

Joseph Cesario¹, David J. Johnson², and Heather L. Eisthen^{3,4}

¹Department of Psychology, Michigan State University; ²Department of Psychology, University of Maryland; ³Department of Integrative Biology, Michigan State University; and ⁴BEACON Center for the Study of Evolution in Action, Michigan State University



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Abstract

A widespread misconception in much of psychology is that (a) as vertebrate animals evolved, "newer" brain structures were added over existing "older" brain structures, and (b) these newer, more complex structures endowed animals with newer and more complex psychological functions, behavioral flexibility, and language. This belief, although widely shared in introductory psychology textbooks, has long been discredited among neurobiologists and stands in contrast to the clear and unanimous agreement on these issues among those studying nervous-system evolution. We bring psychologists up to date on this issue by describing the more accurate model of neural evolution, and we provide examples of how this inaccurate view may have impeded progress in psychology. We urge psychologists to abandon this mistaken view of human brains.

Keywords

nervous-system evolution, triune brain, automaticity, perception-behavior link, dual process

The purpose of this article is to clarify a widespread misconception in psychological science regarding nervous-system evolution. Many psychologists believe that as new vertebrate species arose, evolutionarily newer complex brain structures were laid on top of evolutionarily older simpler structures; that is, that an older core dealing with emotions and instinctive behaviors (the "reptilian brain" consisting of the basal ganglia and limbic system) lies within a newer brain capable of language, action planning, and so on. The important features of this model, often called the *triune-brain theory*, are that (a) newer components are literally layered outside of older components as new species emerge, and (b) these newer structures are associated with complex psychological functions we reserve for humans or, if we are feeling generous, for other primates and social mammals (see Figs. 1a and 1b). As Paul MacLean (1964), originator of the triune-brain theory, stated,

man, it appears, has inherited essentially three brains. Frugal Nature in developing her paragon threw nothing away. The oldest of his brains is basically reptilian; the second has been inherited from lower mammals; and the third and newest brain is a late mammalian development which reaches a pinnacle in man and gives him his unique power of symbolic language. (p. 96)

This belief, although widely shared and stated as fact in psychology textbooks, lacks any foundation in evolutionary biology.

Our experience suggests that it may surprise many readers to learn that these ideas have long been discredited among people studying nervous-system evolution. Indeed, some variant of the above story is seen throughout introductory discussions of psychology and some subareas within the discipline. We provide a few brief examples, illustrate what is wrong with this view, and discuss how these ideas may have impacted psychological research.

Within psychology, a broad understanding of the mind contrasts emotional, animalistic drives located in older anatomical structures with rational, more complex psychological processes located in newer anatomical

Corresponding Author: Joseph Cesario, Michigan State University, Department of Psychology, East Lansing, MI 48823 E-mail: cesario@msu.edu



Fig. 1. Incorrect views (a, b) and correct views (c, d) of human evolution. Incorrect views are based on the belief that earlier species lacked outer, more recent brain structures. Just as species did not evolve linearly (a), neither did neural structures (b). Although psychologists understand that the view shown in (a) is incorrect, the corresponding neural view (b) is still widely endorsed. The evolutionary tree (c) illustrates the correct view that animals do not linearly increase in complexity but evolve from common ancestors. The corresponding view of brain evolution (d) illustrates that all vertebrates possess the same basic brain regions, here divided into the forebrain, midbrain, and hindbrain. Coloring is arbitrary but illustrates that the same brain regions evolve in form; large divisions have not been added over the course of vertebrate evolution.

structures. The most widely used introductory textbook in psychology states that

in primitive animals, such as sharks, a not-so-complex brain primarily regulates basic survival functions. . . . In lower mammals, such as rodents, a more complex brain enables emotion and greater memory. . . . In advanced mammals, such as humans, a brain that processes more information enables increased foresight as well. . . . The brain's increasing complexity arises from new brain systems built on top of the old, much as the Earth's landscape covers the old with the new. Digging down, one discovers the fossil remnants of the past. (Myers & Dewall, 2018, p. 68)

To investigate the scope of the problem, we sampled 20 introductory psychology textbooks published between 2009 and 2017. Of the 14 that mention brain evolution, 86% contained at least one inaccuracy along the lines described above. Said differently, only 2 of the field's current introductory textbooks describe brain evolution in a way that represents the consensus shared among comparative neurobiologists. (See https://osf .io/r6jw4/ for details.)

Examples of this mistaken view are readily found throughout subareas in psychology. In social cognition, this distinction has been a foundation for dual-process models of automaticity, some of which contrast fast and uncontrollable processes with slower and controllable processes. For example, Dijksterhuis and Bargh (2001), discussing their model of a direct link between perception and behavior, write that

when new species develop, this is done by adding new brain parts to existing old ones. . . . The frog and fish, in other words, are still in us. The advantage that humans have is that we also possess new inhibiting or moderating systems. (p. 5)

This widely cited idea is that the behavior of many animals is inflexibly controlled by external stimuli because their brains consist of older structures capable only of reflexive responses, whereas humans and other "higher" animals possess newer systems that allow behavioral flexibility because of added functions such as control and inhibition (Dijksterhuis, Bargh, & Miedema, 2000).

Examples of MacLean's model of brain evolution appear in other areas, including models of personality (Epstein, 1994), attention (Mirsky & Duncan, 2002), psychopathology (Cory & Gardner, 2002), market economics (Cory, 2002), and morality (Narvaez, 2008). Nonacademic examples are too numerous to fully review. The idea of an older animalistic brain buried deep within our newer, more civilized outer layer is referenced widely. Carl Sagan's (1978) Pulitzer Prizewinning book, *The Dragons of Eden*, and Steven Johnson's (2005) *Mind Wide Open* were both popular books that drew heavily on this idea, and Sagan's book played a large role in bringing these ideas to nonacademic audiences.

What's Wrong?

The above examples illustrate several misunderstandings of nervous-system evolution. The first problem is that these ideas reflect a scala naturae view of evolution in which animals can be arranged linearly from "simple" to the most "complex" organisms (Fig. 1a). This view is unrealistic in that neural and anatomical complexity evolved repeatedly within many independent lineages (Oakley & Rivera, 2008). This view also implies that evolutionary history is a linear progression in which one organism became another and then another. It is not the case that animals such as rodents, with "less complex" brains, evolved into another species with slightly more complex brains (i.e., with structures added onto the rodent brain), and so on, until the appearance of humans, who have the most complex brains yet. This misunderstanding and the theoretical problems that follow have been discussed within comparative psychology since the 1960s (Hodos & Campbell, 1969; LeDoux, 2012).¹

Instead, the correct view of evolution is that animals radiated from common ancestors (Fig. 1c). Within these radiations, complex nervous systems and sophisticated cognitive abilities evolved independently many times. For example, cephalopod mollusks, such as octopus and cuttlefish, possess tremendously complex nervous systems and behavior (Mather & Kuba, 2013), and the same is true of some insects and other arthropods (Barron & Klein, 2016; Strausfeld, Hansen, Li, Gomez, & Ito, 1998). Even among nonmammalian vertebrates, brain complexity has increased independently several times, particularly among some sharks, teleost fishes, and birds (Striedter, 1998).

Along with this misunderstanding comes the incorrect belief that adding complex neural structures allows increased behavioral complexity—that structural complexity endows functional complexity. The idea that larger brains can be equated with increased behavioral complexity is highly debatable (Chittka & Niven, 2009). At the very least, nonhuman animals do not respond inflexibly to a given stimulus. All vertebrate behavior is generated by similar neural substrates that integrate information to produce behavior on the basis of evolved decision-making circuits (Berridge, 2003).

The final-and most important-problem with this mistaken view is the implication that anatomical evolution proceeds in the same fashion as geological strata, with new layers added over existing ones. Instead, much evolutionary change consists of transforming existing parts. Bats' wings are not new appendages; their forelimbs were transformed into wings through several intermediate steps. In the same way, the cortex is not an evolutionary novelty unique to humans, primates, or mammals; all vertebrates possess structures evolutionarily related to our cortex (Fig. 1d). In fact, the cortex may even predate vertebrates (Dugas-Ford, Rowell, & Ragsdale, 2012; Tomer, Denes, Tessmar-Raible, & Arendt, 2010). Researchers studying the evolution of vertebrate brains do debate which parts of the forebrain correspond to which others across vertebrates, but all operate from the premise that all vertebrates possess the same basic brain-and forebrain-regions.

Neurobiologists do not debate whether any cortical regions are evolutionarily newer in some mammals than others. To be clear, even the prefrontal cortex, a region associated with reason and action planning, is not a uniquely human structure. Although there is debate concerning the relative size of the prefrontal cortex in humans compared with nonhuman animals (Passingham & Smaers, 2014; Sherwood, Bauernfeind, Bianchi, Raghanti, & Hof, 2012; Teffer & Semendeferi, 2012), all mammals have a prefrontal cortex.

The notion of layers added to existing structures across evolutionary time as species became more complex is simply incorrect. The misconception stems from the work of Paul MacLean, who in the 1940s began to study the brain region he called the *limbic system* (MacLean, 1949). MacLean later proposed that humans possess a triune brain consisting of three large divisions that evolved sequentially: The oldest, the "reptilian complex," controls basic functions such as movement and breathing; next, the limbic system controls emotional responses; and finally, the cerebral cortex controls language and reasoning (MacLean, 1973). MacLean's ideas were already understood to be incorrect by the time he published his 1990 book (see Reiner, 1990, for a critique of MacLean, 1990). Nevertheless, despite the mismatch with current understandings of vertebrate neurobiology, MacLean's ideas remain popular in psychology. (A citation analysis shows that neuroscientists cite MacLean's empirical articles, whereas non-neuropsychologists cite MacLean's triune-brain articles. See https://osf.io/r6jw4/ for details.)

So What?

Does it matter if psychologists have an incorrect understanding of neural evolution? One answer to this question is simple: We are scientists. We are supposed to care about true states of the world even in the absence of practical consequences. If psychologists have an incorrect understanding of neural evolution, they should be motivated to correct the misconception even if this incorrect belief does not impact their research programs.

A more practical question concerns the benefits to psychological science if psychologists changed their mistaken views of neural evolution. Consider the consequence of believing that humans have unique neural structures that endow us with unique cognitive functions. This belief encourages researchers to provide species-specific explanations when it might be more appropriate to recognize cross-species connections. In other words, by anointing certain brain regions and functions as special, researchers treat them as special in their research (see Higgins, 2004).

To illustrate, consider the dual-process theories found throughout much of psychology. In an *Annual Review of Psychology* article, Evans (2008) summarizes that a "recurring theme in dual-process theories" (p. 259) across content areas is the proposal of "two architecturally (and evolutionarily) distinct cognitive systems" (p. 255), with System 1 preceding System 2 in evolutionary development. This division of psychological functions into evolutionarily older animalistic drives versus evolutionarily newer rational thought is exemplified by research on willpower, which has historically been dominated by a framing that contrasts "hot," immediate, and emotional choices with "cool," long-term, and rational choices. Should I eat the ice cream, which tastes good now, or the salad, which I know is better for me in the future? In the classic marshmallow studies, delaying gratification by waiting to eat the marshmallows is seen as a good result—indicating more willpower (Shoda, Mischel, & Peake, 1990). This framing is expected given that the starting point of this research was the Freudian psychodynamic position, which contrasted hot animalistic drives with cool rational processes.

Framing willpower as long-term planning versus animalistic desires leads to the questionable conclusion that delaying gratification is not something other animals are capable of if other animals lack the evolutionarily newer neural structures required for rational long-term planning. Although certain aspects of willpower may be unique to humans, this framing misses the connection between willpower in humans and decision-making in nonhuman animals. All animals make decisions between actions that involve trade-offs in opportunity costs. In this way, the question of willpower is not "Why do people act sometimes like hedonic animals and sometimes like rational humans?" but instead, "What are the general principles by which animals make decisions about opportunity costs?" (Gintis, 2007; Kurzban, Duckworth, Kable, & Myers, 2013; Monterosso & Luo, 2010).

In evolutionary biology and psychology, life-history theory describes broad principles concerning how all organisms make decisions about trade-offs that are consistent with reproductive success as the sole driver of evolutionary change (Daly & Wilson, 2005; Draper & Harpending, 1982). This approach asks how recurrent challenges adaptively shape decisions regarding opportunity trade-offs. For example, in reliable environments, waiting to eat a second marshmallow is likely to be beneficial. However, in environments in which rewards are uncertain, such as when experimenters are unreliable, eating the single marshmallow right away may be beneficial (Kidd, Palmeri, & Aslin, 2013). Thus, impulsivity can be understood as an adaptive response to the contingencies present in an unstable environment rather than a moral failure in which animalistic drives overwhelm human rationality.

Research motivated by this more accurate understanding of brain evolution has been integrative, bringing together research on willpower, inhibition, future discounting, and delay of gratification with evolutionary and developmental approaches (Fawcett, McNamara, & Houston, 2012; McGuire & Kable, 2013). It also has been generative, asking questions that would not make sense from a dual-process perspective on human willpower, such as whether the lack of inhibition that comes from exposure to adverse environments might be just one component of a set of cognitive adaptations designed to enable successful navigation of those environments (Frankenhuis & de Weerth, 2013).

Of course, asking about a specific species' cognitive or behavioral repertoire can yield important insights about both evolutionary history and the nature of a species' current phenotype (e.g., Tomasello, 2009; Tooby & Cosmides, 2005). After all, humans—like every animal—faced unique environmental challenges that shaped their evolutionary trajectory. But believing that humans possess unique neural structures tied to specific cognitive functions may send researchers down a path of research that is misguided and may inhibit connections with other fields.

Conclusion

Perhaps mistaken ideas about brain evolution persist because they fit with the human experience: We do sometimes feel overwhelmed with uncontrollable emotions and even use animalistic terms to describe these states. These ideas are also consistent with such traditional views of human nature as rationality battling emotion, the tripartite Platonic soul, Freudian psychodynamics, and religious approaches to humanity. They are also simple ideas that can be distilled to a single paragraph in an introductory textbook as a nod to biological roots of human behavior. Nevertheless, they lack any foundation in our understanding of neurobiology or evolution and should be abandoned by psychological scientists.

Recommended Reading

- Gawronski, B., & Cesario, J. (2013). Of mice and men: What animal research can tell us about context effects on automatic responses in humans. *Personality and Social Psychology Review*, 17, 187–215. A comprehensive review comparing nonhuman- and human-animal models of behavior and automatic responses.
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- Kaas, J. H. (2013). The evolution of brains from early mammals to humans. Wiley Interdisciplinary Reviews: Cognitive Science, 4, 33–45. A review of principles of basic mammalian brain evolution by a leader in the field.
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Transparency

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ORCID iD

Joseph Cesario 🝺 https://orcid.org/0000-0002-1892-4485

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Note

1. Hodos and Campbell's (1969) admonitions could still apply today: "No teleost fish ever was an ancestor of any amphibian, reptile, bird, or mammal. . . . Thus, to say that amphibians represent a higher degree of evolutionary development than teleost fish is practically without meaning since they have each followed independent courses of evolution" (pp. 339–341).

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