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Your Brain Is Not an Onion with a Tiny Reptile Inside

Joseph Cesario¹, David J. Johnson², and Heather L. Eisthen³

¹Department of Psychology, Michigan State University

²Department of Psychology, University of Maryland, College Park

³Department of Integrative Biology and BEACON Center for the Study of Evolution in Action,

Michigan State University

Abstract

A widespread misconception in much of psychology holds that (1) as vertebrate animals evolved, "newer" brain structures were added over existing "older" brain structures and (2) these newer, more complex structures endowed animals with newer and more complex psychological functions, behavioral flexibility, and language. This belief, though widely shared in our introductory 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

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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) lie 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 (1) newer components are literally layered outside of older components as new species emerge, and that (2) 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 *Figure 1A, 1B*). As Paul MacLean (1964, p. 96), 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."

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

Our experience suggests it may surprise many readers to learn that these ideas have long been discredited among those 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 structures. The most widely-used introductory textbook in psychology (Myers & Dewall, 2018, p. 68) states:

"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..."

To investigate the scope of the problem, we sampled 20 introductory psychology textbooks published between 2009 and 2017. Of the 14 that mention of brain evolution, 86% contained at least one inaccuracy along the lines described above. Said differently, only two of the field's current introductory textbooks describe brain evolution in a way that represents the consensus shared among comparative neurobiologists. (Details in *Supplemental Material*.)

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, p. 5), discussing their model of a direct link between perception and behavior, write:

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...

This widely-cited idea is that the behavior of many animals is inflexibly controlled by external stimuli because their brains consist of older structures only capable of reflexive

responses, whereas humans and other "higher" animals possess newer systems that allow behavioral flexibility due to 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 & Gardener, 2002), market economics (Cory, 2002), and morality (Narvaez, 2008). Non-academic examples are too numerous to fully review. The idea of an older animalistic brain buried deep without our newer, more civilized outer layer is referenced widely. Carl Sagan's (1978) Pulitzer prize-winning 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 non-academic 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 arriving at humans with 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

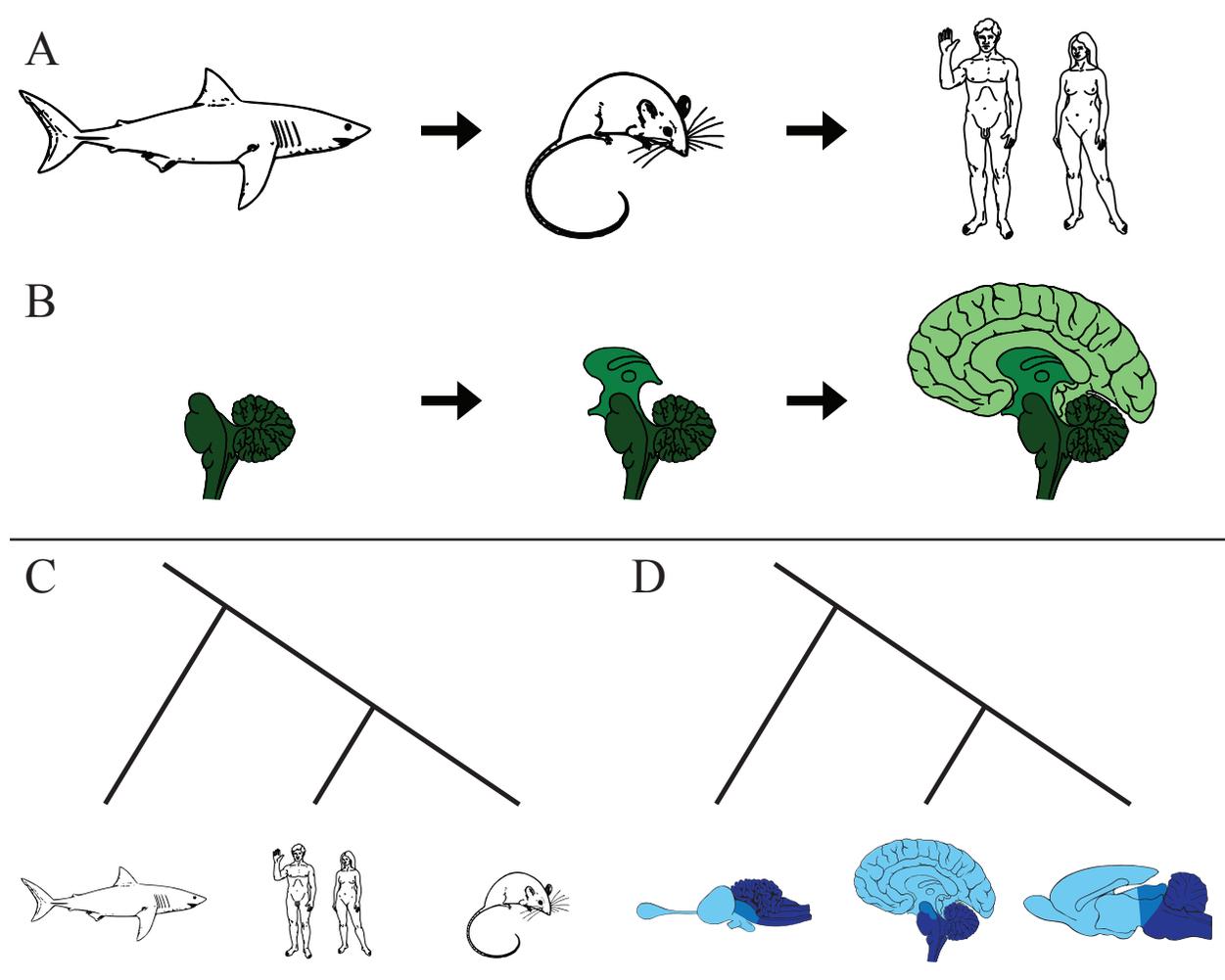


Figure 1.

Top Panel: An incorrect view of evolution (A) and the brain (B), illustrating 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 (A) is incorrect, the corresponding neural view (B) is still widely endorsed. **Bottom Panel:** A correct view of evolution (C) and organization of the brain (D). The evolutionary tree (C) illustrates that animals do not linearly

increase in complexity but radiate 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.

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, like 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 et al., 1998). Even among non-mammalian 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 allow 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 based on 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 pre-date vertebrates (Dugas-Ford et al., 2012; Tomer et al., 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. While there is debate concerning the relative size of the prefrontal cortex in humans compared to non-human 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 humans possess a “triune brain” consisting of three large divisions that evolved sequentially: The oldest “reptilian complex” controlling basic functions like movement and breathing; next the limbic system controlling emotional responses;

and finally the cerebral cortex controlling language and reasoning (MacLean, 1973). MacLean's ideas were already understood to be incorrect by the time he published his 1990 book (Reiner, 1990). Nevertheless, in spite of the mismatch with current understandings of vertebrate neurobiology, MacLean's ideas remain popular in psychology. (See *Supplemental Materials* for a citation analysis showing that neuroscientists cite MacLean's empirical papers whereas non-neuro psychologists cite MacLean's triune brain papers.)

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* chapter, 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 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. While certain aspects of willpower may be unique to humans, this framing misses the connection between “willpower” in humans and decision-making in non-human 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 where rewards are uncertain, as when experimenters are unreliable, eating the single marshmallow now 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 all animals—faced unique environmental challenges that shaped our 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 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 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.

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Author Contributions

JC and HLE conceived the manuscript. All authors contributed to writing/revising and approved the final version of the manuscript for submission.

Endnotes

1. Hodos and Campbell's 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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Recommended Readings

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.

Hodos, W., & Campbell, C. B. G. (1969). Scala naturae: Why there is no theory in comparative psychology. *Psychological Review, 76*, 337–350.

*A classic paper illustrating how beliefs about hierarchy across animal species inhibits scientific progress.

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 mammalian basic brain evolution by a leader in the field.

Krubitzer, L. A., & Seelke, A. M. (2012). Cortical evolution in mammals: the bane and beauty of phenotypic variability. *Proceedings of the National Academy of Sciences, 109*(Supplement 1), 10647-10654.

*A good discussion of within- and between-species variability in cortical evolution.

Reiner, A. (1990). An explanation of behavior: The Triune Brain in Evolution. *Science, 250*, 303–305.

*A clear and thoughtful criticism of MacLean's 1990 book on the Triune brain.

Supplemental Material #1
Introductory Psychology Textbook Survey

Note that we report on all textbooks we examined.

I. Description of brain evolution contains one or more errors:

1. Cervone, D., & Caldwell, T.L. (2015). *Psychology: The science of person, mind, and brain*. New York: Worth Publishers.

"The twentieth century's most renowned conceptual model of the brain, proposed by the neuroscientist Paul MacLean (1990), similarly identifies a three-part, bottom-to-top organization of brain structures. MacLean's model is known as the *triune brain*... MacLean contended that the three levels of brain emerged at different points in the evolution of Earth's species. The *reptilian brain*, the lowest of the three brain regions, is evolutionarily ancient. It has existed since the evolution of reptiles. The *paleomammalian* (ancient mammal) *brain*, the midlevel brain system, is newer, yet still quite old. It reached its full development with the evolution of mammals, more than 100 million years ago. The *neomammalian* (new mammal) *brain* is the newest and highest-level brain system. It reached its fullest development in our species, *Homo sapiens*... you possess not only the unique brain of a modern human, but also, tucked underneath, the brain of a nonhuman mammal and, beneath that, the brain of a reptile" (p. 87-88).

2. Charlton, S.R., Sobel, K., & Sobel, S. (2017). *Psychology: The science of who we are*. Southlake, TX: Fountainhead Press.

"Our brains are built from the ground up, with parts that promote basic survival inherited from our most primitive ancestors at the bottom, and more sophisticated, evolutionarily recent structures built on top" (p. 68).

3. Davis, S.F., & Palladino, J.J. (2010). *Psychology* (6th ed.). Upper Saddle River, NJ: Pearson/Prentice Hall.

"[ranking animals from frog, pigeon, cat, chimpanzee, to human]: the cortex in lower animals such as frogs or cats is smooth and not very thick. The more complex the brain, the rougher the cortex" (p. 71).

4. Feist, G.J., & Rosenberg, E.L. (2015). *Psychology: Perspectives and connections* (3rd ed.). New York: McGraw Hill.

"The three major regions of the brain, in order from earliest to develop to newest, are the hindbrain, the midbrain, and the forebrain... The oldest brain region is the hindbrain... The next brain region to evolve after the hindbrain was the smallest of the three major areas, the midbrain... The last major region to evolve was the largest part of the human brain, the forebrain" (p. 92-93).

5. Gazzaniga, M., Heatherton, T., & Halpern, D. (2016). *Psychological science* (5th ed.). New York: Norton.

"The limbic system serves as the border between the parts of the brain that evolved earliest (the hindbrain and the midbrain) and the part that evolved more recently (the cerebral cortex)" (p. 55).

6. Grison, S., Heatherton, T.F., & Gazzaniga, M.S. (2017). *Psychology in your life* (2nd ed.). New York: Norton.

"[The limbic system] serves as the border between the evolutionarily older parts of the brain (the brain stem and the cerebellum) and the evolutionarily newer part (the cerebral cortex)" (p. 94).

7. Huffman, K., & Sanderson, C.A. (2014). *Real world psychology*. Hoboken, NJ: Wiley.

"Fish and reptiles have smaller, less complex brains than do cats and dogs. The most complex brains belong to whales, dolphins, and higher primates, such as chimps, gorillas, and humans" (p. 53). [Authors' note: The accuracy of this claim is very dependent on how "complexity" is defined. If complexity is defined in terms of structure, as most of the other examples here, then it would be

classified as incorrect. However, as no definition is given in the text, one might classify this as a "grey area" example.]

8. King, L.A. (2014). *The science of psychology* (3rd ed.). New York: McGraw Hill.
 "...let's stop for a moment and examine how the brain evolved. The brains of the earliest vertebrates were smaller and simpler than those of later animals. Genetic changes during the evolutionary process were responsible for the development of more complex brains with additional parts and interconnections (Durrant & Ellis, 2013). [comparing rat, cat, chimpanzee, and human brains:] In both the chimpanzee's brain and (especially) the human's brain, the hindbrain and midbrain structures are covered by a forebrain structure called the *cerebral cortex*" (p. 80).
9. Licht, D.M., Hull, M.G., & Ballantyne, C. (2017). *Psychology* (2nd ed.). New York: Worth Publishers.
 "This [cerebral cortex] outermost section of the brain is also the part that is "newest," or most recently evolved compared to the "older" structures closer to its core. We know this because researchers have compared the brains of humans with those of other primates. The structures we share with our primate relatives are considered more primitive, or less evolved, than the structures that are unique to humans" (p. 77).
10. Marin, A.J., & Hock, R.R. (2016). *Psychology in a dynamic world*. Boston: Pearson.
 "In general, the structures of the brain are arranged in a hierarchical fashion. The analogy of a triple-dip ice cream cone is useful to illustrate how the human brain has evolved from the brains of simpler organisms (Linden, 2007). For example, the lizard brain is like a single scoop of vanilla, the cat brain has a second scoop of chocolate, and the human brain has a third scoop of strawberry on top. Over time, the human brain evolved primarily by adding on rather than reconfiguring; therefore, it still contains the scoop of original vanilla it shares with other creatures like birds and fish" (p. 62).
11. Myers, D.G., & Dewall, C.N. (2018). *Psychology* (12th ed.). New York, NY: Worth Publishers.
 "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..." (p. 68).
12. Schacter, D.L., Gilbert, D., & Wegner, D.M. (2011). *Psychology* (2nd ed.). New York: Worth Publishers.
 "The forebrain undergoes further evolutionary advances in vertebrates. In lower vertebrate species such as amphibians (frogs and newts), the forebrain consists only of small clusters of neurons at the end of the neural tube. In higher vertebrates, including reptiles, birds, and mammals, the forebrain is much larger, and it evolves in two different patterns. Reptiles and birds have almost no cerebral cortex. By contrast, mammals have a highly developed cerebral cortex... This forebrain development has reached its peak -- so far -- in humans... The human forebrain... allows for some remarkable, uniquely human abilities: self-awareness, sophisticated language use, social interaction, abstract reasoning, imagining, and empathy, among others" (p. 106-107).

II. Substantially correct description of brain evolution:

1. Cacioppo, J.T., & Freberg, L.A. (2016). *Discovering psychology: The science of the mind* (2nd ed.). Boston: Cengage Learning.
 "Hominins were not the only creatures who evolved large brains and considerable intelligence. The other primates, elephants, and whales are not lacking in these areas. Although the challenges

of finding food, avoiding predators, and navigating through territories require considerable intelligence, these ecological challenges are no match for the complexity of social life faced by the hominins. The major factor distinguishing human intelligence from intelligence of other species is the richness and complexity of the social behavior supported by the human brain. Managing the abilities to distinguish friend and foe; imitate the behavior of others; use language to communicate; recognize and anticipate the emotions, thoughts, and behavior of others; maintain relationships; and cooperate required the evolution of a special brain (Cacioppo, Berntson, et al., 2002; Hrdy, 2005; Roth & Dicke, 2005). Comparisons of the challenges faced by different species support a stronger role for social complexity than for ecological complexity in building bigger brains (Cacioppo & Decety, 2011a; Dunbar & Schultz, 2007)" (p. 91).

No mention of the midbrain or hindbrain being evolutionarily older, or of the forebrain being added over evolutionary time.

2. Lilienfeld, S.O., Lynn, S.J., Namy, L.L., & Woolf, N.J. (2009). *Psychology: From inquiry to understanding*. Boston: Pearson.

"In terms of evolutionary development of brain regions, the *neocortex* is a relatively recent addition. That's what we mean by a "new" (the prefix *neo-* means "new") brain area. Our neocortex accounts for the vast majority of our cerebral cortex. It's present in all mammals, yet absent in birds and reptiles. Compared with other mammals, evolution has enabled the human neocortex to attain a larger size in proportion to our bodies. We have more cortical areas and more connections than do other species" (p. 110).

No mention of the midbrain or hindbrain being evolutionarily older, or of the forebrain being added over evolutionary time.

III. No description of brain evolution:

1. Breedlove, S.M. (2015). *Principles of psychology*. Oxford: Oxford University Press.
2. Comer, R., & Gould, E. (2010). *Psychology around us* (2nd ed.). Hoboken, NJ: John Wiley & Sons.
3. Gleitman, H., Gross, J., & Reisberg, D. (2011). *Psychology* (8th ed.). New York: Norton.
4. Kalat, J.W. (2017). *Introduction to psychology* (11th ed.). Boston: Cengage Learning.
5. Krause, M., & Corts, D. (2016). *Psychological science: Modeling scientific literacy* (2nd ed.). Boston: Pearson.
6. Weiten, W. (2017). *Psychology: Themes and variations* (10th ed.). Boston: Cengage Learning.

*Supplemental Material #2***Citations of MacLean Across Psychology & Neuroscience**

To illustrate the difference between psychologists and neurobiologists in the popularity and utility of MacLean's ideas, we used Thompson Reuters' *Web of Science* to examine all journal articles published over the decade spanning 2006 – 2015 that cite MacLean's work. We find great differences in the citations of MacLean's theoretical papers, in which he put forth the ideas that constitute the triune brain hypothesis, and his empirical papers, which largely focus on neuroanatomical studies and electrophysiological investigations of brain areas in animals involved in species-typical behavior, such as communication and parenting behavior. Specifically, we tested whether his theoretical papers are more likely to be cited in psychology journals and whether his empirical papers are more likely to be cited in neurobiology journals.¹

Among the 98 journal articles in the last decade that cited MacLean's theoretical papers, 34 papers (35%) are in psychology journals. Among the 140 articles citing his empirical papers, 26 papers (19%) are psychology journals. This difference in the type of papers cited in psychology journals is statistically significant (Fisher's exact test, two-tailed, $p < 0.004$), demonstrating that psychologists cite MacLean's theoretical papers at a higher rate than they do his empirical papers.

Among the 98 citing MacLean's review papers, 35 papers (36%) are in neurobiology journals. Among the 140 articles citing his empirical papers, 88 papers (63%) are neurobiology journals. Again, this difference is statistically significant (Fisher's exact test, two-tailed, $p < 0.001$). Thus, we conclude that neurobiologists do not shun MacLean's work completely and find much of it to still be of value; they simply find his empirical work to be of much greater value than his speculations about brain evolution.

¹ Psychology journals were defined as those with titles containing the particle "psycho" (to exclude psychiatry journals), as well as "biobehavioral," "biosocial," "bioscience," "behavioral science," "emotion," "parenting," "human development," "family therapy," or "relationship therapy." Neurobiology journals were defined as those with titles containing the particle "neur," as well as "brain," "cortex," "CNS," "epilepsy," "radiology," or "magnetic resonance."