

Being in Tune With Your Body: The Emergence of Interoceptive Processing Through Caregiver–Infant Feeding Interactions

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ABSTRACT—*Interoception—the ability to perceive and respond to internal bodily sensations—is fundamental for the continuous regulation of physiological processes. Recently, it has been suggested that because infants depend completely on their caregivers for survival, the development of interoceptive processing emerges as a result of early dyadic interactions, and relies on caregivers’ ability to respond to and meet infants’ physiological needs. In this article, I examine how both caregivers’ and infants’ own characteristics contribute to the emergence and development of infants’ interoceptive processing. In particular, by focusing on feeding interactions, I suggest that infants build expectations about the cause of their internal sensations via a dynamic process of interoceptive distinction between self and other. This developmental account provides a framework that considers the complexity of early dyadic exchanges, and offers novel hypotheses for research investigating the mechanisms*

involved in the ontogeny of interoceptive processing and eating behaviors.

KEYWORDS—*dyadic interaction; feeding; interoception*

Before being able to express themselves verbally, infants actively engage in embodied, turn-taking, and rhythmic communication with their caregivers (Trevarthen & Aitken, 2001). Through these exchanges, infants are thought to gradually acquire information about their own bodies’ boundaries and capability for action by learning to bind in space and time information across multiple senses, such as vision, touch, and proprioception (the perception of the body’s position and movement) (Brinck et al., 2017). Although body perception is critical for infants’ ability to interact with the external environment, focusing on how infants integrate various streams of sensory and motor information overlooks what might be a critical component of body awareness essential for human survival: the ability to sense, interpret, and integrate signals about the physiological condition of the body (i.e., states such as heart rate, body temperature, itch, pain), also known as interoception (Craig, 2002; Critchley et al., 2004). In the past two decades, interest has increased in the study of interoception and, perhaps due to the multifaceted nature of the concept, different definitions and classifications have been proposed across the literature (Khalsa et al., 2018; Murphy et al., 2017; Quadt et al., 2018). However, the exact mechanisms through which interoceptive processing emerges and develops remain largely unknown.

Recently, researchers suggested that as a result of infants’ social-emotional dependence, the development of interoceptive processing relies on caregivers’ ability to respond to and meet babies’ physiological needs during the first months of life (Atzil et al., 2018; Fotopoulou & Tsakiris, 2017). In this article, I offer a developmental account of interoceptive processing that builds on these recent frameworks, and further highlights the importance of focusing on how both caregivers and infants contribute

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to the regulation of infants' internal states. Specifically, individual differences in the way infants initially detect and interpret signals to infer the state of their bodies moment by moment (i.e., perception) influence how these cues are conveyed to caregivers. Once a change in physiological state (e.g., hunger) is signaled, the caregiver's job is to recognize the infant's cues and respond with a specific behavior (e.g., feeding or changing a diaper) to meet the infant's needs. Through gradual but constant adjustments, the behaviors put in place within these interactions contribute to the infant's ability to dynamically anticipate perturbations and achieve long-term stability (i.e., allostasis; Petzschner et al., 2021; Sterling, 2012).

The kind of interoceptive learning that occurs during caregiver–infant interactions is exemplified in the feeding context. Because of its soothing function, feeding represents the primary regulatory mechanism of physiological state in newborns (Porges & Furman, 2011). However, the intrinsic social nature of human infant feeding suggests that both infants' own characteristics and caregivers' feeding behaviors contribute directly to the integration of infants' bodily experiences. On the one hand, infants have to correctly detect and communicate hunger and fullness signals originating in their bodies. On the other, from the outside, caregivers have to first identify and then promptly and appropriately respond to infants' cues. Through this cause–effect learning embedded in the caregiver–infant relationship in the first year of life, the boundaries between self and other are gradually differentiated and infants can move from predominantly caregiver-regulated feeding (i.e., other-regulated body) to a more independent, self-regulated body (see Hodges et al., 2020 for an account of self-regulation during feeding interactions). Over time, how in tune children are with their own body might depend on the delicate balance of these early reciprocal exchanges.

First, I discuss the development of interoceptive processing in infancy by illustrating the critical role of caregiver–infant interactions in light of recent research and theory. Then, I examine how, through feeding exchanges, infants develop the ability to accurately respond to and regulate their internal environment via a dynamic process of self-other distinction and blurring that is inherently bound to the dyad. I close with a discussion of empirical avenues for future developmental studies.

THE EMERGENCE OF INTEROCEPTIVE PROCESSING WITHIN THE DYAD

The ability to sense and integrate signals about the outside world in relation to one's own body (exteroception) is thought to develop through multisensory associations, such as the ability to detect contingencies between visual and proprioceptive stimulation (Rochat, 2009). In particular, embodied, turn-taking, and rhythmic communications in which infants engage with their caregivers are thought to facilitate self-other distinctions (Trevarthen & Aitken, 2001), suggesting that the multisensory

associations that infants form through dyadic interactions represent the primary sources of learning about one's own body. Although a few studies have provided evidence for some sensitivity to interoceptive signals in early infancy (e.g., Fairhurst et al., 2014; Maister et al., 2017), it is unclear whether interoceptive abilities develop as a result of similar processes.

Recently, the *embodied mentalization* account (Fotopoulou & Tsakiris, 2017) proposed that contingent, reciprocal exchanges with caregivers shape not only infants' body perception from the outside, but primarily their ability to interpret physiological states and maintain allostatic regulation (see also Atzil et al., 2018; Ciaunica & Crucianelli, 2019). Specifically, although infants can and do signal changes in internal bodily states (e.g., they rub their ears when their energy levels run low), it is ultimately up to caregivers to turn their attention to infants to change their physiological state until their needs are met (e.g., by rocking the child to sleep). Over time, reiterations of experiences of attunement (i.e., where the caregiver responds to the infant's requests) and misattunement (i.e., where the interaction between infant and caregiver is disrupted; e.g. Ainsworth, 1969) result in infants' ability to interpret what the body really needs at any given point.

Many studies on parent–infant synchrony and attachment have demonstrated that this biological and behavioral dyadic coordination is important for infants' socioemotional development and self-regulation (DiCorcia & Tronick, 2011; Feldman et al., 1999), providing (indirect) support for the idea that proximal exchanges between infants and caregivers are critical for the development of infants' ability to regulate their internal states. Converging evidence shows that coregulation during dyadic interactions promotes the development of stress response (Welch, 2016). In addition, proximal interpersonal interactions, such as those involving touch by the caregiver and breastfeeding, directly affect infants' physiological arousal and vagal development (see Crucianelli & Filippetti, 2020, for a review of the role of touch in development; Fotopoulou & Tsakiris, 2017; Quigley et al., 2017).

Infants play a critical role in these initial interactions, too. How effectively infants communicate their needs can significantly influence caregivers' response to their cues. For example, newborns have to seek the attention of their primary caregivers to regulate their temperature, maintain stable glucose levels, and be soothed from uncomfortable bowel movements due to the ongoing maturation of the intestinal barrier. Thus, the extent to which infants perceive a change in bodily state (e.g., at what point they react to a perturbation) and the way they communicate the perceived change (e.g., the quality and persistence of the signaling) are critical for initiating the interaction and therefore, for eliciting a response from a caregiver that results in having their needs met.

Converging evidence supporting this hypothesis shows that infants can adjust incoming stimulation and signal their needs accordingly, for example, by communicating their demands with

subtle cues at first and gradually increasing their cries for attention until the caregiver provides a response that is consistent with their demand (Beebe & Stern, 1977). Additionally, research on infants' cries demonstrates that several acoustic features of infants' cries are closely linked to their arousal levels (Porter et al., 1986), suggesting that the ways infants signal their needs change as a function of specific variations in bodily states (Wood & Gustafson, 2001). Thus, although caregivers ultimately determine whether infants' needs are acknowledged, babies are responsible for whether and how effectively their changes in internal states are perceived and signaled in the first place.

The fact that infants are in charge of successfully recognizing and conveying their demands suggests that they must perceive (consciously or unconsciously) that a perturbation of the interoceptive system has taken place. A few studies suggest that interoceptive processing emerges in infancy (Fairhurst et al., 2014; Maister et al., 2017). In one, researchers used a looking behavior paradigm to test whether 5-month-olds could differentiate visual stimuli that move in synchrony with their own heartbeats from visual stimuli that move out of synchrony (Maister et al., 2017). Infants displayed a visual preference for cardiac visual-auditory asynchrony, suggesting the presence of interoceptive sensitivity. Additionally, using the heartbeat evoked potential (HEP) as a cortical index of interoceptive processing, infants who displayed greater discrimination between synchronous and asynchronous cardiac rhythms also showed larger HEP amplitude. Although these results are compelling and represent the only direct evidence that infants are sensitive to interoceptive sensations, they do not explain the mechanisms underlying its development.

Specifically, how the ability to sense and respond to changes in interoceptive states emerges and develops across the lifespan is still debated. Interoceptive processing in adulthood has been explained by prediction error minimization mechanisms (predictive coding framework; Barrett & Simmons, 2015), whereby incoming sensory inputs are interpreted in light of prior beliefs derived from past events and evaluated in favor of the most likely cause of the current state of the body. Although a complete illustration of the predictive coding framework is beyond the scope of this article, it can provide a useful theoretical model to elucidate the developmental mechanisms of interoceptive processing and the critical interplay between children's own characteristics and parental influences.

As seen in Figure 1, the idea is that the ways infants perceive and signal their changes in physiological states elicit behavioral responses from others (i.e., their caregivers), gradually leading to the development of expectations about the origin of each change in bodily state perceived (see Atzil et al., 2018, for a similar account on the development of predictions through caregiving). Once a caregiver has become aware of her infant's signals, she is responsible for correctly interpreting the cues, and responding appropriately and promptly to them (Ainsworth, 1969).

Disruptions at any of these levels have implications for the development of interoceptive processing. If an infant's communication of his feelings of discomfort and a caregiver's response to the infant's cues (e.g., prompting the infant with food; see Figure 1, scenario A) are consistent, subsequent occurrences of similar changes in sensations lead to analogous inferences on the likely cause of the current state of the body (e.g., hunger) in the infant, which in turn guide his expression of the cues that led to the offer of food in previous transitions (Harshaw, 2008). Through interoceptive learning derived from the associations built through caregiver–infant interactions, the infant's internal environment is dynamically regulated as the incoming interoceptive signals and past experience are gradually matched, and their links are strengthened over time (Atzil et al., 2018).

However, disruptions may occur due to the caregiver's behavior, the infant's disposition or—as I propose here—a combination of the two. For example, if the infant's perception of his needs is delayed or his signaling is unclear (e.g., due to temperamental traits), the caregiver may respond in a way that is inconsistent with the infant's needs (e.g., she may change the baby's diaper rather than feeding him), thus impeding regulation (see Figure 1, scenario B). Also, despite the infant's clear communication of changes in physiological states, the caregiver's response may be incorrect (e.g., she may misinterpret what the baby needs), inappropriate (e.g., she may play with him when he is tired), delayed, or even completely lacking (see Figure 1, scenario C).

At each of these points, the infant will be unable to build reliable priors about his needs and instead would need to either frequently revise how these are signaled (in the case of a caregiver's misinterpretations and inappropriate responses) or in extreme cases (e.g., when responses are severely delayed or lacking), withdraw altogether. Through this dynamic process of attunement and misattunement that considers influences from both the caregiver and the infant, boundaries between bodily states derived from the self or the other (i.e., the caregiver's response to the infant's needs) may blur or differentiate. In the next section, I focus on how interoceptive self-other distinction versus blurring develops by considering feeding interactions.

INTEROCEPTIVE BLURRING AND DISTINCTION DURING FEEDING

During dyadic exchanges, infants build predictions about the origin of changes in their bodily state, so regularities of both caregivers' and infants' behaviors (i.e., their consistency, timing, and quality) are critical in establishing a responsive interaction that promotes the ability to accurately attribute the origin of bodily states to the self or to others. I refer to this ability as interoceptive self-other distinction.

Responsive feeding entails bidirectional and transactional relationships, whereby the infant provides cues that reflect both his biological needs and his disposition (Kent et al., 2006;

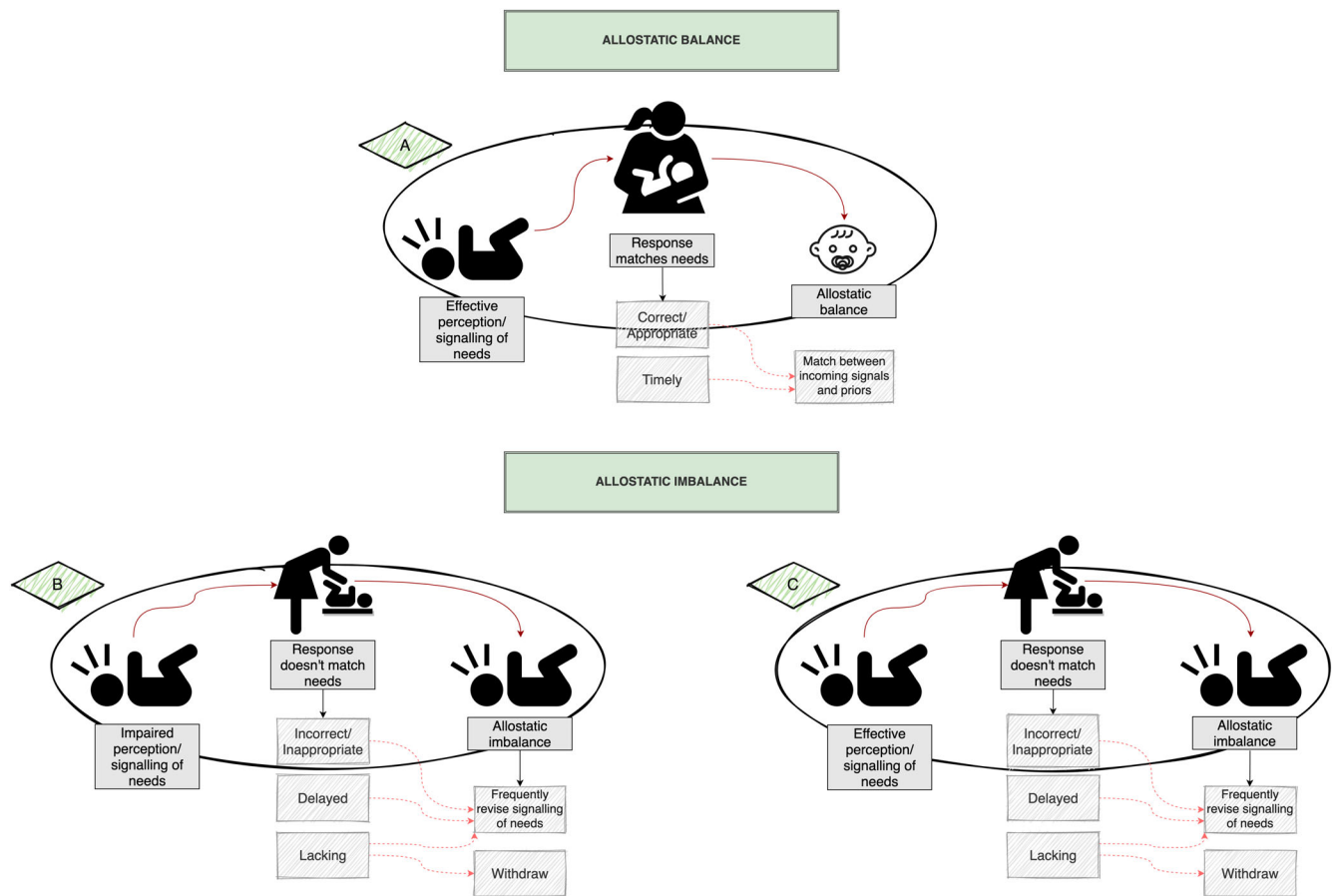


Figure 1. A schematic model of infants' development of interoceptive processing and allostatic regulation.

Note. Depending on how a change in physiological states is perceived and expressed by the infant, the caregiver will respond in a way that might or might not match the infant's need. In the most common scenario (A), a change in the state of the body is promptly communicated to the caregiver. However, if the infant's perception of his needs is impaired or his signaling is unclear (scenario B), or if the caregiver's response is inconsistent or completely lacking (scenario C), allostatic imbalance may arise as a result of systematic breaks in the interactions. The crying baby and breastfeeding images are by Luis Prado from the Noun Project.

Ounsted & Sleigh, 1975). Responsive feeding also presumes that the caregiver can respond promptly to these signals by matching the infant's demands (DiSantis et al., 2011). Research on the development of feeding behaviors suggests that, although infants are capable of adjusting the amount of food they consume to maintain stable caloric intake (Hodges et al., 2013), during the first year of life, caregivers can modify the start and end of feeding through their behaviors, thus affecting infants' food intake. For example, unresponsive feeding practices in which a caregiver overrides or misinterprets an infant's cues (e.g., restricting feeding or feeding to soothe an infant) influence the child's weight gain (Brown & Lee, 2011; Farrow & Blissett, 2006; Jansen et al., 2019; Stifter & Moding, 2015).

Because parental control during feeding leaves little space for the child's ability to detect, identify, and respond to his own internal bodily signals, these feeding practices may contribute to the blurring of interoceptive self-other boundaries and influence infants' future appraisal of these sensations. In particular, by favoring her own perception of needs, the caregiver can

disregard the infant's own hunger and fullness cues, leaving the child unable to build reliable and robust predictions that allow him to distinguish between changes in his own physiological states and the external prompts provided by the caregiver (see Tylka et al., 2015). The more the times the infant is not given the opportunity to sense and appraise the state of his body, the more likely he is to associate a variety of changes in internal sensations (e.g., emotional states such as anger or anxiety) with food intake. Although this hypothesis is compelling, researchers should test this proposition experimentally by directly measuring infants' regulation of hunger and satiety cues.

Nonetheless, and as mentioned earlier, impairments in the perception of or clarity in the expression of interoceptive cues on the infant's part can also promote disruptions in the feeding interaction. Thus, the association highlighted earlier will be amplified if the infant already shows inherent difficulties perceiving or signaling changes in his internal states (Farrow et al., 2018). In these cases, caregivers are more likely to miss or misinterpret infants' demands, and to alter their feeding practices in

response to the babies' predispositions toward food (e.g., Ashcroft et al., 2008). Indeed, infants' tendency to overeat in response to external food cues and emotions is associated with restrictive feeding practices (Schneider-Worthington et al., 2020), suggesting that the feeding environment may magnify children's characteristics and contribute to difficulties in the ability to discern among bodily states.

Similarly, temperamental traits can also affect feeding relationships. For example, infants who fuss and cry more frequently are more susceptible to excessive weight gain (Anzman-Frasca et al., 2014), especially if caregivers are more likely to offer food in response to these episodes (Stifter et al., 2015). These studies suggest that repeated occurrences of feeding exchanges in response to negative affect can foster associations between feeding/food and emotional states that are unrelated to hunger. Thus, enduring predispositions such as appetitive and temperamental traits may elicit an environment conducive to the development of disordered eating behaviors, for example, by leading caregivers to consistently respond with food to infants' distress that is not related to hunger, promoting the association between food and emotion regulation. These associations are also apparent—and difficult to disentangle—in conditions such as infantile colic, in which regulatory difficulties are thought to be at the core of excessive crying (Daelemans et al., 2018), and in which feeding problems and high levels of parental stress often co-occur (Scott-Jupp, 2018).

Overall, the available evidence demonstrates that both infants and caregivers can shape feeding transitions and influence infants' development of interoceptive boundaries. Unresolved disruptions in the cause–effect learning embedded in the caregiver–infant feeding interaction can eventually lead to a blurring between infants' own bodily states and caregivers' response to infants' needs. This interoceptive self–other blurring can have consequences for the ability to identify the interoceptive system being perturbed, to respond appropriately to these perturbations and, eventually, to master self-regulatory development, leaving the child unable to progress from feedings that are partly regulated by the caregiver to a more independent, self-regulated body.

CONCLUDING REMARKS AND LOOKING AHEAD

From the moment they are born and under typical circumstances, infants establish a feeding relationship with their primary caregivers via either breastfeeding or bottle-feeding transitions. From these first feeding interactions, infants and caregivers have to gradually adjust to each other's behaviors until they reach a feeding rhythm that is carefully balanced by both parties at each point in time. Building on recent theories of interoceptive development (Atzil et al., 2018; Fotopoulou & Tsakiris, 2017), I proposed that this balance gives rise to a gradual interoceptive self–other distinction that depends on factors related to both caregivers and infants.

Although I have suggested that studying the development of early feeding interactions can provide insights into the

developmental mechanisms underlying interoceptive processing, the hypotheses I have proposed in this article could be generalized to other interoceptive channels. For example, because the quality of caregiving has been associated with sympathetic reactivity in infants (Enlow et al., 2014), less responsive dyadic interactions could negatively affect the development of interoceptive processing of cardiac rhythm. Researchers should examine the psychophysiological processes that may explain how the processing of different interoceptive channels develops via early dyadic interactions.

Researchers should also use methods from developmental cognitive neuroscience to examine the neural basis underlying the development of interoceptive processing in infancy, by focusing on the interplay between caregiver and infant exchanges and how it changes dynamically as a function of interoceptive predictions about allostasis. In this regard, hyperscanning methods have gained more attention in recent years as a way of studying coordinated neural activity during parent–infant interactions as a biomarker of parents' sensitivity and children's development of emotion regulation (see Levy et al., 2021, for a review). Researchers could monitor oscillatory brain responses during interpersonal synchrony following situations of controlled homeostatic perturbations, examining how breakdowns at different levels of caregiver–infant synchrony affect different elements of perception.

One of the key questions of interoception relates to the developmental origins of interoceptive processing. By examining the caregiver–infant interaction as it unfolds, researchers may be able to elucidate the etiology and direction of causality between caregivers' and infants' influences, and how these change over time. Longitudinal designs may be able to identify patterns of changes across development and isolate the contribution of each individual factor. For example, the feeding interaction is subject to continuous changes and adjustments during the first 2 years of life. Thus, it would be interesting to combine observational and neural measures to longitudinally track the development of caregiver–infant feeding transitions from the nursing period to independent feeding in light of interoceptive self–other blurring and distinction, and to examine how emerging learned behavior and reward circuits can override visceral systems (Zeltser, 2018). In addition, studying the ontogeny of interoceptive processing may have wider implications for the field. By examining the factors that modulate the development of interoceptive processing, researchers may be able to shed light on disorders associated with impairments in interoception, such as anxiety and eating disorders (Murphy et al., 2017).

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