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Editorial overview: Survival behaviors and circuits

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From the moment that organic molecules combined to spawn the first living cells, the principles of evolution took the steering wheel to produce self-replicating organisms capable of surviving a myriad of physiological and ecological challenges. Among these challenges are those that occur in response to threats to well-being, low nutritional and energy supplies, imbalance of fluids or electrolytes, and variations in environmental temperature [1,2]. These survival requirements are met in complex organisms by performing a symphony of defensive, ingestive, thermoregulatory, and reproductive behaviors. When such behaviors occur in organisms with brains that can subjectively represent internal states and external stimuli, we scientists often speak of emotions and feelings. But it is important to keep in mind that these survival needs, and even survival behaviors themselves, predate nervous systems, and thus exist not to generate subjective experiences (e.g. fear or hunger), but to allow the individual and species to meet its survival needs [3].

In recent years, interest in the notion of survival behaviors and their corresponding neural circuits has increased. Within mammals, neural circuits necessary for meeting primordial challenges to well-being are highly conserved [4–7]. These so-called 'survival circuits' provide built-in ways of responding to life's challenges. A common function of all survival circuits is the optimization of behaviors that promote viability and allow gene replication take place by facilitating the evasion of predators and other sources of harm, maximizing the efficiency of energy consumption and foraging, and enhancing mating success [1,2,8–14]. Survival behaviors are, in part, controlled by innate survival circuits which are a first line of response to challenges and opportunities. They are supported by physiological states in the brain and body (global organismic states) that coordinate diverse brain activities and prioritize instrumental responses that may, on the basis of successful past experience, be useful in coping with the challenge or benefiting from the opportunity [1,15,16]. Additionally, survival circuits and global organismic states complement more recently evolved cognitive capacities underling deliberation, decision making, and consciousness [17–21]. A challenge is to avoid projecting human subjective states onto animal behavior in the absence of evidence that such attributions should be made [8,22–26]. As recently noted by leading consciousness researchers, the human brain is the only physical system that unequivocally possesses consciousness [27].

The theme of survival behaviors and circuits was explored recently at a meeting held at New York University (NYU) in in April 2017, and funded by the Templeton World Charity Foundation, and NYU. The short reviews presented in this special issue represent contributions by researchers who

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attended the meeting, but also other whose research is relevant. Together, the papers provide a fresh look at the relation of survival and emotion in an evolutionary and integrative context.

At face value, this issue brings together an unlikely collection of experimentalists and thinkers from the diverse fields of philosophy, ethology, social psychology and cellular physiology to human and animal neuroscience. Although broad in scope, these papers merge on two central ideas. First, survival circuits exist to control behavioral and physiological functions, rather than to generate conscious emotions; in organisms that can be conscious of their own brain's state [28–29], they contribute to emotional feelings but do not dictate them. Second, survival circuits interact the process of keeping organisms alive. Thus, to understand survival states, organisms must be view as unified systems.

This issue fortuitously answers several of, and extends on, Tinbergen's four questions. The *functional-adaptive value* of the defensive survival circuits is addressed by Mobbs, who proposes that to understand the adaptive value of fear and anxiety, researchers should understand the natural conditions that evoke them. Blanchard examines the role of survival circuits in risk assessment, making the novel link to default and saliency networks and McNaughton and Corr introduce the fascinating idea of internal and external risk assessment. Suddenhof, Bulley and Miloyan take a unique perspective on the role of prospection in survival, which involves future risk assessment and aids in the organism's ability to avoid future dangers. Hayden shifts the debate of adaptive value across to the field of foraging theory, suggesting that economic choices during other survival behaviors (e.g. feeding) should be an integral part of the survival circuit theory.

The *mechanistic (causal) question* relates to the physiology of the survival circuitry is highlighted by several papers. Scarantino puts forward a new Basic Emotion Theory to address the critical question of how to separate subjective, phenomenological, behavioral, and motivational systems when trying to understand the how survival circuits function. Canteras examines the mechanistic role of the hypothalamus in predatory and social threats and how this region influences emotional memory, while Yamaguchi and Lin make the link between the hypothalamus, dopaminergic systems and aggression. Petrovich goes further by discussing the role of hypothalamic feeding circuits in survival circuits through adaptive control mechanisms that utilizes cognitive processes to dynamically assess and update internal and external changes. Finally, Kim and Jung propose that to better understand the mechanism of fear, and by proxy survival circuits, researchers should attempt to create paradigms that are grounded in the interaction between behaviorism and ethology and sample a range of threatening situations that organisms are likely to encounter in the wild.

Learning and regulation of the survival circuitry are addressed by several authors. Fanselow puts forward the novel idea that natural selection has created a behavioral system involves three critical elements. These include first, a set of prewired responses that have proven over phylogeny to be effective at defense (e.g. flight, flight and freezing). Second, A rapid Pavlovian learning system, that identifies threats and promotes prewired defensive behaviors. And third, a learning system that has the ability to match the most effective defensive behavior to the current situation. De Voogd, Hermans and Phelps theorize about the large scale defensive survival circuits associated with the regulation of fear in humans, while Cohen and Ochsner examine how training can alter the survival circuits allowing us to adapt to the challenges of the environment. Orederu and Schiller address the role of extinction in the survival circuits and proposes two parallel pathways, first, fast extinction involved in quick learning and second, slow extinction that takes longer to learn whether the stimulus is safe or not. Olsson, FeldmanHall, Haaker and Hensler make the link from survival circuits to social learning. They argue for a need to investigate how human social-cognitive circuits are involved in learning about threat. Indeed, Chaniotis takes an historical perspective to suggest that social and cultural factors affect the evaluation, control, arousal, and display of emotions.

Tinbergen's question of *phyologeny-evolution* of the survival circuits across taxa is addressed by Martinez-Garcia and Lanuza who provide evidence that survival circuits involved in mediating appetitive and aversive are similar across vertebrates. These authors focus on several structures including the central amygdala and tegmentostriatal circuits that are similar in all mammals and support the notion that these structures have evolved across species because they facilitate survival. This leads to the question of how these circuits are different in humans. Barrett and Finley propose that reflexive survival behaviors are purposeful and discuss this in the context of species-general versus species-specific contributions to emotion. Taking a philosophical perspective, Jaworski tackles the question of conscious and nonconscious states involved in survival behaviors. The theme of phylogeny is a critical when trying to separate survival circuits from conscious fear, something that makes human defensive responses different from any other species.

The *ontogeny-developmental* question of the survival circuits is examined in two papers. Meltzoff and Marshall extend on the survival circuits by proposing that infants have a 'social survival circuit' enables infants to flexibly acquire novel behaviors by imitating other members of their culture. Sullivan and Opendak tackle the role of development transitions in survival circuits. These authors suggest that defensive responses to threat change over development, moving from a protection by the caregiver to independence and engagement of the defensive survival circuitry. Both Meltzoff and Marshall and Sullivan and Opendak make the important point that when studying defensive behaviors and their corresponding survival circuits, researchers should consider the ontogeny of the organism and the role the social-maternal environment plays in the formation of these circuits.

An addition to Tinbergen questions is *Maladaptation* question of survival circuits or how these circuits breakdown in psychiatric disorders. Gagne, Dayan and Bishop link the defensive survival circuit to Post Traumatic Stress Disorder (PTSD), yet extend it to computational models where, for example, PTSD may result from difficulties with terminating off-line simulations focused on negative events. Young and Craske make the leap between survival circuits and disorders of affective and propose that researchers should move beyond the traditional fear condition paradigm and investigate how other parts of the survival circuitry (e.g. reward systems) contribute to psychopathology. This is further elaborated on by Taschereau-Ducmouchel, Liu and Lau who propose new treatments that by-pass conscious feelings of fear and potentially target survival circuits directly. Similarly, Hayes and Hofmann examine the influence of survival circuits in the clinic by proposing that psychotherapy can be of help in increasing access to 'unconscious' processes, reducing their automatic impact, and allowing humans to override maladaptive processes engaged by defensive survival circuits.

In sum, the papers in this issue come together to demonstrate the importance of understanding survival circuits on many different levels. Such depth of analysis will allow for a thorough understanding of the survival circuits including how these circuits differ across species, development and are impaired in psychiatric disorders. Further, it is hoped that the theories and empirical data discussed in this issue will invigorate researchers to take new approaches to understanding how the brain responds to a variety of natural threats and use this knowledge to elucidate the nature of a variety of psychiatric disorders and their comorbidity.

Conflict of interest

Nothing declared.

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