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Constructing emotion through simulation

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Evidence increasingly suggests that simulations implement patterns of prior experience to construct one's current experience, whether that experience is oriented in the past, in the here and now, or in the future. Simulation is the mechanism by which the brain capitalizes on prior learning to efficiently navigate the situation at hand. This review examines the latest developments in theory and empirical research that address simulation during emotional phenomena. Integration of evidence across multiple literatures suggests that simulation accounts provide a unifying framework across many different emotional phenomena and highlights the importance of investigating dynamics, complexity, and variation in emotional experiences moving forward.

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Imagine you are out hiking on a crisp fall day. As leaves crackle under your feet, you catch a glimpse of a snake a few feet away and abruptly stop. Seconds later, you exhale as you realize that the snake is an unusually curvy piece of wood, and your body slowly begins to relax. Experiences like this one provide a glimpse into the inner workings of the brain — the simulation that is happening in every moment. Simulation refers to probabilistic patterns of prior experience that dynamically construct one's current experience [1••,2••,3]. In the brain, simulations are implemented as top-down prediction signals that underlie neural activity across sensory and motor cortices, including interoceptive and visceromotor cortices [1••,4]. These predictions, as an 'internal model,' change dynamically, often as sensory input deviates from them. Consider our hiking scenario. Neural simulations constructed the experience of seeing a snake, a probabilistic inference, which was then revised as sensory input deviated from prediction signals specifying the snake's appearance. Through moment-to-moment simulation, the brain capitalizes on prior learning to navigate the situation at hand. Anticipating based on prior experiences, and then adjusting if necessary, is the most efficient means of preparing the body for what might happen next [1••].

Simulation is a unifying framework across recent cognitive science theories (e.g., [5,6]), neuroscience models (e.g., [4,7,8•]), and approaches to emotion (e.g., [1••,9]), and stands in contrast to classic theories that encapsulate emotion, cognition, or perception (e.g., [10–12]). Many empirical findings demonstrate how perceptual and cognitive phenomena are grounded in simulation (for reviews, see [7,13,14]). Theoretical and empirical work across several literatures is beginning to address simulation during emotional phenomena. This review integrates these recent developments on the nature of emotion by successively addressing how simulations underlie regulating the body, are situated and dynamic, and are assembled using language.

Regulating the body

In recent accounts, top-down simulations drive visceromotor and skeletomotor actions and construct sensory perceptions during perceptual, cognitive, and emotional phenomena [1••,2••]. Extensive evidence in perception, for example, demonstrates that top-down simulations distort sensory information based on what is predicted to occur, shaping perception and attention through expectation [2••,8•,15]. Most recently, these accounts are building on models of exteroceptive perception and motor action to address regulating the body through simulation [16••]. From this perspective, even in-the-moment emotional experiences that feel 'triggered' and that have been described as 'basic' are constructed through simulations that mobilize the body to interface with the world [1••]. This top-down approach is a clear departure from classic modular approaches in which perception and emotion remain encapsulated from 'higher level' conceptual simulation or processing that occurs at a later stage (e.g., [10,12]).

Predictive coding models of brain function specify the column-level prediction and error computations that underlie how top-down simulations are implemented across sensory and motor cortices (for reviews, see [1••,8•,17,18]). Recent models extend this framework to the visceromotor action and interoception that underlies regulating the body. More specifically, the Embodied Predictive Interoceptive Coding (EPIC) model [16••] specifies a model of top-down simulation in which cortical regions that send descending, efferent visceromotor signals to the body are integrated with those that receive ascending, afferent interoceptive signals from the body (for an extension of the EPIC framework, see [1••,4] and for other discussions of interoceptive prediction, see [19,20]). In this model, simulation is integral to anticipating the body's needs, or allostasis. Allostasis refers to anticipating changes in the body's internal milieu and preparing to meet those needs before they arise, which is how the body's many physiological systems are efficiently kept in balance [21–23,24•]. This occurs via limbic cortices (e.g., anterior cingulate, ventral anterior insula) initiating visceromotor signals to the hypothalamus and brainstem nuclei that regulate the autonomic, neuroendocrine, and immune systems. These visceromotor limbic regions also send the predicted sensory consequences of visceromotor changes — interoceptive simulations — to primary interoceptive cortex (as well as to the other sensory cortices and to motor cortex).[1] Comparing a simulation (i.e., prediction signal) to ascending sensory input from the internal milieu of the body results in interoceptive prediction error. There are then multiple routes to dynamically minimizing prediction error over time, including changing prediction signals or changing how the sensory input is sampled [16••].

Initial neuroanatomical and functional connectivity findings suggest EPIC is a viable model of brain function [1••], although it remains to be tested in many respects. Evidence that top-down simulations underlie early sensory processing is accruing across the exteroceptive sensory modalities and also during multisensory integration (for reviews, see [2••,4,8•,15,26,27]). Initial evidence is suggestive that top-down processing of interoceptive activity also occurs [16••,19,28,29]. A recent synthesis demonstrated integration of the interoceptive/allostatic system described above using evidence from tract-tracing studies in macaque monkeys, intrinsic functional connectivity in multiple large-scale samples (assessed in 'resting state' data), and the behavioral relevance of this connectivity emerging in individual differences [30•]. During an affective task, individuals showing stronger intrinsic connectivity within the specified allostatic/interoceptive system also demonstrated stronger concordance between subjective ratings of arousal and objectively measured arousal in the body (changes in the sympathetic nervous system). These findings highlight the promise of predictive coding approaches for illuminating individual differences in emotional experience (see also [31]). Many recent articles are building on initial findings to develop implications for mental health, using this computational framework to generate new hypotheses about changes through which psychopathology emerges, including early vulnerabilities and later crippling manifestations in physical health (e.g., [16••,32–34]).

Situating dynamically

Grounding emotional phenomena in simulation removes sharp divisions between emotion, perception, and cognition. Instead, emotional experiences become distinguished by the coordinated visceromotor, motor, and perceptual changes that occur as simulations mobilize the body to interface with the world (which underlie feelings, behaviors, expressions, and so on). Because these coordinated changes reflect the situation at hand, recent theoretical developments emphasize situating emotion [35••,36]. Returning to our 'snake mistake' example, consider happening upon the same atypically curvy piece of wood in a trendy home décor store. In this situation, you likely would not initially mistake it for a snake and would likely experience the situation very differently, perhaps with pleasant interest. Situated approaches to the mind view the brain as a coordinated system designed to dynamically implement context-specific, multimodal patterns to navigate situations [2••,6,35–40]. Because the multimodal aspects of situations tend to repeatedly co-occur, during emotional phenomena and during many other kinds of phenomena, the simulations that construct these experiences typically involve coordinated facets of a situation [35••,37,41]. From this perspective, the situation plays a critical role in the emergence of an emotion and should not be considered a separate phenomenon from it [36,37].

Neuroscience evidence increasingly points to the possibility that a myriad of situated emotional phenomena could be constructed through coordinated and interacting neural systems that are not specific to emotion [42–44,45•]. Any given experience of emotion is grounded in a series of dynamically changing, situated simulations, which is reflected in distributed and time-varying neural patterns across structurally and functionally distinct networks. Consistent with this approach, a major insight of meta-analyses examining the brain bases of emotion is that regions consistently implicated during emotion are distributed across multiple, large-scale networks that are involved in many different psychological phenomena [46•,47]. A recent synthesis further suggests that the highly-connected cortical limbic regions implicated in these meta-analyses and discussed in much research on emotion coordinate situated simulation across sensory and motor systems, dynamically integrating body and world, and constructing a unified conscious experience [4]. These discoveries are initiating research that increasingly employs more ecologically valid paradigms to induce situated and dynamic multimodal experiences that parallel what occurs in the real world (for a special issue on emotion in multimodal settings, see [48•]). Initial research indicates that, in general, shifts into emotional and motivational states are associated with increased functional connectivity across disparate brain regions (for recents

[1] This direction of prediction flow from viseromotor regions to primary interoceptive cortex is grounded in Barbas and colleagues model of corticocortical connections, in which prediction signals flow from less-developed granular regions (e.g., visceromotor regions) to more-developed granular regions (e.g., primary interoceptive cortex) [25].

reviews, see [49,50••]), which is consistent with the idea that coordinated activity mobilizes the body to interface with the world. When intense subjective feelings of fear, anger, or sadness emerged in a naturalistic movie-viewing context, for example, distributed circuitry anchored in the amygdala and subgenual anterior cingulate involved in regulating the body showed greater connectivity with distributed insula-based circuitry involved in orienting attention [51•].

Because, in situated simulation approaches, the situations that characterize individuals' lives differ, it becomes an empirical priority to investigate variation in emotional repertoires. Taking this approach, a recent large-scale study revealed that 'emodiversity' — experiencing diverse emotions in daily life (broadly construed) — is associated with better mental and physical health outcomes [52•]. Consistent with this finding, accumulating evidence is demonstrating that more granular experiences of emotional situations in day-to-day life are protective [53,54•]. Individuals who tend to distinguish between negative emotional experiences (e.g., differentiating sadness, fear, anger) are less likely to engage in destructive behavior or to experience severe anxiety or depression [55,56]. Individuals who tend to distinguish between positive emotional experiences (e.g., differentiating amusement, joy, pride) exhibit greater psychological resilience [57] and those who tend to experience greater diversity in their positive emotions exhibit lower circulating levels of inflammation [58]. Furthermore, several recent experiments demonstrate that meaningful situational variation occurs even within common categories of emotion that we refer to with the same word (e.g., fear, anger, sadness, disgust, happiness) [35••,44,59,60]. This recent research demonstrates the value of situated approaches in unlocking a mechanistic understanding of individual differences underlying human suffering and flourishing [41].

Assembling via language

Simulation accounts draw attention to shared mechanisms underlying 'online' experiences of emotions unfolding in the world, and thinking and talking about these experiences 'offline,' a focus that emerges when emotion, cognition, and perception are not assumed to function separately [61]. It was probably easy for you to imagine experiencing the 'snake mistake' situation in the woods presented earlier, simply by reading a few short sentences. During many emotional phenomena, language is a vehicle for assembling simulations, especially when a situation is not presently occurring — to anticipate a future scenario, recount a past episode, and so on ([61,62]; see also [63,64]). As words provide details that increasingly situate the experience, top-down predictions cascade across distributed brain networks, including motor and sensory systems, to construct experience during what is described as remembering, imagining, and so on. From this perspective, situated simulation is a common neural mechanism for navigating many different emotional phenomena that occur in daily life: experiences oriented in the past, in the here and now, or in the future.

Innovative studies examining emotional phenomena that emerge through language are providing initial support for this view. A recent meta-analysis revealed that imagining emotional experiences from a first-person perspective, by listening to or reading scenarios, is consistently associated with changes in behavior, experience, and peripheral physiology, and thus underlies one of the more powerful induction techniques for studying emotions in the lab [65]. Neuroimaging paradigms drawing on these induction techniques are increasingly demonstrating that top-down simulations extending into primary sensory and motor cortices underlie these emotional experiences. Studies in which participants imagined 'being there' in an emotional real-world scenario showed distributed neural activity that extended into primary visual, motor, and somatosensory cortices [37,66]. In another study, participants who showed greater similarity in their subjective emotional experiences while listening to short narratives also showed greater similarity in patterns of neural activity in primary visual and auditory cortex [67]. Recent evidence suggests that simulation also occurs throughout the sensory and motor systems involved in regulating the body. Neural activity in primary interoceptive cortex and brainstem regions involved in visceromotor regulation was observed during imagined scenarios that involved detailed descriptions of bodily changes [66]. An intriguing possibility is that immersion rich in situational detail involves simulation throughout the sensory and motor systems in which the brain ignores prediction error generated by sensory input, which is why the imagined experience feels 'real' [61].

Recent evidence suggests that simulation also occurs during rapid language comprehension tasks in which participants are not instructed to immerse in mental imagery. These experiments often manipulate body positions and actions during language comprehension to investigate simulation. If top-down simulations implemented across motor and sensory cortices as prediction signals underlie comprehension, then activity in the body will manifest as prediction error in the brain that speeds or slows performance in the comprehension task. In one such innovative study, temporarily paralyzing facial muscles involved in expressing emotion via botox injections selectively slowed comprehension of sentences describing emotional situations [68]. This result suggests that simulation of facial actions contributes to understanding emotional experiences communicated through language. A growing literature of similar findings suggests that situated simulation underlies comprehending words that refer to emotions (for recent reviews, see [69••,70,71]).

The implications of these emerging literatures are far-reaching, including the power of words and conversation in regulating the body, and, vice versa, the power of physical activity to disrupt or facilitate thought patterns [61,69••]. While these initial findings are striking, it is important not to lose sight of the complexity of many emotional phenomena. Theoretical reviews increasingly emphasize that prediction is occurring across hierarchies in the brain, at many different levels, with the goal of reducing overall prediction error (e.g., [4,72]). The term simulation conveys that prediction signals throughout the hierarchy are not divorced from motor and sensory activity, but these signals may reflect multi-modal compression at some levels. With this in mind, it is important to consider whether there are probabilistic representations in the linguistic system and/or forms of abstraction that should either be further developed within the simulation framework or distinguished from it (for a recent review of these issues, see [73]). Much remains to be learned about how language dynamically constructs emotional phenomena, not only during the more 'offline' emotional experiences reviewed here, but also during 'online' experiences enmeshed in the world.

Moving forward

This review contributes to a growing literature addressing simulation during many different psychological phenomena. Grounding emotion in simulation reveals dynamics, variation, and complexity in emotional phenomena that is often overlooked and that warrants empirical attention. Moving forward, a largely unexplored research question in this domain is how the simulations that underlie emotional experiences in different situations develop and change across the lifespan — the learning that occurs through prediction and error and the role that language plays in this learning [41]. Situated simulation accounts suggest that relationships in childhood are critical in forming emotional repertoires, and further suggest that, even in adulthood, emotional experiences can be altered in the moment and refashioned for the long-term in many different ways. This frontier in emotion science thus provides a new optimism about addressing many of the mental health challenges in today's world.

Conflict of interest statement

Nothing declared.

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