Developing Broad Brains: The importance of an early introduction to evolutionary thinking in undergraduate neuroscience programs

Megan D. Gall[1,2*&] and Justin Touchon[1,2&]

[1] Biology Department, Vassar College, 124 Raymond Ave., Poughkeepsie, NY 12604, USA

[2] Program in Neuroscience and Behavior, Vassar College, 124 Raymond Ave., Poughkeepsie, NY 12604, USA

[&] Authors made equal contributions

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Megan Gall OrcID: 0000-0003-0032-8164

Justin Touchon OrcID: 0000-0002-1643-348X

*Corresponding author

Email: megall@vassar.edu

Phone: 845-437-7115

Abstract

There have been a number of calls for neuroscience to embrace a wider range of model systems. Authors of these opinion pieces have emphasized the inherent value of explicitly evolutionary and comparative work in neuroscience and the value of diversity in applied and biomedical research. However, few of these papers address the role of undergraduate neuroscience education in preparing students to pursue, much less value, evolutionary and comparative neuroscience. Here, we argue that the field of neuroscience would benefit from the explicit inclusion of evolutionary and comparative neuroscience in introductory courses. We first review the state of introductory neuroscience curricula and available teaching materials, before discussing the importance of an early introduction to evolutionary and comparative ideas, challenges to incorporating these ideas into introductory courses, and finally offer a number of strategies to increase student awareness of the diversity of systems available for neuroscience research. We speculate that introducing students to evolutionary and comparative neuroscience early in their education may increase retention of students with an evolutionary or comparative bent, which may increase the number of researchers interested in pursuing these questions in their careers, while also making students bound for health, biomedical research, or engineering professions more aware of the value of evolutionary and comparative approaches.

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43 ## Introduction

44 Throughout his career, Peter Narins has been a champion of integrative and comparative biology.
45 His work has ranged from molecules to behavioral ecology, spanned taxa, and revealed
46 fascinating exceptions to our mammal-centric understanding of hearing. Many of the other
47 articles in this special issue are likely to reflect on his accomplished career as a scholar.
48 However, he was also an important force in the development of young scientists. Whether
49 working to provide a summer science institute for high school teachers or winning teaching
50 awards for his field biology course that exposed students to the joys and challenges of field-
51 based animal research, he excelled at preparing a future generation of scientists. One student said
52 of their experience in the field biology course "One thing you can be sure of, was that Dr. Narins
53 was right alongside us, on hands and knees, in hopes of taping the oh-so-elusive calls of the male
54 coqui. When we became discouraged, whether it [was] due to a bad night in the field or
55 malfunctioning equipment, Dr. Narins was always there with a word of encouragement"
56 (https://alumni.ucla.edu/awards/peter-m-narins/). These formative experiences in the
57 "classroom" do more than just prepare students for careers — they open their eyes to the
58 diversity of research questions waiting to be answered.

59 Despite the enormous growth in the field of neuroscience over the last two decades, there has
60 been comparatively little growth in funding and publication of comparative neuroscience work
61 (Zupanc and Rössler 2022). A number of recent review and perspective pieces have highlighted
62 the importance of comparative research in neuroscience or the framing of neuroscience questions
63 in an evolutionary framework (Manger et al. 2008; Carlson 2012; Hale 2014, 2019; Wagner et al.
64 2024). Some highlight Krogh's principle that for every question there is an interesting organism
65 best suited for study (Beetz 2024) or that animals are worthy of investigation because they are
66 interesting in their own right (Yartsev 2017). Others have emphasized the importance of studying
67 neuroscience problems in multiple species as common mechanisms may better elucidate the
68 function of human systems (Carlson 2012; Laurent 2020; Banerjee et al. 2026). Still others
69 suggest that "bio-inspired" design and technological advances (Díaz-García et al. 2023; Zhao et
70 al. 2024; Boufidis et al. 2025) may benefit from evolutionary thinking (Miikkulainen 2025).
71 Clearly, there are many valuable reasons to look outside the common *C. elegans*, *Drosophila,*
72 zebrafish and rodent models of neural function.

73 These perspective pieces have primarily focused on the level of the established P.I., post-doc, or
74 graduate student, while the importance of the undergraduate curriculum has largely been ignored.
75 It has been our experience that many neuroscience undergraduates are unaware of the diverse
76 systems available for study, much less the potential benefits of studying such diversity (Hale
77 2019). It has also been our experience that exposure to a broad range of study systems — both
78 less traditional model organisms and truly non-model ones — opens doors to students who might
79 have been otherwise turned away by neuroscience as a field. To the best of our knowledge, there
80 are not available data to support a causal link between introductory course content and

81 persistence in a particular major; however, we have had a number of our own students tell us that
82 they continued with a Neuroscience and Behavior major due to the comparative content they
83 were introduced to early in their college careers. For other students, those destined to be
84 physicians or clinical researchers for example, exposure to diverse organisms makes them more
85 aware of the limitations of work restricted to single model systems, the medical advances that
86 have only been made possible by studying a diverse range of species, and hopefully an
87 appreciation for the value of comparative and evolutionary neuroscience.

88 Therefore, in this perspective piece, we highlight the importance of early exposure to
89 comparative and evolutionary neuroscience for undergraduate students. We focus first on the
90 current state of the neuroscience curricula for undergraduates, before turning our attention to the
91 value of an early exposure for undergraduates that will be pursuing diverse career goals. Finally,
92 we address the challenges in adopting this approach and offer suggestions for ways to
93 incorporate these ideas into undergraduate curricula.

94 The State of Undergraduate Neuroscience Curricula

95 We first asked two questions. (1) Are comparative and evolutionary ideas represented in the
96 curricula for undergraduate neuroscience majors? (2) If comparative and evolutionary ideas are
97 represented, do students encounter them early in the major, or are they only introduced in upper
98 division courses or elective courses? Our goal here was to do a "temperature check" of
99 undergraduate programs, rather than perform an exhaustive review of the place of evolution in
100 all undergraduate programs, which might be more appropriate for the primary literature.
101 Therefore, to address these questions we took three approaches. First, we reviewed the
102 undergraduate neuroscience program websites and course catalog descriptions for 42 of the top-
103 ranked US-based colleges and universities in US News and World Report (23 nationally-ranked
104 research universities and 19 nationally-ranked liberal arts colleges, see supplemental material) to
105 determine whether their messaging about the field of neuroscience was consistent with our
106 experience that evolution is underrepresented. We reviewed the descriptions of the department,
107 program, or major on both the official websites and the course catalog, looking for explicit
108 mentions of following words associated with comparative biology or evolution: comparative,
109 evolution, taxa, species, ecology, neuroethology, and environment. The full text of the
110 descriptions from websites and course catalog can be found in the electronic supplementary
111 material (ESM). Second, we reviewed the course catalog descriptions, and syllabi when
112 available, for introductory neuroscience courses at each of those colleges and universities to
113 determine the extent to which students are introduced to comparative and evolutionary
114 approaches early in their academic careers. Note that we only considered specific introductory
115 neuroscience or behavioral neuroscience courses, even though many undergraduate neuroscience
116 majors require students to take several introductory biology or psychology courses, which may
117 expose students to some evolutionary thinking. We also reviewed online course catalogs and
118 program descriptions to determine if comparative or evolutionary perspectives were present in

119 upper-division or elective course descriptions. Finally, we reviewed 16 currently available (i.e.
120 "in print") textbooks for introductory neuroscience or behavioral neuroscience courses and
121 assessed the relative amount of each book dedicated to evolutionary or comparative neuroscience
122 topics, as well as the degree to which topics were framed in a comparative or evolutionary lens.
123 To select our texts we took three approaches. First, we informally polled our faculty peers to
124 determine which books they were using in their courses. Second, we visited the websites of each
125 of the major textbook publishers and reviewed all of the available texts for neuroscience or
126 neurobiology, selecting those that appeared appropriate for an introductory course. Third, we
127 searched for open access books in OER Commons, Open Stax, and via Google using the
128 keywords neuroscience, neurobiology, physiological psychology, and behavior. We attempted to
129 include texts that covered a range of publishing models, as well as the duration of time in use
130 (see Table 1). While not an exhaustive list, we believe this covers the majority of texts that are
131 currently available for an introductory course and provides an overview of the predominant
132 perspectives taught in introductory neuroscience curricula.

133 **Neuroscience program and introductory course descriptions**

134 We found that, overall, comparative and evolutionary ideas were rarely explicitly articulated in
135 publicly available materials in which neuroscience programs described themselves. Six of the 42
136 institutions included at least one word associated with comparative or evolutionary approaches in
137 their descriptions of the programs. A seventh program did include a mention of evolution, but
138 only in the context of humans. Of the six programs that mentioned evolution or comparative
139 biology, most introduced these ideas either at the senior level or in elective courses that would
140 reach only a subset of majors. This is in contrast to cellular and molecular mechanisms,
141 development, and human cognition, which were ideas present in the majority of program
142 descriptions (see electronic supplementary material).

143 Syllabi were only publicly available for four introductory courses, and so we instead focused on
144 course descriptions from online course catalogues or program websites. These descriptions
145 reflect the public messaging about the content of the courses, but may lack in the nuance that can
146 be found in a syllabus. Therefore, it is possible that some of the courses here do include
147 comparative or evolutionary material, even if it is not formally described in the course
148 description. Only two introductory course descriptions ("Neurobiology and Behavior I:
149 Introduction to Behavior" at Cornell University and "Introduction to Neuroscience" at College of
150 the Holy Cross) explicitly included evolutionary or comparative ideas. The introductory course
151 at a third program (University of Chicago's "Foundations of Neuroscience" course) included a
152 partial focus on the "development and evolution of the nervous system". Most introductory
153 course descriptions at liberal arts colleges did not mention evolutionary concepts, although our
154 own institution's introductory course does mention "comparative systems in neuroscience and
155 behavior". Comparative ideas were more prevalent in upper division elective courses. Given that
156 many programs offer neuroscience courses that originate in either a Biology or Psychology

157 department, we looked for courses that had a specific focus in neuroscience, as opposed to
158 merely a course in animal behavior, for example. Of the 42 programs we examined, we found
159 that nine offered advanced elective courses in Neuroethology or a similar topic under a different
160 name (see ESM). Another eight programs have elective courses listed that were more specifically
161 focused on nervous system or brain evolution (e.g., the University of Chicago's "Evolution and
162 the Nervous System", Columbia University's "Brain Evolution"or Bowdoin College's "Brain,
163 Behavior, and Evolution"), although some of these indicated that the evolutionary breadth was
164 limited to just mammals. These courses were somewhat more prevalent at research universities,
165 with 11 of the 17 courses occurring at large research universities and six at liberal arts colleges
166 (see ESM).

167 **Neuroscience textbooks**

168 Textbooks are often an important consideration when designing a course. While not all
169 instructors design their course around a single textbook, it is not uncommon for introductory
170 courses to assign a text that accompanies lectures and assignments. These textbooks, therefore,
171 are a key component in advertising to students the conceptual boundaries or core components of
172 the field.

173 We found that, overall, evolutionary and comparative ideas were minimally represented in
174 introductory texts. Only four of the sixteen texts included chapters that were explicitly
175 comparative in nature (Breedlove and Watson 2023, Kirby et al. 2024, Martin et al. 2020,
176 Striedter 2015), with an additional text having a partial chapter with a comparative focus (Gaskin
177 2019). Four of these texts are from a traditional publisher (Oxford University Press; Breedlove
178 and Watson 2023, et al. 2020, Striedter 2015 and Sage College Press; Gaskin 2019) and one is an
179 open-access text available through Open Stax (Kirby et al, 2024). These chapters represent a
180 relatively minor proportion of the total content (from ~0.2 to 10%), with the majority of content
181 focused on structure, mechanisms, and development, particularly of vertebrate central nervous
182 systems. Additionally, these chapters often come towards the end of the book as "add-on"
183 chapters, rather than foregrounding comparative and evolutionary concepts early in the text.

184 Table 1. Comparative Coverage in Introductory Neuroscience Textbooks

Textbook (edition)	Authors / Editors	Year	Publisher	Publishing Model	Total chapters	Dedicated "comparative" chapters	Approximate share
Neurobiology: A Functional Approach (1st)	Striedter, G.F.	2015	Oxford University Press	Traditional	16	2	10%
Introduction to Behavioral Neuroscience (1st)	Kirby, E.D., Glenn, M.J., Sandstrom, N.J., and Williams, C.L.	2024	Open Stax	Open Access	19	1	10%
Behavioral Neuroscience (10th)	Breedlove, S.M. and Watson, N.V.	2023	Oxford University Press	Traditional	19	2	5%
From Neuron to Brain (6th)	Martin, A.R., Brown, D.A., Diamond, M.E., Cattaneo, A., and De-Miguel, F.F.	2020	Oxford University Press	Traditional	30	1	3%
Behavioral Neuroscience: Essentials and Beyond (1st)	Gaskin, S.	2019	Sage College Publishing	Traditional	15	0.2	1%
Discovering Behavioral Neuroscience (4th)	Freberg, L.A.	2019	Cengage	Traditional	16	0[1]	1%
Behavioral Neuroscience (1st)	Spilich, G.	2023	Wiley	Traditional	17	0[1]	1%
Neuroscience (7th)	Augustine, G.J., Groh, J.M., Huettel, S.A., LaMantia, A-S., White, L.E., and Purves, D.	2023	Oxford University Press	Traditional	34	0	0%
Neuroscience: Exploring the Brain (5th)	Bear, M., Connors, B., and Paradiso, M.A.	2025	Jones & Bartlett Learning	Traditional	25	0	0%

Principles of Neural Science (6th)*	Kandel, E.R., Koester, J.D., Mack, S.H. and Siegelbaum, S.A.	2021	McGraw Hill	Traditional	64	0	0%
Foundations of Neuroscience	Henley, C.	2021	Michigan State University Libraries	Open Access	40	0	0%
The Open Neuroscience Initiative	Lim, A.	2021	College of Science and Health Full Text Publications	Open Access	16	0	0%
Neuroscience Online*	Department of Neurobiology and Anatomy	2025	McGovern Medical School at UTHealth	Open Access	45	0	0%
Foundations of Behavioral Neuroscience (10th)	Carlson, N.R. and Birkett, M.A.	2022	Pearson	Traditional	17	0	0%
Brain and Behavior: An Introduction to Behavioral Neuroscience (7th)	Garrett, B. and Hough, G.	2025	Sage College Publishing	Traditional	15	0	0%
Introduction to Neuroscience	Hedges, V.	2022	Michigan State University Libraries	Open Access	68	0	0%

*indicates advanced level texts that are sometimes used for introductory courses

[1]chapter on human nervous system evolution

186 Only two books (Kirby et al. 2024, Striedter 2015; Table 1) explicitly state in their prefaces that
187 species diversity and/or evolution are core lenses through which nervous systems should be
188 viewed. However, even these two books foreground human, or at least mammalian, brains and
189 their organization in the early chapters, with more explicit comparative or evolutionary topics
190 primarily found in later chapters. Two additional books included chapters with human
191 evolutionary content, but had very little focus on non-mammalian species (Freeberg 2019,
192 Spilich 2023; Table 1).

193 Two excellent books do exist that compile examples from across a broad array of animals ["The
194 Neuroethology of Predation and Escape" by Sillar et al. (2016) and "Behavioral Neurobiology"
195 by Zupanc (2010)], but as these books are geared towards upper-level undergraduates and
196 graduate students, we did not consider them in our review of introductory textbooks. We do
197 however discuss them below.

198 Our survey of neuroscience and behavior programs, their introductory curricula, and the
199 textbooks used in those courses suggests that evolutionary and comparative concepts are fairly
200 underrepresented in the ways that introductory neuroscience is presented to students, and
201 possibly in the course content itself. We feel it is fair to say that evolutionary and comparative
202 perspectives are certainly not a core lens through which neuroscience is viewed, and taught, in
203 many programs. Indeed, it seems that most undergraduate neuroscience curricula outsource
204 teaching evolutionary concepts to biology departments and the introductory courses of those
205 programs.

206 Why introduce evolutionary and comparative frameworks in Introductory 207 Neuroscience?

208 Introductory courses are both tricky and vitally important. These are the courses in which
209 students get their earliest exposure to the concepts and practices in the field, and their breadth
210 means that they define for students the boundaries of a given field (Basu et al. 2017, 2021). At
211 perhaps their most basic level, introductory courses let students know the variety of subfields
212 they may encounter with further study, and therefore they help students know the possibilities
213 that lay ahead of them and if those possibilities seem interesting enough to pursue for a degree.
214 Although hard data seem to be lacking, most educators have anecdotal accounts of students
215 whose career and life choices were profoundly impacted by material they encountered in an
216 introductory class. The material that students are exposed to in introductory courses can thus
217 influence their perceptions of the discipline and shape their trajectories. It may be obvious, but
218 students that are not exposed to concepts in their coursework are unlikely to know those concepts
219 exist at all.

220 While there is surprisingly little recent work on the impact of introductory courses on major
221 selection, there is a large body of work focused on feelings of belonging in STEM fields (e.g.,

Kessel and Nelson 2011; Rainey et al. 2018). Introductory STEM courses can have a disproportionately negative effect on historically underserved or excluded groups (Hatfield et al. 2022) and research suggests that student experiences in introductory STEM courses have profound implications for student outcomes. For example, students that feel a greater sense of belonging in STEM courses are more likely to pursue a major in a STEM field (Rainey et al. 2018). By extension, the content students encounter in introductory courses may impact whether students feel that this is a field to which they would like to belong.

One way that instructors can increase the number of students that feel they "belong" in introductory neuroscience courses is to increase the breadth of material that is taught. Introductory courses that focus almost exclusively on human or rodent systems are likely to drive away students with an inclination for comparative studies. However, by judiciously choosing examples from across the animal kingdom that have led to drug discoveries or clinically-relevant mechanisms, students that are destined to be clinicians or physicians or researchers working with traditional neuroscience model organisms may gain an appreciation of the importance of these diverse systems for medical fields (examples are provided in a subsequent section, Figs 1-4), or perhaps even for their inherent value.

Indeed, we see several primary benefits to exposing students to evolutionary and comparative neuroscience concepts early on. First, by setting up more students with at least a basic understanding of the evolution of the nervous system, we are likely to improve the quality of questions asked by future neuroscience researchers. It is important for researchers to understand not just the advantages of traditional model systems, which are admittedly many, but also their limitations. Secondly, exposure to taxonomic and evolutionary breadth will improve the ability of all students to think critically and comparatively, something equally important for researchers as for the many students that choose not to pursue neuroscience as a career. Additionally, many neuroscience curricula are heavily "fact-based". A conceptual framework grounded in evolution provides a scaffold on which to hang the details of the nervous system, which can improve student learning outcomes. Adding evolutionary context can help neuroscience and pre-health students — who are often focused on the fine details — develop broadly integrative thinking. In other words, understanding the evolutionary context in which neurons or nervous systems evolved can help neuroscience students see the forest, in addition to the trees.

What are the obstacles to including these ideas in an introductory curriculum?

For educators that might be interested in adding more breadth to their introductory curriculum, there can be considerable obstacles to overcome. Perhaps one of the greatest of these obstacles is the lack of textbook options to teach from (see Table 1). Having a useful and authoritative reference text is an incredibly valuable resource for an introductory course. Unfortunately, few of the widely available textbooks we reviewed contain chapters on or discussion of the diversity

259 of nervous systems across animals, nor do they pay service to the tremendous amount that we
260 have learned from animals such as *Aplysia* sea slugs, *Loligo* squids, or *Drosophila*, much less the
261 far less well known but equally amazing mountain chickadees (*Poecile gambeli*), crayfish
262 (*Procambarus clarkii*), cuttlefish (*Sepia officinalis*) and others. These species, when discussed,
263 typically serve as stand-ins for humans. None of the available textbooks use an evolutionary lens
264 as the primary way to understand the structural and functional diversity of nervous systems.
265 Textbooks routinely refer to "the brain" or "the eye", generally referring to the human or perhaps
266 a generic mammalian nervous system, completely ignoring that animals possess a tremendous
267 array of "brains" and "eyes." Some programs we reviewed, such as Grinnell College, have
268 endeavored to create their own textbook, borrowing from the open access texts we reviewed
269 above, but these still lack a sense of evolutionary breadth.

270 Equally challenging is the fact that most neuroscience faculty employed at colleges and
271 universities were themselves trained in, and continue to conduct research using, traditional model
272 systems such as mice or rats. It is perfectly sensible that faculty teach what they know best, and
273 so professors taught from a traditional neuroscience curriculum are likely to recapitulate that
274 educational structure themselves. The flipside of the abundance of traditionally-trained faculty is
275 that the faculty members that conduct neuroscience research with non-traditional animals are
276 likely vastly outnumbered (Zupanc and Rössler 2022). This is reflected in the curricular
277 recommendations from the Faculty for Undergraduate Neuroscience (FUN), which places a
278 heavy focus on psychology and cellular/molecular content, with evolution suggested as a
279 potential elective course at the intermediate level (Wiertelak et al. 2018). More recently,
280 evolution was adopted as a core concept in neuroscience (Chen et al. 2023); however, it was
281 ranked as least important among the core concepts by faculty and was one of the concepts most
282 commonly suggested for elimination from neuroscience core concepts. This general lack of
283 interest in evolutionary and comparative ideas is further reflected in the attendance of researchers
284 at professional conferences. A total of 2,636 abstracts were submitted to six meetings of the
285 International Congress on Neuroethology that were held between 2010 and 2022 (Beetz 2024).
286 In contrast to this, at the 2025 annual meeting of the Society for Neuroscience alone, the number
287 of "late-breaking" abstracts was *capped* at 2,500 abstracts.

288 A related (and perhaps obvious) point to the lack of textbook resources and faculty to teach
289 broad neuroscience is that the preponderance of neuroscience research has been conducted with
290 traditional model organisms, and so the vast majority of the recent knowledge and examples
291 available to teach do indeed come from mice, non-human primates, *Drosophila*, zebrafish, and
292 *C. elegans* (Laurent 2020). Thus, even for faculty who are interested in developing a curriculum
293 that incorporates evolutionary breadth in neuroscience, there is simply less knowledge to draw
294 from, as compared to the detailed minutiae we know of the rodent and human nervous systems.

295 Lastly, although increasing the breadth of examples taught at the introductory level should have
296 the effect of retaining a broader diversity of students interested in neuroscience, some instructors

297 may have concerns that it could also alienate some students that are singularly focused on
298 understanding human neuroscience. Indeed, many institutions feel constrained in their course
299 offerings due to economic realities driven by enrollment patterns. Many students enter college
300 knowing they want to go to medical school or to graduate school to study a particular
301 mammalian model. Instructors or department and program chairs may worry that these students
302 will be turned off by learning about cnidarians or cone snails or electric eels. We are fortunate, at
303 our institution, to have significant flexibility in our course content. Many of our pre-medical
304 students take our comparative animal physiology or animal structure and diversity courses,
305 which have limited human content. These students have excellent success on the MCAT and the
306 institution has high medical school acceptance rates. However, we do not have programs in
307 nursing or other health professions that require more explicit human content at the undergraduate
308 level. We recognize that not all instructors or institutions will be able to spend large amounts of
309 time in introductory courses on comparative or evolutionary ideas. Instructors with concerns
310 about losing this pre-health population might consider a judicious selection of comparative
311 examples that highlight *medically-relevant* contributions from a broad array of species (Figs. 1-
312 4), which would be a valuable step in exposing students to a wider range of taxa. For instructors
313 with more flexibility, they may consider implementing more explicit evolutionary material.

314 What should we do?

315 There are many things that we can do to make the introductory curriculum reflect the diversity of
316 nervous system form and function in animals. Some of our suggestions are relatively modest
317 changes that are fairly easy to implement, while others might cost political capital or require
318 significant time investments. Here we begin with the easy and build to the challenging, pointing
319 to resources where they exist. We recognize that not all instructors will have the ability to
320 implement all of these changes, so we suggest incorporating ideas as time and institutional
321 flexibility allows.

322 The first recommendation is to use, or encourage your colleagues to use, language that suggests
323 to students that substantial structural, functional, phylogenetic, and mechanistic diversity exists
324 in animal nervous systems. As we noted above, many textbooks present content in a way that
325 suggests an archetype, rather than acknowledging diversity. While fully rectifying this issue
326 requires a significant time investment, altering the language you use in your classroom is
327 relatively straightforward and should not come at the exclusion of other material. The simplest
328 change we recommend, therefore, is to avoid using phrases such as “the brain” or “the eye”,
329 which suggest that there is a canonical brain or a canonical eye. Often, the brains or eyes in
330 question are human brains, or in some cases the brains of rodent models, which falsely implies to
331 students that neuroscience is solely focused on, or is at least limited to, mammalian systems.
332 Instead, we suggest adopting language that acknowledges the multiplicity of nervous, sensory,
333 and motor systems: i.e., “brains” and “eyes” and “muscles”.

Certainly, pluralizing canonicalized language is not sufficient, although it is an important first step and is quite easy to implement. Our second recommendation would be to include a very small amount of life history information about model organisms when they are presented in textbooks or in a course and once again, we feel that this would not be so onerous as to necessitate the removal of existing material. For instance, when introducing the work of Hodgkin, Huxley, and Katz many instructors talk about "***the*** squid giant axon". Here is a great chance to note that individuals of species in the genus *Loligo* move through their environments via jet propulsion by contracting their mantles (Young 1938; Ward and Wainwright 1972; Keynes 2005). These squids are preferred prey items of a number of visually-oriented predators, including seals, toothed whales, and large fish. When a squid encounters a predator, it must respond rapidly. Information transferred through the giant axon leads to rapid contraction of the mantle causing water to shoot out of the siphon, rapidly propelling the squid backwards and away from danger (Otis and Gilly 1990; Llinás 1999). Simultaneously the squid releases ink which obscures the vision of the predator. This is a very real life-or-death situation and responses must be fast. Larger neurons conduct information more quickly and the giant axons of squids are among the largest known axons, similar in size to mechanical pencil lead (action potentials in squids of this genus travel at approximately 10–20 m/s). These squids were chosen for electrophysiological investigation due to the relative simplicity of studying potentials in such a large axon. However, the large axon is, itself, a product of evolutionary processes: selective pressure for rapid escape behavior in the face of predation. Similar context can be given to the study of memory in individuals of the genus *Aplysia*, foraging and color vision in human and non-human primates; nocturnality, somatosensation and cortical representation in mice, or chemoreception in *Drosophila* seeking suitable substrates for egg-laying.

Our third recommendation is to emphasize diversity and use non-mammalian examples of neuroscience principles. Krogh's principle states that for every research question there is an organism best suited for interrogation, and this is certainly true in neuroscience. While the majority of detailed neuroscience data do come from rodent models, there are many times when a non-model organism not only provides as good an example as a model species, but perhaps a better one. Two excellent sources of primarily non-model organism neuroscience examples can be found in "The Neuroethology of Predation and Escape" by Sillar et al. (2016) and "Behavioral Neurobiology" by Zupanc (2010). While these books are geared towards upper-level undergraduates and graduate students, examples can easily be worked into an introductory context. We also recommend Striedter (2023), which offers a number of excellent suggestions for incorporating evolution into neuroscience teaching. "Neurobiology: A Functional Approach" by Striedter (2019) and "Introduction to Behavioral Neuroscience" by Kirby et al. (2024) seem to be the best options for introductory texts (Table 1). We offer four examples of how comparative ideas can be incorporated into material traditionally found in introductory courses in the following section.

Our fourth recommendation is to emphasize that behavior, sensory reception, and motor output existed before neurons (and long before brains)! Sensory, nervous, and motor systems evolved in response to selective pressures. For instance, bacteria are capable of chemotaxis, a “low-level” behavioral response (Wadhams and Armitage 2004), with chemoreception leading to a motor response in flagella. Not only do they lack a nervous system, they lack membrane bound organelles! Paramecia have been described as “swimming neurons” (Brette 2021). These single-celled organisms, by definition, lack a nervous system. However, they are capable of sensation, information transfer, and motion. Paramecia respond to glutamate, an indicator of potential food, can produce calcium-based action potentials, and are an inexpensive model system for inquiry-based laboratories and investigation of taxis behaviors. Moreover, many of the molecular signatures of neurons have homologs in single-celled organisms like choanoflagellates (Colgren and Burkhardt 2022). Long before brains existed, ctenophores and cnidarians (Bosch et al. 2017) evolved nerve nets and sensory organs for detecting light and gravity, likely modifications of the earlier systems evolved in single-celled organisms (Moroz 2015). These systems were then further organized, centralized, and eventually cephalized in bilaterians (Martín-Durán and Hejnol 2021; Sachkova 2024), allowing for increasingly complex behavior.

Our fifth recommendation is to get involved in teaching, or structuring the curriculum for, the introductory neuroscience and behavior program at your institution. Readers of this paper are likely already interested in comparative and evolutionary representation in neuroscience. If your primary teaching responsibilities are in upper-undergraduate or graduate level courses, consider a guest lecture in introductory neuroscience. Motivated current and future faculty have opportunities to drive the curricula at their institutions and can advocate for the inclusion of comparative and evolutionary ideas. This may be a relatively large lift, but we believe it can have an important impact in preparing future neuroscientists. We have developed teaching materials (lectures and short-format labs) that are available upon request from the authors.

Our final recommendation is perhaps the most challenging to implement. We have identified the lack of a cohesive text for teaching undergraduate neuroscience through an evolutionary or comparative lens as a significant barrier to implementing this approach in the introductory curriculum. Therefore, we suggest that motivated readers consider collaborating on introductory textbooks that consider the mechanism, development, and structure/function of nervous systems in a comparative or evolutionary context. There are a number of things to consider here. For instance, there may not be a strong market for an introductory text with an evolutionary or comparative framing, given the current state of neuroscience education, and as such a traditional publishing model may not be feasible. Open access texts can reach a large population, but the monetary return for authors is minimal. Moreover, authors will need to consider how their institutions value textbook authorship in promotion, tenure, and merit review. However, we believe this is a critical and necessary step towards centering evolutionary and comparative ideas in introductory neuroscience courses.

410 ## Examples of ways to incorporate comparative ideas into introductory
411 ## neuroscience

412 ***Action potentials and voltage-gated ion channels: Cone snail venom.***

Fig. 1 A cone snail consuming a fireworm. Credit: Richard Zerpe, Creative Commons Attribution-Share Alike 2.0 Generic License

A core concept in all introductory neuroscience courses is the role of voltage-gated ion channels in propagating action potentials. Cone snail venom, i.e. conotoxins, offer an interesting example to probe student understanding of these concepts. Cone snails in the genus *Conus* are slow moving predators of worms, molluscs, and impressively, fish (Fig. 1). Cone snails have evolved potent cocktails of neurotoxins (conotoxins), with some species producing 100s of different toxins simultaneously (Olivera et al. 1990; Olivera 1997). These neurotoxins have very
426 diverse and specific neurological effects;
427 acting on voltage-gated sodium- (Na_V),
428 potassium- (K_V), and calcium- (Ca_V) channels,
429 among others. Amazingly, this represents just a small subset of all conotoxins. In some cases,
430 these toxins may hold voltage-gated ion channels open, and in others they may keep them closed
431 (Olivera 1997). Not only are these animals and their venoms inherently fascinating, they provide
432 an excellent way for students to explore the roles of ion channels in action potentials. What
433 happens to a neuron if voltage-gated Na channels are held open? What about blocking the
434 opening of voltage-gated K channels? What if both occur at the same time? For students
435 interested in medicine, instructors can highlight the opportunity for drug development and health
436 interventions made possible by studying cone snail venom (Nelson 2004; Azam and McIntosh
437 2009; Halai and Craik 2009).

438 ***Synaptic transmission: Venomous snakes and electric eels***

Fig. 2 Three species that were invaluable in the purification and characterization of nicotinic acetylcholine receptors. Left, electric rays (*Torpedo marmorata*), center, electric eels (*Electrophorus electricus*) and right, many banded kraits (*Bungarus multicinctus*). Credit: Left, Philippe Guillaume, Creative Commons Attribution 2.0 Generic license. Center KOS, GNU Free Documentation License. Right, Lin Chen Wen Creative Commons Attribution-Share Alike 4.0

439 Another key concept in introductory neuroscience is synaptic transmission. Most courses cover
440 transmission at neuromuscular junctions mediated by nicotinic acetylcholine receptors (nAChR).
441 Our understanding of these receptors is thanks in large part to work on species such as electric
442 rays (*Torpedo californica, T. marmorata)* and eels (*Electrophorus electricus*, Changeux 2020,

Fig. 2). In the 1930s it was recognized that electric organs had structures that resembled modified motor end plates. Then, in the 1940s David Nachmansohn found that electroplaques had nearly 400-500 times the acetylcholinesterase (AChE) activity of mammalian tissues per unit mass (Nachmansohn 1959). Subsequently, nAChRs were purified and characterized from these species, thanks in large part to their high concentrations (Chang 1974; Lindstrom et al. 1983). Purification was possible through affinity binding of nAChRs to α-bungarotoxin (α-BGT), a neurotoxin produced by many-banded kraits (*Bungarus multicinctus*), which are extremely venomous snakes. This α-BGT blocks neuromuscular transmission without affecting AChE (Chang and Lee 1963; Changeux et al. 1970). There is an opportunity, here, to link back to the cone snails in the previous example. One class of conotoxins, α-conotoxins, also target nAChRs, and are primarily antagonists of muscle receptors (Azam and McIntosh 2009). Prey injected with α-conotoxins lose muscular control and exhibit flaccid paralysis, allowing the snails to ingest the prey item. This is also a great chance to connect biochemistry to behavior and evolution, as the exact cocktail of toxins produced by each species appears to be driven by shifts in the types of prey taken by each species (Koch et al. 2024).

Cortical representation of sensory information: Star-nosed mole somatosensation

Fig. 3 Star-nosed moles (*Condylura cristata*) are small, semi-aquatic moles found in the Northeastern United States and Eastern Canada. Their habitat and foraging has, presumably, selected for a keen tactile sense. They have a unique star-nose with high spatial resolution, as well as large forepaws and claws for digging. The somatosensory cortex of star-nosed moles has a large volume devoted to the star and forepaws. Credit: Left, National Park Service, Right, Donna Naughton Creative Commons Attribution-Share Alike 4.0

A third concept in many introductory courses is the cortical representation of sensory information. In addition to the human examples, it is useful for students to understand that (1) the distribution and abundance of sensory receptors is generally linked to the ecology of animals and (2) that spatial information and relative "importance" of sensory information is broadly preserved in cortical representations. Star-nosed moles (*Condylura cristata*) are excellent for this purpose (Fig. 3). These semi-aquatic moles spend much of their time in low to no-light environments and have evolved an exquisite tactile sense via 22 appendages that extend in a star shape from the nose (Catania 2011, 2012). These rays have a greatly expanded cortical representation. The spatial relationship of the rays on the star is maintained in the spatial organization of the neocortex, with representations found in the primary (S1) and secondary (S2) somatosensory cortex (Catania 2011, 2012). A third representation of the star (S3) is visible caudal to S2, which is unlike somatosensory representations in other mammals. Additionally, one of the rays is significantly overrepresented both in the cortex and in peripheral innervation, suggesting a tactile "fovea" that is more similar, in many ways, to the organization of the visual system in humans, rather than the somatosensory system.

474

475 ***Evolutionary diversity in the neurological basis of behavioral phenotypes***

Fig. 4 Three species that vary in the expression and mechanisms underlying pair bonding behavior: prairie voles (*Microtus ochrogaster*), meadow voles (*Microtus pennsylvanicus*), and deer mice (*Peromyscus maniculatus*). Credit: Left, Nastacia Goodwin, Creative Commons Attribution-Share Alike 4.0 International. Center Chuck Homler / FocusOnWildlife.Me, Creative Commons Attribution-Share Alike 4.0 International. Right, Seney Natural History Association, Creative Commons Attribution-Share Alike 2.0 Generic license

476 A fourth key concept is that evolution may have acted on the nervous system in various ways in
477 different lineages to achieve similar behavioral phenotypes. An excellent example of this is the
478 modulation of reproductive and social behaviors. Critically important here is that there are a
479 diversity of ways in which behaviors may be modulated. However, many mechanisms are
480 thought to be ubiquitous when they have only been demonstrated in one (or a small number of)
481 organism(s). A great example is monogamy and male parental care in voles (Fig. 4). There has
482 been considerable research investigating the neurological mechanisms underlying pair-bonding
483 in voles, and the influence of vasopressin and oxytocin in the brain. However, monogamy in
484 voles represents a single evolutionary event. Despite this, the mechanism in voles — that
485 vasopressin and the distribution of its receptors in the hypothalamus and ventral pallidum
486 modulate the degree of monogamy and paternal care — is often taught or assumed to be *the*
487 mechanism of monogamy and parental care across a range of species, if not all species.
488 However, research with other rodents, such as *Peromyscus* mice, suggests that this mechanism is
489 in fact not ubiquitous at all (Turner et al. 2010). This example serves to emphasize that there can
490 be multiple answers to a single question ("how do animals evolve mongamy?") and can help
491 promote integrative thinking amongst neuroscience undergraduates.

492

493 **Conclusions**

494 It is impossible to calculate the number of lives that have been positively impacted by Peter
495 Narins. Not only did he inspire countless others with his research, but his teaching broadened the
496 horizons of students bound for any number of future careers. One of his strengths, and what
497 made him such an appealing and engaging educator, was his view that we should consider the
498 nervous systems of all animals. In line with this, there have been a number of calls for an
499 increased focus on evolutionary and comparative neuroscience research, including several in the
500 *Journal of Comparative Physiology*. However, we have demonstrated here that the current state
501 of undergraduate curricula in the United States does not currently reflect this aspirational
502 breadth. Although we have identified a number of barriers to the inclusion of evolutionary and
503 comparative framing in neuroscience curricula, we feel these are largely surmountable, some

504 with relatively little effort, and we offer several suggestions for a path forward. Introducing
505 students to evolutionary and comparative ideas early in their careers will help build interest in
506 evolutionary and comparative research, which may fuel new discoveries akin to those that
507 transformed our understanding of the nervous system in the first place and which also came from
508 diverse animal systems. Additionally, for students interested in medical or technology careers,
509 increasing the breadth of material taught in introductory courses can increase student
510 appreciation of the value of comparative work for medicine or bio-inspired technology.

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517

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