



Editorial overview: Sensitive and critical periods

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Catherine Hartley is an Associate Professor of Psychology and Neural Science at New York University. Her research focuses on characterizing the changes in cognitive representations and computations that inform learning and decision-making across development, and how dynamic changes in brain circuits give rise to these functions. A goal of her research is to understand the costs and benefits associated with how individuals learn and make decisions at different developmental stages, as well as how specific learning and decision-making biases contribute to psychological vulnerability or resilience. Her research is supported by the National Science Foundation, the National Institute of Mental Health, the Templeton World Charity Foundation, the Jacobs Foundation, and the NYU Vulnerable Brain Project.

Willem E. Frankenhuis is an Associate Professor of Psychology at Utrecht University in the Netherlands. He works at the intersection between developmental psychology and evolutionary biology. His research centers on developmental plasticity, the ability to adjust development based on environmental conditions and physiological state. His theoretical work uses mathematical modeling to explore how natural selection shapes mechanisms of plasticity, across generations. His empirical work studies how, within generations, these mechanisms adaptively tailor individuals to local conditions based on experience. Dr. Frankenhuis' empirical research focuses on hidden talents, abilities that are enhanced by adversity. His research is supported by the Netherlands Organization for Scientific Research (V1.Vidi.195.130), the James S. McDonnell Foundation (220020502), and the Jacobs Foundation (2017 1261 02).

Sensitive and critical periods are central topics in the life sciences. Evidence concerning when experience exerts the greatest impact on individual development has implications for a range of societal issues, including maternal and prenatal health policies, the timing of treatments and interventions, and natural resource management via control of pests and diseases.

Thus, sensitive and critical periods are studied in a variety of disciplines. On the one hand, this division of labor has clear benefits: researchers can use ideas and measures best suited to their particular subject matter. On the other hand, there are costs: scientists in different fields often do not know about each other's work, because they publish in different journals, attend different meetings, and use different concepts and terms. As a result, they are less likely to benefit from each other's theories, methods, and findings. Specifically, researchers miss out on theories that illuminate their data and predict new observations; on methods that disentangle factors that are currently confounded in their studies; and on mechanisms in other species that offer insight into, or at least provide clues to, mechanisms operating in the species they study (Frankenhuis & Nettle, 2020).

Researchers studying different species can learn from each other. All animals are part of the same tree of life. Having descended from common ancestors, they may have inherited the same (or closely related) developmental mechanisms. Moreover, even if animals occupy different branches on the tree of life, natural selection may have shaped their mechanisms in similar ways if these mechanisms solve similar challenges (e.g., predicting future conditions based on current experiences). Thus, building bridges strengthens individual areas of research and advances consilience, i.e., the integration of all sciences.

The goals of this special issue

The short-term goal of this issue is, therefore, to help researchers of sensitive periods in different disciplines learn about each other's work. The longer-term goal is for information to flow across bridges between currently disconnected areas of research, creating scope for synergies. Hence, this issue includes contributions from researchers from different fields, including developmental psychology, cognitive neuroscience, evolutionary biology, and biological anthropology.

There are many connections between the contributions in this issue, not all of which can be showcased in this introduction. Therefore, we have organized this introduction into four broad themes, although most papers touch upon several themes. These themes are, in the order of their presentation: the evolution of sensitive and critical periods, the neurobiological and cognitive mechanisms governing critical and sensitive periods,

methodological challenges in studies of sensitive and critical periods, and the application of knowledge about sensitive and critical periods to treatment, intervention, and policy.

The evolution of sensitive and critical periods

Sensitive and critical periods are widespread in all classes of organisms: mammals, birds, fish, reptiles, amphibians, invertebrates, and plants. However, there is also variation in sensitive and critical periods:

- between species in the same trait – for instance, some birds learn their songs early in life, others throughout their lifetimes;
- between individuals from the same species – for instance, individual variation in brain plasticity resulting from variation in genes, experience, or both; and
- between traits within a single individual – for instance, some cognitive systems adjust more readily than others to changes in social or environmental conditions (e.g., when previously institutionalized children are adopted into a loving family).

What factors and processes explain such variation between species, individuals, and systems? This general question, of course, does not have a simple answer. Rather, it offers the contours of a coloring picture that we can all help to complete.

This picture includes the questions which sensitive and critical periods are biologically adaptive (i.e., have been favored by natural selection), and what their functions are (i.e., how variation in plasticity across ontogeny has promoted survival and reproduction). Lea and Rosebaum (2020) review the main hypotheses that evolutionary biologists have proposed to explain why sensitive and critical periods typically exist early in life. English and Barreaux (2020) discuss how some of these hypotheses have been tested in insects and how others can be tested in future research. Kuzawa (2020) discusses how mammalian mothers may convey information to their offspring that reflects distinct timescales of her experience. Mariette (2020) reviews the recent discovery that in birds prenatal sounds may provide information for embryos to finetune their phenotypes to the current environment. Sachser et al. (2020) discuss sensitive and critical periods at later life stages, particularly in adolescence, in rodents; and so do Laube and Fuhrmann (2020) for humans. Humphreys and Salo (2020) argue that human infants' and children's developmental responses to early adversity are best understood in light of the experiences these age groups typically had over the course of human history, rather than what is normative in contemporary societies.. Finlay (2020) uses case studies to illustrate that evolutionary accounts should consider not only adaptive explanation, but also

phylogeny and biophysics. Not all sensitive and critical periods are adaptive.

The neurobiological and cognitive mechanisms governing critical and sensitive periods

Experience exerts a pronounced influence on brain development. Neural circuits supporting both basic perceptual (e.g., vision, hearing) and higher-level cognitive processes (e.g., language, social cognition) exhibit sensitive and critical periods during which the presence or absence of specific environmental inputs alters their organization and function. Moreover, as brain development is progressive and hierarchical, experiences that influence the tuning of a neural circuit during an early sensitive period may have downstream effects on the organization of circuits with later sensitive periods. This biological embedding of experience within neural circuits involves a diverse set of physiological and cognitive mechanisms. Research has begun to elucidate how experiences become encoded in neural activity that shapes the organization of brain circuits, the mechanisms that govern the opening, closure, and sequencing of sensitive periods, and the consequences of sensitive periods for specific cognitive functions.

The papers in this issue cover a broad range of mechanisms. Hsu et al. (2020) discuss the role of maternal hormones as mediators of developmental outcomes during prenatal sensitive periods in birds. Lin et al. (2020) propose that sensitivity of the dopaminergic system to the reinforcement statistics of the environment may organize the development of corticostriatal circuits that support learning and decision making in mammals. Sullivan and Opendak (2020) and Gee (2020) discuss the influence of early caregiving experience on the development of neural circuits governing emotional learning and regulation in rodents and humans, respectively. Cheng et al. (2020) present evidence from studies of deaf and blind individuals that the functional specialization of a fronto-temporal language network depends on linguistic experience (spoken or sign language) during a sensitive period in childhood. Thompson and Steinbeis (2020) argue that during early infancy, environmental complexity and contingent caregiver interactions scaffold the development of several component processes of executive function, including attention and sense of instrumental control. Pehune (2020) reviews evidence that early musical training facilitates diverse aspects of music cognition through its effects on the sequential refinement of interactive auditory processing systems in the brain. Lövdén and Lindenberger (2020) propose that learning can be viewed as a sequential process of expansion, exploration, selection, and refinement of brain circuits, and discuss evidence for such structure in the experience-dependent plasticity that occurs in motor learning. Underscoring the

complexity of biological mechanisms of sensitive period regulation, Callaghan (2020) presents evidence that interaction between central and peripheral systems may allow microbiota to serve as regulators of plasticity within learning and memory systems.

Methodological challenges in studies of sensitive and critical periods

Researchers who seek to identify sensitive or critical periods and their underlying mechanisms face a number of methodological challenges. The identification of sensitive periods requires longitudinal assessment of the effects of experience. In humans, longitudinal data collection is inherently challenging, and researchers cannot readily achieve the level of experimental control that is possible in animal models. Moreover, even in well-controlled laboratory studies, procedural differences in experimental protocols can make the integration of findings across research groups challenging (Chaby et al., 2020). Several articles within this issue discuss such methodological challenges and suggest best practices for addressing them. Gabard-Durnham and McLaughlin (2020) review criteria for inferring sensitive periods, discuss the merits and shortcomings of methodological approaches that have been used to study sensitive periods in human development (e.g., environmental and pharmacological manipulations, computational modeling), and suggest novel approaches that may also prove fruitful. Hartshorne (2020) argues that the study of sensitive periods requires larger and more diverse samples than those readily acquired in laboratory studies and advocates for massive online experiments as a promising alternative.

The study of sensitive periods in higher-order cognitive abilities poses unique inferential challenges as these functions typically depend on diverse lower-level abilities, which may themselves be tied to distinct regulatory mechanisms. Woodward and Pollak (2020) discuss how the involvement of diverse mechanisms in affective processing (e.g., facial recognition, reward processing, fear conditioning) presents a challenge for isolating sensitive periods in emotional development, and underscore the importance of distinguishing between effects of early experience and evidence of a sensitive period. Pascalis et al. (2020) similarly note that sensitive periods for face processing and language development likely interact, and that distinct experience influencing one system may also affect the other. Kievit (2020) proposes that sensitive periods in cognitive development might be better conceptualized as extended periods during which early

experience alters the strength or nature of the interactions between cognitive domains.

The application of knowledge to treatment, intervention, and policy

As our understanding of the mechanisms of plasticity increases, so do options to apply this knowledge in treatment, intervention, and policy. Through experiential manipulations and pharmacological treatments, researchers are already able to alter the timing or duration of sensitive periods in some neurobiological systems, or reinstate heightened plasticity after its closure. Such interventions might, in the future, be leveraged in clinical contexts to improve mental and physical health outcomes, enabled by policy. While applying any causal intervention in humans merits careful ethical consideration, our knowledge of sensitive and critical periods offers many potential avenues for facilitating desirable individual and societal outcomes.

Chaby et al. (2020) discuss the mechanisms that underpin heightened sensitivity to stress during adolescence, and suggest how findings in animal models might be leveraged to predict risk for stress-related psychopathology and develop targeted treatments. Pitchik et al. (2020) discuss the dynamic interaction between maternal depression and child development, and discuss the potential effects of three classes of interventions on maternal mental health and child developmental outcomes. Noble and Giebler (2020) discuss the influence of socioeconomic inequality on brain structure and function, proposing diverse experiential mechanisms that might contribute to such effects. They discuss a clinical trial assessing the influence of a monthly cash gift on developmental trajectories of children from low-income homes, an example of a causal manipulation of a complex target (i.e., socioeconomic status) that can directly inform evidence-based social policies, even when the mechanisms that drive these effects are not yet fully understood.

Conclusion

We are delighted to have had the opportunity to develop this issue with researchers studying a variety of mechanisms in a range of animals. This issue provides researchers with opportunities to learn about each other's work – theories, methods, and findings – and start building bridges, which jointly compose an infrastructure that not only enriches individual areas of research, but also enables synergies across them. We hope this issue will offer a small step towards more integration of the natural and social sciences and thus increase consilience, i.e., the integration of all sciences.