

Modeling the evolution and development of emotions

Abstract

I argue that emotion research needs formal (mathematical) theory to address two central questions. How does evolution shape mechanisms of emotion development across generations, depending on environmental conditions? How do these mechanisms generate emotions, based on lifetime experience and current context? Formal modeling enables researchers to state ideas clearly and precisely, deduce predictions, and evaluate the fit between theory and data.

Keywords: evolution; development; learning; cognition; danger; fear.

© 2019, American Psychological Association. This paper is not the copy of record and may not exactly replicate the final, authoritative version of the article. Please do not copy or cite without authors' permission. The final article will be available, upon publication, via its DOI: [10.1037/dev0000732](https://doi.org/10.1037/dev0000732)

Modeling the evolution and development of emotions

A journalist asked: “Which contributes more to personality, nature or nurture?” Donald Hebb famously replied: “Which contributes more to the area of a rectangle, its length or its width?” (Meaney, 2004). This analogy brilliantly exposed the misconceptions that nature and nurture are additive and zero-sum (more nature implies less nurture, and vice versa). In reality, all traits of organisms, *phenotypes*, result from interactions between nature and nurture.

Still, other misconceptions persist. Some scientists ask whether a given ability or behavior results from evolution *or* development. However, all phenotypes result from development. And all development results from evolved mechanisms interacting with ontogenetic and current contexts. Therefore, all phenotypes have both an evolutionary history and a developmental history. Evolution and development are nested processes operating on different timescales. Across generations, only some developmental mechanisms make it through the sieve of evolution; within generations, these mechanisms tailor individuals’ phenotypes to local conditions (Frankenhuis, Panchanathan, & Barrett, 2013). In this commentary, I will argue that formal modeling can illuminate both processes of adaptation.

In developmental psychology, evolutionary perspectives are traditionally associated with ‘innate’ phenotypes. However, nothing in the predominant view in biology entails that adaptive phenotypes are: not learned, present at birth, fixed across ontogeny, and universal in the species (Frankenhuis & Del Giudice, 2012). Far from it. Natural selection often results in developmental mechanisms that produce different phenotypes in different environmental conditions (e.g., stress response systems adapt to current levels of danger). These mechanisms generate some phenotypes early in life (e.g., bilateral symmetry of the human body) and others later (e.g., pubertal traits). And, they may produce maladaptive phenotypes in a subset of individuals (e.g.,

who misperceive the level of danger in their environment due to chance events) (Frankenhuis & Del Giudice, 2012). Nonetheless, all of these phenotypes result from development *and* evolution. Even novel phenotypes, constructed for the first time in the current generation, have evolutionary histories, through the mechanisms that construct them (e.g., statistical learning mechanisms used to master modern technologies) (Barrett, 2015).

Rather than view evolution and development as zero-sum, therefore, it is better to ask two complementary questions. First, how do evolutionary processes (including but not limited to natural selection) shape developmental mechanisms, depending on environmental conditions? And second, how do these mechanisms construct phenotypes, based on lifetime experience and current context? These questions feature in several articles in this special issue.

LoBue & Adolph (2019) ask what learning mechanisms infants and children use to tailor their levels of fear to potential dangers, based on cultural context and personal experience. Stern et al. (2019) discuss the developmental roots of empathy. Pereira et al. (2019) argue that infants and children learn actively by selecting behaviors that are likely to provide useful information about the world. Hammond & Drummond (2019) state that positive emotions facilitate infants' prosocial development, enabling their integration into family and community life. All of these papers, and others, discuss the adaptive mechanisms that infants and children use to tailor their brains, minds, and bodies to local conditions, based on lifetime experience and current context. Although my commentary will focus on the development of fear, many of the points I make apply to other emotions as well, and some apply generally to all phenotypes.

Developing fear adaptively

To understand what a person is arguing for, it helps to understand what they are arguing against (Cosmides & Tooby, 1997). LoBue & Adolph (2019) argue against two different nativist

views about infants' and children's acquisition of fear of snakes, spiders, heights, and strangers: that it is adaptive for these fears to be present at birth (*innate knowledge*); and, that it is adaptive to be born with 'prepared' learning mechanisms that acquire these fears rapidly based on limited experience (*prepared learning*). These authors argue for fear development depending on cultural context and personal experience (*contextual learning*).

The authors make two arguments against these nativist views. First, the current empirical record simply does not support the prevailing hypothesis that fear of snakes, spiders, heights, and strangers is present at birth or develops early in life. Second, it would not be adaptive – indeed, it would even be maladaptive (reduce survival and reproduction) – for these fears to be present at birth or develop early, without consideration of cultural context and personal experience. I am sympathetic to both arguments, but with caveats. Before discussing these arguments, I present criteria for identifying fear.

Many studies have found that infants and children attend more to dangerous stimuli (e.g., spiders) compared with non-dangerous stimuli (e.g., butterflies). LoBue & Adolph (2019) argue that such perceptual bias is, by itself, not enough to establish the presence of fear. In addition, criteria should include behavioral (e.g., avoidance) and/or physiological evidence (e.g., changing heart rate) (Buss, 2011). I agree. Surveying the empirical record using these criteria, the authors only find evidence for fear of strangers in *some* infants and *some* experimental designs. For snakes and spiders, they find evidence that young children actually *like* them. For heights, the evidence is mixed and can be interpreted in different ways. For instance, many infants do not show adaptive behavior; they crawl over the edge of a cliff. LoBue & Adolph (2019) do not argue that fear of snakes, spiders, and heights never develop early in life. Rather, they argue that their development depends on context and individual differences (see also Feldman Barrett,

2009). Now we return to the two arguments against nativist views of fear development (innate knowledge and prepared learning) these authors make.

First, in their discussion of the empirical record, LoBue & Adolph (2019) focus on learning about snakes, spiders, heights, and strangers. I understand this focus because research on these stimuli has deep traditions. However, I was surprised to see no mention of recent work on early learning about plants (Wertz & Wynn, 2014a, 2014b) – another ancestrally recurrent threat – especially because this research seems to meet LoBue & Adolph's (2019) criteria for identifying fear. Specifically, this work does seem to provide behavioral evidence consistent with fear, in addition to differential looking in response to plants. For instance, infants exhibit more social looking toward adults when confronted with plants compared to other object types (Elsner & Wertz, 2019) and are more reticent to touch plants than other stimuli (Wertz & Wynn, 2014a; Włodarczyk, Elsner, Schmitterer, & Wertz, 2018). It is worth noting that Wertz and colleagues have themselves only interpreted their findings as support for prepared learning about plants, without claiming such learning is accompanied by fear emotions (Włodarczyk et al., 2018). Future research that includes physiological measures could provide illuminating evidence.

Similarly, my colleagues and I have argued for prepared learning about danger, without claiming that such learning is accompanied by fear emotions (Barrett, Peterson, & Frankenhuus, 2016). Our cross-cultural research shows that children better memorize danger information than non-danger information (Barrett & Broesch, 2012; Barrett et al., 2016; Broesch, Barrett, & Henrich, 2014). In addition, we have proposed that parameter settings of prepared-learning mechanisms may be influenced by local danger and cultural context. For instance, preliminary evidence suggests that Ecuadorian children from Shuar communities, for whom dangerous animals are a relevant threat, learn which unfamiliar animals are dangerous faster than American

children from Los Angeles and better remember this information one week later (Barrett et al., 2016). Although we have argued for prepared learning, our data – like most of the data reviewed by LoBue & Adolph (2019) – might be explained by general learning mechanisms coupled with perceptual bias. In order to know which type of learning architecture is more likely to account for the data, it would be helpful to formalize both accounts (creating clear, precise descriptions of how fear develops according to each account) and compare their predictions with existing data.

The evolution of contextual learning

Second, I share LoBue & Adolph's (2019) view that researchers have been seduced too easily by nativist hypotheses of fear development. These authors write: "Although fear of snakes/spiders, heights, and strangers might be adaptive in some instances, heightened attention to these stimuli, the ability to perceive affordances for action when presented with these stimuli, and the ability to evaluate their meaning based on context is far more adaptive: These behaviors encourage infants to explore new things while maintaining the flexibility to develop a fear if they discover that a stimulus is truly threatening."

Although I agree that there are benefits to learning based on context, such learning also has costs (e.g., time and energy invested in collecting, storing, and retrieving information). When is learning based on context more adaptive than innate knowledge or prepared learning? The adaptive value of different learning mechanisms will depend on the statistical structure of the environment. Specifically, it will depend on such variables as the rate of environmental change over space and time, both between and within generations, and the extent to which developing organisms are able to infer their current conditions and predict future conditions (Frankenhuis, Nettle, & McNamara, 2018). Using formal modeling, evolutionary biologists have rigorously

explored this issue for decades (see references in sections 2 and 3 of Frankenhuis, Panchanathan, & Barto, 2018), but this literature is not discussed. Here, the authors have missed an opportunity to build a bridge with biology and to highlight the need for formally modeling the evolution of contextual learning vs. innate knowledge and prepared learning, and to emphasize the need for empirical studies that measure the relevant environmental statistics (Frankenhuis, Nettle, & Dall, 2019).

In formal models of evolution, the goal is typically not to fit a statistical or computational model to data; rather, it is to start with basic evolutionary principles (e.g., population genetics), make additional assumptions about a phenomenon of interest (e.g., development, cognition), and explore what developmental mechanisms or phenotypes are likely to result from evolution. The utility of any particular model will depend, of course, on the assumptions it makes and how well it is constructed and analyzed, as with arguments in natural language (Frankenhuis et al., 2018). The advantage of formal modeling is that it enables researchers to state an idea clearly in cases where natural language might be ambiguous (using math rather than words), deduce predictions (based on logic rather than reasoning, which is subject to biases), and evaluate the fit between theory and data (more precision in predictions). Darwin recognized the value of mathematics. Almost 200 years ago, he wrote in his *Autobiography*: “I have deeply regretted that I did not proceed far enough at least to understand something of the great leading principles of mathematics; for men thus endowed seem to have an extra sense” (1828–1831).

Biology has moved well beyond ‘just-so evolutionary stories’ (i.e., post-hoc adaptive rationalizations of observations). For instance, some biologists build formal (mathematical) models to predict which phenotypes are adaptive in particular environmental contexts and then breed (i.e., experimentally evolve) animals in those contexts to observe whether the *predicted*

phenotypes result from natural selection (e.g., fruit flies, which have short generation times) (Kawecki et al., 2012). Conducting such studies with humans is not feasible, nor desirable, but formally modeling hypotheses about the evolution of development is, and such modeling can spur theoretical and empirical progress in psychology, as it does in the other life sciences (Cohen, 2004; Servedio et al., 2014).

Although there are many models of the evolution of development and learning that are relevant to the current discussion (Dunlap, Austin, & Figueiredo, 2019), I am not aware of any models that simultaneously compare the fitness of contextual learning, innate knowledge, and prepared learning in different environmental conditions. I hope that researchers will build such a model, because it could provide valuable insights into debates in developmental psychology. A model could include such variables as: the base rate of encountering potential dangers within a lifetime; fluctuations in these base rates over time (environmental autocorrelation); the accuracy with which these danger can be discriminated from background noise (cue reliability); the costs and benefits of false positives (detecting danger when there is none) and false negatives (not detecting danger when there is one); other agents that are learning about danger, and whose behaviors convey information about the level of danger of particular entities (a form of social transmission), and so on. Readers interested in building such a model may consider using the framework of signal detection theory (see Lynn & Feldman Barrett, 2014, for a tutorial), with sequential decisions (Trimmer, Ehlman, McNamara, & Sih, 2017), combined with Bayesian updating. Pereira et al. (2019) provide an accessible introduction to Bayesian modeling in their supplement, noting that such models are increasingly used in psychology. A bridge with biology could be made here, too, as a parallel trend is occurring in the modeling literature that explores the evolution of development (Stamps & Frankenhuis, 2016).

In addition to bringing rigor, formal modeling adds conceptual clarity. LoBue & Adolph (2019) argue that conceptual confusion is hindering progress in the study of fear development. I agree. As these authors explain, this confusion results in large part from jingle-jangle fallacies: researchers using different terms to denote the same thing, or the same term to denote different things. I make one addition: natural language is typically more ambiguous than formal language. For instance, hypothesizing that a given trait (e.g., developmental plasticity) is adaptive in a variable environment leaves unspecified how environmental conditions precisely vary (e.g., at what rate, over space and/or time). Formalizing ideas resolves ambiguities by stating ideas and predictions in mathematical terms (Epstein, 2008; Smaldino, 2017).

Models are not reality

Mathematical models make ideas precise and transparent, reveal whether ideas are logically coherent, and allow deduction of clear predictions. However, these models cannot tell us what the world is actually like. To know this, we must measure. For instance, a formal model that compares contextual learning with innate knowledge and prepared learning might show that under a wide range of plausible environmental conditions (e.g., autocorrelation in the range that ecologists commonly observe in nature, cue reliabilities in the range that vision scientists have documented for relevant types of stimuli), contextual learning is the most adaptive. Assuming we think our model captures key aspects of reality, this result should increase the credibility of the contextual learning account compared with the others. However, our investigation does not stop here. Our next step would be to conduct empirical research to measure relevant environmental dimensions and determine their actual statistical properties. Obtaining such data is challenging, but it is certainly possible and has been done in some cases (for review, see Frankenhuis et al., 2019).

Adaptation is about the fit between organisms and their environments. Developmental psychological theory would benefit from using formal modeling to explore hypotheses about the adaptive mechanisms that infants and children use to tailor their phenotypes to their ontogenetic and current contexts. Formal models are the norm in biology, for good reasons: they have several advantages over natural language. However, we should not confuse models for reality. We need to assess our model assumptions (e.g., environmental statistics), test model predictions (e.g., how people learn about danger or develop fear), and revise models or build new ones based on fresh empirical data. As Nobel Laureate Robert Millikan wrote in 1924: “Science walks forward on two feet, namely theory and experiment. ... Sometimes it is one foot that is put forward first, sometimes the other, but continuous progress is only made by the use of both.”

References

- Barrett, H.C. (2015). *The shape of thought: How mental adaptations evolve*. Oxford University Press, New York.
- Barrett, H. C., & Broesch, J. (2012). Prepared social learning about dangerous animals in children. *Evolution and Human Behavior*, *33*, 499–508.
doi:10.1016/j.evolhumbehav.2012.01.003.
- Barrett, H. C., Peterson, C. D., & Frankenhuis, W. E. (2016). Mapping the cultural learnability landscape of danger. *Child Development*, *87*, 770-781. doi:10.1111/cdev.12495
- Broesch, J., Barrett, H. C., & Henrich, J. (2014). Adaptive content biases in learning about animals across the life course. *Human Nature*, *25*, 181–199. doi:10.1007/s12110-014-9196-1.
- Buss, K. A. (2011). Which fearful toddlers should we worry about? Context, fear regulation, and anxiety risk. *Developmental Psychobiology*, *47*, 804-819. doi:10.1037/a0023227
- Cohen, J. E. (2004). Mathematics is biology's next microscope, only better; biology is mathematics' next physics, only better. *PLoS biology*, *2*, e439.
doi:10.1371/journal.pbio.0020439
- Cosmides, L., & Tooby, J. (1997). Evolutionary psychology: A primer. Retrieved from:
<http://www.psych.ucsb.edu/research/cep/primer.html>
- Dunlap, A. S., Austin, M. W., & Figueiredo, A. (2019). Components of change and the evolution of learning in theory and experiment. *Animal Behaviour*, *147*, 157-166.
doi:10.1016/j.anbehav.2018.05.024
- Elsner, C., & Wertz, A. E. (2019). The seeds of social learning: Infants exhibit more social looking for plants than other object types. *Cognition*, *183*, 244-255.

doi:10.1016/j.cognition.2018.09.016

Epstein, J. M. (2008). Why model? *Journal of Artificial Societies and Social Simulation*, *11*, 12.

Feldman Barrett, L. (2009). Variety is the spice of life: A psychological construction approach to understanding variability in emotion. *Cognition and Emotion*, *23*, 1284-1306.

doi:10.1080/02699930902985894

Frankenhuis, W. E., & Del Giudice, M. (2012). When do adaptive developmental mechanisms yield maladaptive outcomes? *Developmental Psychology*, *48*, 628-642.

doi:10.1037/a0025629

Frankenhuis, W. E., Nettle, D., & Dall, S. R. X. (2019). A case for environmental statistics for early life effects. *Philosophical Transactions of the Royal Society B*, *374*,

20180110. doi:10.1098/rstb.2018.0110

Frankenhuis, W. E., Nettle, D., & McNamara, J. M. (2018). Echoes of early life: Recent insights from mathematical modeling. *Child Development*, *89*, 1504–1518.

doi:10.1111/cdev.13108

Frankenhuis, W.E., Panchanathan, K., Barrett, H.C. (2013). Bridging developmental systems theory and evolutionary psychology using dynamic optimization. *Developmental Science*, *16*, 584–598. doi:10.1111/desc.12053

Frankenhuis, W. E., Panchanathan, K., & Barto, A. (2018). Enriching behavioural ecology with reinforcement learning methods. *Behavioural Processes*. Advance online publication.

<https://doi.org/10.1016/j.beproc.2018.01.008>

Hammond, S. I, & Drummond, J. K. (2019). Rethinking emotions in the context of infants' prosocial behavior: The role of interest and positive emotions. *Developmental Psychology*.

Kawecki, T. J., Lenski, R. E., Ebert, D., Hollis, B., Olivieri, I., & Whitlock, M. C. (2012).

Experimental evolution. *Trends in Ecology & Evolution*, 27, 547-560.

doi:10.1016/j.tree.2012.06.001

LoBue, V., & Adolph, K. A. (2019). Fear in infancy: Lessons from snakes, spiders, heights, and strangers. *Developmental Psychology*.

Lynn, S. K., & Feldman Barrett, L. (2014). “Utilizing” signal detection theory. *Psychological Science*, 25, 1663-1673. doi:10.1177/0956797614541991

Meaney, M. J. (2004). The nature of nurture: Maternal effects and chromatin remodeling. In J. T. Cacioppo, & G. G. Berntson (Eds.), *Essays in social neuroscience* (pp. 1–14). Cambridge: MIT Press.

Pereira, M. R., Barbosa, F., de Haan, M., & Ferreira-Santos, F. (2019). Understanding the development of face and emotion processing under a predictive processing framework. *Developmental Psychology*.

Servedio, M. R., Brandvain, Y., Dhole, S., Fitzpatrick, C. L., Goldberg, E. E., et al. (2014). Not just a theory—the utility of mathematical models in evolutionary biology. *PLoS Biology*, 12, e1002017. doi:10.1371/journal.pbio.1002017

Smaldino, P. E. (2017). Models are stupid, and we need more of them. In R. R. Vallacher, S. J. Read, & A. Nowak (Eds.), *Computational social psychology* (pp. 311–331). New York, NY: Routledge.

Stamps, J., & Frankenhuis, W. E. (2016). Bayesian models of development. *Trends in Ecology and Evolution*, 31, 260-268. doi:10.1016/j.tree.2016.01.012

Stern, J. A., Botdorf, M., Cassidy, J., & Riggins, T. (2019). Empathic responding and hippocampal volume in young children. *Developmental Psychology*.

Trimmer, P. C., Ehlman, S. M., McNamara, J. M., & Sih, A. (2017). The erroneous signals of

detection theory. *Proceedings of the Royal Society B*, 284, 20171852.

doi:10.1098/rspb.2017.1852

Wertz, A. E., & Wynn, K. (2014a). Thyme to touch: Infants possess strategies that protect them from dangers posed by plants. *Cognition*, 130, 44–49.

doi:10.1016/j.cognition.2013.09.002

Wertz, A. E., & Wynn, K. (2014b). Selective social learning of plant edibility in 6- and 18-month-old infants. *Psychological Science*, 24, 874–882. doi:10.1177/0956797613516145

Włodarczyk, A., Elsner, C., Schmitterer, A., & Wertz, A. E. (2018). Every rose has its thorn: Infants' responses to pointed shapes in naturalistic contexts. *Evolution & Human*

Behavior, 39, 583–593. doi:10.1016/j.evolhumbehav.2018.06.001