Alimentary Epigenetics: A Developmental Psychobiological Systems View of the Perception of Hunger, Thirst and Satiety.

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Alimentary epigenetics: A developmental psychobiological systems view of the perception of hunger, thirst and satiety ☆

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A B S T R A C T

Hunger, thirst and satiety have an enormous influence on cognition, behavior and development, yet we often take for granted that they are simply inborn or innate. Converging data and theory from both comparative and human domains, however, supports the conclusion that the phenomena hunger, thirst and satiety are not innate but rather emerge probabilistically as a function of experience during individual development. The metatheoretical perspective provided by developmental psychobiological systems theory provides a useful framework for organizing and synthesizing findings related to the development of the perception of hunger, thirst and satiety, or alimentary interoception. It is argued that neither developmental psychology nor the psychology of eating and drinking have adequately dealt with the ontogeny of alimentary interoception and that a more serious consideration of the species-typical developmental system of food and fluid intake and the many modifications that have been made therein is likely necessary for a full understanding of both alimentary and emotional development.

Hunger, thirst and satiety must be numbered among the most powerful influences on mood, behavior and development. After well over a century of modern scientific research on the subject, however, we still lack an adequate understanding of human eating (cf. Herman, 1996), including the phenomena of hunger, thirst and satiety. What is hunger? What is thirst? What is satiety? How

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do they develop over the course of individual ontogeny? How do they vary over the course of days, weeks, months and lifetimes? How does this development and variation interact with and/or influence the myriad psychological and behavioral processes that psychologists take interest in?

The vast majority of research and theory has focused on questions of the first type. That is, on discovering the underlying essences of these phenomena. A great deal of progress has thus been made with respect to understanding the *biological* and *behavioral* bases of hunger, thirst and satiety. A full treatment of these phenomena must, however, necessarily encompass their biological, behavioral, perceptual and cognitive aspects. All of these moreover are undoubtedly intimately interrelated, function simultaneously and, as the current paper will highlight, *develop* and change over time. A growing body of evidence suggests that the various systems involved in the regulation of food and fluid intake undergo substantial development and organization postnatally. The gastrointestinal (GI) tract and enteric nervous system, for example, are not fully developed at birth (Gershon, 1998). Their development and functioning are thus susceptible to a variety of perinatal environmental influences (e.g., Fåk, Ahrné, Molin, Jeppsson, & Weström, 2008; Rautava & Walker, 2007; Thompson, Wang, & Holmes, 2008), including nutrition-induced alterations of gene expression and patterns of DNA methylation (Waterland, 2006). Vagal[1] sensory innervation of the GI tract is similarly incomplete at birth and is thus open to ontogenetic influences, some of which have potentially serious consequences for health (Fox & Murphy, 2008).

The current paper will nonetheless focus on only one aspect of the complex system of influences that determine food and fluid intake: the development of the *perception* and *cognitive understanding* of hunger, thirst and satiety. The paper will thus focus on the interoceptive experience of appetitive motivation or *alimentary interoception* and on how human and non-human animals come to understand the relation of such interoceptive information to their own behavior and to exteroceptive stimuli in the environment. This paper will make the case that the available evidence favors the somewhat counterintuitive conclusion that, despite their critical role to survival, the phenomena of hunger, thirst and satiety are not "innate," "hard-wired" or genetically "programmed," but are instead the product of individual development (cf. Birch, 1998; Birch & Fisher, 1998; Blumberg, 2005; Booth, 1992; Le Magnen, 1998).

To make such a statement is *not* to claim that they are not or cannot be *inherited*, but only that the mechanism for their inheritance is largely extra-genetic[2] and that their expression is thus open to substantial experiential or ontogenetic influence. Such a claim finds support in data and theory from a number of fields, including developmental biology, developmental psychobiology and developmental evolutionary biology. The emerging consensus within these fields is that organisms inherit not simply a set of genes or a fixed genetic "program" but rather highly complex, structured developmental systems or "manifolds", of which DNA is only a part (e.g., Avital & Jablonka, 2001; Gottlieb, 1971; Gottlieb, 1997; Gottlieb, 2002a; Harper, 2005; Jablonka & Lamb, 2005; Johnston & Edwards, 2002; Lickliter & Honeycutt, 2003; Oyama, 2000; Oyama, Griffiths, & Gray, 2001). These inherited systems consist of a host of developmental resources, both internal and external to the organism, that tend to be conserved over time and which can thus contribute to the reliable reoccurrence of species-typical phenotypes over the course of generations. This expanded view of inheritance allows for potential non-genetic inheritance of even critical phenotypic outcomes, including food preferences, metabolism, thermoregulatory abilities, attachment and/or filial preferences, sexual preferences, predatory/anti-predatory behavior and phenomena such as hunger, thirst and satiety (see Blumberg, 2005; Jablonka & Lamb, 2005; Lickliter, 2005, for reviews).

The first part of the paper will provide an overview of developmental psychobiological systems theory. Next, theory and research supportive of a developmental psychobiological systems view of alimentary interoception will be reviewed. The paper will argue that neither developmental psychology nor the psychology of eating and drinking have adequately dealt with the subject of alimentary

[1] The vagus is the primary nerve connecting and carrying information between the GI tract and brain (Zhu, Wu, Owyang, & Li, 2000).

[2] Sometimes referred to as epi-, exo- or supra-genetic inheritance. All of these terms generally signify non-genetic inheritance, with the exception of the term *epigenetic*, which has a very different meaning in the fields of genetics and molecular biology than it does as typically employed in the field of psychology.

interoception and its development. The paper will also argue that a rethinking of alimentary interoception from a developmental psychobiological systems perspective, with particular emphasis on the species-typical system of food and fluid intake and the many modifications that have been made therein, will likely be far more fruitful for future researchers and theorists than simplistic evolutionary approaches.

Overview of developmental psychobiological systems theory

Developmental psychobiological systems theory is rooted historically in a number of different sources, including Lehrman's (1953, 1962) transactional approach to behavioral development, Schneirla's (1959) research and theory on animal behavior and Kuo's (1967) critique of both learning psychology and ethology (see Gottlieb, Wahlsten, & Lickliter, 2006; Oyama, 2000). Kuo (1967), for example, argued against strict behaviorism in favor of a broader, synthetic and developmental approach to behavior, writing that:

> ...the relationship between the behaving organism and its environment is an extremely complex and variable dynamic process...*behavior* is far more than the visible muscular movements. Besides such movements, the morphological, the physiological (biophysical and biochemical) changes, the developmental history of the animal, and the ever-changing environmental context are interwoven events which are essential and integral parts of behavior...In other words, *the study of behavior is a synthetic science*...the qualitative and quantitative analysis of the dynamic relationship between the organism and the external physical and social environment (p. 25).

Kuo thus advocated a far broader scope for and more interdisciplinary approach to the study of behavior than that espoused by traditional behavioral psychology.

Gottlieb's theory of *probabilistic epigenesis* (e.g., 1971, 1997, 2002b, 2007) builds on and draws out in a more formal way many of the principles implied by Kuo's epigenetic theory. The theory of probabilistic epigenesis is generally juxtaposed with the idea of *predetermined* epigenesis, which characterizes the influence of genes on development as a strictly unidirectional one, yielding a kind of direct "readout" of the "information" encoded in the genome. The notion of *probabilistic* epigenesis, in contrast, characterizes phenotypic outcomes as inherently probabilistic functions of developmental processes, entailing *bidirectional* interaction or *coaction*[3] between and within all levels of the organism–environment system (cf. Gottlieb et al., 2006). From this perspective, genetic, cellular, extracellular, physiological, neurological and all other influences (e.g., social, cultural) *coact* over time to produce phenotypic outcomes.

With respect to evolution, developmental psychobiological systems theory emphasizes that what are "selected for" over the course of generations are not isolated or isolatable genes or genomes but entire "developmental manifolds", or organism–environment systems (Gottlieb, 1971). These systems generally include at least (1) a relatively persistent physical environment, with relatively persistent chemical, thermal, physical and/or structural features, (2) a relatively persistent ecological milieu (including particular plants, parasites, fungi, bacteria, etc.) and, in the case of humans and other social animals, (3) a social or cultural milieu, potentially containing territories, customs, traditions, organizations, technology, language, knowledge, etc. (Gottlieb et al., 2006; Jablonka & Lamb, 2005). There is thus a great deal of room for both phenotypic stability and phenotypic variability contained in almost any organism's *extra-genetic* inheritance. As Blumberg (2008) writes, "there really is no need to hard-wire that which is learned quickly and efficiently through experience...behavior...can be molded under the guiding influence of persistent and mundane external factors" (pp. 36–37). A *genetic* "coding" for the relatively stable features of *extra-genetic* inheritance would make little sense from a biological standpoint, as it would mean less adaptive flexibility or plasticity for organisms that must

[3] The terms coaction and coact are employed by Gottlieb and others to highlight the fact that the "interaction" is not merely statistical interaction between isolated or isolatable variables and/or processes, but *coaction* between inseparable components of a dynamic system. Along these lines, Gottlieb and Halpern (2002) have criticized what they term the "analysis of variance mentality": that because two variables or factors can be isolated statistically, through the use of analysis of variance, they act (or interact) in the real world as isolated, independent contributors to the outcomes under study.

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persist under variable and changing environmental circumstances (cf. Ramsay, Seeley, Bolles, & Woods, 1996).

Psychobiologists have long taken a critical stance toward thinking guided by and oriented around concepts such as "instinct" and adjectives such as "innate", "inborn" and "instinctive", while also struggling to avoid the reification of artificial dichotomies based on such concepts (e.g., "nature" vs. "nurture", "innate" vs. "acquired"). Knight Dunlap (1919, 1922), founder of the short-lived journal *Psychobiology*, was one of the first major critics of such concepts and thinking. Dunlap (1922) wrote, for example:

> At the present time, I can see no way of distinguishing usefully between instinct and habit. All reactions are definite responses to definite stimulus patterns, and the exact character of the response is determined in every case by the inherited constitution of the organism *and* the stimulus pattern. All reactions are instinctive: all are acquired. If we consider instinct, we find it to be the form and method of habit-formation: if we consider habit, we find it to be the way in which instinct exhibits itself. Practically, we use the term *instinctive reaction* to designate any reaction whose antecedents we do not care, at the time, to inquire into; by *acquired reaction*, on the other hand, we mean those reactions for whose antecedents we intend to give some account. But let us beware of founding a psychology, social, general, individual, on such a distinction (p. 94).

The psychobiologist Lehrman (1953) later argued famously against the use of the term "instinct" in the field of ethology, writing that:

> Any instinct theory which regards "instinct" as immanent, preformed, inherited, or based on specific neural structures is bound to divert the investigation of behavior development from fundamental analysis and the study of developmental problems. Any such theory of "instinct" inevitably tends to short-circuit the scientist's investigation of intraorganic and organism–environment developmental relationships which underlie the development of "instinctive" behavior (p. 359).

Both Dunlap (1922) and Lehrman (1953) emphasize that we often use adjectives like "innate" and "instinctive" to describe a behavior or phenotype whose development we simply have not taken the time to investigate carefully and that such terms frequently have the effect of stifling developmental investigations of such outcomes. If an outcome is innate, why investigate it any further?

Mameli and Bateson, (2006) have recently put forward a philosophical critique of the concept of "innateness". These authors point out the high degree of conceptual confusion frequently caused by the use of the term. Its possible definitions range from "present at birth", "not acquired" and "not learned" to "genetically determined", "highly heritable" and "species-typical" (Mameli & Bateson, 2006, p. 177). These authors in fact tabulate 27 possible definitions of the term and point out that none of these provides an entirely adequate translation of the folk concept of "innateness" into a scientifically useful one. The various possible definitions of the term do not necessarily correlate with one another and it has yet to be shown whether or not they form any scientifically useful clusters (Bateson & Mameli, 2007). These authors conclude that it is best to avoid the use of the term entirely in science until such evidence is obtained. Throughout the current paper the term "innate" will thus be used only in the negative and then only to mean "unlearned", "not acquired" and "genetically pre-programmed".

In place of terms such as "innate" and artificial dichotomies such as "nature vs. nurture" and "innate vs. acquired" developmental psychobiological systems theorists have long advocated the systematic and unbiased exploration of the complexity embodied in the system(s) under study (e.g., Gottlieb, 1971; Lehrman, 1962). Investigations stemming from this framework have discovered a great many subtle (sometimes referred to as *non-obvious*) bidirectional interactions between the various possible levels of analysis, many of which are highly important for an understanding of both development and evolution (see Blumberg, 2005). Gottlieb (1971, 1997), for example, elaborated the non-obvious influence that prenatal exposure to a species-typical rearing environment has on the early development of perceptual preferences in ducklings. Gottlieb found that ducklings do not exhibit their normal species-typical preference for the maternal call of their own species—a preference that can easily appear to be "innate"—unless they experience their own embryonic vocalizations, which sound nothing like the maternal call of their species, during late prenatal development. As another example, the Brownheaded cowbird (*Molothrus ater*) is a brood parasitic species (that lays its eggs in the nests of other species, which then raise its hatchlings as their own) that has long been thought to have innate capacities of species-recognition and species-typical song production. Meredith West and Andrew King (e.g., West & King, 1985, 1988; King & West, 1983, 1989) have, however, elaborated the non-obvious influence on male song repertoire of subtle movements made by female cowbirds—movements hardly visible to the unaided human eye—that have the effect of shaping juvenile male song production. The deliberate study of such non-obvious factors, often driven by the dogged investigation of otherwise unusual or unexpected results, has shown that much of what has traditionally been categorized as simply *genetic* or *innate* turns out, on closer examination, to be the product of normally occurring *experience* within a normally occurring, species-typical developmental system or rearing environment (cf. Blumberg, 2005; Gottlieb, 1971; West & King, 1987).

An important generalization that can be made from developmental psychobiological systems theory is that the specific consequence(s) of a modification to a developmental system or species-typical rearing environment can seldom be predicted in advance of making the modification, or on *a priori* grounds. The complex system of factors, interactions and/or coactions that make up a given system entail that a modification at any point (physically, by adding, subtracting or altering the quantity and/or quality of some element, and/or temporally, by delaying or advancing some element) can potentially have reverberations or consequences throughout the system or at any given node of the system. The connection(s) between cause and effect may thus be far from obvious or intuitive in a complex and dynamic developmental system. Just as the knocking out of a gene may have unexpected effects or no obvious effect at all on an organism's development or on a given phenotypic outcome, modifying the nature, amount and/or timing of non-genetic developmental resources can have unpredictable and sometimes unexpected consequences for development (e.g., Blumberg, 2005; Columbus & Lickliter, 1998; Lickliter, 1993; Sleigh & Lickliter, 1997).

Applied to the area of the development of alimentary interoception, a developmental psychobiological systems perspective holds much promise for the generation of novel and potentially interesting and important questions and discoveries. Simply asking the questions, 'What is (or was) the species-typical rearing environment for *Homo sapiens*?' and 'What modifications to this species-typical rearing environment, particularly to the species-typical system of food and fluid intake, have been made during the last several centuries?' illustrate the kind of thinking that a developmental psychobiological systems perspective warrants. These questions, particularly the second, are empirically and historically answerable questions, as opposed to mere speculations about the evolutionary antecedents of modern outcomes. Although the current paper will not focus on these questions per se, the paper hopes to encourage such thinking by reviewing, for the first time,[4] what is currently known about the development of alimentary interoception.

The development of hunger, thirst and satiety

There have been many barriers to the study of the development of hunger, thirst and satiety but the greatest has surely been the tendency to assume such phenomena to be inborn, instinctive or innate. This same barrier has blocked or hindered progress in a number of other domains within psychology and related fields over the course of the last century (see Blumberg, 2005). Prior to Hebb (1949) the question of the development of hunger was largely ignored, as the predominant opinion was that hunger was simply inborn—something so critical to life, so essential to survival, that it could not possibly have been left to chance and learning. In other words, if anything were to be flawlessly inherited or genetically "programmed" it would be a critical outcome like hunger. Hunger was thus taken to be something which functions perfectly from the start, requiring little or no experiential input. As Bruch states (1969), "Hebb felt that in a phenomenon such as hunger the role of learning is often dismissed because the function has been traditionally conceived of as an innate drive, as a basic part of the organism's physiological endowment, subject only to the most superficial modifications" (p. 96).

[4] See Blumberg (2005) for a partial review of the comparative literature on the topic.

Although several early theorists acknowledged that experiential input or learning played an important role in hunger (e.g., Bash, 1939; Carlson, 1931; Hoelzel, 1927; Knapp, 1905; Wada, 1922), the questions of *how* this takes place was typically ignored. It was also taken for granted that this development always goes smoothly (e.g., Janowitz & Grossman, 1949). Hebb (1949) argued, in contrast, that many of the contradictions in the literature on hunger and eating were the result of the neglect to take into account the influence of cognition and development. Hebb's suggestion, particularly with respect to the development of alimentary interoception, has, however, largely been ignored in the six decades since he put it forward (see Birch, 1998; Birch & Fisher, 1998; Birch & Fisher, 2000; Blundell, 1979, for notable exceptions). A growing body of research and theory, both comparative and human, nonetheless points to the soundness of Hebb's proposal. A review of this research and theory will follow.

The development of hunger, thirst and satiety in non-human animals

The ethologist Spalding (1873) and the psychologists Baldwin (1896) and Thorndike (1899) were among the first to take an interest in the development of alimentary interoception. Each of these scientists made observations consistent with the view that, despite an "instinctive" or "innate" tendency to consume once in contact with water, domestic chicks must learn to associate thirst with drinking behaviors and with the exteroceptive qualities of water during early development. Baldwin (1896), for example, commented that:

> In the case of the fowl's drinking, it is not the mere fact that drinking and eating may differ in the degree to which the performance is congenital...but that instincts (in this case drinking) may be only half congenital, and may have to be supplemented by imitation, accident, intelligence, instruction, etc., in order to act, even when the actions are so necessary to life that the creature would certainly die if the function were not performed. That is the interesting point (p. 669).

Breed (1911) later made observations confirming these conjectures: in general, chicks initially came into contact with food or water accidentally and/or through social facilitation. As Breed writes:

> The chicks, left to develop naturally in the vicinity of food and water, usually found the water by fortuitous pecking or...in imitation of other chicks. By imitation here I mean that the performance of drinking by one chick in the presence of another sometimes stimulated that other itself to perform the drinking act (p. 76).

Despite these observations, Breed nonetheless adhered to the view that thirst is innate, believing that he had merely failed to test the development of drinking under conditions adequate to demonstrate this.

The ethologist Craig (1912, 1918) made extensive observations of Ring-doves (*Turtur risorius*) supportive of a developmental account of thirst. Craig (1912) concluded similarly that initial contact with water in pigeons is normally accidental, but is followed immediately by reflexive swallowing. The pigeons Craig studied showed no sign of an "innate" connection between the exteroceptive qualities of water and the act of drinking. On occasion individual pigeons even had to be shown how or else forced to drink by Craig. It took many repetitions for some birds, even after some experience drinking, to establish a reliable connection between the interoceptive stimulus to drink (thirst) and the exteroceptive qualities of water. According to Craig (1912):

> The dove does not instinctively give a drinking response to the sight or sound of water, nor to the touch of water on distal parts of the body...The young dove first gets its bill into the water, probably, chiefly by pecking: either pecking at objects in the water that attract its attention, or pecking in imitation of old birds...Though doves instinctively imitate pecking, they do not instinctively imitate drinking as such (p. 275).

The initial contact with water under conditions of thirst in these pigeons was thus not the result of an inborn connection between thirst and water but due largely to trial and error and/or social influences. In explaining his results, Craig introduced the distinction between the *appetitive* and *consummatory* components of motivated behavior: the *appetitive* components being very much influenced by experience and learning and the *consummatory* components being largely reflexive or "instinctive".

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Nearly half a century later, Kuo (1967) summarized similar experiments of his own investigating the development of alimentary interoception in pigeons and reported results similar to those described by Craig. According to Kuo, following a period of isolation, one group of pigeons:

> ...established the drinking habit without previous experience in one to six trials. This was done by placing a cup of water in front of the thirsty bird; if it failed to drink without help, the head was pressed down to make the beak touch the water. In every case, the pigeon started drinking immediately. This was repeated until the pigeon started to drink without help at the sight of water (p. 145).

In another group, pigeons were allowed to observe other birds eating and drinking following a period of isolation and, according to Kuo, acquired normal eating and drinking behavior as a consequence.

W.G. Hall and his colleagues, in a more recent series of studies with rat pups, have provided results consistent with this early body of research. Hall, Arnold, and Myers (2000), for example, found that chow- and liquid-diet-reared pups responded differently when dehydrated via sodium chloride injections at 21 days of age. Pups reared on chow responded with shorter latencies to drink and larger quantities consumed than pups reared entirely on a liquid diet, suggesting that pups reared on chow had learned to associate dehydration with the need to ingest water and that liquid-reared pups had not. In a second experiment, these authors demonstrated that a single experience with acute injection-induced dehydration was sufficient for the learning of an appetitive response in liquid-reared pups. According to Hall et al.:

> In the typical postweaning rearing situation, these peripheral signals as a matter of course become paired with drinking water, an experience that we now conclude is required for the assembly of a coordinated sequence of appetitive responses to dehydration...the experience of drinking water while dehydrated, rather than just the experience of dehydration or rehydration per se, appears to be required for the acquisition of the appetitive behavior (pp. 103–104).

In a subsequent study, Myers and Hall (2001) explicitly demonstrated this last point: only rat pups that experienced pairings of dehydration with oral ingestion of water *while dehydrated* were found to show appropriate responses to acute dehydration. Pups that had been non-orally rehydrated by the experimenters showed no evidence of such learning. Changizi, McGehee, and Hall (2002) extended these findings to hunger and food ingestion, finding that only rats that experienced pairings of food-deprivation with food ingestion subsequently showed appropriate orienting and food-seeking behaviors when later deprived of food.

In summary, a small but growing body of comparative research provides support for Hebb's (1949) suggestion that the perception of hunger, thirst and satiety is not innate, but must emerge during individual development. Although the majority of these studies have focused on thirst and fluid ingestion, the available studies on food ingestion (e.g., Changizi et al., 2002) point to little difference between the two systems in this regard. To paraphrase Baldwin (1896), the interesting thing about such studies is that they seem to point to incredibly haphazard or sloppy design. Why has something so critical to life been left to the vagaries of individual development? How could evolution be so reckless? Not long recovered from thinking about the world in terms of design by an omnipotent, omniscient creator, we still expect a kind of rational design from the invisible hand of nature (cf. Blumberg, 2005). From a developmental psychobiological systems perspective, however, the reliable reoccurrence of a species-typical rearing environment, containing species-typical resources, in species-typical amounts and with species-typical timing, and opportunities for species-typical experience of and/or interaction with such resources can provide ample ground for the reliable reoccurrence of even critical phenotypic outcomes.

The development of hunger, thirst and satiety in humans

Bruch's theory

The psychiatrist Bruch (1961, 1969, 1970, 1971, 1973, 1991) expanded Hebb's (1949) ideas and applied them to the development of disordered eating in humans. Bruch argued that perturbations in the human infant–caregiver feeding system can provide the ground for aberrations in the development of psychological characteristics like autonomy as well as the perception or awareness of internal states like hunger and satiety. Bruch's theory was premised on the idea that, "hunger awareness, and that of other biological needs, is not innate biological knowledge but that learning is necessary for them to become organized into recognizable patterns" (1969, p. 93). Bruch also argued that, "discriminating awareness of hunger itself is not present at birth and develops, accurately or distortedly, through reciprocal transactional feedback patterns of experience" (p. 97). Bruch believed that many of her patients with eating disorders had disturbed or inaccurate interoceptive abilities, particularly the inability to appropriately recognize and respond to sensations of hunger and satiety. A central component of Bruch's theory was that this deficit in interoceptive awareness (IA) was a direct result of abnormal or deviant early experience with feeding and food intake.

In Bruch's view, infants reflexively give off a variety of cues indicating their internal feelings and states; for example, crying or engaging in oral behavior when feeling discomfort (cf. Wright, 1987). It is the *appropriateness* of caregiver responses to such infant-initiated cues, however, that determines whether correct learning of associations between such internal sensations or "needs" and external conditions and stimuli will occur (Bruch, 1969). The idea advocated by Bruch is that there is no innate knowledge that a particular configuration or set of internal sensations has to do with food, eating behaviors and/or exteroceptive food-related cues. The initial sensation of "hunger" is simply an undifferentiated, unpleasant feeling, whose relation to the infant's behavior and other stimuli must be learned through reciprocal interactions with caregivers. As this knowledge must be acquired within a socio-cultural milieu, there is a great deal of potential plasticity or malleability with respect to exactly how alimentary interoception develops or fails to develop in a given individual. Bruch argued that some children learn to pair too broad a range of interoceptive feelings or sensations with the need for food and "hunger", leading to cases of developmental obesity, whereas others learn to eat completely irrespective of interoceptive signals, sometimes leading to or at least contributing to the symptomatology and/or development of anorexia nervosa.

Buck's theory

A modern restatement of Bruch's theory is provided by Buck (1989a, 1989b, 1993, 1999), who characterizes the caregiver of the human infant as akin to a living biofeedback machine and terms the process by which children learn to identify the meaning or significance of internal sensations—both "drive" states such as hunger and thirst as well as emotional states and feelings—*social biofeedback*. As Buck (1999) writes:

> Children learn about their subjectively experienced feelings and desires largely through feedback form others responding to their expressive behaviors. This is termed *social biofeedback* because the behavior of the other provides the child with feedback about a bodily process that is otherwise inaccessible to the child (p. 307).

From this perspective, children can be socialized to have varying degrees of interoceptive and/or emotional competence or incompetence depending on the appropriateness of caregiver response to infant and child cues.[5]

Discussing the therapeutic application of adult biofeedback training, Miller and Dworkin (1978) employ the following analogy:

> ...I should like to return to the example of the novice golfer, who is learning to sink a putt. If both the golfer and coach are blindfolded, they will not know whether any putt succeeds or fails. Most patients are strikingly poor at correctly perceiving their visceral responses...The availability of biofeedback, like removal of the blindfold from the golfer and his coach, should be useful for any response that can be learned, but whose learning is impeded by inadequate perception of that response (p. 1277).

[5] Gergely and Watson (1996) make a case for a similar theory (also termed *social biofeedback theory*) and for the importance of early social biofeedback for the development of emotion and affect regulation.

Applying the same metaphor to the theories of Bruch and Buck, the caregiver can be seen as analogous to the coach, who may, for a variety of reasons, be "blindfolded" and thus unable to perceive and/or respond appropriately to infant and/or child cues. The newborn can be viewed as akin to the novice golfer, "blindfolded" by his/her lack of innate knowledge of the game. The caregiver thus functions like a mirror or biofeedback device, in which the child will experience a more or less accurate or distorted reflection of him/herself and from which he/she will be able to perceive more or less useful information about his/her internal feelings and states and their relation to his/her own behavior and to the outside world.

Alimentary interoception and emotional development

Two important correlates of Hebb, Bruch and Buck's thinking about the development of alimentary interoception are that emotional and appetitive/motivational processes are closely interrelated during early development and that correct *differentiation* of emotional and alimentary needs likely occurs only with appropriate differential caregiver response to infant and child cues. Bruch (1970), for example, wrote that, "the inability to differentiate 'hunger,' the need to eat, from other signals of bodily discomfort and from emotional tensions appears to be the outcome of incorrect and confusing early learning" (p. 498). Hebb (1949) wrote similarly that, "until such learning has occurred, it appears that the only direct effect of the need of some particular food, or of food in general, is restlessness, emotional disturbance, and malaise" (p. 205).

Although the distinction between motivation and emotion is generally taken for granted (e.g., Grossman, 1966; Mogg, Bradley, Hyare, & Lee, 1998), the boundary between motivational and emotional processes is likely far less distinct. Hunger, for example, has the potential to be a highly emotional experience (e.g., Cannon, 1912, 1915; Carlson, 1931; Russell, 2005). According to Cannon (1915):

> On the same plain with pain and the dominant emotions...is the sensation of hunger. It is a sensation so peremptory, so disagreeable, so tormenting, that men have committed crimes in order to assuage it. It has led to cannibalism...It has resulted in suicide. And it has defeated armies... (p. 232).

Although there are few empirical studies directly investigating the impact of hunger, thirst and satiety on emotion and emotional experience, a large and growing body of research suggests a far closer relationship than has traditionally been thought (cf. Dess, 1991, 2001).

A number of comparative studies, for example, have found a general correlation between food-deprivation and certain forms of aggression in rats, mice and fish (e.g., Adams, Cowan, Marshall, & Stark, 1994; Fredericson, 1950; Poulsen, 1977; Rohles & Wilson, 1974; Wada, 1922). There is also a large literature suggesting that food restriction and starvation are frequently associated with impulsivity, hyperirritability and aggressiveness in humans (see Fessler, 2003). Prolonged food-deprivation or semi-starvation can also result in severe depression and other psychological disorders (e.g., Brozek, Guetzkow, Vig Baldwin, & Cranston, 1951; Keys, Brozek, Henschel, Mickelsen, Taylor, 1950). The few studies that have investigated the influence of normal interprandial (between meal) food-deprivation on mood in humans moreover suggest that there is likely a substantial entrainment of mood or affect with the daily rhythm of food intake under ordinary circumstances (e.g., Monello & Mayer, 1967; Owens et al., 2000). Evidence suggestive of a similar relationship between thirst and affect has also begun to accrue in recent years (e.g., Acevedo, Gill, Goldfarb, & Boyer, 1996; Backhouse, Biddle, & Williams, 2007; de Araujo, Kringelbach, Rolls, & McGlone, 2003).

A tight coupling between motivational and emotional systems and processes makes a good deal of sense biologically, as survival depends critically on the ingestion of adequate water and nutrients. This view is supported by known functional overlap between brain areas involved in motivational and emotional processes (e.g., Cardinal, Parkinson, Hall, & Everitt, 2002; Jones, Dilley, Drossman, & Crowell, 2006; Sewards & Sewards, 2000) and is echoed by modern neuroscientists, who sometimes refer to the phenomena of hunger, thirst and pain as "homeostatic emotions" (e.g., Craig, 2003). Against this backdrop, the idea advocated by Hebb, Bruch and Buck is that there is no innate knowledge of any difference between "emotional" feelings or states and "motivational" ones like hunger, thirst and satiety. Just as infants must be socialized to identify and understand interoceptive alimentary signals through reciprocal interactions with caregivers, so must they be socialized to identify and understand internal emotional feelings and states and their relation to behavior (both expressive and ingestive) and to exteroceptive stimuli (Buck, 1989a). From this perspective, "motivation" and "emotion" are thus largely bio-socio-cultural constructs.

Fig. 1 is an attempt to illustrate the model of normal emotional/motivational development suggested by Hebb, Bruch and Buck's thinking. Buck and colleagues have argued that disturbances within the early social biofeedback system and consequent deficits in emotional competence are likely at play in the development of a variety of childhood behavior disorders as well as conditions such as schizophrenia and alexithymia (Buck, 1993; Buck, Goldman, Easton, & Smith, 1998). *Alexithymia* is a condition characterized by a marked inability to identify and/or put emotional states and experiences into words (Lesser, 1981). It can be predicted, on Bruch and Buck's theory, that children will be unable to build correct associations between emotional and/or motivational vocabulary and internal states without the experience of interactions with caregivers conducive to the acquisition of such learning (i.e., accurate caregiver interpretation of and/or appropriate response to child cues). Along similar lines, Schachter, Goldman, and Gordon (1968) state that:

> Obviously, attaching a particular label to any particular internal or visceral syndrome is a learned, cognitively and socially determined act...Whether or not the label 'hunger' is applied to the feelings associated with this physiological symptom has...little to do with the symptom itself, but is a good part determined by the individual's developmental feeding history. If feeding is usually coincidental with these symptoms one can reasonably anticipate that the label 'hunger' will be applied to this set of feelings and that the individual will behave in a manner appropriate to this coincidence of label and symptoms. If feeding is chronically inappropriate to physiological conditions, there is probably little reason to anticipate that the label 'hunger' will be applied... (p. 91).

From this perspective, the quality of the early infant–caregiver social biofeedback system can potentially determine: (1) sensitivity to and/or accuracy for recognition of internal feelings and states (i.e., interoceptive awareness), (2) the ability to correctly interpret and/or reason about internal feelings and states (i.e., interoceptive competence) and (3) the ability to describe and/or communicate internal feelings and states (i.e., expressive competence). Interoceptive competence, in theory, can be sepa-

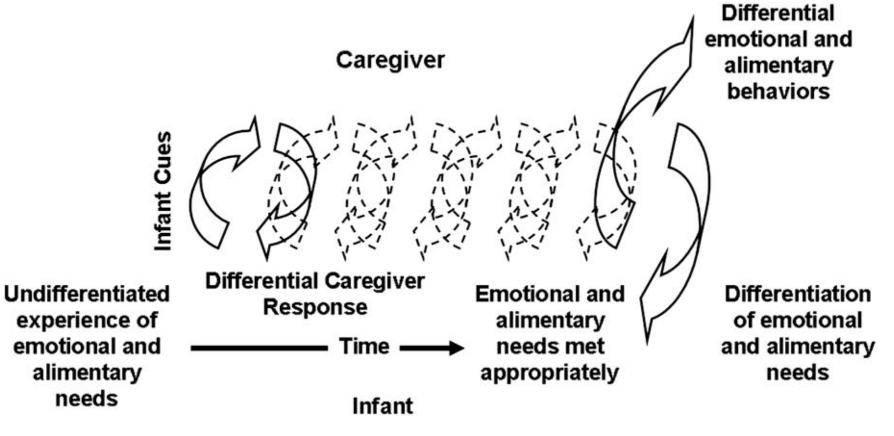

Fig. 1. An illustration of the model of motivational and emotional development suggested by the ideas of Hebb, Bruch and Buck. Initially, there is little or no differentiation of emotional and alimentary needs. Over time, via reciprocal processes of feedback and socialization (social biofeedback) with a caregiver or caregivers who is/are attentive to infant cues and respond(s) differentially to emotional and alimentary needs, the infant or child learns to discriminate these needs as distinct and to behave differentially in response to them. The end result is an individual who can accurately identify and appropriately satisfy emotional and alimentary needs. Numerous factors not illustrated here (e.g., culture, historical circumstances, caregiver pathology, infant temperament) can affect the caregiver and/or infant side of the social biofeedback system, potentially resulting in poor awareness, discrimination and/or differentiation of emotional and alimentary needs.

rated further into *emotional competence*, or competence identifying, interpreting and reasoning about emotional states, and *motivational competence*, or competence identifying, interpreting and reasoning about motivational states like as hunger, thirst and satiety.

Case studies supportive of Bruch's theory

There are a number of sources of anecdotal support for Bruch's theory, including many case studies reported by Bruch herself. In one of these, for example, the mother of one of Bruch's anorexic patients had become obsessed, beginning in the girl's infancy, with making her skinny baby "plump and pleasant" (Bruch, 1973, p. 49). This obsession inevitably included a feeding regime in accordance with the mother's wishes, ideas and ultimate goal; the child's feelings and needs, being irrelevant, were ignored. Describing this patient, Bruch states that, "...she expressed with startling and dramatic directness what I have come to recognize as crucial issues in many patients with serious eating disorders, namely the basic delusion of not having an identity of their own, of not even owning their body and its sensations, with the specific inability of recognizing hunger as a sign of nutritional need" (p. 50).

Ainsworth and Bell (1969) describe a number of potentially problematic feeding patterns observed in a study of 26 mother–infant dyads. In two of these patterns, the mothers labeled their behavior "demand feeding" (feeding the babies when they demand to be fed) and yet their babies were "conspicuously overfed." In one group this was done in an attempt to gratify or please the baby and in the other it was done in an attempt to "stuff the baby full" so that the baby would sleep for a long period of time and thus demand little attention. According to the authors, the mothers in the first group "wanted their babies to be happy, but tended to treat too broad a spectrum of cues as signals of hunger" (p. 145). Another pattern emerged in mothers who used "staving off" as a strategy even though they declared themselves to be feeding the babies on demand. Ainsworth and Bell describe these mothers as follows:

> These mothers all declared their intention to feed on demand...But they referred frequently...to their hope that the baby would get onto a schedule...They maintained the fiction of demand feeding by mechanisms of denial. They refused to recognize hunger signals when they occurred...These were mothers who...would have been pleased to make feeding a happy time. But, probably because their babies were too hungry and upset when they were finally fed, feedings were tense and unhappy (pp. 146–147).

Yet another pattern was that in which mothers were simply impatient while feeding and thus inconsistent as a result. These mothers, according to Ainsworth and Bell, showed an inability to understand and tolerate the natural pauses that occur during feeding and thus tended to terminate feeding prematurely. In still another pattern, displayed in only one case, the mother fed the child on an extremely rigid schedule and "was almost completely impervious to the baby's signals, and...fed him almost entirely at her own timing" (p. 148). In a final category were mothers who fed their infants in a highly arbitrary manner. In one instance, for example, the mother was extremely controlling and even sadistic and "could not bear the way her baby defied her by refusing to sleep, wake, feed, and smile in accordance with her will". The variety of patterns described by these authors give some credence to Bruch's theory, suggesting that there are likely many possible routes by which the early human infant–caregiver feeding system can become perturbed, potentially leading to the kinds of deficits in IA hypothesized to occur under Bruch's theory.

Empirical research supporting Bruch's theory

Infant feeding and the development of hunger, thirst and satiety. Wright, Fawcett, and Crow (1980) studied the dynamics of early feeding in 132 breast- and 58 bottle-fed infants over the course of the first two months of life. It was found that, when tested, the breast-fed infants adjusted their intake to match the length of deprivation: the longer the interval between feeds, the more they consumed and the shorter the interval, the less they consumed. Bottle-fed infants, on the other hand, were found to consume the same amount regardless of the amount of time elapsed since their last feed. This finding suggests that the bottle-fed infants had failed to learn to pair interoceptive signals stemming from food-deprivation and/or exteroceptive temporal cues with postingestive satiety signals. It was also found that by the age of one month a clear diurnal rhythm of consumption developed in the breast-fed infants, who consumed more in the morning and less throughout the day. A similar pattern, however, failed to develop in bottle-fed infants, who consumed roughly the same amount at all feeds throughout the day. In addition, it was found that in bottle-fed infants most pauses or interruptions in the feed were entirely determined by the mother, whereas in the breast-fed group the majority of pauses or interruptions were infant-determined. According to the authors:

> At this gross level of analysis, it is clear that any possible role of the baby in, for example, indicating satiety by actively terminating the feed is minimized in the case of the bottle-fed baby. All such decision-making remains the prerogative of the mother, and there is no indication of a developmental change across the first two months of life. In the case of the breast-fed baby, there seems a greater degree of flexibility (p. 11).

Breast-feeding thus apparently lends itself to a more passive role for the mother and a more active role for the infant during the feed, whereas the technique of bottle-feeding imposes upon the baby an almost entirely passive role, while providing a more active role for the mother.

Wright (1988, 1993) discusses several related findings differentiating the mothers of breast- and bottle-fed infants. In a sample of 166 mother–infant dyads, most mothers who breast-fed reported that there was a time of day when their infant was hungrier than other times, whereas 42% of bottle-feeding mothers reported no change in their infants. Wright points out that there are at least two important structural differences between breast- and bottle-feeding: the degree of infant control over the feed and the presence of exteroceptive cues indicating the quantity of milk ingested by the infant. That is, a breast-fed infant has a great deal more potential for control over the feed, especially in terms of determining its pace and duration. In addition, breast-feeding mothers have no direct exteroceptive access to the amount of milk consumed by their infants, whereas mothers bottle-feeding their infants do. In support for Wright's suggestions, Fisher, Birch, Smiciklas-Wright, and Picciano (2000) found breast-feeding to be associated with greater infant control during feeding and bottle-feeding to be associated both with greater maternal control and higher levels of subsequent energy intake in children at 18-months of age. Farrow and Blissett (2006a) reported data confirming these results, finding that breast-feeding appears to be linked to child intake regulation via its relationship with reduced maternal control of feeding (particularly pressuring children to eat), increased feeding sensitivity and its impact on positive mealtime interactions. Farrow and Blissett (2006b) likewise found that lower amounts of maternal control at 6-months-of-age was associated with infants later showing evidence of self-regulation of both intake and weight gain. That is, infants who were slower initially to gain weight subsequently increased their weight gain whereas infants who gained more weight early later slowed their weight gain. High levels of maternal control, on the other hand, were found to be associated with infants showing consistent weight gain.

Breast-feeding can thus lend itself to less caregiver concern with quantity consumed and the paying of closer attention to infant satiety cues. Bottle-feeding, on the other hand, has the potential to force a caregiver to choose between strictly adhering to his/her own ideas, beliefs, expectations, schedule, etc., or else closely attending to, learning about, and responding to infant cues. Wright (1988) also reports that:

> Breast-feeding mothers appeared more concerned about what could be called the 'psychological environment', e.g., they commented on the importance of both mother and baby enjoying the feed in a relaxed atmosphere. The criteria which mothers used to decide when the baby had had enough to eat vary—the baby stops sucking, is sleepy, looks content, spits out the teat/nipple...42% of breast-feeding mothers recognized falling asleep as a satiety cue compared with 6% of the bottle feeders; and 32% of bottle-feeding mothers stopped feeding only when the baby spat out the teat/nipple compared with 4% of the breast feeders (p. 614).

Bottle-feeding caregivers certainly have the option of ignoring quantity consumed and closely attending to infant satiety cues; bottle-feeding, however, appears to be strongly associated with opposite behaviors, perhaps, as Wright suggests, simply because of the increased saliency of the visual cues provided by the bottle.

It is also possible that maternal anxiety and/or attitude about the quantity of infant consumption can be a factor leading some mothers to choose bottle- rather than breast-feeding from the start. Bramhagen, Axelsson, and Hallström (2006), for example, found two dominant categories with respect to the attitudes mothers generally have about the feeding of children and infants: a more flexible and a more controlling one. Bramhagen et al. describe flexible mothers as showing greater sensitivity and responsivity to their children in feeding situations whereas more controlling mothers rely very little or not at all on child cues, believing that, "they alone...[are] responsible for the child's food intake" (p. 31). It is thus possible that a mother with a more controlling attitude might choose bottle-feeding simply because of the increased control it provides. This idea is supported by Taveras et al. (2004), who reported finding that mothers who breast-fed, especially mothers who breast-fed longer, employed less restrictive or controlling feeding practices when their children were one year of age.

Direct tests of Bruch's theory. Consistent with Bruch's theory, disturbed IA is widely held to be a central component of eating disorders (e.g., Garner, Garfinkel, & Moldofsky, 1978; Lilenfeld, Wonderlich, Riso, Crosby, & Mitchell, 2006) and is measured by standard diagnostic tools for the assessment of eating pathology (e.g., the Eating Disorder Inventory; Garner, 1991). A number of prospective studies have found poor IA to be a predictor for the development of eating disorders (Killen et al., 1996; Leon, Fulkerson, Perry, & Early-Zald, 1995) and to be significantly lower in individuals recovered from eating disorders compared to non-eating-disordered individuals (e.g., Caspar, 1990; Leon, Fulkerson, Perry, Keel, & Klump, 1999; Lilenfeld et al., 2000). In addition, IA has been found to be negatively correlated with alexithymia, both in patients with eating disorders (Garner, 1991; Sexton, Sunday, Hurt, & Halmi, 1998; Taylor, Parker, Bagby, & Bourke, 1996) and in non-clinical samples (e.g., Quinton & Wagner, 2005). Sexton et al. (1998), for example, found that anorexics had significantly higher alexithymia scores than both bulimics and controls. Such evidence strongly supports Bruch's theory and is suggestive of the kind of relationship between interoceptive ability and expressive competence that is predicted by both Bruch and Buck's theories.

Despite such evidence, few studies have directly tested Bruch's theory. Coddington and Bruch (1970) devised a method of introducing a nutritive substance into the stomachs of subjects without them having exteroceptive access to cues indicating the quantity ingested. It was found that both markedly underweight and overweight subjects had more difficulty with the task than did normal weight individuals, regardless of pathology. These subjects were more inaccurate at determining the quantity they had consumed based on interoceptive cues of satiety than normal weight individuals. According to the authors:

> Considerable difficulty was encountered when subjects were asked whether they were "hungry" indicating how poorly defined this concept is, or how many people have difficulties with their internal perception. A few felt "hungry" at the start and not at the end...A few subjects (all of them of abnormal weight) described a variety of sensations...but no awareness of hunger or satiation (p. 573).

Garfinkel (1974) performed another test of Bruch's theory which suggested that anorexics may have disturbed perception of satiety but not hunger. According to Garfinkel:

> Both patients and controls perceive hunger as a feeling of gastric emptiness. The only differences in the experience of hunger are the patients' negative affect, their increased urge to eat, and their preoccupation with thoughts of food...controls experience satiety as a fullness in the stomach, while patients with anorexia nervosa experience satiety without any gastric sensations, as bloating or as fullness alternating with no sensations (p. 312).

These patients showed an inability to perceive sensations of satiety and tended to respond to this interoceptive deficit in two distinct manners. One group, which was found to be associated with a better treatment outcome, responded by relying entirely on external cues (e.g., by being served by others, eating everything on the plate, never asking for more). The other group, associated with a poorer treatment outcome, responded, "by continuously avoiding foods, develop[ing] food fads, induc[ing] vomiting, or abusing laxatives" (p. 314).

Robinson (1989) studied interoceptive ability in anorexics, bulimics and controls and, similar to Garfinkel (1974), found anorexics to have a disturbed sense of satiety but not of hunger perception. Anorexic patients were found to have a significantly lower correlation between gastric contents and urge to eat than controls. Controls reported feeling calm following a meal whereas anorexics reported sensations of fullness and/or bloating. Owen, Halmi, Gibbs, and Smith (1985), on the other hand, reported evidence suggesting that eating disordered individuals have a disturbed sense of both hunger and satiety compared to control subjects. Rolls et al. (1992) reported that, although anorexics with bulimic features had some ability to adjust their food intake to dietary preloads, their reports of hunger, thirst and satiety differed significantly from those of control and bulimic subjects. In a more recent study, van Strien and Ouwens (2007) moreover reported finding a correlation between poor interoceptive awareness, alexithymia and the tendency of women to overeat under conditions of stress rather than showing more "natural" reduced consumption under such conditions.

Anorexia, early feeding and GI difficulties. An additional way that control can be exerted over the feeding situation is by choosing to schedule or else arbitrarily feed rather than feed an infant on demand (Ainsworth & Bell, 1969). Steiner, Smith, Rosenkranz, and Litt (1991) found that mothers of patients with anorexia nervosa reported far higher use of schedule than demand feeding during the early feeding of these patients than the mothers of matched controls. More specifically, the mothers of anorexics reported having schedule fed the patient in 50% (and the siblings of patients in 61%) of the cases, compared to 12% of cases for mothers of matched controls. To explain these findings, the authors suggested that the mothers of these anorexic patients may have been less confident in their own mothering abilities and that the patients, additionally, may have been "more placid and less demanding" (p. 166) as infants. Chatoor, Egan, Getson, Menvielle and O'Donnell (1987) studied patterns of mother–infant interactions during both play and feeding in 42 cases of infantile anorexia[6] and 30 matched controls. These authors found that during both feeding and play, mothers of control infants positioned their infants better for reciprocal interaction, waited more often for the infant to initiate interactions, and were more pleasant toward their infants. The mothers of anorexic infants, in contrast, showed poorer positioning of their infants, handled their infants more often, more abruptly and more roughly, made more negative and critical comments toward their infants, and were more unresponsive and overriding of their infants' cues.

Reflecting on their clinical work with such mothers, Chatoor, Egan, Getson, Menvielle, and O'Donnell (1987) identified two major groups: one in which mothers reported having had intense conflicts with their own mothers—conflicts which "spilled over" into their relationship with their own infants—and another group, in which mothers had developed a kind of "blind spot" in dealing with their infants. Describing this later group, Chatoor et al. write that:

> These dyads had usually experienced some transient feeding difficulties when the infant was ill, which seemed to have "sensitized" the mother to worry excessively about the infant's growth. These mothers seemed to feel insecure in their mother role and measured their competence by how well the infant ate. Because of high anxiety during feeding, these mothers were unable to read the infant's cues correctly. Feeding became an increasingly frustrating task as the toddler refused to eat in an effort to assert more autonomy and control (p. 539).

These findings highlight, again, that there are likely numerous possible routes by which salutary infant–caregiver interaction and/or IA might fail to develop or else become disturbed during early development.

Of relevance to this issue, in a study of 51 adolescents with anorexia nervosa and 51 matched controls, Råstam (1992) found higher rates of reported GI problems of various kinds in the early feeding histories of anorexics compared to controls. Consistent with the observations of Chatoor, Egan, Getson, Menvielle, and O'Donnell (1987), Råstam speculated that GI difficulties may have led to heightened parental anxiety about feeding the child and thus greater chances of the child developing anorexia

[6] Infantile anorexia, distinct clinically from anorexia nervosa, can emerge from early infancy to 3 years of age and generally involves food refusal and acute or chronic malnutrition (see Chatoor, 1989; Poinso, Viellard, Dafonseca, & Sarles, 2006).

nervosa later in life. It has long been known that there is an association between early GI disturbances (e.g., diarrheal infections) and infant feeding practices (e.g., Bullen & Willis, 1971; Ketsela, Asfaw, & Kebede, 1990). Ciampolini, Vicarelli, and Bini (1991), for example, reported a link between the manner of infant feeding (schedule vs. demand), blood sugar levels and the occurrence of chronic diarrhea in 2-year old children. These authors argued that the use of demand feeding combined with the habitual use of non-starchy vegetables may help educate children such that they do not overeat and develop GI disturbances following weaning. Ziyane (1999) similarly reported that breast-fed infants are far less likely to suffer from diarrheal attacks than infants who are either non-breast-fed or weaned prematurely.

Ciampolini, Borselli, and Giannellini (2000) reported results from a longitudinal study in which a specific infectious agent, *Helicobacter pylori*, was found to be associated with schedule of feeding, blood glucose levels at feeding time and the occurrence of gastrointestinal problems. *H. pylori* is a bacteria capable of colonizing the lining of the stomach that has been found to be strongly associated with the development of a variety of cancers (e.g., Amieva & El-Omar, 2008; Hecht, 2007; Hsu et al., 2007; Suzuki, Hibi, & Marshall, 2007) and has been classified as a Class I carcinogen by the World Health Organization (Williams & Pounder, 1999). In Ciampolini et al.'s (2000) study, caregivers were preventatively trained to identify signals of metabolic hunger (indexed by glycemia lower than 4.7 mmol/L) and to feed their child accordingly, in addition to making dietary modifications and increasing the child's physical activity. The authors measured serum antibodies to *H. pylori* upon the entry of healthy infants (negative for *H. pylori*) into the study and at 4, 8 and 12 year follow-ups. Across all follow-ups, seropositivity for *H. pylori* was found to be 4.7% in the intervention group compared to 30.2% in controls. The authors also reported results from a recovery study in which both children and young adults (60 months to 25 years) positive for anti-*H. pylori* were recruited and either assigned to an intervention (similar to the previous study) or a control condition. After one year 62.5% of subjects in the intervention group had lost seropositivity for *H. pylori* compared to 13% in the control condition. This series of studies suggests connections between schedule of feeding and GI disturbances that may be of direct relevance to the ontogeny of IA as well as the reported occurrence of GI difficulties in the feeding histories of anorexics (e.g., Steiner et al., 1991).

Ciampolini (2006) recently reported that by training mothers to pair measures of their 2-year-olds' blood glucose levels with requests for food, food intake could be substantially reduced in these children. Ciampolini and Bianchi (2006) have termed the initial interoceptive signal to feed, which correlates with a *gradual* drop in blood glucose levels to less than 85 mg/dl on average, "initial hunger" and have argued that this signal represents (or is at least correlated with) an "unconditioned" hunger.[7] Ciampolini and Bianchi report that most adults are normally incapable of identifying the sensations corresponding to such "initial hunger", but can be trained to utilize blood glucose measurements as feedback to learn to identify such sensations and adapt their food intake accordingly. This is not necessarily a simple process, according to these authors, as there are many factors that can confound the accuracy of such measurements and their relation to underlying interoceptive signals to feed.

Research on dietary restraint. There has long been a notion that some people are more "external" and others more "internal" with respect to the cues that predominantly motivate their food intake (e.g., Nisbett, 1968; Schachter, 1968; Schachter, 1971). The related concept of *dietary restraint* refers to a deliberate cognitive attempt to restrain one's eating (irrespective of internal cues), in attempt to avoid overeating and weight gain. The unrestrained eater, in contrast, is characterized as the eater who eats primarily in response to internal cues and is much less affected by external cues (e.g., Herman & Mack, 1975). Studies both in the laboratory and real world settings have supported the conclusion that restrained eaters tend to overeat and unrestrained eaters tend to eat less when depressed and/or stressed (e.g., Cools, Schotte, & McNally, 1992; Herman, Polivy, Lank, & Heatherton, 1987; Polivy & Herman, 1976; Wardle, Steptoe, Oliver, & Lipsey, 2000). In addition, a number of studies have found that restrained eaters do not and that unrestrained eaters do adjust their food intake in laboratory

[7] As opposed to transient blood glucose declines that appear to be a largely learned physiological response to impending intake-related homeostatic disturbance (see Ramsay et al., 1996; Woods, 1991).

eating tasks when given dietary "preloads" prior to the task (e.g., Hibscher & Herman, 1977; Ruderman & Christensen, 1983).

Despite such findings, there have been relatively few studies aimed at the question of the *development* of dietary restraint. There is a great deal of evidence that child-feeding practices can have a large impact on what cues children learn to use to regulate their food intake (cf. Birch & Fisher, 1996; Johnson & Birch, 1994). In one study, for example, two groups of adults were given different instructions on how to treat their children: in one group, the adults were instructed to deliberately focus children on internal cues of hunger and satiety, openly discussing with the children the relation of such cues to intake regulation, and in the other group, the children were made to eat on a fixed schedule and deliberately focused on external cues (Birch, McPhee, Shoba, Steinberg, & Krehbiel, 1987). Similar to the findings Wright (1988, 1993) obtained comparing bottle- and breast-fed infants, these authors found evidence that children who were focused on interoceptive cues later showed an ability to adjust their intake to the actual energy content of ingested foods whereas the children who were focused on exteroceptive cues showed no such ability.

In a study of mothers with eating disorders, mothers with postpartum depression, healthy control mothers and their 12-month-old infants, Stein et al. (2001) found that the mothers with eating disorders were more controlling of their infants and that the variable that most predicted maternal control was maternal dietary restraint. Tiggemann and Lowes (2002) similarly reported a correlation between parental control of eating and maternal dietary restraint. Fisher and Birch (1999) likewise reported that parental restrained eating predicted both maternal restriction of their 3–6-year-old daughters' eating and the tendency of these girls to overeat under conditions of unrestricted access to snack foods. Francis and Birch (2005) similarly found that mothers who were more preoccupied with weight reported more restriction of their 9–11-year-old daughters' food intake and that these girls, in turn, showed more restrained eating than the daughters of women less preoccupied with food intake. In a study of 5-year-old girls and their parents, Carper, Fisher, and Birch (2000), additionally, found evidence that parental pressure and control of children's eating may encourage the early development of patterns of restrained and disinhibited eating in girls.

Birch, Fisher, and Davison (2003) found that 5-year-old girls whose mothers employed more restrictive feeding practices reported more eating in the absence of hunger at 7- and 9-years of age than girls whose mothers employed less restrictive practices. Girls who were already overweight at 5-years of age and who had mothers who employed restrictive feeding practices, however, were found to show the greatest amount of weight gain. Birch and Fisher (2000) reported correlations both between maternal and daughter relative weights, which they hypothesized to reflect both genetic and shared environmental effects, and between maternal control and the relative weight of the daughter. These authors argue that their data support a model of bidirectional influence between parent and child in which, "daughters' weight status influenced mothers' perceptions of daughters' risk of overweight, which in turn influenced mothers' child-feeding practices" (p. 1059). In a longitudinal study of 105 Dutch children, Vogels et al. (2006) similarly reported finding that body weight during the first year of life, high paternal body mass index (BMI) and maternal dietary restraint were significantly correlated with child overweight at age 12. Although these authors did not comment upon the issue, it possible that maternal restraint and/or eating pathology also affected both paternal BMI and infant weight at 1-year-of-age, in addition to these factors affecting maternal dietary restraint (cf. Birch & Fisher, 2000).

Findings such as these highlight the impact of child-feeding practices on the development of intake regulation as well the likelihood that cognitive characteristics such as dietary restraint may be largely the product of learning during early development. In recent years, there have nonetheless been several attempts to relate dietary restraint to genetic inheritance in general (e.g., de Castro & Lilenfield, 2005; Neale, Mazzeo, & Bulik, 2003; Provencher et al., 2005) and/or specific genetic polymorphisms (e.g., Vogels et al., 2005). In a study of 202 nuclear families (282 men and 402 women), Provencher et al. (2005), for example, reported a low heritability estimate of 5.5% for dietary restraint, as measured by the Three-Factor Eating Questionnaire (TFEQ; Stunkard & Messick, 1985). De Castro and Lilenfield (2005), on the other hand, argue for a significant genetic inheritance of dietary restraint, based on a heritability analysis of monozygotic (MZ) and dizygotic (DZ; both same- and opposite-sex) twins. These authors found that "genetic effects" accounted for 44% of the variance on the cognitive restraint scale of the TFEQ and 58% of the variance on the Restraint Scale score (Herman & Polivy, 1980), although this later value fell to 30% when BMI was included as a covariate in the analysis. De Castro and Lilenfield point out that this finding suggests that, ''the apparent heritability of dietary restraint, as measured by the Restraint Scale, is due, at least in part, to its covariation with body size, which is highly heritable'' (p. 452). These authors also acknowledge that inheritance is larger than genes, writing that, ''genes strongly influence the individual's nutrient intake and body weight as the integral of a large number of diverse heritable environmental, social, psychological, and physiologic factors'' (p. 454). Neale et al. (2003), however, performed a study of Caucasian, same-sex female MZ and DZ twins in which they examined the heritability of the three main components of the TFEQ ('Disinhibition', 'Hunger' and 'Restraint'). These authors reported a 45% (.32–.57) heritability of dietary disinhibition, compared to 8% (.00–.38) and 0% (.00–.30) heritabilities of 'Hunger' and dietary restraint, respectively.[8]

The development of thirst in humans

Bruch's ideas about the development of hunger and its satiation should, in theory, apply equally well to the development of thirst in humans. Given the existing comparative literature on the ontogeny of thirst in non-human animals (e.g., Changizi et al., 2002; Craig, 1912), this would seem particularly likely. The internal motivation or ''drive'' for the ingestion of water in humans is, however, far more imperative in the short-term than that of hunger, as humans can go for long periods without eating but are far more tied to water—we need to ingest it more frequently and in greater relative quantities—than most other land animals. It is thus possible that, for humans, thirst is ''hard-wired'' to a far higher degree than hunger. Swallowing and fluid ingestion are known to develop prenatally in humans and similar species (Ross, El-Haddad, Desai, Gayle, & Beall, 2003; Ross & Nijland, 1998) and there is substantial evidence that the physiological and neural systems involved in thirst and fluid ingestion are also ''programmed'' prenatally in response to conditions *in utero* (El-Haddad, Desai, Gayle, & Ross, 2004; El-Haddad & Ross, 2006; Mansano, Desai, Garg, Choi, & Ross, 2007; Perillan, Costales, Vijande, & Arguelles, 2007; Perillan, Costales, Vijande, & Arguelles, 2008).

There has, however, been no research to date investigating the postnatal ontogeny of thirst in humans, so it is currently unknown to what extent thirst is in fact ''hard-wired'' at birth. One unexplored possibility is that there is little inborn differentiation of hunger and thirst in newborn mammals, given that the mammalian developmental system of food/fluid intake involves both needs being met simultaneously via the ingestion of breast milk. If this is the case, mammals may have to learn to differentiate hunger and thirst later in development, during or following weaning (cf. Hall et al., 2000). On the other hand, breast-feeding does not provide the infant with a homogenous food. A key difference between breast milk (provided directly from breast to the infant) and substitutes is in fact that breast milk changes nutritional composition during the feed (Hall, 1975). The foremilk is thin, watery and has relatively little nutritional content compared to the hindmilk, which is available later in the feed (if the infant continues to feed from the same breast) and contains far greater quantities of fats and other nutrients (e.g., Bishara, Dunn, Merko, & Darling, 2008; Saarela, Kokkonen, Koivisto, 2005). It is thus possible that the nutritional difference between foremilk and hindmilk allows for the differential satisfaction of thirst and hunger in breast-fed infants, something not possible for bottle-fed infants, who consume a relatively homogenous mixture. Hall (1975) argued, for slightly different reasons, that the foremilk/hindmilk nutritional difference may be important for the development of appetite regulation, providing a potential connection between bottle-feeding and the development of obesity. As there is little empirical data addressing the postnatal development of thirst in humans, however, speculations such as these must await empirical investigation.

The development of hunger, thirst and satiety: Summary and synthesis

In accord with the comparative literature, Hebb (1949) suggested that hunger is not innate but must be acquired during early development. Building on Hebb's ideas, Bruch theorized that the perception of hunger and satiety are not innate but are instead learned via caregiver responses to

[8] Values in parentheses are 95% confidence intervals.

infant-initiated cues (Bruch, 1969). This theory provided a good explanation for the difficulties encountered by many of Bruch's eating disordered patients and was supported by reconstructions of their feeding histories (e.g., Bruch, 1971). Numerous deviant patterns were found in these histories, all falling under the category of inappropriate and/or or inconsistent responses to infant cues. Several empirical studies with anorexic and obese individuals have provided at least partial support for Bruch's theory (e.g., Coddington & Bruch, 1970; Garfinkel, 1974; Robinson, 1989) and disturbed IA is now widely considered to be a hallmark of eating disorders (e.g., Lilenfeld et al., 2006). Bruch's theory also finds a more modern restatement in Buck's (1993, 1998) conception of the human caregiver as akin to a *living biofeedback machine*, responsible for socializing the infant both as to the meaning or significance of the full range of his/her motivations and emotions as well as the appropriate means of communicating this experience.

There is a large and rapidly growing literature on the negative effects of maternal eating disorders (e.g., Cooper, Whelan, Woolgar, Morrell, & Murray, 2004; Patel, Wheatcroft, Park, & Stein, 2002; Russell, Treasure, & Eisler, 1998; Senior, Barnes, Emberson, & Golding, 2005; Stein, Woolley, Cooper, & Fairburn, 1994; Stein, Woolley, & McPherson, 1999; Stein et al., 2001, 2006; Whelan & Cooper, 2000), depression (e.g., Chronis et al., 2007; Murray, Fiori-Cowley, Hooper, & Cooper, 1996), anxiety (e.g., Farrow & Blissett, 2005; Kaitz & Maytal, 2005) and substance abuse (e.g., Eiden, 2001) both on infant and child development in general and on the appropriate feeding of children and infants. Cooper et al. (2004), for example, found that mothers with eating disorders provided more disorganized mealtime environments and were also more controlling when interacting with their children. Murray et al. (1996) found that mothers with postpartum depression (PPD) were less sensitively attuned to the needs of their infants and more overriding of their infant's cues than mothers without PPD. Farrow and Blissett (2005) similarly reported maternal anxiety to be correlated with more controlling and restrictive feeding practices and Stein et al. (2001) found mothers with eating disorders to be more verbally controlling with their 1-year-old infants than mothers without eating disorders. Hagekull, Bohlin, and Rydell (1997), in addition, reported a connection between maternal sensitivity in general and the development of feeding problems in infancy.

This literature, when combined with studies examining qualitative patterns of interaction between mothers and infants during feeding (e.g., Ainsworth & Bell, 1969) and studies examining developmental influences on cognitive characteristics such as dietary restraint (e.g., Birch & Fisher, 2000; Stein et al., 2001), make clear that there is ample opportunity for the kinds of deficits in alimentary interoception that Bruch hypothesized to exist in eating disordered individuals to develop under real world circumstances. Independent of maternal and/or paternal psychopathology, the situation of a new mother dealing with an infant in general and with the feeding situation in particular can be highly stressful for both mother and infant. The birth of a child often precipitates a sharp decline in marital satisfaction (e.g., Meijer & van den Wittenboer, 2007) and has been found to facilitate the development of eating pathology in some women (Stein & Fairburn, 1995). Caregivers can also become anxious as a result of a child become ill, failing to meet growth and/or weight expectations (Chatoor, Egan, Getson, Menvielle, & O'Donnell, 1987) and/or having food-related allergies.

Occasionally disturbances to the infant–caregiver feeding system are imposed by medical necessity, as occurs when infants and children are fed via tube, either nasogastrically or by gastrostomy (Mason, Harris, & Blissett, 2005). Such children frequently have difficulty adjusting to and often actively resist oral feeding upon termination of their treatment (Geertsma, Hyams, Pelletier, & Reiter, 1985; Mason et al., 2005). The reasons for this difficulty are still poorly understood, but it has been suggested that social interactions with parents and/or parental anxiety may play at least some role (see Mason et al., 2005). The availability of food and/or water is an additional "contextual" factor that is obviously critical to the functioning of the early infant–caregiver feeding system. Food insecurity can, in theory, impact the infant–caregiver feeding system on multiple levels, including acting as a stressor on caregivers, adversely affecting the nutritional composition and/or flavor of breast milk (or the availability of substitutes), and potentially altering both infant responsiveness to caregivers and caregiver responsiveness to infants.

Characteristics of the child (e.g., temperament, expressiveness) inevitably interact or coact with caregiver characteristics and contextual factors in facilitating, maintaining and/or disrupting the salutary functioning of the infant–caregiver feeding system (cf. Ammaniti, Ambruzzi, Lucarelli, Cimino &

D'Olimpio, 2004; Satter, 1995). As Wright, Parkinson and Drewett write (2005), "Successful feeding in infancy depends on a complex interaction between caregiver and child, which could potentially become disordered as a result of characteristics or behaviors of either parent or child, or a mismatch between the two" (p. 1263). An infant trait such as expressiveness—which might be tied to individual differences in the biological substrates for interoception—for example, can potentially have a large impact on the types of responses elicited from a caregiver (Wright, 1987). A highly expressive infant might elicit more frequent feeding and/or social interaction than is needed, whereas a less expressive infant might receive less feeding and/or social interaction than is optimal (cf. Wright, 1987). Bruch's theory assumes that from birth there are reliable connections at least between internal physiological signals of deprivation or "need" and reflexive behavioral displays of discomfort (Wright & Crow, 1982). A great deal of variability in interoceptive ability has, however, been found in adults (e.g., Craig, 2004; Katkin, 1985; Vaitl, 1996)—including sex differences (e.g., Katkin, Blascovitch, & Goldband, 1981; Whitehead & Drescher, 1980)—and it is possible that natural variation in the quantity or quality of interoceptive sensory information available to newborns can substantially modulate early interactions with caregivers. An infant characteristic like temperament, on the other hand, has the potential to modulate the affective responses of caregivers to infants during feeding interactions. According to Ammaniti, Ambruzzi, Lucarelli, Cimino, and D'Olimpio (2004):

> ...already in the first year of life, difficult manageability of the child, characterized mainly by irritability, negative emotionality and irregularity in the basic rhythms (feeding and sleeping) can interact with the "vulnerability" of the mother, who presents anxious and depressive symptoms or negative eating attitudes which interfere with empathic recognition of the signs of hunger and fullness in the child (p. 269).

In support for this idea, Blissett and Farrow (2007) found, based on maternal self-report, that infant temperament moderated maternal use of controlling feeding practices at 1 and 2 years of age. There are numerous ways caregivers can respond to the potentially stressful situation of feeding an infant or child, many of which may be disruptive to the formation and/or functioning of the infant–caregiver feeding system (e.g., Ainsworth & Bell, 1969; Drummond, Wiebe & Elliot, 1994) and thus potentially detrimental to the development of IA in infants and children (cf. Bruch, 1969).

The introduction and proliferation of bottle-feeding must certainly be considered one of the largest modifications of the species-typical developmental system of food and fluid intake yet accomplished. Consistent with the predictions of Bruch's theory and of direct relevance to a developmental psychobiological systems view of alimentary interoception, the work of Wright (1988, 1993) and his colleagues (Wright et al., 1980) demonstrates that there are several important differences between breast- and bottle-fed infants. This line of research illustrates that what might seem to be a fairly inconsequential modification of the early feeding situation might, in addition to its widely known negative impact on various aspects of health, including immunity and morbidity (e.g., Wright, Parkinson, & Scott, 2006), have important consequences for the development of alimentary interoception. Bottle-feeding appears to lend itself to greater maternal control of feeding and less maternal responsiveness to infant-initiated cues, is associated with deficits in the ability of infants to regulate their intake (Wright, 1988, 1993), and is likely associated with deficits in alimentary interoception. A number of large scale epidemiological studies have in fact reported a significant negative correlation between breast-feeding and the later development of obesity (e.g., Dewey, 2003; Owen, Martin, Whincup, Smith, & Cook, 2005; von Kries et al., 1999). Breast-feeding undoubtedly causes physiological and epigenetic effects related to weight regulation and the prevention of obesity (e.g., effects on ghrelin cell development and ghrelin levels; Fåk, Friis-Hansen, Weström, & Wierup, 2007). Such effects may nonetheless be mediated as much by the structural, behavioral and social correlates of breast-feeding as the nutritional composition of breast milk.

If the theory advocated by Hebb, Bruch and Buck is correct, deficits in IA may often be accompanied by deficits in interoceptive and/or expressive competence—deficits spanning the motivational-emotional spectrum. Such deficits could potentially lead to problems in social and/or emotional development and could thus play a role in the development of childhood behavior disorders (cf. Buck, 1993; Buck et al., 1998) as well as overt eating disorders (e.g., Bruch, 1971; Bruch, 1981). In addition, such deficits could potentially contribute to the development of affective disorders such as depression, which tend to be strongly associated with eating abnormalities (e.g., Beck, 1975; Devlin & Walsh, 1989; Paykel, 1977; Polivy & Herman, 1976). There is a great deal of comorbidity between affective and eating disorders (e.g., Godart et al., 2007; Salbach-Andrae et al., 2008) in general, the cause(s) of which are still poorly understood. The theory advocated by Hebb, Bruch and Buck posits that there is little or no innate differentiation of "emotion" as distinct from hunger, thirst and satiety during early development and that caregivers must socialize infants as to the significance of the full range of their motivations and emotions (Buck, 1998). This theory thus allows for the possibility that certain individuals may be less aware of and thus more likely to confuse motivational and emotional needs and feelings, potentially contributing to the facilitation, maintenance and/or recurrence of affective and/or eating disorders.

Taken as a whole, there is substantial support for the ideas advocated by Craig, Hebb, Bruch and Buck, as well as for a developmental psychobiological systems account of alimentary interoception. Although studies such as those of de Castro and Lilenfield (2005) point to a significant heritability of cognitive outcomes such as dietary restraint, a developmental psychobiological systems view emphasizes that behavior genetic studies, even of twins reared apart, cannot possibly partial out the influence of environmental and genetic effects, no matter how sophisticated the statistical technique, both because genes are but one of many heritable developmental resources (resources that typically go unmeasured in such studies) and because development and individual experience simply do not begin at birth (see Gottlieb, 1995, 2003; Oyama, 2000).

Summary and conclusions

This paper has reviewed a growing body of research and theory, both comparative and human, converging on the conclusion that alimentary interoception—the perception of hunger, thirst and satiety—is not inborn or innate but must be acquired or learned, usually during early development. The similar theories and ideas put forward independently by Craig (1912, 1918), Hebb (1949), Bruch (1969) and Buck (1989a) have been shown to be generally correct by a growing body of empirical research. Fig. 2 is an attempt to provide a visual representation of the combined model suggested by this theory and research. From this perspective, the infant is not born a *tabula rasa*: there are initially some relatively "hard-wired" or reflexive connections between biological signals indicating need for food and/or water and expressive behaviors like crying, along with consummatory and other reflexes (e.g., rooting) and basic taste preferences. Apart from these, the neonate is neither born with any innate or pre-wired connections between particular interoceptive sensations and nutritive stimuli in the environment, nor between such stimuli and the behaviors that come to be involved in ingestion. Any such connections must be acquired during ontogeny through processes of socialization or social biofeedback. During development, expressive and ingestive behaviors are socialized and, depending upon the quality of caregiving received and the likely influence of numerous contextual and cultural factors, the infant may grow to have a differentiated sense of emotional and alimentary needs (interoceptive awareness and/or competence) and of how to appropriately express (expressive competence) and meet those needs (emotional/motivational competence) within a given social environment.

To assert that infants are born with an innate or instinctive sense of hunger, thirst and/or satiety is to hold that neonates are born with genetically inherited, innate "knowledge." Such an assertion is, however, not supported by developmental and biological science and is inconsistent with the wider conception of inheritance embodied in developmental psychobiological systems theory. Organisms inherit far more than DNA. The postulation of innate knowledge is unnecessary if extra-genetic features of an organism's inherited developmental system or niche more or less guarantee the reliable emergence of such knowledge with normal levels and timing of species-typical interaction with and/or experience of those features. In the case of the development of alimentary interoception, infants must learn to make cognitive connections between interoceptive stimuli, their own behavior(s) and external appetitive stimuli through interaction and experience within a socio-cultural milieu and/or ecological niche. In more altricial species, like humans, this generally occurs through reciprocal processes of feedback and socialization with caregivers (Bruch, 1961, 1969). Caregivers thus function like *biofeedback* providers for developing human infants and children (Buck, 1989a). This is a view

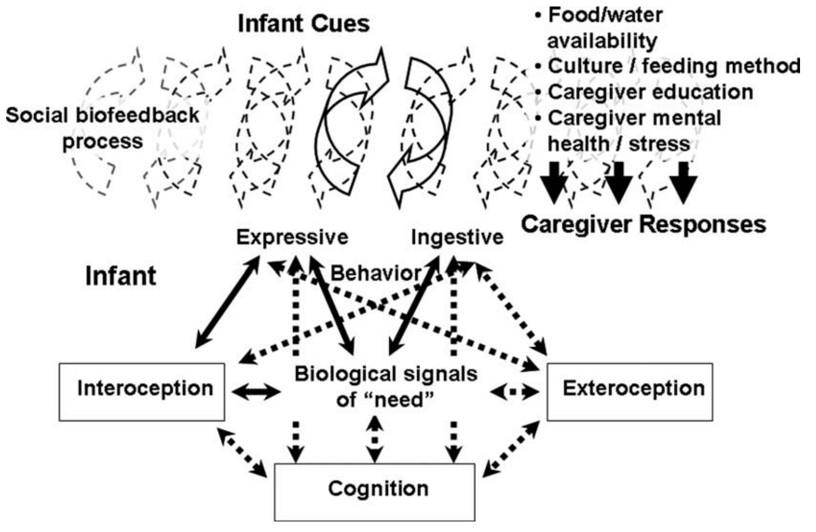

Fig. 2. A simplified illustration of the combined model of interoceptive development (for altricial species) suggested by the research and theory reviewed in the current paper. This model combines elements of the theories and ideas put forward by Craig (1912, 1918), Hebb (1949), Bruch (1961, 1969) and Buck (1989a). The "social biofeedback" process consists of reciprocal interactions in which infant and/or child cues are interpreted and responded to by a caregiver or multiple caregivers. In this model, infants are not born with an innate interoceptive sense or knowledge of hunger, thirst and satiety, but must acquire such skills and knowledge through processes of social biofeedback. If infant cues are responded to appropriately (i.e., differentially with respect to actual infant needs) then the infant/child's expressive and ingestive behaviors will come to be appropriately socialized for adaptation within a given socio-cultural environment. The dark arrows illustrate that this model acknowledges some relatively "hard-wired" or reflexive connections between physiological signals of biological need, interoceptive experience and expressive behavior (e.g., crying). The dashed arrows illustrate connections that must be established during postnatal development. The model is dynamic and non-hierarchical: all arrows are double-sided, indicating bidirectional relationships between physiological signals, interoceptive experience, exteroceptive experience, cognition and behavior. Physiological signals of biological need, for example, undoubtedly modulate interoception, exteroception, cognition and behavior, in addition to being affected both directly and indirectly by these.

consistent with the emerging consensus that views the mother as a critical developmental resource within the typical mammalian developmental system (Moore, 2007). In more precocial species (e.g., chickens and quail), other normally occurring features of the organism's inherited niche (e.g., a mother and/or other conspecifics who are prone to peck in the vicinity of ingestible items and/or the mere presence of ingestible items) likely guarantee the emergence of hunger, thirst and satiety under species-typical conditions (e.g., Breed, 1911).

It may be argued that this paper has simply erected and attacked a "straw man" and that no serious researcher today believes that eating is wholly genetically and/or evolutionarily determined. Such a claim, however, is misplaced given that the purpose of the present paper is to argue for a developmental psychobiological systems view of *alimentary interoception* and to review, for the first time, the existing empirical and theoretical literature bearing upon the development of alimentary interoception. The acknowledgment that learning is critically involved in almost all aspects of appetitive development is ubiquitous in the modern field of eating psychology (e.g., Birch, 1998; Booth, 1992; Capaldi, 1996; Le Magnen, 1998). A *developmental psychobiological systems* perspective, particularly with respect to alimentary interoception is, however, generally missing. With the exception of L.L. Birch and her colleagues (e.g., Birch & Fisher, 1998, 2000; Birch et al., 2003; Fisher & Birch, 1999), the development of alimentary interoception appears to be taken for granted by researchers and theorists working within the domain of the psychology of eating and drinking.

In one textbook on the subject, for example, few references to the many empirical studies cited in the present review supportive of a developmental view of alimentary interoception can be found except for a passing reference to Wright's studies, several references to Birch's studies and several references to Bruch's trade books (Logue, 1991, 2004). In the more recent version of this text, *The Psychology of Eating and Drinking*, the author moreover treats Bruch primarily as a "psychodynamic" theorist, writing that:

> According to this view, it's understandable that a child might come to eat when frightened or lonely, since he or she has associated feeding with security and a mother's love. Alternatively, if early caregivers are wise in feeding a child and respond well to the child's biological needs, they can teach the child to consume food only when it's really needed. Although the psychodynamic approach seems an eminently reasonable one, we have little in the way of research findings to make its conclusions significant for experimental psychologists (p. 30).

This characterization of Bruch's theory is overly simplistic and inadequate, particularly given that Bruch explicitly abandoned the psychoanalytic approach to eating disorders because she found that it simply did not work with eating disordered patients (e.g., Bruch, 1970). As this review highlights, there is also a large and growing body of research supportive of the views advocated by Bruch. In a chapter of the same text dedicated to drinking and thirst likewise no references to any of the empirical studies suggesting a developmental account of thirst (e.g., Changizi et al., 2002; Craig, 1912, 1918) can be found. In another textbook on the subject, Ogden (2003) similarly portrays Bruch as a psychodynamic theorist, while also omitting any reference to research and theory supportive of a developmental account of alimentary interoception. The text, *Why We Eat What We Eat: The Psychology of Eating*, edited by Capaldi (1996), however, does a far better job of emphasizing the influence of development and learning on nearly all aspects of eating.

It is arguable that developmental psychobiological systems theory may provide a far better metatheoretical basis for the science of eating and drinking than the approach currently provided by evolutionary psychology. Evolutionary explanations of eating and eating related behaviors are gaining rapidly in popularity and proliferation (e.g., Nesse, 1964; de Graaf, 2006; de Ridder & van den Bos, 2006; Gatward, 2001; Guisinger, 2003; Lieberman, 2006; Polivy & Herman, 2006; van den Bos & de Ridder, 2006). Logue (2004), for example, puts forward a strictly evolutionary account of eating at the beginning of her text. Polivy and Herman (2006) similarly argue for an evolutionary view of eating, writing that:

> ...imposing an evolutionary interpretation does not ordinarily involve the sort of experimentation required to establish causality; rather, phenomena are reinterpreted in a fashion consistent with evolutionary principles. The criterion for establishing the value of the present exercise is whether or not it provides a coherent and illuminating interpretation that was heretofore neglected (p. 31).

This description highlights that the kind of intellectual exercise often involved in the application of evolutionary principles to fields like eating in some ways bears closer resemblance to postmodern philosophy than scientific psychology. De Ridder and van den Bos (2006) similarly argue that, "adopting an evolutionary point of view is compelling as it provides a rather straightforward account of a once adaptive mechanism that has become maladaptive in a society that is characterized by the abundance of food" (p. 1).

To argue that processes of evolution have in no way shaped eating behavior would be absurd. It should be sufficient to point out, however, that such simplistic thinking stands in stark contrast to the data and theory reviewed in the present paper and to a developmental psychobiological systems perspective, which views all phenotypic outcomes as emergent, probabilistic functions of a host of interactions and/or coactions over the course of individual development. This is not an anti-evolutionary position, as has been claimed elsewhere (e.g., MacDonald & Hershberger, 2005). A developmental psychobiological systems perspective simply demands a fuller, less simplistic conception of evolution and natural selection—or a *biologically plausible evolutionary psychology* (Lickliter & Honeycutt, 2003). Entire developmental systems are "selected for" (cf. Blumberg, 2005; Jablonka & Lamb, 2005; Rollo, 1995) and these *evolved-systems-as-a-whole* and all modifications therein must be taken into account by researchers and theorists adopting evolutionary approaches to complex behaviors such as eating and drinking.

Evidence is mounting, for example, against the view that the modern epidemics of obesity and diabetes are *merely* the result of a mismatch between our ancient genes and modern obesogenic environ-

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ment (e.g., de Ridder & van den Bos, 2006; Lieberman, 2006). Such a view is too simplistic to capture the complexity involved in the production of such outcomes and ignores the mounting evidence suggesting that mismatches due to intrauterine and perinatal epigenetic programming may be far more prevalent and more important, particularly from a public-health standpoint (e.g., Bateson, 2001, 2007; Bateson et al., 2004; Fowden, Giussani, & Forhead, 2006; Gluckman, Hanson, Spencer, & Bateson, 2005; Hales & Barker, 1992; Martin-Gronert & Ozanne, 2005; Ross et al., 2003; Wells, 2007). Given the number of modifications that have been made to our species-typical rearing environment, particularly to our species-typical developmental system of food and fluid intake, the need for a developmental psychobiological systems approach to eating and appetitive development is arguably urgent.

On the flip side of the coin, the topics of eating and appetitive development have not been a central concern for modern developmental psychologists. In the 77 chapters that make up the four volumes of the *Handbook of Child Psychology* (Damon & Lerner, 2006), for example, not a single chapter is dedicated to the development of eating, drinking or appetite. Likewise, in the 80 chapters that make up the *Handbook of Parenting* (Bornstein, 2002), not a single chapter is dedicated to eating, drinking, appetite or to the feeding infants and children. Apparently we have progressed far beyond the Freudian preoccupation with basic biological functions—eating and drinking are not important for child development and the provision of food and drink is not an important aspect of parenting. In the 67 chapters that make up *Developmental Psychopathology* (Cicchetti & Cohen, 2006) a single chapter does, however, focus on the effects of nutrition on brain development. Taken as a whole, this is obviously a highly unsatisfactory situation, particularly given that it is the state of affairs in a society wherein obesity and other eating disorders, along with related medical conditions such as diabetes, have reached epidemic proportions (cf. Faith, Fontaine, Baskin, & Allison, 2007; Flegal, 2005; Levitsky, 2005; Mokdad et al., 2001). It gives the impression of a socio-cultural blindspot of enormous proportions (cf. Booth, 1994). It is a blindspot that can nonetheless be remedied by a redirection of theoretical, scientific and educational efforts toward a truly interdisciplinary, integrative science of appetitive development.

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