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Bio-behavioral synchrony promotes the development of conceptualized emotions

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As adults, we have structured conceptual representations of our emotions that help us to make sense of and regulate our ongoing affective experience. The ability to use emotion concepts is critical to make predictions about the world and choose appropriate action, such as 'I am afraid, and going to run away' or 'I am hungry and going to eat'. Thus, emotion concepts have an important role in helping us maintain our ongoing physiological balance, or *allostasis.* We will suggest here that infants can learn emotion concepts for the purpose of allostasis regulation, and that conceptualization is key component in emotional development. Moreover, we will suggest that social dyads facilitate concept learning because of a robust evolutionary feature seen in newborns of social species: they cannot survive alone and depend on conspecifics for allostasis regulation. Such social dependency creates a robust driving force for social learning of emotion concepts, and makes the social dyad, which is designed to regulate the infant's allostasis, an optimal medium for concept learning. In line with that, we will review evidence showing that the neural reference space for *emotion* overlaps with neural circuits that support *allostasis* (striatum, amygdala, and hypothalamus) and *conceptualization* (medial prefrontal cortex, posterior cingulate cortex), and that their developmental trajectories are interrelated, and depend on synchronous social care.

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Self-regulation in adulthood biologically depends on social regulation in early life

Among social species, such as mammals and most birds, newborns cannot survive on their own, and completely rely on a dedicated caregiver to regulate their ongoing physiological balance, or *allostasis* [1•,2•]. Newborns need social assistance in regulating their energy expenditure, temperature and immune function [3•], and accordingly, early life care ensures the newborn's survival and growth. Importantly, while mothers repeatedly regulate their offspring's allostasis, they also foster the development of self-regulation [4•,5]. Offspring brain development depends on the provisioning of adequate maternal care in early life, particularly in neural circuitry involved in allostasis, including the nucleus accumbens (NAcc), amygdala, and hypothalamus-pituitary-adrenal axis (HPA axis) [4•,6••,7]. It was demonstrated in mice that insufficient regulation of pups' allostasis, such as in cases of maternal separation [8] or low levels of maternal care [9], cause lasting modifications of the allostasis regulation system, reducing its efficiency to accommodate stressful events [6••]. Specifically, insufficient maternal care causes increased sensitivity of neuroendocrine and behavioral stress response, including a long term increase in HPA axis reactivity, changes in glucocorticoid receptor expression in the hippocampus, and increased basal levels of corticosterone [8], all key allostatic agents [6••]. The manifestations of such neuroendocrine changes relate to the animal's behavioral phenotype of self-regulation, including decreased exploration and increased inhibition behaviors in pups [10•]. In addition to these HPA effects, early life social care has consequences for the developmental trajectory of limbic-motivational regions supporting allostasis, and the shaping of behavior. For example, offspring of low maternal behavior dams show a decreased density of benzodiazepine receptors in the amygdala, less expression of estrogen receptors in the hypothalamus, and altered dopaminergic release in reward regions, behaviorally manifested by increased indices of anxiety-like behavior and decreased maternal sensitivity later in life (for review see [10•]). Thus, the development of the neural infrastructure needed for allostatic self-regulation in adulthood depends on social regulation of allostasis in early life, which also 'programs' the offspring's long-term behavioral phenotype of self-regulation.

Synchrony is a strategy for social regulation of allostasis

One efficient strategy to regulate someone else's allostasis is with bio-behavioral *synchrony*. Parent–infant bio-behavioral synchrony is the matching of behavior, affective states, and biological rhythms between parent and child, organized in an ongoing coherent pattern [11••]. In humans, parent–infant synchrony has been thoroughly studied and synchronous parenting behavior was found to be a reliable proxy for parent–infant attachment, and reflects parental sensitivity and attunement to the infant [11••]. Synchrony predicts optimal emotional development, including the ability to recognize emotion in others and to self-regulate emotion [11••]. Synchronous caregiving is often considered the source of infants' affective regulation, which sets the ground for optimal emotional development [11••]. On the contrary, children raised without experiencing sufficient social synchrony will suffer from atypical emotional development [11••,12•]. However, while parent–infant synchrony is established as important for attachment and affective regulation, we propose here that synchrony regulates much more than the infant's affect; synchrony is evolutionarily predisposed to keep infants alive. Starting from gestation, a mother controls her fetus's allostasis via mother-fetus physiological synchronization [13]. After birth, mothers continue to regulate the infants' allostasis [14–16] using the same synchrony strategy. Mothers regulate their infants' temperature by holding them close so that their temperatures synchronize [15]. Mothers regulate their infants' arousal with voice (by singing, or speaking loudly or softly) [17], synchronizing their heart rates [18]. Mothers regulate their infants' immune function by breastfeeding, synchronizing their gut-macrobiota and antigen-specific antibodies [19]. Synchrony is an efficient strategy for social regulation of allostasis in multiple physiological systems. Critically, when a caretaker consistently cares for the infant via synchrony, in addition to ensuring survival, she/he implicitly creates an optimal environment for learning.

Synchronous care facilitates learning of abstract (emotion) concepts

Early social care determines the development of offspring self-regulation [20]. In contrast with other species, humans are special because they have the cognitive ability to link abstract[a] concepts to the regulation of allostasis. Infants learn to categorize information based on co-occurrence probability via *statistical learning* [23–25]. Detecting structure within the environment is a critical step in development, from a meaningless stream of unpredicted sensory information to populations of instances grouped into categories that can be mentally represented as concepts [25–27] (for example, with experience the spatial statistical regularity in facial features perceived by the infant, will gradually be conceptualized as a 'face'). Within social dyads, caretakers implicitly facilitate statistical learning, by providing temporal conditioning between concept learning and the reward gained from social interaction. This is consistent with the broader view that infants are 'rational constructivists' who are actively sampling information in their environment [28]. Caretakers act as both the tutor (introducing new concepts, often with language) and the reinforcement (via the social regulation of allostasis). Since allostasis is regulated by a social agent, certain social concepts appear to be the first and most robust concepts to be learned: the conditioning between *allostasis* and *human* will result in a rapid and powerful learning of a fundamental social concept: *mommy* (i.e. the agent that repeatedly makes it all better) [29]. Similarly, this concept can be *daddy*, or other caretaker(s) who consistently meets the allostatic needs of the infant. Once fundamental social concepts for caregivers are learned, infants will gradually acquire other culturally relevant concepts, introduced by caretakers, and aid in the regulation of allostasis.

Emotion concepts are among the concepts that best predict an individuals' ability to regulate their own allostasis throughout the lifespan [30]. Affect can be thought of as the interoceptive consequences of allostatic changes. As such, the properties of affect, namely valence and arousal, can be defined using the concept allostasis: valence represents the subjective experience of deviation from allostasis (negative valence) or regaining allostasis (positive affect), and we can further speculate that arousal represents the amplitude of the change. Emotion concepts help to organize affective states within a given situation into meaningful events based on past experiences. These concepts convey and organize information about eliciting circumstances, actions and predicted outcomes. Critically, emotion concepts are not static representations, they are flexible predictions that are populated by a set of variable instances—they are grounded [31] by modality specific information tied to the situations in which they occur [32,33]. Simply invoking an emotion concept can have a powerful impact on the experience or perception of affective (i.e. allostatically relevant) information [34]. As such, emotion concepts shape behavior and physiology [35], serving as tools to regulate allostasis.

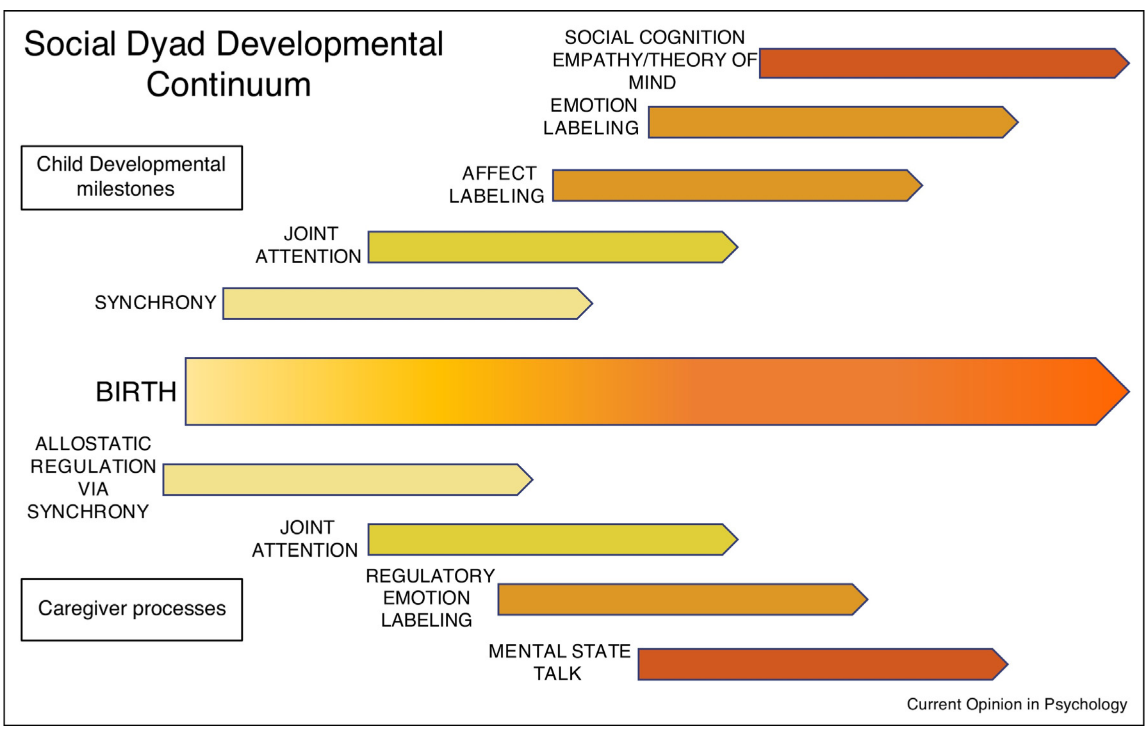
Beginning in early development, emotion concepts are built in the context of social dyads. Infants learn new concepts by synchronizing their attention with others, during instances of joint attention [36] and by harnessing the power of language. Emotion categories are not made of homogenous instances of experience, and not all instances within an emotion category (for example 'fear') look alike, feel alike, or have the same biological signature [37•]. We have proposed that language (including *words* for emotions) helps to overcome the abstract, varied and situated nature of emotional instances [37•,38•]. Words overcome variation by serving as an 'essence placeholder' or 'glue' to join the instances into a category [39]. Acquisition of emotion concepts appears to start broadly. Rudimentary concepts for affective states — displeasure and pleasure reliably appear first [40••], and broadly indicate

[a] Here we use the term abstract to refer to emotion concepts as relatively less physically or spatially constrained than other more 'concrete' concepts. This does not imply that these concepts cannot also be 'grounded' in the sense that their representation relies on whole brain patterns of activity and impacts the periphery. Indeed, there is ample evidence that emotion concepts are grounded in different sensory and motor modalities [21] (for review see [22]).

allostatic status (e.g. *negative affect* — deviation from allostasis versus *positive affect* — regaining allostasis). Detailed emotion concepts (e.g. *anger* or *sadness*) emerge more slowly over early childhood [40••]. In the social dyad, language use guides the complex statistical learning about emotions [41]. Caretaker use of emotion words (as well as other mental language, including words for thoughts and desires) predicts later offspring use of emotion terms [42]. Importantly, early caregiver use of emotion words is most frequently directed at labeling the infant's state (as opposed to self-labeling in the adult) in the context of regulation [43], serving to directly tie these concepts to an infant's allostasis. Moreover, prevalence of joint-attention in the social-dyad within the first year of life predicts the degree to which a child uses emotion language later on [44]. Thus, the social dyad is a vehicle that promotes the temporal conditioning between the use of emotion concepts and allostasis regulation. In synchronous dyads, this emotion concept learning is augmented by reinforcement from allostasis regulation, such that synchronous care facilitates the development of functional abstract (e.g. emotion) concepts.

Caregiver construction of emotions is a social strategy designed to acknowledge and eventually regulate the infant's allostasis [6••]. The caretaker, who is attuned to their infant's allostasis, constantly organizes their infant's momentary subjective experience into constructed emotion categories. Humans can learn to categorize instances of their own affective experience into emotion categories by relying on these early experiences conferred by the social dyad [45]. Children gradually learn to share their own emotions with others, and later to infer and share the emotions of others [46,47]. As such, emotion is inherently a social feature of experience. Learning to independently categorize subjective experience into emotion categories is a milestone in emotion development [48,49], which depends on synchronous care (Figure 1). Correspondingly, emotion concepts also vary considerably cross-culturally [50] because the situations, actions, social perspectives, etc., that are highlighted by a shared concept vary based on the values and structure of a culture. Different cultures use different modes of regulating the nervous system with concepts. For example some cultures appear to conceptualize 'affective'

Figure 1



A dyadic continuum of emotion development. Infants' developmental milestones are contingent on caregiver provisioning of allostasis regulation and language use. As caregivers regulate the infants' allostasis, infants gain experience in the rudimentary social skill of synchrony. Thereafter, as attention develops [53], infants learn to share their attention with the caretaker [54], and to synchronize conceptual knowledge. Synchronous parenting fosters the child's ability to use concepts [55•], and parental use of mental state language promote children to label their own emotions [42] and later to infer and represent other people's mental states [42,43,46]. Children rely on the social conditioning between emotion concepts and allostasis for the development of social cognition, as they learn to use emotion concepts for understanding and regulating other people's allostasis. The color gradient represents the development of concepts; darker color indicates the infant's growing ability to represent concepts and therefore engage in self-regulation. Synchronous caregivers carefully adjust their input per the infant's developmental stage.

events with less mentalization but more action concepts [51•,52•], suggesting that there may be uncharted cultural variability in allostasis regulation, and the optimal trajectory for the social dyadic continuum (Figure 1).

Caregiver processes are critical for conceptualization and emotion development

As illustrated in Figure 1, a cascade of caregiver processes unfold across development, which promote conceptualization, and allow for emotion development in the infant to occur. Variability in the quality of caregiver processes can impact this developmental trajectory of emotion. In cases of insufficient maternal regulation, the optimal developmental trajectory shifts to place infants at risk of psychopathology [56]. It was recently demonstrated that mothers who suffer from post-partum depression are less synchronous with their infants, and such reduced social synchrony disrupts the infant's emotion regulation [57•]. The authors suggested that compromised regulation of emotion is behaviorally transferred from the depressed mother to her infant. It was separately demonstrated that parent–infant synchrony promotes children's use of concepts [12•], and reduced maternal responsiveness among post-partum depressed mothers impairs infants' concept learning [58]. Mothers suffering from post-partum depression use less infant directed speech and show difficulty in establishing and maintaining events of joint attention [55•]. Accordingly, post-partum maternal depression adversely affects infants' language development [55•]. Moreover, aberrant social experience among abused children is associated with children's perceptions of emotion expressions, such as higher sensitivity to anger cues [59•]. Importantly, lack of early emotion socialization can be remediated in part by later caregiver use of emotion language (i.e. introduced to adopted children at three years of age) [60], suggesting some flexibility in the ideal developmental trajectory, and marking the importance of childhood experience in emotion development.

Building on this evidence that social experience and maternal care are crucial for both concept and emotion development, it is suggested here that synchrony, emotion and conceptualization are interrelated. We propose that synchronous care supports optimal emotion development because it fosters the conceptualization of emotional events, which is critical for self-regulation. The shift in emotion development seen in pathological dyads could be the result of impaired conceptualization due to insufficient maternal regulation. Thus, the mechanistic role of conceptualization in emotion development across childhood warrants future empirical investigations.

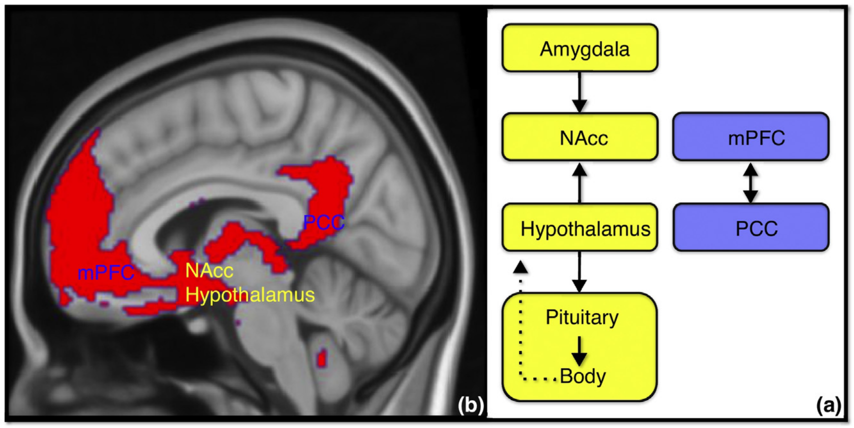
Common neural reference space for emotion, allostasis, conceptualization and synchronous maternal care

Inspecting the neural circuits that support conceptualization of emotion corresponds with the theoretical and empirical links between emotion concepts and allostasis. The neural reference space for emotions, as assessed in neuroimaging meta-analysis [61••], can be decomposed to regions associated with conceptualization, including the medial prefrontal cortex (mPFC) and posterior cingulate cortex (PCC) [62], and regions associated with allostasis, particularly the striatum, hypothalamus and amygdala [6••]. These regions are consistently recruited in studies of any discrete emotion category, including fear, disgust, happiness, sadness and anger [61••]. Thus, these regions are not specific to one emotion category, but instead are involved when emotions are conceptualized as *a category*. This suggests that humans can associate neural features supporting allostasis and conceptualization when categorizing emotions.

The use of concepts for allostasis regulation is not suggested to be specific to emotion. Instead it is suggested to be a domain general mechanism for regulation and learning. Conceptualization supports social and self-regulation, while allostasis regulation reinforces and fosters concept learning. The same subcortical neural circuits associated with allostasis and cortical circuits associated with conceptualization (both consistently involved in emotion), are also involved in social processing [63], and specifically in synchronous mothering, as demonstrated in mothers' brains [64•]. Synchronous mothers who are extremely attuned to their infants' allostasis have increased neural connectivity between the cortical circuit supporting conceptualization (mPFC and PCC) and the subcortical circuit supporting allostasis (NAcc, hypothalamus and amygdala) [64•]. Moreover, highly synchronous mothers show stronger striatal dopaminergic responses to their infant [64•]. Striatal dopamine, which was linked to maternal synchrony [64•], is a key allostatic agent [65–67]. Thus, it seems that neural circuits that support allostasis regulation and those supporting conceptualization are domain general neural circuits, which interact to realize different kinds of experiences, including emotion (regulation) and social regulation (Figure 2).

Similar to the developmental trajectory of emotion, the neural circuitry that supports conceptualization takes years to develop [72]. The neural association between the PCC and mPFC, is not wired at birth [73••] and strengthens linearly throughout adolescence [74]. Interestingly, there is a temporal link between the maturation of this mPFC-PCC circuit and children's ability to use concepts [75,76], and to self-regulate their emotions [77••]. In addition to the cortical circuit potentially supporting conceptualization, the cortico-limbic association, which potentially links conceptualization to allostasis, also takes years to develop. The mesolimbic dopaminergic system, which has a role in detecting allostatic deviations [78], matures very early in life, whereas mesocortical system, involved in cortico-limbic integration, continue to

Figure 2



Neural circuits supporting allostasis and conceptualization associate in the human brain to support multiple mental experiences, including emotion. **(a)** A neural model for allostasis (yellow) and conceptualization (blue). The amygdala, nucleus accumbens (NAcc), hypothalamus and connecting pituitary secretory gland are involved in allostasis regulation [6••]. The hypothalamus-pituitary endocrine system is a brain–body feedback pathway, which regulates the adrenal gland (via the HPA axis), but also gonadal and thyroid function, altogether controlling multiple allostatic processes including growth, reproduction, immunity, stress and metabolism [68]. The medial prefrontal cortex (mPFC) and posterior cingulate cortex (PCC) have been shown to be involved in humans' mental ability to hold and use internal representations of concepts [62,69]. **(b)** In humans, these regions are intrinsically connected, forming a neural network [63] that associates limbic circuits (in yellow) with cortical circuits (in blue), potentially demonstrating a functional association between allostasis and conceptualization. Neural function in this circuitry has been associated with different experiences, including emotion [70••], social functioning [71] and synchronous bonding [64•].

develop into early adulthood [67]. It was recently documented that in the presence of mothers, children not only show improved affective regulation, they also show improved neural connectivity between the amygdala and mPFC [79••]. This suggests that caregivers support the infant's self-regulation via consolidation of the infants' cortico-limbic pathways [79••], which potentially links allostasis regulation to conceptualization.

Conclusions

Evidence suggests that while mothers synchronously care for their infants, using brain circuitry involved in conceptualization and allostasis [64•], infants gradually develop the equivalent neural circuitry [73••], providing the infrastructure for cognitive and emotional skills. With maturation of this neural circuitry, children develop independence in using emotion concepts to regulate their own allostasis. Moreover, with synchronous care, the social dyad becomes a template: children are experientially trained to become social experts, eventually learning to use emotion concepts to regulate their own, and other people's allostasis. This hypothesized mechanism for intergenerational transmission of emotion incorporates the important epigenetic and post-natal influences on emotion development, and points to future research that will assess emotion as an acquired scheme of culturally relevant concepts.

Conflict of interest statement

Nothing declared.

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