

2. Siviter, H., and Muth, F. (2020). Do novel insecticides pose a threat to beneficial insects? *Proc. Biol. Sci.* 287, 20201265.
3. Woodcock, B.A., Isaac, N.J.B., Bullock, J.M., Roy, D.B., Garthwaite, D.G., Crowe, A., and Pywell, R.F. (2016). Impacts of neonicotinoid use on longterm population changes in wild bees in England. *Nat. Commun.* 7, 12459.
4. Rundlöf, M., Andersson, G.K.S., Bommarco, R., Fries, I., Hederström, V., Herbertsson, L., Jonsson, O., Klatt, B.K., Pedersen, T.R., Yourstone, J., et al. (2015). Seed coating with a neonicotinoid insecticide negatively affects wild bees. *Nature* 521, 77–80.
5. Siviter, H., Richman, S.K., and Muth, F. (2021). Field-realistic neonicotinoid exposure has sub-lethal effects on non-*Apis* bees: A meta-analysis. *Ecol. Lett.* 24, 2586–2597.
6. Siviter, H., Brown, M.J.F., and Leadbeater, E. (2018). Sulfoxaflor exposure reduces bumblebee reproductive success. *Nature* 561, 109–112.
7. Sgolastra, F., Medrzycki, P., Bortolotti, L., Maini, S., Porrini, C., Simon-Delso, N., and Bosch, J. (2020). Bees and pesticide regulation: Lessons from the neonicotinoid experience. *Biol. Conserv.* 241, 108356.
8. Topping, C.J., Aldrich, A., and Berny, P. (2020). Overhaul environmental risk assessment for pesticides. *Science* 367, 360–363.
9. El Agrebi, N., Traynor, K., Wilmart, O., Tosi, S., Leinartz, L., Danneels, E., de Graaf, D.C., and Saegerman, C. (2020). Pesticide and veterinary drug residues in Belgian beeswax: Occurrence, toxicity, and risk to honey bees. *Sci. Total Environ.* 745, 141036.
10. Traynor, K.S., Tosi, S., Rennich, K., Steinhauer, N., Forsgren, E., Rose, R., Kunkel, G., Madella, S., Lopez, D., Eversole, H., et al. (2021). Pesticides in honey bee colonies: establishing a baseline for real world exposure over seven years in the USA. *Environ. Pollut.* 279, 116566.
11. Donley, N. (2019). The USA lags behind other agricultural nations in banning harmful pesticides. *Environ. Heal.* 18, 44.
12. Sgolastra, F., Hinarejos, S., Pitts-Singer, T.L., Boyle, N.K., Joseph, T., Lückmann, J., Raine, N.E., Singh, R., Williams, N.M., and Bosch, J. (2019). Pesticide exposure assessment paradigm for solitary bees. *Environ. Entomol.* 48, 22–35.
13. Pisa, L., Goulson, D., Yang, E.-C., Gibbons, D., Sánchez-Bayo, F., Mitchell, E., Aebi, A., van der Sluijs, J., MacQuarrie, C.J.K., Giorio, C., et al. (2017). An update of the Worldwide Integrated Assessment (WIA) on systemic insecticides. Part 2: impacts on organisms and ecosystems. *Environ. Sci. Pollut. Res.* 28, 11749–11797.
14. EFSA (2022). Revised guidance on the risk assessment of plant protection products on bees (*Apis mellifera*, *Bombus* spp. and solitary bees). <https://connect.efsa.europa.eu/RM/s/publicconsultation2/a017U0000011fdP/pc0217>.
15. Campbell, J.W., Cabrera, A.R., Stanley-Stahr, C., and Ellis, J.D. (2016). An evaluation of the honey bee (Hymenoptera: Apidae) safety profile of a new systemic insecticide, flupyradifurone, under field conditions in Florida. *J. Econ. Entomol.* 109, 1967–1972.
16. Franklin, E.L., and Raine, N.E. (2019). Moving beyond honeybee-centric pesticide risk assessments to protect all pollinators. *Nat. Ecol. Evol.* 3, 1373–1375.
17. Goulson, D. (2015). Neonicotinoids impact bumblebee colony fitness in the field: a reanalysis of the UK's Food & Environment Research Agency 2012 experiment. *PeerJ* 3, e854.
18. Willis Chan, D.S., and Raine, N.E. (2021). Population decline in a ground-nesting solitary squash bee (*Eucera pruinosa*) following exposure to a neonicotinoid insecticide treated crop (*Cucurbita pepo*). *Sci. Rep.* 11, 4241.
19. Hayward, A., Beadle, K., Singh, K.S., Exeler, N., Zaworra, M., Almanza, M.T., Nikolakis, A., Garside, C., Glaubitz, J., Bass, C., et al. (2019). The leafcutter bee, *Megachile rotundata*, is more sensitive to N-cyanoimidine neonicotinoid and butenolide insecticides than other managed bees. *Nat. Ecol. Evol.* 3, 1521–1524.
20. Siviter, H., Matthews, A.J., and Brown, M.J.F. (2022). A Combined LD50 for Agrochemicals and Pathogens in Bumblebees (*Bombus terrestris* [Hymenoptera: Apidae]). *Environ. Entomol.* 51, 378–384.
21. Linguadoca, A., Jürison, M., Hellström, S., Straw, E.A., Šima, P., Karise, R., Costa, C., Serra, G., Colombo, R., Paxton, R.J., et al. (2022). Intra-specific variation in sensitivity of *Bombus terrestris* and *Osmia bicornis* to three pesticides. *Sci. Rep.* 12, 17311.
22. Klein, O., Roessink, I., Elston, C., Franke, L., Jütte, T., Knäbe, S., Lückmann, J., van der Steen, J., Allan, M.J., Alscher, A., et al. (2022). Results of ring-testing of a semifield study design to investigate potential impacts of crop protection products on bumblebees (Hymenoptera, Apidae) and a proposal of a potential test design. *Environ. Toxicol. Chem.* 41, 2548–2564.
23. Siviter, H., Bailes, E.J., Martin, C.D., Oliver, T.R., Koricheva, J., Leadbeater, E., and Brown, M.J.F. (2021). Agrochemicals interact synergistically to increase bee mortality. *Nature* 596, 389–392.
24. Linguadoca, A., Rizzi, C., Villa, S., and Brown, M.J.F. (2021). Sulfoxaflor and nutritional deficiency synergistically reduce survival and fecundity in bumblebees. *Sci. Total Environ.* 795, 148680.
25. Tosi, S., and Nieh, J.C. (2019). Lethal and sublethal synergistic effects of a new systemic pesticide, flupyradifurone (Sivanto®), on honeybees. *Proc. Biol. Sci.* 286, 20190433.
26. More, S., Bampidis, V., Benford, D., Bragard, C., Halldorsson, T., Hernández-Jerez, A., Bennekou, S.H., Koutsoumanis, K., Machera, K., Naegeli, H., et al. (2021). A systems-based approach to the environmental risk assessment of multiple stressors in honey bees. *EFSA J.* 19, e06607.
27. Topping, C.J., Brown, M., Chetcuti, J., de Miranda, J.R., Nazzi, F., Neumann, P., Paxton, R.J., Rundlöf, M., and Stout, J.C. (2021). Holistic environmental risk assessment for bees. *Science* 371, 897.
28. Woodcock, B.A., Bullock, J.M., Shore, R.F., Heard, M.S., Pereira, M.G., Redhead, J., Ridding, L., Dean, H., Sleep, D., Henrys, P., et al. (2017). Country-specific effects of neonicotinoid pesticides on honey bees and wild bees. *Science* 356, 1393–1395.
29. Milner, A.M., and Boyd, I.L. (2017). Toward pesticidevigilance. *Science* 357, 1232–1234.

Q & A

Joseph LeDoux

Joseph LeDoux is a University Professor and the Henry and Lucy Moses Professor of Science, and Professor of Neural Science, Psychology, Psychiatry, and Child and Adolescent Psychiatry at New York University. He also directs the Emotional Brain Institute at NYU. His work is focused on the brain mechanisms of emotion, memory, and consciousness. LeDoux has received numerous awards for his research, including the Fyssen Prize in Cognitive Science, The Karl Spencer Lashley Prize from the American Philosophical Society, and the William James Award from the Association for Psychological Science. He is an elected member of the American Academy of Arts and Sciences and of the National Academy of Sciences USA and is the 2023 President-Elect of the Association for the Scientific Study of Consciousness. LeDoux is the author of several books, including *The Emotional Brain*, *Synaptic Self*, *Anxious* (2016 APA William James Book Award), and *The Deep History of Ourselves* (finalist for the 2020 Pen America E.O. Wilson Award for Literary Science Writing). His forthcoming book, *The Realms of Existence, is due out in October 2023*. As a side line, he is the lead singer and songwriter in the rock band *The Amygdaloids* and in the acoustic duo *So We Are*.

**What turned you on to science in the first place?** I grew up in small town in South Louisiana in the ‘boomer’ generation. Like many of my cohort, as a teen I wanted to be a rock and roller. I was not inclined towards science. I did poorly in math in high school, and the only science class I remember taking is chemistry. My major in college at Louisiana State University was business administration, and I steered clear of science there as well, except for a class that, these days, would be called ‘physics for dummies.’ I went on to receive a master’s in marketing, also at LSU, during which I got interested in psychology, and, in particular, why people buy the stuff they buy. The last

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psychology class I took at LSU was taught by Robert Thompson who did research on memory in rat brains. I ended up working in his lab for a few months, and three years later, in 1978, I had a PhD in Psychology from Stony Brook University for research I did on consciousness in split-brain patients. A career is not necessarily launched along a straight line.

**How did you get started in your specific field of research?** My mentor at Stony Brook, Mike Gazzaniga, was very open minded, and didn't hold it against me that I had little formal scientific background. I didn't get much course knowledge in grad school either, since the PhD program was research based and had few course requirements — the only one of any substance was a class on behaviourist psychology, which reflected the fact Stony Brook was one of the last bastions of behaviourism. But the lack of course work didn't matter since my PhD research on consciousness in 'split-brain' patients was not a hi-tech adventure and didn't require a lot of technical or neuroscience expertise.

**What is the best advice you've been given?** Truth be told, I did feel like an imposter. All the other students had some kind of relevant educational background. So, one day I told Mike I thought I should learn some biochemistry. He said, why would you want to do that? Out of context, that may sound like a flippant, if not strange, response. But the context was that he felt I should focus on the big questions of psychology — what is the mind? How does consciousness come about? If I needed biological support, I could always collaborate with, or even hire, someone. That advice came in handy when I joined Don Reis' lab at Cornell Medical School in 1979 as a post-doc. He had every major neurobiological technique of the day. My research goal was to understand brain systems that control behaviours in rats that, in humans, are correlated with fear. Through on-the-job training, and especially by collaborating, I published state-of-the-art neurobiological research. By the time I joined NYU in 1989 as an associate professor, my career as a wet-lab, behavioural neuroscientist

was well established, even though I myself was not an expert in most of the procedures used in my lab. Like Mike advised, I simply hired post-docs who were experts.

**Who were your key early influences?**

Sigmund Freud; B.F. Skinner; Karl Lashley; Robert Thompson; Mike Gazzaniga; Don Reis. I came across Freud in a psychology course at LSU. I was intrigued by him, but I didn't know how to articulate what he meant to me. Skinner's behaviourist approach captivated me and I wrote to him about using his models to understand consumer behaviour. He wrote back that he felt it was wrong to use scientific psychology to manipulate consumer choices. I was actually more into consumer protection, but I was very impressed to get Skinner's letter, which motivated me to leave business. While working in Robert Thompson's lab I came across the ideas of Karl Lashley on memory and consciousness. Thompson had worked with Lashley, which made me feel like I had a scientific past. Mike Gazzaniga taught me to think and write. But Lashley was also in Mike's intellectual past, and that made me doubly connected to him. The trifecta was complete when I received the Lashley Award from the American Philosophical Society. Putting it all together, Don Reis provided me state-of-the-art neurobiological techniques and collaborators, allowing me to ask Gazzaniga-like psychological questions about emotional behaviour using the behaviourist methods I had learned from Thompson. I will explain Freud later.

**If you had to choose a different field of biology, what would it be?**

I wouldn't want to be any other kind of biologist. Maybe because, if anything, I think of myself as a psychologist who flirted with neuroscience, and the psychology/neuroscience interface really is all I know and care about. Of course, all psychological functions are biological functions, but as a scientific identity you can be a psychologist without ever thinking about the nervous system, and a neuroscientist without ever thinking about the genes and molecules that concern most biologists.



Joseph LeDoux, playing his 'heavy mental' songs, in Kåkkå Kverulankaterdalen (the cathedral of quarrels) in Stavanger, Norway. Photo by Karsten Hegland.

**Do you have a favourite science book?**

Early on, as I was trying to make the transition from business to behavioural neuroscience, I immersed myself in several books: Robert E. Silverman's *Psychology*; J.P. Chaplin and T.S. Krawiec's *Systems and Theories of Psychology*; C.S. Hall and G. Lindzey's *Theories of Personality*; and Joseph Altman's *Organic Foundations of Animal Behaviour*. Long after becoming a professor at NYU, I learned that Silverman published his book while teaching psychology at NYU in the early 70s, when Mike Gazzaniga was a professor there, just before moving to Stony Brook.

**What do you think are the biggest problems in your field?**

Neuroscience is in an age of technical wizardry. We can turn genes on and off and control brain circuits and behaviours. But the question is, what are we looking for, and will we know it when we see it? This is where Gazzaniga's advice above really rings true. We need to be as rigorous in our concepts and interpretations as in our data collection and analysis. A big part of the problem is that psychology has special linguistic impediments not faced by other sciences. In the late 1950s, George

Mandel and William Kessen noted that physicists, astronomers, and chemists don't need to take seriously commonsense ideas about nature because people's beliefs and attitudes about the stars, matter and energy, and chemical elements don't affect the subject under investigation. But psychologists do have to pay attention because people's beliefs about the mind influence their thoughts and actions in daily life and are thus an important part of what psychology is all about. For example, when biologists name a gene with a common language term like *hedgehog*, no one mistakes that for the animal of the same name. But when psychologists refer to a behaviour with a term derived from human introspection, like fear, the assumption is that the mental state of fear has some special relation to the behaviour, and also to the brain circuit that controls the behaviour. From time to time, we need to step back and evaluate the language of science. It's not that mental state words like fear are not useful. It's just that they should be used for mental states, and not be automatically assumed to be causes of behaviour in animals or humans just because the mental state is correlated with the behaviour in humans.

**How do you feel about applied versus basic science?** When I was just getting started as a scientist, I steered clear of applications. Having so little formal training in science I was trying to do my best to mimic the way a real scientist would think about basic versus applied research — that applied science lacked the beauty and purity of basic science. Then the more I got to know about research on emotions like fear and anxiety, the more I realized that the reason treatments for fear and anxiety disorders were not very good was because basic science notions about these states were wrong. The problem started with Darwin and his acolytes in the late 19<sup>th</sup> century. They viewed emotions as states of mind inherited from mammalian ancestors. In the early 20<sup>th</sup> century, behaviourists banned this kind of anthropomorphic talk about mental states. But they continued to use mental state terms like fear and anxiety to describe behaviours. Treatments for problems with fear and anxiety emerging in the

mid 20<sup>th</sup> century were influenced by the behaviourist approach. Today, the focus remains on using behaviour as a marker for mental disorders, with little concern for the mental part of the problem. The assumption is that behaviour is a better readout of 'fear' than the feeling of fear. But so long as the mental part of mental disorders is marginalized, people will suffer mentally. In retrospect, I think that's what I understood in Freud but didn't know how to articulate.

**Is there too much emphasis on big data-gathering collaborations as opposed to hypothesis-driven research by small groups?** Big data and hypothesis driven research both have a place. But both could use more emphasis on the conceptual underpinnings of the research. Scientists are taught how to collect and analyse data. Philosophers are taught to think. It might be helpful if scientific education could include a bit of this kind of training as well.

**If you would not have made it as a scientist, what would you have become?** Well, I always wanted to be a musician as a kid. Decades later, being a scientist actually made that possible in ways I never expected. In 2005 or so we had a band composed of NYU researchers that played songs about mind and brain at holiday parties — Manic Depression, Mother's Little Helper, 19<sup>th</sup> Nervous Breakdown. We called ourselves 'The Amygdaloids', since a lot the work I and other band members were doing was on that part of the brain. Then I wrote a couple of these mind-brain songs myself for a gig that was written up in a local newspaper with the headline 'Heavy Mental'. We went on to record several heavy mental albums (see The Amygdaloids YouTube channel) and played countless gigs in NY and on the road. As an acoustic duo, two of us have travelled the world doing gigs in cities where I have lectured.

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## Quick guide

# Hoover the talking seal

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**Hoover, who?** Hoover (1971–1985; **Figure 1**) was a male harbor seal (*Phoca vitulina*) famous for imitating human speech, who spent most of his life at the New England Aquarium in Boston, USA. Initially raised by a Maine fisherman, Hoover began imitating English phrases once he reached sexual maturity. The seal's repertoire included "hello there", "come over here", "hurry", "hey hey", and "Hoover". Hoover provides an unparalleled example of speech mimicry — a form of vocal learning — in seals.

**How did a seal learn to parrot human speech?** Hoover was an orphaned seal, found at Bethel Point, Maine, in 1971 and rescued a few weeks after his birth. George Swallow took the orphaned pup home, handfeeding and frequently speaking to him. Growing fast, Hoover was donated to the New England Aquarium at about three months. He started producing speech-like sounds much later, around his fifth birthday. Hoover produced his speech-like vocalizations typically in the water, from a vertical position, followed by bubble blowing. These vocal displays were especially frequent during breeding season, and often appeared directed at female seals, suggesting that these vocalizations may have acted as 'breeding songs' like those produced by male harbor seals. Importantly, the aquarium staff did not train Hoover to produce these displays.

**Did Hoover faithfully copy speech, or simply trick us into thinking he does?** One might think that Hoover was no different from some 'YouTube stars', like Siamese cats or Huskies that say 'Mama' or 'I love you'. Human perception is so attuned to finding (speech) patterns that some animals may trick our brains into hearing speech sounds where no such similarity exists. However, in the case of Hoover there is solid evidence for speech

