Neuroimaging support for discrete neural correlates of basic emotions: A voxel-based meta-analysis. *Journal of Cognitive Neuroscience*, 22, 2864-2885.
- Wilson-Mendenhall, C. D., Barrett, L. F., Simmons, W. K., & Barsalou, L. W. (2011). Grounding emotion in situated conceptualization. *Neuropsychologia*, 49, 1105-1127.
- Yeo, B. T., Krienen, F. M., Sepulcre, J., Sabuncu, M. R., Lashkari, D., Hollinshead, M., et al. (2011). The organiza

tion of the human cerebral cortex estimated by functional connectivity. *Journal of Neurophysiology*, 106, 1125–1165.

Emotion beyond brain regions: Networks generate cognitive–emotional interactions

Luiz Pessoa, Department of Psychology, University of Maryland

For over a century, neuroscience has held tight to a framework of *computations as performed by brain regions*. Accordingly, when brain scientists sought to understand the brain basis of emotion, a search for key areas was initiated. With time, several of them were put forward, including emotion “centers” such as the hypothalamus and amygdala. The continued search for the “emotional brain” eventually led to an expanded list of emotion-related subcortical and cortical areas among which the orbitofrontal cortex, the anterior insula, the anterior cingulate cortex, in addition to the ones above, are very popular ones. Depending on how one counts, the list can easily add up to more than a dozen regions.

Two issues are immediately evident. The first is that the list is extremely difficult to define. Consider, for instance, the problem of defining the “limbic” brain, an effort that has essentially failed, although the term continues to be as popular as ever – unfortunately. The second, and the one I would like to discuss here, is that recent understanding of anatomical pathways reveals architectural features that show that cortex and subcortex are part of a connectivity system that allows for massive distribution and aggregation of neural signals (Swanson, 2000; Modha & Singh, 2010). It is thus not surprising that much research has revealed that brain regions are involved in many functions, and that similar functions are performed by many regions. The mapping between structure and function is thus both *pluripotent* (one-to-many) and *degenerate* (many-to-one) (Edelman & Gally, 2001).

Based on these notions, a network perspective is needed for the understanding of the interactions between emotion, motivation, perception, and cognition (Grossberg, 1980; Barbas, 1995; Damasio, 1999; Mesulam, 1999; Pessoa, 2008; 2013). Briefly, networks of brain regions collectively support behaviors: the *network itself is the unit*, not the brain region. Processes that support behavior are not implemented by an individual area, but rather by the interaction of multiple areas, which are dynamically recruited into multi-region assemblies (Figure 1).



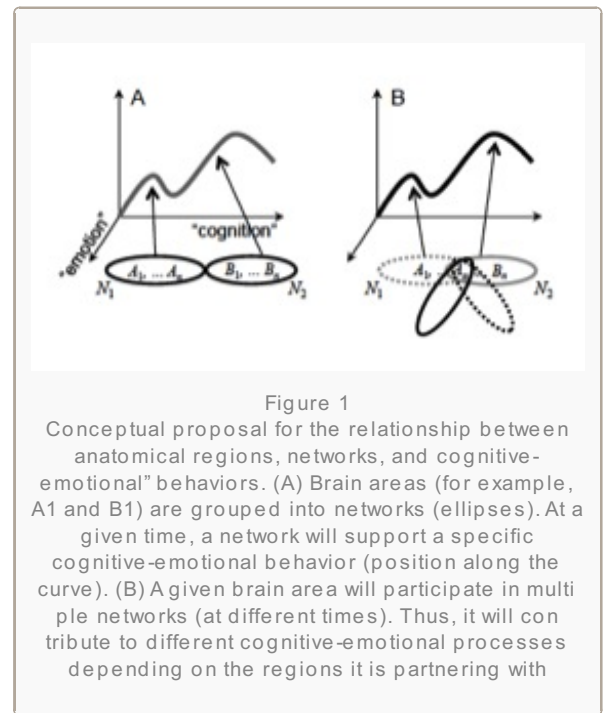
However, importantly, whereas a network perspective is needed for a fuller characterization of the mind–brain, it should not be viewed as a panacea. For one, the challenges posed by the many-to-many mapping between regions and functions is not dissolved by the network perspective. Indeed, one should not anticipate a one-to-one mapping when the network approach is adopted – counter to the recent trend of labeling networks with specific functions. Additionally, decomposition of brain regions in terms of meaningful clusters, such as the ones generated by recent “network science” algorithms (Newman, 2010), does not by itself reveal “true” subnetworks. Given the complex and multi-relational relationship among regions, multiple decompositions will offer different viewpoints of how to understand their interdependency.

Within a distributed computation perspective, the emphasis shifts from attempting to understand the brain one region at a time, to understanding how coalitions of regions support the mind–brain. Insofar as brain regions are not the unit of interest, they should not be viewed as “cognitive” or “emotional”. Traditionally, however, regions whose function involves homeostatic processes and/or bodily representations have been frequently viewed as “emotional”, whereas regions operating on more abstract information – such as those involved in problem solving and planning – have been viewed as “cognitive”.

Consider the extensive communication between the amygdala and visual cortex (incidentally, an architectural feature seen in primates only): efferent amygdala projections reach nearly all levels of the visual cortex (Amaral et al., 2003). Thus, visual processing takes place within a context that is defined by signals occurring in the amygdala (as well as the orbitofrontal cortex, pulvinar, and other regions), including those linked to affective significance (Pessoa & Adolphs, 2010). Consider also the connectivity of prefrontal cortex. Although the amygdala is not connected to all PFC territories, a “one-step” property of amygdala–prefrontal connectivity is present: amygdala signals reach nearly all prefrontal regions with a single additional connection within PFC (e.g., pathways between medial and lateral PFC; see Averbeck & Seo, 2008). Thus, cognitive–emotional interactions abound in the prefrontal cortex.

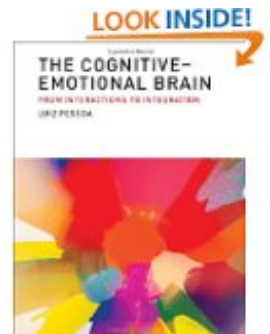
More generally, given inter-region interactivity, and the fact that networks intermingle signals of diverse origin, although a characterization of brain function in terms of networks is needed, the networks themselves are best conceptualized as neither “cognitive” nor “emotional”. The preceding discussion anticipates an important notion: emphasizing interactions among brain regions that are supported by direct, strong structural connections is misleading. Understanding structural connectivity is essential, but it is *not* sufficient. Although, at first glance, the notion of an architecture anchored in physical connections is clear cut, the boundary between an anatomy and function quickly blurs when we consider specific anatomical factors such as the receptor subtypes involved, the presence and proportion of excitatory and inhibitory interneurons, and the strength of the connections. The existence of complex circuits with multiple feedforward and feedback connections and the existence of diffuse projection systems further complicates the picture.

Thus, to understand how regions and networks contribute to brain function, it is *necessary* to identify the way regions are *functionally connected*. Devised to characterize how neurons interact, functional connectivity was initially defined as the “temporal coherence” among the activity of different neurons, as measured by cross-correlating their spike trains (Gerstein & Perkel 1969); or, more generally, the “temporal correlation between neurophysiological (functional) measurements made in different brain areas” (Friston et al., 1993). Understanding functional connectivity is vital, because it will frequently deviate from that expected from simply considering



structural information. Overall, architectural features guarantee the rapid integration and distribution of information even when robust structural connections are not present, and support functional interactions that are heavily context dependent.

What are the implications of these “network ideas” for understanding emotion? Together, they suggest that the mind–brain is *not* decomposable in terms of categories such as “emotion” and “cognition”. Although versions of this idea have been advanced by others too (e.g., Damasio, 1999; Mesulam, 1999; Lindquist et al., 2010), the present proposal differs from these in important ways as outlined in a recent book entitled *The Cognitive-Emotional Brain: From Interactions to Integration* (Pessoa, 2013). In a nutshell, the neural basis of emotion and cognition should be viewed as governed less by properties that are intrinsic to specific sites and more by contextually determined interactions among multiple brain regions. In this sense, emotion and cognition are *functionally integrated systems*, namely, they more or less continuously impact each other’s operations (see Bechtel & Richardson 2010). What ensue are organisms that navigate their ecological niches successfully.



References

- Amaral, D. G., Behniea, H., and Kelly, J. L. (2003). Topographic organization of projections from the amygdala to the visual cortex in the macaque monkey. *Neuroscience*, 118(4), 1099–1120.
- Averbeck, B. B., and Seo, M. (2008). The statistical neuroanatomy of frontal networks in the macaque. *PLoS Computational Biology*, 4(4), e1000050.
- Barbas, H. (1995). Anatomic basis of cognitive-emotional interactions in the primate prefrontal cortex. *Neuroscience and Biobehavioral Reviews*, 19(3), 449–510.
- Bechtel, W., and Richardson, R. C. (2010). *Discovering Complexity: Decomposition and Localization as Strategies in Scientific Research* (2nd ed.). Cambridge, MA: MIT Press.
- Damasio, A. R. (1999). *The Feeling of What Happens: Body and Emotion in the Making of Consciousness*. New York: Harcourt Brace.
- Edelman, G. M., and Gally, J. A. (2001). Degeneracy and complexity in biological systems. *Proceedings of the National Academy of Sciences of the United States of America*, 98(24), 13763–13768.
- Friston, K. J., Frith, C. D., Liddle, P. F., and Frackowiak, R. S. (1993). Functional connectivity: The principal-component analysis of large (PET) data sets. *Journal of Cerebral Blood Flow and Metabolism*, 13(1), 5–14.
- Gerstein, G. L., and Perkel, D. H. (1969). Simultaneously recorded trains of action potentials: Analysis and functional interpretation. *Science*, 164(3881), 828–830.
- Grossberg, S. (1980). How does a brain build a cognitive code? *Psychological Review*, 87(1), 1–51.
- Lindquist, K.A., Wager, T.D., Kober, H., Bliss-Moreau, E., Barrett, L.F. (2012). The brain basis of emotion: a meta-analytic review. *Behavioral & Brain Sciences*, 35(3), 121–143.
- Mesulam, M.-M. (1981). A cortical network for directed attention and unilateral neglect. *Annals of Neurology*, 10, 309–325.
- Modha, D. S., and Singh, R. (2010). Network architecture of the long-distance pathways in the macaque brain. *Proceedings of the National Academy of Sciences of the United States of America*, 107(30), 13485–13490.
- Pessoa, L. (2008). On the relationship between emotion and cognition. *Nature Reviews Neuroscience*, 9(2),

148–158.

Pessoa, L. (2013). *The cognitive-emotional brain: From interactions to integration*. Cambridge: MIT Press.

Pessoa, L., and Adolphs, R. (2010). Emotion processing and the amygdala: From a “low road” to “many roads” of evaluating biological significance. *Nature Reviews. Neuroscience*, 11(11), 773–783.

Swanson, L. W. (2000). Cerebral hemisphere regulation of motivated behavior. *Brain Research*, 886(1–2), 113–164.

Imaging the Emotional Brain

Stephan Hamann, Department of Psychology, Emory University

Recent decades have witnessed a knowledge explosion about all aspects of brain function. Neuroscience studies of emotion have also multiplied, using a wide array of methods from the molecular to the systems level across multiple species. Relatively recently, functional neuroimaging, primarily in the form of functional MRI (fMRI) has assumed a leading role in examining the brain basis of human emotion, with hundreds of papers published to date investigating a wide range of emotion phenomena. Substantial advances have been made in understanding the neural mechanisms involved in specific emotion domains, ranging from facial emotion processing to emotional memory. However, so far there has been surprisingly little high-level integration of affective findings across domains, and a coherent and organized consensus framework for understanding the neural underpinnings of emotion from the findings of neuroimaging studies has remained elusive.



In light of this, what have we actually learned from this proliferation of neuroimaging studies that illuminates fundamental aspects of emotion and their neural representation? What has neuroimaging added that would not have been known otherwise? Here I will focus on a few major ways that neuroimaging has contributed to the overall endeavor of understanding the emotional brain and highlight some challenges and future directions.

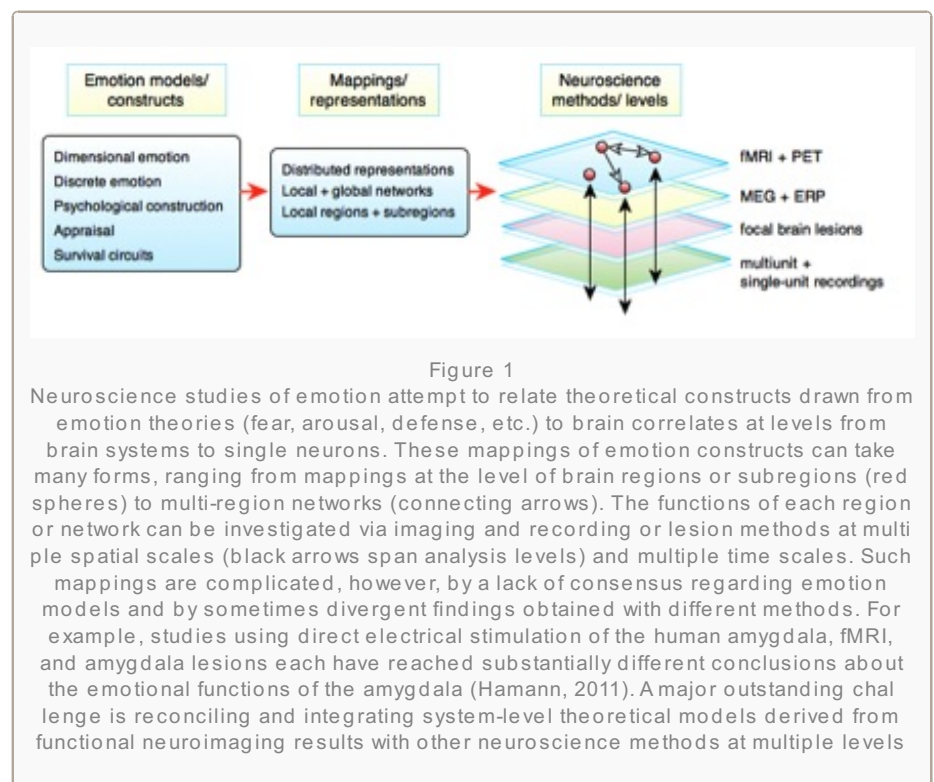
Many neuroimaging studies, including those of emotion, have focused on “brain mapping”, the mapping or association of brain functions to brain structures with the goal of elucidating the brain’s functional organization. But unlike a world map which has well-defined and universally recognized components and boundaries such as mountains and oceans, there is no similar agreement on the components and boundaries of maps of the emotional brain. Neuroimaging studies based on different psychological emotion views such as discrete basic emotions (e.g., fear), affective dimensions (e.g., arousal), or survival relevant circuits (e.g., defense) map essentially different theoretical constructs onto the brain, creating multiple model-dependent maps that complicate attempts to summarize across studies (see Figure 1 for discussion).

The process of mapping emotion in the brain is ultimately only as successful as these emotion models and their constructs, highlighting how theories of emotion play a critical role in determining the basic components and boundaries of maps charting the brain basis of emotions.

Despite these challenges, techniques such as neuroimaging meta-analysis have elucidated some key principles and have played an important role in recent theoretical debates (Hamann, 2012). For example, one major debate has focused on whether the separate emotions such as fear and disgust that are posited by discrete basic emotions theories actually map onto activation in unique brain regions in neuroimaging studies, as would be expected if each emotion had a dedicated neural circuit. If basic emotions are not reflected in brain activations, this would call into question the neural validity of such theories (Lindquist, Wager, Kober, Bliss-Moreau, & Barrett, 2012).

Neuroimaging meta-analyses can analyze associations between brain activation and emotion function across multiple studies. On the one hand, these analyses have found that basic emotions are indeed reflected in consistently greater activation in particular brain regions, allowing one to predict the brain regions likely to be activated during a particular emotion (Vytal & Hamann, 2010). However, meta-analyses have generally failed to find one-to-one mappings between emotions and brain regions, suggesting that it is generally invalid to infer a single emotion, basic or otherwise, from activation of an isolated region, despite the popularity of this type of inference (Poldrack, 2011; Stevens & Hamann, 2012). Instead, each brain region plays many different functional roles across multiple emotional situations, depending on the affective context and the broader network of other interacting regions active at the same time (Anderson, Kinnison, & Pessoa, 2013; Barrett & Satpute, 2013). A region such as the amygdala is like a highly versatile actor, best known for certain genres but able to play a wide range of roles depending on the ensemble of other actors interacting in a given scenario (e.g., fear, reward, arousal, novelty detection), rather than being like a typecast actor who plays the same role in every film (e.g., only fear).

These findings are not consistent with traditional basic emotion views that require dedicated emotion-specific brain regions that are not used for other emotions or other cognitive functions. However, they are consistent with theoretical variations on the basic emotions theme that allow for more flexible types of mappings between emotions and the brain, such as those that propose networks of brain regions as a more appropriate level of mapping between emotions and brain (Hamann, 2012). Preliminary evidence of the potential of network level analyses comes from fMRI studies that have used multivariate pattern classification methods, which can detect subtle patterns of activity reliably associated with mental states, even when those patterns are widely distributed across the brain. Studies using such methods have successfully distinguished and decoded multiple basic emotions from distributed patterns of brain activity, both within and across individuals, often in cases where standard fMRI analyses focused on individual regions fail to detect differences between emotions (Kassam, Markey, Cherkassky, Loewenstein, & Just, 2013; Peelen, Atkinson, & Vuilleumier, 2010).



Another major contribution of neuroimaging is its role in promoting new theoretical advances in affective science. fMRI occupies a special spatiotemporal niche among neuroscience methods, which enables the simultaneous investigation of activity across the entire brain, at multiple spatial scales, and at time scales well-suited for studying emotion. Powerful neuroimaging tools have also been developed for synthesizing and analyzing results from multiple studies in search for emergent patterns across studies. fMRI's ability to record and analyze brain activation associated with emotion representations at multiple spatial and temporal scales facilitates the formulation and testing of alternative views of brain mechanisms of high-level emotion models. Although other methods such as neuropsychological lesion studies have also been fertile ground for theoretical development (Damasio, 2005), many recent theoretical advances and debates regarding emotion have centered on findings from neuroimaging, highlighting this method's importance in driving theoretical change.

A promising theoretical development is the recent focus on identifying key adaptive survival challenges shared across species and the associated *survival circuits* that mediate a coordinated set of adaptive brain and behavioral responses (LeDoux, 2012). Survival circuits differ from basic emotions in that they are defined by brain circuits and adaptive functions that are conserved across mammals, rather than by subjective emotional experience (LeDoux, 2012). Although individual survival circuits do not map directly onto basic emotion categories, there are conceptual similarities between proposed circuits such as defense against harm and basic emotions such as anger and fear. Survival circuits have yet to be systematically investigated in human fMRI studies. A key question for such studies is whether survival circuits can be mapped consistently onto specific, evolutionarily conserved brain regions and networks.

Neuroimaging is ultimately only one method among many in the affective neuroscience toolbox, and like any method it has important limitations, such as limits on spatial and temporal resolution and its essentially correlational nature. The concept of *converging operations* (Bechtel, 2002) refers to the use of complementary evidence from multiple techniques or levels to corroborate experimental conclusions, overcoming weaknesses of individual techniques. A future challenge for affective science will be to apply this approach more systematically, to bridge and integrate across levels of analysis, brain organization, multiple methods and species. Initial efforts at such integration have shown that different methods can yield contradictory findings, highlighting the magnitude of the challenge ahead. Studies using permanent and reversible brain lesions to determine whether particular regions are critical for emotional function, versus merely correlated with it, will be particularly important in complementing neuroimaging's correlational findings. Finally, another major challenge will be to achieve greater theoretical consensus regarding the representation and organization of emotion, which will promote synthesis across all levels of affective neuroscience and help to integrate multiple competing maps of the emotional brain into a common framework.

References

- Anderson, M. L., Kinnison, J., & Pessoa, L. (2013). Describing functional diversity of brain regions and brain networks. *NeuroImage*, 73, 50–58. doi:10.1016/j.neuroimage.2013.01.071
- Barrett, L. F., & Satpute, A. B. (2013). Large-scale brain networks in affective and social neuroscience: towards an integrative functional architecture of the brain. *Current Opinion in Neurobiology*, 23(3), 361–372. doi:10.1016/j.conb.2012.12.012
- Bechtel, W. (2002). Aligning multiple research techniques in cognitive neuroscience: Why is it important? *Philosophy of Science*, 69(S3), S48–S58. doi:10.1086/341767
- Damasio, A. (2005). *Descartes' Error: Emotion, Reason, and the Human Brain*. Penguin.
- Hamann, S. (2011). Introduction to the Special Issue on the human amygdala and emotional function. *Neuropsychologia*, 49(4), 585–588.
- Hamann, S. (2012). Mapping discrete and dimensional emotions onto the brain: controversies and consensus.

Trends in Cognitive Sciences, 16, 458-466.

Kassam, K. S., Markey, A. R., Cherkassky, V. L., Loewenstein, G., & Just, M. A. (2013). Identifying Emotions on the Basis of Neural Activation. *PLoS ONE*, 8(6), e66032. doi:10.1371/journal.pone.0066032

LeDoux, J. (2012). Rethinking the Emotional Brain. *Neuron*, 73(4), 653–676. doi:10.1016/j.neuron.2012.02.004

Lindquist, K. A., Wager, T. D., Kober, H., Bliss-Moreau, E., & Barrett, L. F. (2012). The brain basis of emotion: A meta-analytic review. *Behavioral and Brain Sciences*, 35(03), 121–143.

Peelen, M. V., Atkinson, A. P., & Vuilleumier, P. (2010). Supramodal Representations of Perceived Emotions in the Human Brain. *Journal of Neuroscience*, 30(30), 10127–10134. doi:10.1523/JNEUROSCI.2161-10.2010

Poldrack, R. A. (2011). Inferring Mental States from Neuroimaging Data: From Reverse Inference to Large-Scale Decoding. *Neuron*, 72(5), 692–697. doi:10.1016/j.neuron.2011.11.001

Stevens, J. S., & Hamann, S. (2012). Sex differences in brain activation to emotional stimuli: A meta-analysis of neuroimaging studies. *Neuropsychologia*, 50(7), 1578–1593.

Vytal, K., & Hamann, S. (2010). Neuroimaging support for discrete neural correlates of basic emotions: a voxel-based meta-analysis. *Journal of Cognitive Neuroscience*, 22(12), 2864–2885.

Get to Know Iris Mauss!

Iris Mauss, Department of Psychology, University of California, Berkeley

The research I conduct together with my students and collaborators examines emotions and how people regulate them, often with a focus on how these processes affect people's psychological health (lab website: www.ocf.berkeley.edu/~eerlab/). In particular, we have studied three aspects of emotions: the degree of coherence among different components of emotional responses, people's ability to regulate emotions once they are "up and running," and individual and cultural differences in what people believe about emotions.



Emotion Coherence

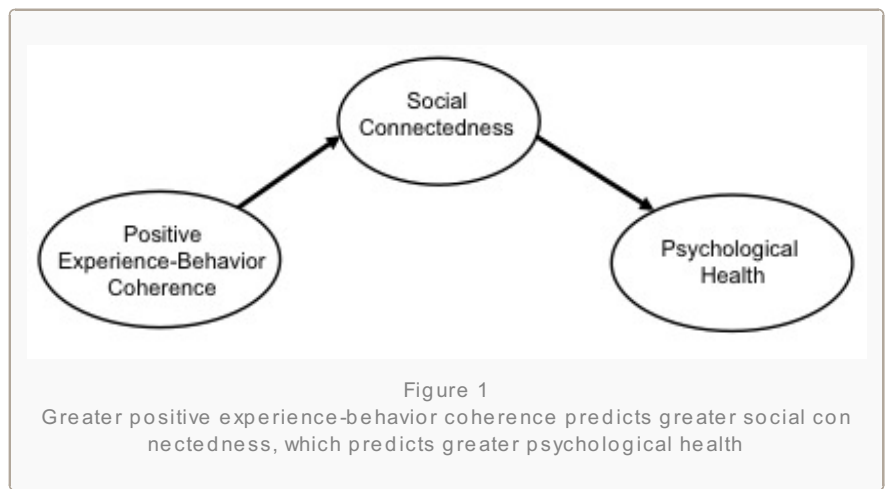
Emotion theories – and lay intuition – posit that people's emotional experiences, behaviors, and physiological responses are coordinated during emotional episodes (Ekman, 1992; Levenson, 1994; Panksepp, 1994). For instance, when we feel anxious, we have a strong sense that our heart is racing and our palms are sweaty. Despite the pervasiveness of this *emotion coherence hypothesis*, empirical support for it is surprisingly limited (Mauss & Robinson, 2009). This intriguing gap led us to develop a new approach to emotion coherence. Rather than examining coherence *across individuals* (e.g., comparing people who are experiencing different levels of anxiety), we assessed coherence *within individuals across time* by continuously measuring participants' emotional experiences, behaviors, and autonomic physiology as they experienced a range of emotions (Mauss, Levenson, McCarter, Wilhelm, & Gross, 2005). When using this approach, these emotion responses were indeed linked. Importantly, however, coherence varied a great deal across individuals, ranging from none to almost perfect coherence.

This wide range of individual differences in coherence was a springboard to examine an important question: might emotion coherence *serve a function*? Take coherence between experience and behavior, for example. Coherence of emotional experiences and behavior may support social processes while dissociation of behavior and experience might disturb them (e.g., someone who smiles without *feeling* happy might appear inauthentic). The social benefits of experience-behavior coherence, in turn, might contribute to greater psychological health. A longitudinal study confirmed this prediction (Mauss, Shallcross, et al., 2011). People with greater experience-behavior coherence in a laboratory experiment exhibited better psychological health on a follow-up survey two years later. As is illustrated in Figure 1, social connectedness mediated this association, suggesting experience-behavior coherence enhances health because it supports social functioning.

Emotion Regulation

Humans do not just passively experience their emotions. Instead, they actively regulate them, often with the goal of decreasing negative emotion (Gross, Richards, & John, 2006). Our research explores the effectiveness of different emotion regulation strategies. At the center of our research is a paradox: intentionally trying to avoid emotions (“I will stop feeling angry!”) often exacerbates them, perhaps because it directs attention to the very experience it is trying to avoid.

How then can people decrease negative emotions?



We have documented three promising emotion-regulation strategies which bypass an intentional focus on decreasing emotion. In the first strategy, people reappraise the situation that precedes their emotional experience so as to experience less negative emotion (Gross, 1998). For example, a person who got into a fight with a friend could reappraise it as a valuable disagreement that will ultimately deepen the friendship. A second route to decreasing negative emotion is *not* to control it but rather to *accept* it, as is the case when one embraces one's sadness over a loss as a normal response (Hayes, Wilson, Gifford, Follette, & Strosahl, 1996; Segal, Williams, & Teasdale, 2002; Shallcross, Ford, Floerke, & Mauss, 2013). Paradoxically, acceptance may allow people to pay less attention to the negative emotion, and therefore feel it less. While reappraisal and acceptance have quite different proximal goals (reappraisal is aimed at changing how one thinks about the emotional situation while acceptance is aimed at accepting one's emotional responses) both have the same outcome: decreased experience of negative emotion. Finally, *automatic emotion regulation* avoids intention altogether by associating certain situations unconsciously with emotion-regulation goals (Mauss, Bunge, & Gross, 2007). For example, in cultures that discourage anger in social situations, people may over time automatically associate social situations with the goal of decreasing anger.

For each of these strategies, we have documented with laboratory experiments and correlational studies that they effectively decrease negative emotions and increase psychological health (Hopp, Troy, & Mauss, 2011; Mauss, Cook, Cheng, & Gross, 2007; Mauss, Cook, & Gross, 2007; Shallcross, Troy, Boland, & Mauss, 2010). For example, we measured reappraisal ability by assessing how much participants could use reappraisal to modulate their experiential and physiological responses to sad films. We then showed that reappraisal ability predicted psychological health in people who had recently experienced stressful life events (e.g., a divorce). As depicted in Figure 2, among participants with low reappraisal ability, stress severity was related to depressive symptoms; but among participants with high reappraisal ability, depressive symptoms were low and not related to stress severity (Troy, Wilhelm, Shallcross, & Mauss, 2010).

More recently, we have begun to look beyond the individual in explaining links between emotion regulation and health outcomes. Our thinking is that few individual-level factors have invariant effects. Rather, the usefulness of individual-level factors usually depends on *their context*. For instance, when stressors are controllable, regulating one's own emotions instead of changing one's situation may be counterproductive (Troy, Shallcross, & Mauss, in press). In support of this idea, we found that reappraisal ability protected stressed participants from depression – but only when stress was uncontrollable (e.g., a family member's death). When stress was more controllable (e.g., a conflict at work), greater reappraisal ability was associated with *more* depression (Figure 3).

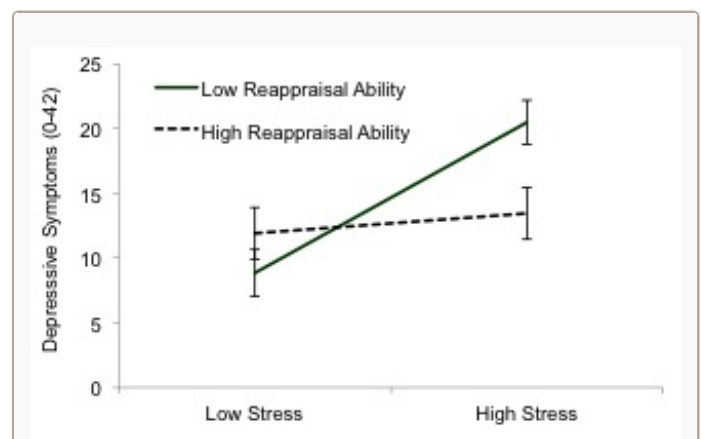


Figure 2
Depressive symptoms as a function of stress severity and reappraisal ability. Reappraisal ability protects participants from the harmful effects of stress on depression

Beliefs about Emotion

Our third line of work explores how people's beliefs about emotions affect their emotions, emotion regulation, and health (Mauss & Tamir, in press). We focus on two sets of beliefs: 1) beliefs regarding whether emotions should be controlled, or, *emotion control values*; and 2) beliefs regarding which emotions one should experience, or, *valued emotions*.

A potent source of emotion control values is culture (Markus & Kitayama, 1991; Tsai, Knutson, & Fung, 2006). In a laboratory study, for instance, we found that Asian Americans value emotion control more than do European Americans, and, accordingly, experience less anger than European Americans in response to an anger provocation (Mauss, Butler, Roberts, & Chu, 2010). A second study documented the power of these cultural values to impact health-relevant processes. Reflecting that Asian Americans, relative to European Americans, value emotion control more, emotion control values were linked to an adaptive pattern of cardiovascular challenge for Asian-American participants. In contrast, for European-American participants, emotion control values were associated with a maladaptive pattern of cardiovascular threat (Mauss & Butler, 2010).

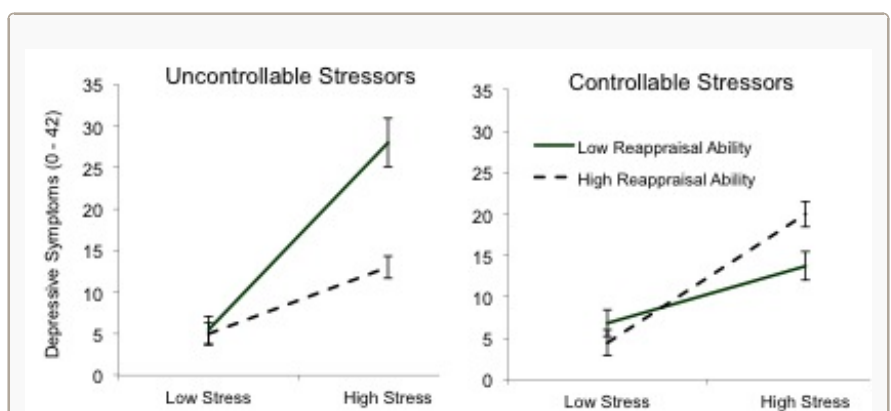


Figure 3
Depressive symptoms as a function of stress severity, stress controllability, and reappraisal ability. Reappraisal ability is protective in the context of relatively uncontrollable stressors but harmful in the context of relatively controllable stressors

Beliefs about which emotions one should experience also influence health. We have focused on happiness as an emotion that people have particularly strong beliefs about (Ford & Mauss, in press; Gruber, Mauss, & Tamir, 2011). Combining evidence from experimental and individual-difference approaches, we find that – paradoxically – the more people value happiness the more unhappy and at risk for depression they are (Mauss, Tamir, Anderson, & Savino, 2011). These effects appear to be due to people being more likely to be disappointed when they believe they should feel very happy. Broadly, these findings show that how people think about emotions – their emotion beliefs and values – plays a profound role in the experience and regulation of emotion.

Concluding Comment

Affective science is a relatively new research area. Yet for centuries, philosophers and scientists have debated questions such as: What is an emotion? What functions do emotions serve? Should people control their emotions, and if so, how can they do so? How are emotions and their regulation involved in health, disease, and the ‘good life’? Our research speaks to these questions by examining emotion coherence, emotion regulation, and people’s values and beliefs about emotion. In exploring these questions, we hope to contribute to a better understanding of emotions, their regulation, and their implications for health.

To know more about Iris, check out the video below, which is part of the very interesting [Experts in Emotion Series](#) directed by [June Gruber](#) at Yale University.

References

- Ekman, P. (1992). An argument for basic emotions. *Cognition & Emotion*, 6, 169-200.
- Ford, B. Q., & Mauss, I. B. (in press). The paradoxical effects of pursuing positive emotion: When and why wanting to feel happy backfires. In J. G. J. Moskowitz (Ed.), *Positive emotion: Integrating the light and dark sides*. Oxford: Oxford University Press.
- Gross, J. J. (1998). Antecedent- and response-focused emotion regulation: Divergent consequences for experience, expression, and physiology. *Journal of Personality and Social Psychology*, 74, 224-237.
- Gross, J. J., Richards, J. M., & John, O. P. (2006). Emotion regulation in everyday life. In D. K. Snyder, J. Simpson & J. N. Hughes (Eds.), *Emotion regulation in couples and families: Pathways to dysfunction and health* (pp. 13-35). Washington, DC: American Psychological Association.
- Gruber, J., Mauss, I. B., & Tamir, M. (2011). A dark side of happiness? How, when, and why happiness is not always good. *Perspectives on Psychological Science*, 6, 222–233.
- Hayes, S. C., Wilson, K. G., Gifford, E. V., Follette, V. M., & Strosahl, K. (1996). Experiential avoidance and behavioral disorders: A functional dimensional approach to diagnosis and treatment. *Journal of Consulting and Clinical Psychology*, 64, 1152-1168.
- Hopp, H., Troy, A. S., & Mauss, I. B. (2011). The unconscious pursuit of emotion regulation: Implications for psychological health. *Cognition and Emotion*, 25, 532-545. doi: 10.1080/02699931.2010.532606
- Levenson, R. W. (1994). Human emotion: A functional view. In P. Ekman & R. J. Davidson (Eds.), *The nature of emotion*



Figure 4
The pursuit of happiness can backfire, or, as Nathaniel Hawthorne wrote, “Happiness is like a butterfly which, when pursued, is always beyond our grasp, but, if you will sit down quietly, may alight upon you”

otion: *Fundamental questions* (pp. 123-126). New York: Oxford University Press.

Markus, H. R., & Kitayama, S. (1991). Culture and the self: Implications for cognition, emotion, and motivation. *Psychological Review*, 98, 224-253.

Mauss, I. B., Bunge, S. A., & Gross, J. J. (2007). Automatic emotion regulation. *Social and Personality Psychology Compass*, 1, 146-167. doi: 0.1111/j.1751-9004.2007.00005.x

Mauss, I. B., & Butler, E. A. (2010). Cultural context moderates the relationship between emotion control values and cardiovascular challenge versus threat responses. *Biological Psychology*, 84, 521-530.

Mauss, I. B., Butler, E. A., Roberts, N. A., & Chu, A. (2010). Emotion control values and responding to an anger provocation in Asian-American and European-American individuals. *Cognition and Emotion*, 24, 1026-1043.

Mauss, I. B., Cook, C. L., Cheng, J. Y. J., & Gross, J. J. (2007). Individual differences in cognitive reappraisal: Experiential and physiological responses to an anger provocation. *International Journal of Psychophysiology*, 66, 116-124.

Mauss, I. B., Cook, C. L., & Gross, J. J. (2007). Automatic emotion regulation during anger provocation. *Journal of Experimental Social Psychology*, 43, 698-711. doi: 10.1016/J.Jesp.2006.07.003

Mauss, I. B., Levenson, R. W., McCarter, L., Wilhelm, F. H., & Gross, J. J. (2005). The tie that binds? Coherence among emotion experience, behavior, and physiology. *Emotion*, 5, 175-190.

Mauss, I. B., & Robinson, M. D. (2009). Measures of emotion: A review. *Cognition and Emotion*, 23, 209-237.

Mauss, I. B., Shallcross, A. J., Troy, A. S., John, O. P., Ferrer, E., Wilhelm, F. H., & Gross, J. J. (2011). Don't hide your happiness! Positive emotion dissociation, social connectedness, and psychological functioning. *Journal of Personality and Social Psychology*, 100, 738-748. doi: 10.1037/a0022410

Mauss, I. B., Tamir, M., Anderson, C. L., & Savino, N. S. (2011). Can seeking happiness make people unhappy? Paradoxical effects of valuing happiness. *Emotion*, 11, 807-815. doi: 10.1037/a0022010

Panksepp, J. (1994). The basics of basic emotions. In P. E. R. J. Davidson (Ed.), *The nature of emotion: Fundamental questions* (pp. 237-242). New York: Oxford University Press.

Segal, Z. V., Williams, J. M. G., & Teasdale, J. D. (2002). *Mindfulness-based cognitive therapy for depression: A new approach to preventing relapse*. New York, NY, US: Guilford Press.

Shallcross, A. J., Ford, B. Q., Floerke, V. A., & Mauss, I. B. (2013). Getting better with age: The relationship between age, acceptance, and negative affect. *Journal of Personality and Social Psychology*, 734-749.

Shallcross, A. J., Troy, A. S., Boland, M., & Mauss, I. B. (2010). Let it be: Accepting negative emotional experiences predicts decreased negative affect and depressive symptoms. *Behaviour Research and Therapy*, 48, 921-929. PMID: PMC3045747.

Troy, A. S., Shallcross, A. J., & Mauss, I. B. (in press). A person-by-situation approach to emotion regulation: Cognitive reappraisal can either hurt or help, depending on the context. *Psychological Science*.

Troy, A. S., Wilhelm, F. H., Shallcross, A. J., & Mauss, I. B. (2010). Seeing the silver lining: Cognitive reappraisal ability moderates the relationship between stress and depression. *Emotion*, 10, 783-795. doi: 10.1037/a0020262

Tsai, J. L., Knutson, B., & Fung, H. H. (2006). Cultural variation in affect valuation. *Journal of Personality and Social Psychology*, 90, 288-307. doi: 10.1037/0022-3514.90.2.288