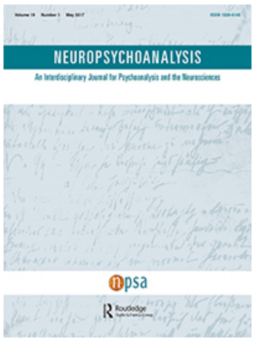

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Shir Atzil & Lisa Feldman Barrett

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COMMENTARY

# Social regulation of allostasis: Commentary on "Mentalizing homeostasis: The social origins of interoceptive inference" by Fotopoulou and Tsakiris

Shir Atzil[a] and Lisa Feldman Barrett[a,b*]

[a] *Athinoula A. Martinos Center for Biomedical Imaging, Massachusetts General Hospital, and Harvard Medical School, Charlestown, MA 02129, USA;* [b] *Department of Psychology, Northeastern University, Boston, MA 02115, USA*

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The paper by Fotopoulou and Tsakiris proposes that the most fundamental features of a human (e.g. the *minimal self*), including sensation, interoception and affect, develop in a relational manner, and rely on self-related concepts (e.g. *mentalizing homeostasis*) learned in a social context. Indeed, a growing body of literature supports this theory and emphasizes the role of social regulation during development. In support of Fotopoulou and Tsakiris, we too propose that the brain is fundamentally designed for allostasis, and that all feeling, thinking and perceiving proceeds with allostasis, its sensory consequences (interoception) and their low dimensional features (affect) at the core. We propose that infants depend on their caretakers for survival, such that social dyads keep the infant alive by promoting learning of a conceptual system for how to make sense of the body in the world. Within social dyads, infants' brains learn to conceptualize interoceptive and other perceptual information in the service of self-regulation. We further propose that the neural capacities for social functioning does not derive from inborn modules, but instead develop within social dyads while caregivers intentionally establish and support allostasis in the infant.

**Keywords:** allostasis; development; social regulation; brain

Humans live with other humans, or else they cannot survive. Specifically, infants depend on social care for maintaining physiological balance. Accordingly, infants' brains develop within social relationships, which begs the question of which neural features are inborn and which develop as a result of expectable input from the social environment. This is often framed as the nature vs. nurture debate. In their paper, Fotopoulou and Tsakiris confront this debate head on, and propose a hypothesis by which the most fundamental neural features are not predetermined, but instead are shaped after birth by social input, including sensory perception (both exteroception and interoception) and primary affective feelings (all of which are commonly assumed to be non-relational and innate) (Fotopoulou & Tsakiris, 2017). Fotopoulou and Tsakiris further suggest that the brain learns predictive models that help to prepare the body for upcoming changes in physiological regulation (which they define as homeostasis), using past knowledge and environmental cues as a guide (Fotopoulou & Tsakiris, 2017; Friston, 2010).

Indeed, the brain is fundamentally designed for maintaining physiological stability and balance (Sterling, 2012). However, in complex organisms living in complex social environments (e.g. humans), optimization of physiology, including regulation of energy balance, reproduction and protection, requires more than maintaining a stable set point or homeostatic threshold. In social species, such as ours, the brain needs to wire itself to the requirements of a dynamically changing environment, which demands (1) a range of physiological states that maintain balance and (2) that the brain predicts physiological needs and attempts to meet them *before* they are required by the body (e.g. if your blood pressure changes after you stand, you faint). The ongoing processes aimed to maintain physiological regulation through prediction and change are called *allostasis* (Ganzel, Morris, & Wethington, 2010; McEwen & Wingfield, 2003; Sterling, 2012). As opposed to homeostasis (which is defined as regulating a system toward a set point (Sterling, 2014)), allostasis considers the need for dynamic physiological balance in an ever-changing environment. We propose that a well-adapted brain keeps the body within an allostatic range of dynamically balanced physiological functions.

In the adult human brain, a complex system for allostasis and its sensory consequences (perceiving the sensory changes from within the body, called interoception) is constantly regulating physiology. The system integrates cortices that regulate the physiological systems of the body (cingulate cortices, anterior insula, medial prefrontal cortex and ventrolateral prefrontal cortex), the hippocampus and connecting amygdala, striatum and hypothalamic secretory

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*Corresponding author. Email: l.barrett@neu.edu pathways, as well as the periaqueductal gray, the parabrachial nucleus and the nucleus tractus solitarius (Ganzel et al., 2010; McEwen & Gianaros, 2010) (see Figure 1). The cortical regions, which are limbic in structure (allocortical or agranular/dysgranular in their cytoarchitectural arrangement (Barbas, 2015)) issue visceromotor and other physiological predictions to the autonomic nervous system, the immune system and the endocrine systems of the body (see Figure 2A). The neurons in most of these allostatic regulation regions directly synapse on the primary interoceptive cortex (located in the dorsal mid to posterior insula) (Kleckner et al., 2017). Via these connections, cortical regulation regions send the predicted sensory consequences of upcoming allostatic changes as interoceptive predictions to the primary interoceptive cortex (Barrett & Simmons, 2015) (see Figure 2B). Ascending interoceptive input from the body travels via small diameter pathways to the mid/posterior insula and are compared with the prediction. The difference is computed as prediction error signals (Barrett & Simmons, 2015). Striatal dopamine, which is sensitive to prediction error signals, supports learning and behavior that improves future predictions (Pessiglione, Seymour, Flandin, Dolan, & Frith, 2006). The hypothalamic–pituitary axis help to control allostasis by releasing endocrine hormones into circulation, regulating the adrenal glands, the gonads and the immune system (Ganzel et al., 2010).

In social species like humans, social interactions are in the service of allostasis. Newborns completely depend on their caretakers for allostasis. Resting-state functional magnetic resonance imaging probing spontaneous brain activity in newborns (Gao, Lin, Grewen, & Gilmore, 2016) revealed that humans are innately equipped with the infrastructure needed to sense the external and internal environment, but the neural infrastructure that enables information integration and prediction develops after birth (Gao et al., 2009). Newborns' brain-function is limited to perception–action regions, rather than multi-modal association cortices seen in adults (Fransson, Aden, Blennow, & Lagercrantz, 2011). Infants learn statistical regularities in the environment and couple them with sensory inputs from their own bodies (both spatial and temporal). Thus, association cortices form probabilistic models that can use environmental cues to predict and prepare for upcoming changes in allostasis. Such multi-modal integration in association cortices, which is key for neural prediction, develops with age. Predictions function like ad hoc concepts (Barrett, 2017b). A predicting brain does not ask "what is this?" but asks "what is this like?" (Bar, 2007), as it categorizes incoming sensory input relative to past experience (Barrett, 2017b). The categorical assembly of sensory events serves as an "essence placeholder" or "glue" to join these instances into a category and enables infants to construct rudimentary abstract concepts (Atzil, Gao, & Barrett, in preparation; Atzil & Gendron, 2017).

With consistent social care, one important concept that infants learn to construct is *caretaker*. Since most caretaker–infant interactions are aimed toward maintaining allostasis in the infant, the social concept *caretaker* contains interoceptive information. The statistical regularities between internal interoceptive sensations in the infant and external sensory experience of the caretaker allow children to associate interoceptive signals of allostasis to the presence of the caretaker. With development, the consistent temporal contingency between the social and interoceptive features of experience makes social information allostatically relevant, as infants will learn to use social information to predict about upcoming changes in allostasis, in the service of self-regulation. Moreover, since interoceptions are experienced as low dimensional representations of affect, the concept of *caregiver* has affective properties (unpleasantness of allostasis deviation and pleasantness of regaining allostasis). Fotopoulou and Tsakiris elegantly coin the term *Mentalizing homeostasis* (Fotopoulou & Tsakiris, 2017) to describe how instances of subjective bodily experiences are grouped into mentally represented categories. Concepts related to exteroception, interoception and affect are usually considered "self-related" (e.g. individual and not relational (Fotopoulou & Tsakiris, 2017)) and are assumed to develop independently from social learning. However, since infants develop in social dyads, these "self-related" concepts, and underlying neural circuitry, develop contingent on social care, and are learned and crafted by social input.

Social care, which is aimed to maintain allostasis in an infant, promotes the conceptual construction of exteroception, interoception and affect. Therefore, improved social regulation of allostasis will better promote the acquisition of such concepts (Atzil, Gao, & Barrett, in preparation; Atzil & Gendron, 2017). Parents who are attuned to their infants' needs will acknowledge and correct even mild allostatic disturbances (Atzil, Gao, & Barrett, in preparation; Atzil & Gendron, 2017). This helps the infant build a fine-tuned internal model of his or her body in the world. We therefore wish to highlight the importance of higher-order social cognition, such as theory of mind, to conceptual development in infants. While Fotopoulou and Tsakiris hypothesize that the caretaker's body is sufficient for the infant developing a conceptual representation of "self" (Fotopoulou & Tsakiris, 2017a), we hypothesize that caretakers use

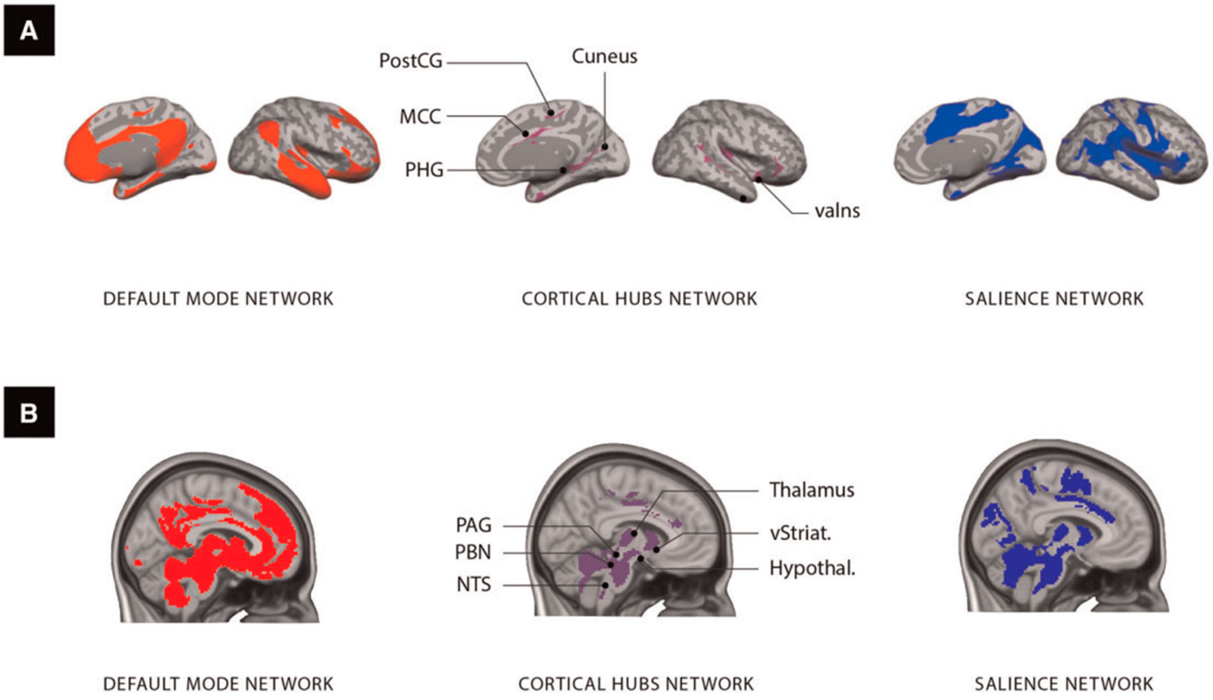

Figure 1. A large-scale system for allostasis and interoception in the human brain. (A) The system implementing allostasis and interoception is composed of two large-scale intrinsic networks (default mode network on the left; salience network on the right) that are interconnected by several hubs (shown in the middle; for coordinates, see Kleckner et al. (2017)). These maps were constructed with resting state BOLD data from 280 participants, binarized at $p < 10^{-5}$, and then replicated on a second sample of 270 participants. (B) The allostasis/interoception system, including subcortical connections, thresholded $P < 0.05$ uncorrected, replicated in 270 participants. Note: vaIns, Ventral anterior insula; MCC, midcingulate cortex; PHG, parahippocampal gyrus; PostCG, postcentral gyrus; PAG, periaqueductal gray; PBN, parabrachial nucleus; NTS, the nucleus of the solitary tract; vStriat., ventral striatum; Hypothal., hypothalamus. Adapted with permission from Kleckner et al. (2017) as adapted in Barrett (Barrett, 2017b; Kleckner et al., 2017b); color figures are available in the online version of this article.

their body and brain to regulate the infant's allostasis, and by that promoting the acquisition of concepts (Atzil, Gao, & Barrett, in preparation; Barrett, 2017a). The role of parental higher-order social cognition in infant development is supported by research on post-partum depressed mothers. Mothers who experience post-partum depression often physically care for their infants, but their theory of mind and attunement to the infants is attenuated, resulting in a shift of developmental trajectories toward social, emotional and cognitive growth (Apter-Levy, Feldman, Vakart, Ebstein, & Feldman, 2013; Granat, Gadassi, Gilboa-Schechtman, & Feldman, 2016). Among healthy mothers, individual differences in mother–infant synchronization (which relies on theory of mind (Atzil, Hendler, & Feldman, 2011)) lead to infants' improved conceptualization (Sohr-Preston & Scaramella, 2006) and emotional development (Feldman, 2007).

Fotopoulou and Tsakiris further state that sensory input deriving from social interaction, such as pleasant human touch, impacts the brain via two parallel neural pathways: the main tactile processing stream (via the thalamus and primary somatosensory cortex) and an additional parallel system, specialized for coding the "affective properties of social touch" (via a different part of the thalamus and posterior insula) (Fotopoulou & Tsakiris, 2017). Moreover, Fotopoulou and Tsakiris claim that the parallel system is specialized for social affective touch, and is not activated by robots or other nonhuman touch (Fotopoulou & Tsakiris, 2017). By contrast, our hypothesis is that part of an infant's concept of *caretaker* (including their touch) involves allostasis, such that human touch becomes understood as inputs that are relevant for allostasis, and are thus represented in the interoception/allostasis network, including the anterior and posterior insula. Specifically, since the predictive brain learns to use social information to prepare for allostasis changes, the provision of human touch involves allostatic predictions (Atzil et al., in preparation; Barrett, 2017b). Thus, the involvement of the insular cortices is not necessarily evidence for a special "social affective touch system", but rather demonstrates the involvement of the interoception/allostasis system (Kleckner et al., 2017) (see Figure 2B). Social regulation of allostasis cannot be dichotomized into social-perception

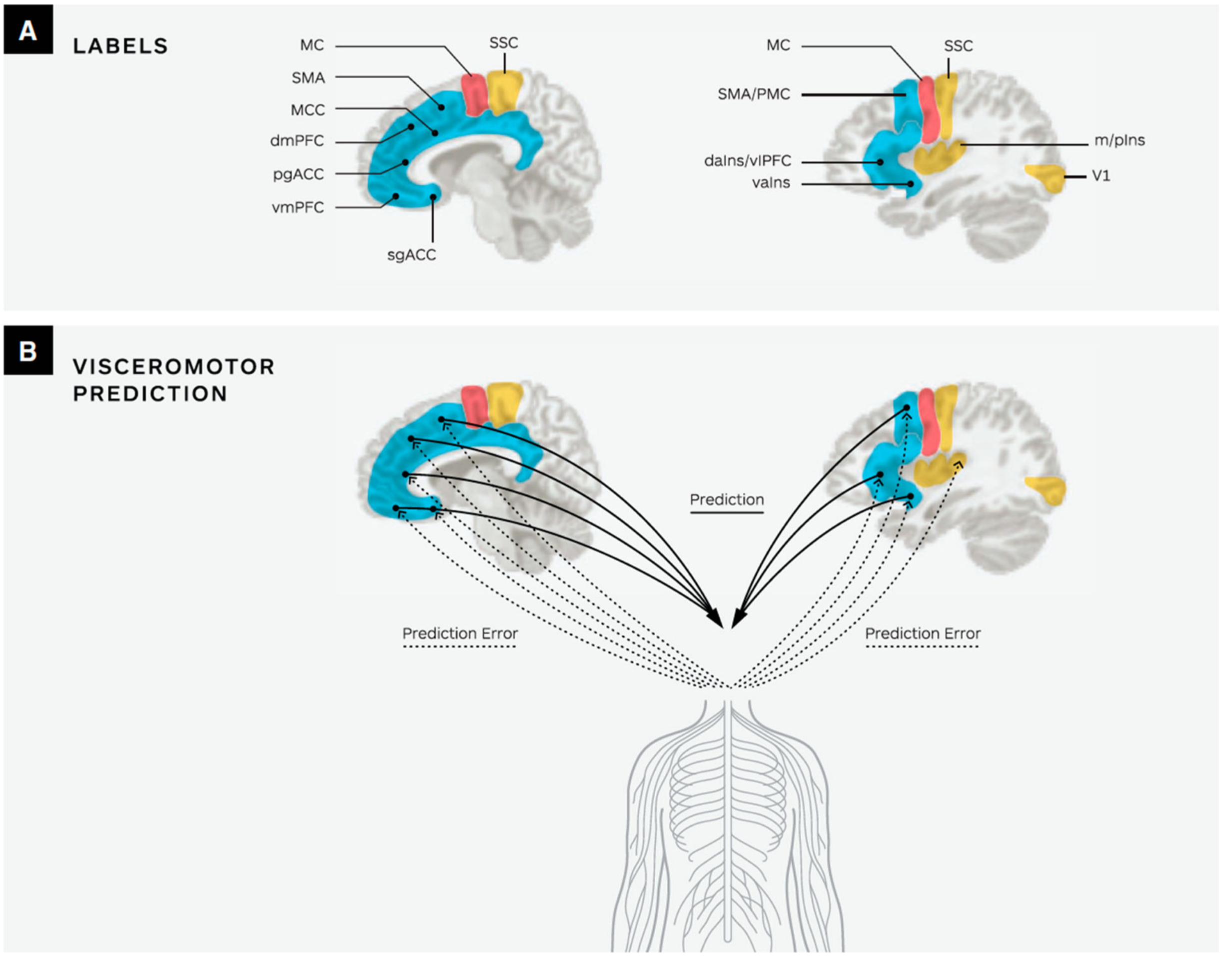

Figure 2. A depiction of visceromotor predictive coding in the human brain. (A) Key limbic and paralimbic vortices (SMA, MCC, dmPFC, pgACC, vmPFC, sgACC) provide cortical control of the body internal milieu. The primary motor cortex is labeled as MC. For simplicity, only primary visual cortex (V1), interoceptive cortex (m/pIns), and somatosensory cortex (SSC) are shown. Subcortical regions are not shown. (B) Limbic cortices initiate visceromotor predictions that descend to the body via the hypothalamus and brainstem nuclei (e.g. PAG, PBN and nucleus of the solitary tract) to regulate the autonomic, neuroendocrine and immune systems (solid lines). The ascending sensory inputs from the internal milieu of the body are carried along the vagus nerve and small diameter C and Aδ fibers to limbic regions (dotted lines). Comparisons between prediction signals and ascending sensory input result in prediction error that is available to update the brain's internal model. Supplementary motor area-SMA; middle cingulate cortex- MCC; dorsomedial prefrontal cortex- dmPFC; pregenual anterior cingulate cortex - pgACC; ventromedial prefrontal cortex- vmPFC; subgenual anterior cingulate cortex- sgACC; middle and posterior insula- m/pIns. Adapted with permission from Barrett (2017b). (See online version for color figures.).

and interoceptive parallel processes. Instead, they are two features of one experience.

Even with these concerns, our view is that the hypotheses raised by Fotopoulou and Tsakiris are novel and important for three reasons. First, they contribute to the long-standing yet relevant nature vs. nurture debate. Fotopoulou and Tsakiris move the debate forward by considering an environmental/social role in the development of the most primary neural features (exteroception, interoception and affect, which they call the *minimal self* (Fotopoulou & Tsakiris, 2017)). Second, Fotopoulou and Tsakiris contribute to the growing body of literature that proposes a role for domain-general processes like homeostasis (and allostasis) in the construction of human mental experience (Atzil, Gao, & Barrett, in preparation; Atzil & Gendron, 2017). The human brain is not a set of inborn universal modules. Instead, human experience is constructed ad hoc for the purpose of allostasis regulation, and depends on social context. Last, Fotopoulou and Tsakiris' hypothesis points to the importance of social interactions for brain development, consistent with other views (Atzil, Gao, & Barrett, in preparation; Barrett, 2017a). It is widely accepted that social input throughout life is important for the development of social cognition (Feldman, 2015). However, social input in early life might not only be responsible for the development of social cognition, but might also shape the entire conceptual system, from complex abstract concepts such as emotions (Atzil & Gendron, 2017), to the most primary sensory concept about the self (Fotopoulou & Tsakiris, 2017).

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No potential conflict of interest was reported by the authors.

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## References

Apter-Levy, Y., Feldman, M., Vakart, A., Ebstein, R. P., & Feldman, R. (2013). Impact of maternal depression across the first 6 years of life on the child's mental health, social engagement, and empathy: The moderating role of oxytocin. *American Journal of Psychiatry*, *170*(10), 1161–1168. doi:10.1176/appi.ajp.2013.12121597

Atzil, S., Gao, W., & Barrett, L. F. (in preparation). *Growing a social brain*.

Atzil, S., & Gendron, M. (2017). Bio-behavioral synchrony and the development of emotion: A role for conceptualization. *Current Opinion in Psychology.*

Atzil, S., Hendler, T., & Feldman, R. (2011). Specifying the neurobiological basis of human attachment: Brain, hormones, and behavior in synchronous and intrusive mothers. *Neuropsychopharmacology*, *36*(13), 2603–2615. http://www.nature.com/npp/journal/v36/n13/suppinfo/npp2011172s1.html

Bar, M. (2007). The proactive brain: Using analogies and associations to generate predictions. *Trends in Cognitive Sciences*, *11*(7), 280–289.

Barbas, H. (2015). General cortical and special prefrontal connections: Principles from structure to function. *Annual Review of Neuroscience*, *38*, 269–289. doi:10.1146/annurev-neuro-071714-033936

Barrett, L. F. (2017a). *How emotions are made.* Boston, MA: Houghton Mifflin Harcourt.

Barrett, L. F. (2017b). The theory of constructed emotion: An active inference account of interoception and categorization. *Social Cognitive & Affective Neuroscience.* doi:10.1093/scan/nsw154

Barrett, L. F., & Simmons, W. K. (2015). Interoceptive predictions in the brain. *Nature Reviews Neuroscience*, *16*(7), 419–429. doi:10.1038/nrn3950

Feldman, R. (2007). On the origins of background emotions: From affect synchrony to symbolic expression. *Emotion*, *7*(3), 601–611. doi:10.1037/1528-3542.7.3.601

Feldman, R. (2015). Sensitive periods in human social development: New insights from research on oxytocin, synchrony, and high-risk parenting. *Development and Psychopathology*, *27*(2), 369–395. doi:10.1017/S0954579415000048

Fotopoulou, A., & Tsakiris, M. (2017). Mentalizing homeostasis: The social origins of interoceptive inference. *Neuropsychoanalysis,* *19*(1), 3–28. doi:10.1080/15294145.2017.1294031.

Fransson, P., Aden, U., Blennow, M., & Lagercrantz, H. (2011). The functional architecture of the infant brain as revealed by resting-state fMRI. *Cerebral Cortex*, *21*(1), 145–154. doi:10.1093/cercor/bhq071

Friston, K. (2010). The free-energy principle: A unified brain theory? *Nature Reviews Neuroscience*, *11*(2), 127–138. http://www.nature.com/nrn/journal/v11/n2/suppinfo/nrn2787_S1.html

Ganzel, B. L., Morris, P. A., & Wethington, E. (2010). Allostasis and the human brain: Integrating models of stress from the social and life sciences. *Psychological Review*, *117*(1), 134–174. doi:10.1037/a0017773

Gao, W., Lin, W., Grewen, K., & Gilmore, J. H. (2016). Functional connectivity of the infant human brain plastic and modifiable. *The Neuroscientist*. doi:10.1177/1073858416635986

Gao, W., Zhu, H., Giovanello, K. S., Smith, J. K., Shen, D., Gilmore, J. H., & Lin, W. (2009). Evidence on the emergence of the brain's default network from 2-week-old to 2-year-old healthy pediatric subjects. *Proceedings of the National Academy of Sciences*, *106*(16), 6790–6795.

Granat, A., Gadassi, R., Gilboa-Schechtman, E., & Feldman, R. (2016). Maternal depression and anxiety, social synchrony, and infant regulation of negative and positive emotions. *Emotion*. Advance online publication. doi:10.1037/emo0000204

Kleckner, I., Zhang, J., Touroutoglou, A., Chanes, L., Xia, C., Simmons, W. K., … Barrett, L. (2017). Evidence for a large-scale brain system supporting allostasis and interoception in humans. *bioRxiv.* doi:10.1101/098970

McEwen, B. S., & Gianaros, P. J. (2010). Central role of the brain in stress and adaptation: Links to socioeconomic status, health, and disease. *Annals of the New York Academy of Sciences*, *1186*(1), 190–222.

McEwen, B. S., & Wingfield, J. C. (2003). The concept of allostasis in biology and biomedicine. *Hormones and Behavior*, *43*(1), 2–15. doi:10.1016/S0018-506X(02)00024-7

Pessiglione, M., Seymour, B., Flandin, G., Dolan, R. J., & Frith, C. D. (2006). Dopamine-dependent prediction errors underpin reward-seeking behaviour in humans. *Nature*, *442*(7106), 1042–1045.

Sohr-Preston, S. L., & Scaramella, L. V. (2006). Implications of timing of maternal depressive symptoms for early cognitive and language development. *Clinical Child and Family Psychology Review*, *9*(1), 65–83. doi:10.1007/s10567-006-0004-2

Sterling, P. (2012). Allostasis: A model of predictive regulation. *Physiology & Behavior*, *106*(1), 5–15. doi:10.1016/j.physbeh.2011.06.004

Sterling, P. (2014). Homeostasis vs allostasis: Implications for brain function and mental disorders. *JAMA Psychiatry*, *71*(10), 1192–1193.