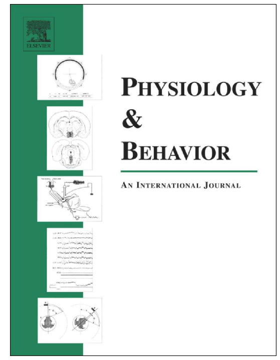

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Understanding infant eating behaviour – Lessons Learned from Observation

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Abstract

Observations of human infants during feeding presents a rich source of data to identify the ways in which hunger, appetite and satiety are communicated in early life. Infants signal appetite through their interest or disinterest in food using a series of communication cues from rapid and transient facial expressions to subtle or potent gestures and bodily movements through to vocalisations and eventually speech. Even in the first days of life facial expressions in response to basic tastes are clearly demonstrated and shared between human infants, other primates and the rat. These sensory typical reactions are said to have biological significance since the positive affective response to sweet taste secures a safe and useful source of energy while an aversive response to bitter may protect against toxicity. However, beyond these shared responses to basic tastes, the human infant has a sophisticated communication system to demonstrate readiness to eat, avid or waning appetite and satiety. Video capture and behavioural coding of infant communication and caregiver responses during meals reveal the dynamic nature of mealtime interactions. Responsiveness to infant cues is influenced by maternal characteristics and mode of feeding. Breastfeeding facilitates communication by enhancing maternal responsiveness and increasing the frequency of engagement and disengagement cues of the infant. This demonstrates the bi-directionality and interdependence of infant communication during a feed, namely that more responsive feeding for example, through breastfeeding, is associated with more proficient communication by the infant. Overall, observational methods have revealed the complex ways in which infants signal energy needs to their caregivers, and in turn these same methods have captured on film the ways in which carers recognise and react to these signals as part of responsive feeding. Potential applications of these methods includes developing interventions to facilitate infant self-regulation through responsive feeding.

Keywords: infant; hunger; appetite; liking; wanting; food intake

In order to investigate basic aspects of a biologically driven behaviour such as eating, psychologists have turned to the origins of their discipline and applied a phenomenological approach. The first and most obvious method to investigate a behaviour is to characterise its basic elements through observation. For those trained in biopsychology the assumption is that observed behaviour reflects underlying physiological processes. Thus for Curt P Richter, behaviour represented a biological phenomenon seeking to maintain physiological balance and so-called “wisdom of the body” (Blass, 1994). The classic studies by Clara Davis (1928, 1939) investigating nutritional wisdom demonstrated that infants aged 8m could choose appropriately from an array of raw and cooked foods to ensure adequate nutrition, growth and wellbeing. The infants selected a variety of foods not simply the most liked nor the most sweet. Whilst the experiment was flawed in many ways including questionable ethics as well as no provision of processed, highly palatable foods, this study revealed the importance of careful observation of very young children revealing their astonishing capacity to select wisely to meet energy and nutrient requirements (see Strauss 2006 for further discussion).

During the milk feeding phase, babies signal to their mothers their need to eat through a systematic process of agitation, orientation towards the breast, mouthing, hand movements to the mouth, progressing to more distress until the hunger cry is heard. It is assumed that mothers will respond to these signals and feed as needed. Beyond the milk feeding period infants signal hunger, satiation, liking and wanting in ever more sophisticated ways and it is the carer’s responsibility to identify then respond to these cues. Responsive feeding will make the difference between healthy feeding, providing too much or too little. This can then impact on body weight. For example, it is assumed that rapid infant weight gain, a known predictor of childhood obesity, may be driven by maternal overfeeding. However, what is not clear is whether mothers are simply responding appropriately to a hungry baby or misreading signals from their infants and providing too much food (Lumeng, 2016). Child eating traits such as fussiness and satiety responsiveness are highly heritable (Llewellyn& Wardle, 2015). Therefore, food-relevant signals produced by infants may reflect underlying traits and temperament and how mothers respond to this may in turn determine whether the infant is fed responsively or not.

So that infant eating behaviour can be investigated, and the role of communication between mothers and their babies understood, a clear set of recognisable behavioural cues are needed. In this paper, the use of observational data including facial expressions, overt behaviours and how mothers respond to these will be discussed. Following in the footsteps of Curt Richter, who was the consummate comparative psychobiologist, the commonalities between human and non-human primate responses to tastes will be considered before then moving on to consider the specific facial expressions, bodily movements, gestures and vocalisation communicated by human infants to their caregivers. If the infant is nutritionally wise expressing "wisdom of the body" then these communication signals should be easily discernible, reliable and responsive to a variety of nutritional challenges. Therefore, liking and wanting signals should differ as a function of the foods offered to infants and this will be explored in relation to acceptance of a novel vegetable. Finally, for the communication to be successful it is not sufficient for infants to signal hunger, satiation, liking and wanting, it is also necessary for the caregiver to understand and respond accordingly to these signals. Therefore, the final section of this paper will explore responsive feeding and how this may vary according to maternal characteristics and mode of feeding.

First tastes – the role of chemical continuity

When does the first experience of food-related sensory stimuli such as taste and smell occur? It is known that this occurs *in utero*. The foetus is exposed to flavours derived from the maternal diet. In his studies of foetal learning, Hepper (1988) exposed pregnant rats to garlic or no garlic, then presented garlic or onion in petri dishes to 12 day old pups. The time spent over each stimulus was recorded and the total amount of time spent on each side of the cage was recorded. Offspring of the dams fed garlic preferred garlic over onion and offspring of the control group showed no preference for either stimulus. This finding was replicated in cross-fostered pups. Therefore, odour learning occurs *in utero* and it is claimed that this is biologically adaptive, providing chemical continuity between the maternal diet, the food preferences of her offspring, serving to enhance kin recognition (Hepper, 1996).

In the human equivalent of these studies, Marlier and Schaal (2005) have shown that newborn babies use both head and mouth movements to indicate preference for odours. These elegant studies have been developed from a long history of assessing olfactory sensitivity in infants, revealing that neonates can detect, discriminate and assign incentive value to various odours. For example, in response to ammonia delivered via a cotton swab to 1-5 day old infants, most will turn their head away from the offensive smell (Schaal, 1988). Soussignan, Schaal and Marlier (1997) investigated the response of 3 day old babies to artificial (vanillin, butyric acid, formula milks) and biological (breast milk, amniotic fluid) odours using recordings of behavioural (facial and oral movements) and autonomic (respiration, differential skin temperature) events. In these studies, nose wrinkling and the "grimace" facial expression were interpreted as disgust for an aversive relative to a positive odour (butyric acid vs vanillin; Soussignan et al 1997). Thus in early life infants communicate like and dislike, acceptance and rejection.

Building on this, in order to assess preference of one odour over another the technique developed by Marlier and Schaal (2005) employed an olfactory paired-choice test. The newborn is supported in a fabric apparatus and gauze pads presented on either side impregnated with either distilled water or milk (human or formula). In this test, the infant's response is video-recorded during 1 min exposures which are counterbalanced to minimise lateral bias of head turning. Overall, oral activation (mouthing) and head orientation were higher in response to human milk over formula milk for both breastfed and formula fed babies. This may be explained by the attractiveness of human milk which contains aromatic compounds familiar to infants via transmission *in utero* and is not dependent on experience since formula fed babies show this same response. During the early postnatal period infants communicate their preference via facial expressions, mouthing or head orientation towards familiar or liked odours.

To determine responses to taste in infants, methods based on the taste reactivity measurements in rodents developed by Grill & Norgren (1978) analyse frame by frame reactions using video recording. The use of dynamic images captured on video has permitted fine-detail analysis of infant facial reactions to taste which is not possible in real time observations.

Newborn responses to different basic tastes have been well characterised. Classically this was demonstrated in the early work of Jacob Steiner (1977). In these studies, pure tastants were given via pipette to newborns to characterise the specific response to sweet, sour, bitter and salty and to investigate affective qualities. Steiner demonstrated distinctive facial expressions of the newborn to the sweet taste (tongue protrusions and "smile"), lip pursing in response to sour tastes and gape to bitter tastes. These facial responses are observed in non-human primates and in collaboration with Kent Berridge, the work of Steiner was extended to understand the "sensory typical" and affective responses to basic tastes across different mammalian species. Berridge (2000) has proposed that human hedonic and aversive reactions are directly related to the taste reactivity patterns of other animals. In the rat and primate there is a shared tongue protrusion in response to sucrose in solution (representing the sweet taste) and shared "gape" in response to quinine in solution (representing the bitter taste). Whilst these responses are similar across species, there are also distinctive elements shown only by humans such as lip pursing to sour tastes and differences in speed of tongue protrusions (Berridge, 2000). For instance, in the human infant tongue protrusions appear to be relatively slow, about 1 per second whilst in New World monkey species, more rapid tongue protrusions are observed at a rate of around 3 per second. Between humans and other non-human primates, responses are similar albeit that they will vary “in proportion to their degree of phylogenetic relatedness” according to Berridge (2000 pg 193). Given that there appears to be a continuum of hedonic and aversive taste reactivity patterns which extends to the rat, it may be argued that these responses are “sensory typical” but do not necessarily indicate affective quality. Generally speaking, palatability corresponds well with the specific sensory qualities of a given taste (for example sweet or bitter), and with whether and how much of that substance will be consumed. But palatability as measured by taste reactivity can be dissociated from intake and so reactivity patterns predict hedonic or aversive responses to the taste but do not necessarily predict ingestion (Berridge, 2000). Studies which therefore seek to understand both liking and intake will measure taste reactivity, behavioural responses and various parameters reflecting ingestion (rate of ingestion, duration of the meal, amount consumed).

In the rodent model, taste preferences can be programmed during foetal development by exposure of the dams to a cafeteria diet (Desai et al., 2014) and by intrauterine growth restriction (Laureano et al 2016). In these contexts, taste preference can be gauged by taste response and intake measures. Using the example of the effect of intrauterine growth restriction, day old rat pups born to food restricted dams were given intra-oral sucrose solution and their response filmed for 90 seconds. Both rhythmic midline tongue protrusions and lateral tongue protrusions were counted using frame by frame analysis of the first 60 seconds to assess hedonic response to the taste of sucrose relative to plain water. Under these conditions, pups born to food restricted dams showed a significant preference for sucrose over water and had a higher frequency of total tongue protrusions than the control pups indicating an exaggerated response to sucrose compared to control. This is especially interesting since these results suggest that in addition to the sensory-typical liking response to sweetness, incentive salience is influenced by nutritional status. Similar methods of filming oral activation are shared between animal and human models, with the underlying assumption that tongue protrusion frequency represents a positive affective response and greater frequency indicates greater incentive salience (wanting).

In the human context, affective responses are inferred by facial expression and by the avidity of appetite for a substance. These responses are assessed in the laboratory by researchers and by asking caregivers (usually mothers) to make a judgment of how much their infant likes a food (Forestell and Mennella, 2007, Forestell and Mennella, 2012, Mennella et al., 2001, Maier et al., 2008). Although this measure of liking can be direct, it is subjective, open to bias and the criteria used to assess liking are not always clear. Even when researchers make subjective judgements of liking instead of mothers, this must be done on the basis of evidence. The variety of cues which mothers and others draw upon to provide information on liking along with hunger, satiation and satiety are important to identify so that behavioural coding systems can be developed to compare within and between infants. In this way a taxonomy of responses can be developed then applied both to understand *how* infants communicate basic needs, the ways in which this changes with development and *what* carers are looking for in responding to these signals.

Approach, avoidance and the ways in which these are communicated

During the first days and weeks of life, human infant communication is largely limited to crying (Illingsworth, 1980). The hunger cry varies in relation to distress and simple approach/avoidance behaviours are easily discernible in the first few days of life. As the infant develops, more complex communication patterns emerge.

Several studies have investigated mothers' perceptions of these feeding cues. These studies have been identified through a systematic research review (McNally et al 2016). Here it was concluded that hunger cues are easier to perceive by mothers than satiation cues, and that feeding cues are easier to interpret as children grow older. The review also found that the behaviours used to signal hunger, appetite and satiety are diverse and variable across and within individuals making the development of any taxonomy of responses challenging. Furthermore, cues are influenced by developmental maturity and mode of feeding. Given that infant feeding is dyadic, both infant (age, sex and temperament) and maternal characteristics (e.g. BMI) interact to affect how feeding cues are perceived.

What then are the signals that mothers use to interpret hunger, appetite and satiety? Anderson et al. (2001) asked mothers what they looked for when deciding readiness for weaning. In this context, perceptions of hunger related both to babies' characteristics (e.g. age, weight) and their behaviour (e.g. rapid rate of milk consumption, agitation, "chewing" their hands) as well as context such as time of day and time since last feed. Mothers reported being able to identify a 'hungry cry'. However, this was differentiated from other cries by time of day rather than the characteristics of the cry itself. Reported satiation cues included expressions of contentment, and being more settled.

Interestingly Wright (1986) reported differences in mothers' interpretation of hunger cues according to the sex of their baby. These differences were of note since the weights taken from before and after feeding indicated that relatively constant volumes of milk were consumed by girls and boys across the day. It appears then that mothers of infants construe male babies as hungrier than females (Wright 1986).

According to Gross et al. (2010) who also examined mothers' perceptions of infant hunger and satiation, four hunger and satiation behaviours were attended to. These were sucking hands and crying to indicate hunger and for satiation - turning the head away and "knowing the baby is full". In this study, identification and response to cues differed according to mode of feeding and to characteristics of the mothers. Mothers who were obese were more likely to identify sucking on hands as a hunger cue and less likely to believe that babies know when they are full. The authors interpreted this mismatch to suggest that obese mothers are more alert and responsive to cues for hunger and less sensitive to signs of fullness which in turn could lead to overfeeding over time. They also found that breastfeeding mothers were more likely to identify sucking on hands as a hunger cue, and this was interpreted as these mothers being more "tuned in" or sensitive to infant hunger than those who formula fed.

Using semi-structured interviews Hodges et al. (2008) investigated cues which prompted mothers to initiate and end feeding. Like Anderson et al. (2001) the authors found mothers used both infant behaviours and external cues (e.g. time) to identify hunger. Typical hunger cues in this study were crying, fussing and licking the lips and these were reported across several age groups (3, 6 and 12 months). Common satiation cues included pulling away, spitting food out and stopping feeding. The authors also found that the prominence, intensity and specificity of infant cues guided decisions about initiating and ending feeds and that mothers found cues easier to interpret with increasing infant age.

Hodges et al. (2013) went on to develop a tool to characterise and code responsive feeding. The Responsiveness to Child Feeding Cues Scale (RCFCS) identified 20 types of hunger cue and 28 types of satiation cue. Hunger and satiation cues were further categorised as 'early' (e.g. increased alertness), 'active' (e.g. excitatory movements) and 'late' (e.g. fussing and crying) in order to reflect changes in cue intensity. They found that mothers were typically more responsive to hunger than satiation cues. The authors interpreted this in the context of the greater urgency and biological imperative of caregivers to respond to hunger compared to satiation. Maternal responsiveness to satiation was predicted by specific maternal characteristics such as lower body mass index, longer breastfeeding duration, and higher educational level. Breastfeeding may facilitate responsiveness to infants and this may later serve to protect infants from overweight and obesity. Although the protective effect has been contested (see Cassazza et al., 2013).

In their study of the changes in feeding cues expressed over time, Hodges et al (2016) observed mother–infant pairs during mealtimes at infant age 3, 6, 9, 12, and 18 months in the home. They used RCFCS at each time point and noticed that fullness cues became more diverse and less subtle over time. For instance in the first 2 observations (3m and 6m) disinterest, falling asleep, decreased muscle tone and activity level signalled fullness but during the later observations pushing or pulling away and communicating "no" verbally became more apparent. In relation to appetite, postural attention and reaching for food increased after 6 months. With time then, motor and language skills develop to enable infants to assert themselves more clearly in relation to readiness to eat and to terminate the meal.

In a longitudinal study of infants Skinner et al (1998) provided mothers with pictures of hunger cues and asked at what age these were displayed by their baby. Infants were aged 2 to 24m and mothers were interviewed at least 6 times out of a possible 10 times. They found that hunger behaviours (e.g. opening the mouth as the spoon approached) appeared at a younger age than satiation behaviours (e.g. closing the mouth to reject food) (4.4 to 5.7 months versus 5.8 to 7.5 respectively). Again this could be explained by the greater survival value of signalling hunger compared to satiation. In this study mothers reported that infants signalled interest in eating by opening the mouth in readiness as food approached, eating steadily, and/or eating a large amount of food. Food dislikes were communicated via facial expressions, and by body movements, such as turning the head or body away from food or throwing food away. These signals of food dislike appeared by 8m of age, and strong indications of food likes and dislikes increased in frequency with age. Overall, mothers reported that their infant's ability to communicate improved in scale and scope over time in tandem with the mother's improved skill in interpreting this communication (Skinner et al., 1998).

In summary, during milk feeding the first form of communication about hunger status is through approach behaviours such as hand to mouth, agitation, orienting towards the breast/bottle, culminating in the "hunger" cry. Satiation is initially signalled through disinterest and sleep and later signalled through avoidance cues such as stopping or slowing down acceptance, turning the head and pulling the body away. As children progress to solid foods, the approach and avoidance behaviours develop further in scale and scope. With maturity infants begin to use language to signal enjoyment of food and to indicate when they do not like or want to eat a specific food. It has been argued that the urgency and survival value of communicating hunger must be simple and dramatic, and therefore takes precedence over other needs. Cues to signal fullness appear later than hunger cues and responsiveness to these may depend on characteristics of the mother including breastfeeding duration, maternal body mass index and education.

Development and application of the Feeding Infant Behaviour and Facial Expression Coding System (FIBFECS)

Research towards developing a "taxonomy" of infant cues which signal approach/avoidance behaviours has progressed through the use of coding systems including the RCFCS. In assessing infant liking, facial expressions have been coded extensively in infants (Mennella and Beauchamp, 1997; Mennella et al., 2001; Forestell and Mennella, 2007, Mennella et al., 2009, Forestell and Mennella, 2012, Soussignan et al., 1997, Rosenstein and Oster, 1988). The Facial Action Coding System; FACS (Ekman and Friesen, 1978) is widely accepted as a measurement tool to code facial expressions in humans by detecting facial movements. Within the FACS the actions of individual or grouped muscles contribute to "action units". As mentioned above, like other non-human primates, humans use these facial expressions to communicate to others. However, in the human face there are many more muscles which can be recruited to display complex emotions such as anger, disgust, happiness and sadness. These facial expressions of emotion are universally understood across cultures (Ekman and Friesen, 1978). It is assumed that facial expressions displayed by babies might also reflect underlying emotional states to encourage communication with their caregiver. Such behaviours will have strong evolutionary significance in promoting appropriate responses from carers. Therefore, the BABY FACS adapted for infants by Oster (1993) reflects the different morphological features between adults and infants. For example, babies have more facial fat and more elastic skin than adults giving a different and a smoother facial response. Facial expression coding from the BABY FACS has been implemented in several studies to assess food liking in infants and older children (Forestell and Mennella, 2012, Forestell and Mennella, 2007, Zeinstra et al., 2009, Mennella et al., 2009, Soussignan et al., 1997, Rosenstein and Oster, 1988).

As a measure of incentive salience, consummatory behaviours include how much is eaten of a given food. This is calculated in simple terms such as weight of food consumed or energy intake but is also reflected in duration of the meal and pace of eating. Here it is assumed that the more a food is wanted, the more will be eaten, the longer the duration of the meal and the faster it will be consumed. It is also assumed that the more a food is liked, the greater its incentive salience and therefore it is more likely to be eaten and in greater amounts than foods less liked. Bringing together consummatory measures with facial expressions (indicating incentive salience) in response to the taste of foods permits a test of these assumptions. In studies where maternal judgement of infant liking is compared to intake measures and facial expressions, it has been found that facial expressions of distaste were inversely associated with eating pace and subjective reports of liking

(Forestell and Mennella, 2012, Mennella and Beauchamp, 1997, Forestell and Mennella, 2007, Mennella et al., 2009). A study by Mennella et al. (2009) examined the effect of exposure to milk formulas with different sensory properties on liking and intake in infants aged 4–9 months. The infants who were familiar with drinking hydrolysed casein formulas (with noticeable bitter, sour, and savoury tastes compared with breast milk), displayed fewer negative facial expressions when eating bitter and savoury cereals compared to the infants who were unfamiliar with such milk. This suggests higher levels of liking of these flavours as a function of experience.

Video coding together with other measures of liking (maternal ratings, researcher judgements and independent coding from facial expressions) provide cross verification of data from two or more sources to improve levels of description and explanation. In a study of weaning age infants, we adapted the BABY FACS to assess liking and wanting, in conjunction with intake, maternal and investigator ratings of liking (Hetherington et al 2016). In this study, infants were randomly assigned to a control group receiving no prior vegetable experience or an intervention involving a step-by-step introduction of novel vegetable flavours added to milk for 12 days and then to cereal for 12 days. This study was designed to test whether exposure to vegetables paired with a familiar and liked food (milk and cereal) would enhance acceptance of the pure vegetable flavour (Hetherington et al 2015). Following the 24 days of exposure, on days 25 and 26 babies were filmed receiving their first taste of pure vegetable puree (carrot on d25 and green bean in d26) and their responses coded. Video recordings were coded using the Feeding Infants: Behaviour and Facial Expression Coding System (FIBFECS; Hetherington et al 2016).

The coding system is divided into two sections with 6 acceptance/rejection behaviours (turns head away, arches back, crying/fussy, pushes spoon away, leans forward and rate of acceptance; see Figures 1 and 2 for examples of turning the head away and disinterest) and 7 facial expression items (brow lowered, inner brow raised, squinting, nose wrinkling, lip corners down, upper lip raised and gaping; see Figures 3 and 4 for examples). Infants were offered 9 consecutive spoonfuls of puree and behaviours and facial expressions were assessed per spoonful. When a spoon offer was rejected, the infant's behaviours were coded for the spoon offer; however facial expressions were not coded because the infant had tasted the vegetable. Four independent trained raters who were blind to the infants' group assignment (experimental or control) conducted the coding. Duration, pace and intake of the vegetables differed by group with the infants from the intervention group showing greater duration, pace and consumption of each vegetable than the infants from the control group. Investigator ratings but not maternal ratings of liking also differed by group assignment in line with predictions (greater rated liking for vegetables in the intervention compared to the control group).

Figures 1 -4 here

The coded behaviours from the FIBFECS also revealed a difference by intervention, thus infants who had been exposed to the vegetables in milk and cereal showed fewer rejection behaviours and a faster rate of acceptance than infants in the control group. However, coded facial expressions from the FIBFECS did not differ by intervention group. Facial expressions were similar by group but differed by vegetable. Carrot produced fewer instances of negative facial expressions such as brow lowered, nose wrinkling, upper lip raised and gape than green bean for both groups of infants. This may be attributable to the sweeter taste of carrots relative to green bean, and might reflect a more general acceptance of this vegetable even in infants who had not yet experienced this specific taste. The total number of rejection behaviours, and overall frequency of aversive facial expressions were inversely associated with intake and duration of eating. The more the food was liked (such as carrot), indicated by fewer facial expressions of distaste and fewer rejections (indicating wanting), the faster the pace of eating, the greater the intake and the longer the duration of the meal. In addition, a faster acceptance rate and fewer rejections were significantly correlated with liking ratings. The FIBFECS scores related to subjective measures of liking (from mothers and investigators) and objective measures of intake (reflecting wanting). However, mothers reported similar levels of liking for vegetables across groups, whereas investigators reported greater liking for vegetables in the intervention group (Nekitsing et al., 2016). Both mothers and researchers discriminated between liking for the different vegetables, and ratings of liking by mothers and researchers correlated significantly with total number of rejection behaviours and aversive facial expressions for the green bean.

Overall, the FIBFECS subscales revealed that experience of vegetables reduced rejection behaviours in weaning age infants, however, facial expressions were determined more by type of vegetable (sweet or bitter) than by experience. Mothers and researchers rated liking and these ratings corresponded well with rejection behaviours and with aversive facial expressions for the more disliked vegetable. Clearly mothers are attending to infant communication whether obvious avoidance behaviours or more subtle facial expressions of dislike. Taken together these are used by mothers to judge whether a food is liked and whether the meal should proceed.

Responsive feeding– cue recognition and the role of feeding method

The extent to which mothers and other carers are able to identify and respond to infant feeding cues will determine whether infants are fed to meet their nutritional needs. Feeding practices and responsiveness to infants influence the early entrainment of appetite control (Disantis et al. 2011; Hurley et al. 2011). The precise mechanisms linking feeding practices and appetite entrainment are not clear, however in their systematic review of the literature DiSantis et al. (2011) proposed a theoretical role for maternal feeding 'responsiveness' in infant and child overweight. 'Responsive' mothers are sensitive to hunger and satiation cues and respond to these appropriately while discordant maternal responses are a proposed risk factor for obesity. Worobey et al. (2009) found lower maternal sensitivity to feeding cues at six months predicted infant weight gain between six and twelve months. Hurley et al. (2011) also found that two types of discordant response, restrictive feeding and indulgent feeding, were associated with a high BMI in infants and young children. DiSantis et al. (2011) proposed a third kind of discordant response, namely maternal pressure to eat, also influenced obesity risk. Assertive prompts to eat and maternal intrusiveness were associated with higher adiposity in toddlers (Lumeng et al., 2012) suggesting that mothers may override the child's internal regulation signals in favour of her own desire to feed. Poor responsiveness to satiation cues by prompting or pressuring infants to eat may affect obesity risk by superimposing maternal expectations of what should be eaten over the infant's ability to self-regulate.

However, the direction of causality between maternal responsiveness and infant adiposity remains unclear. Overfeeding may arise from insensitivity to fullness cues, the use of food to comfort (Worobey et al., 2009), or could arise from the maternal responsiveness to the "hungry baby" as some infants have a more avid appetite than others (Lumeng, 2016). In turn, mothers may restrict intake for children they perceive to over-eat, or may pressure children with small appetites to eat more (Webber et al., 2010).

What then determines whether mothers are responsive to their infants' needs? It has been proposed that mothers who breastfeed might be more responsive than mothers who formula feed assuming that mothers who breastfeed encourage their babies to exert control over feeding initiation and cessation. Formula feeding or feeding breast milk from a bottle situates control for the feed with the mother who can easily judge volume consumed. Feeding from a bottle is associated with parental feeding control and lower ability to self-regulate energy intake (Arenz et al., 2004). Together with feeding practices, feeding mode (breast or bottle) may influence risk of overfeeding. For example, bottle-fed infants were more likely to be encouraged to empty their bottles or cup in late infancy (>6m) than those who were fed directly at the breast (Li et al., 2010). Bottle-feeding, regardless of the type of milk, was also associated with infants' poorer self-regulation and excess weight gain during late infancy (Li et al 2008).

So far it has been argued that infants are capable of increasingly sophisticated ways of communicating appetitive cues including hunger, appetite and satiation. Does the mode of feeding influence the extent to which mothers recognise and respond to these cues? We conducted a series of investigations on the same cohort of infants to examine differences in mealtime interactions between breastfed and formula fed babies assessing both maternal and infant behaviours.

In the first study, a cohort of 73 women from the UK and Israel who had been followed during pregnancy, were then contacted between 2 and 6m postpartum. In this study it was found that maternal BMI predicted feeding on a schedule with heavier mothers feeding less responsively using a schedule to feed. Baby eating traits did not differ by BMI or feeding mode, but using the Baby Eating Behaviour Questionnaire (Llewellyn et al., 2011) general appetite and enjoyment of food were closely linked, as well as slowness in eating and satiety responsiveness (Shloim et al 2014). Since no differences in eating traits were found between breastfed and bottle fed babies as measured through self-report, a two further studies were undertaken to assess feeding behaviour through filmed mealtime interactions.

In one of these investigations, video recording was conducted during the milk feeding phase for 41 of the original sample of Israeli and UK mother–infant dyads. Feeding behaviours were coded using the Simple Feeding Element Scale (Shloim et al., 2015). Mealtime interactions did not vary according to maternal body mass index or country. However, women who breastfed (rather than bottle fed or fed solids) presented fewer distractions during the meal, provided a more ideal feeding environment and fed more responsively.

To examine these interactions in more detail films from twenty-seven mothers (13 breastfeeding; 14 formula feeding) were coded when the infants were aged between 3 and 22 weeks. In particular, the expression of engagement and disengagement cues during the feed were recorded. These cues were identified using a validated list of communication cues developed by Barnard (1994) forming part of the Nursing Child Assessment Feeding Scale (NCAFS). There are 83 feeding cues in all which can be further divided into engagement (n = 19) and disengagement cues (n = 64). Each cue is further described as potent (strong and clear) or subtle. Originally the feeding scale was developed in the nursing context in order to identify problematic parent-child interactions. This scale has been used as a means to detect difficulties caused either by adverse circumstances or developmental delay. The frequency of each cue during the beginning, middle, and end of the feed was recorded. In this analysis only 22 of the possible 83 feeding cues were applied and of these 6 were engagement and 16 disengagement cues. Examples of engagement cues included sucking sounds, mutual gaze, opening the mouth in readiness to feed, whereas examples of disengagement cues included pushing away or back arching. Over time, engagement cues tended to decrease and disengagement cues tended to increase, reflecting the transition from interest in milk to disinterest and satiation. Overall breastfed infants displayed more of both types of cue than formula fed, in particular, engagement cues such as sucking were more apparent at the beginning of a feed in breastfed compared to formula fed babies. Breastfed babies also opened their mouth and indicated greater readiness to eat at the beginning of the feed compared to formula fed infants (Shloim et al., 2017).

In summary, developmental maturity ensures that infants demonstrate more diverse and assertive means of communicating appetitive cues including hunger, appetite and satiation; however, responsiveness to these cues may be influenced by maternal BMI and mode of feeding. There is evidence that breastfeeding mothers are more responsive to their infants and in part, this could be due to the communication proficiency shown by breastfed babies (Shloim et al., 2017).

Conclusions

Following in the footsteps of psychobiologists including Curt Richter, extensive observations of infant feeding have yielded valuable insights into how hunger, appetite and satiation are signalled. Building on the methods developed to assess taste reactivity in the rat, the now classic studies of infant facial expressions to basic tastes show sensory typical behaviours in the human infant shared across species indicative of positive and negative affective responses. Progressing from still photographs to video capture has permitted detailed investigation of the dynamic nature of subtle and strong reactions to taste as well as overt approach and avoidance behaviours in response to different foods. Coding systems such as the RCFCS permit intensive scrutiny of how caregivers recognise and respond to child feeding cues (Hodges et al., 2013). Tools like this can then be applied to mealtime interactions in order to detect the tendency to over or underfeed infants. Similarly, coding schemes such as the FIBFECS have been adapted from existing facial expression and behavioural cue measures to support analyses of liking and wanting in early infancy. The FIBFECS has been applied to detect differences in response to a novel vegetable following an intervention involving repeated exposure and to distinguishing between target foods which differ in taste qualities (Hetherington et al., 2016; Nekitsing et al., 2016). The potential implications of these observational methods include application within infant obesity prevention trials and also as a tool to support caregivers as a feeding aid. The assumption being that infants are capable of self-regulation, but that only through feeding responsively will parents facilitate this capacity. Such proposed applications are yet to be tested. However, interventions designed to promote responsive feeding are worth pursuing given that decisions about mode of feeding and the ways in which parents understand their infants' communication are modifiable. In summary, the psychobiology of human appetite begins by understanding the ways in which infants communicate energy needs and observational approaches have provided investigators with a set of tools with which to conduct this research. There are potential applications of these methods beyond understanding infant communication towards developing interventions to support responsive feeding.

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Figure Legends

Figure 1: Upper panel – one infant turning the head away to the presentation of a novel vegetable

Figure 1: Lower panel – examples of turning the head away

Figure 2: Infant showing disinterest in food offered (turn away from spoon, looking down)

Figure 3: frame by frame facial expressions in response to vegetable (A: mouth open, B: mouth open in readiness to accept food, C: food tasted, D: nose wrinkling, E: nose wrinkling and inner brow lowered)

Figure 4: frame by frame facial expressions in response to novel vegetable (A: smile, mouth open, B: tongue protruded, mouth open, C: lip corners down, nose wrinkling, eyes squinched)

Figure 1

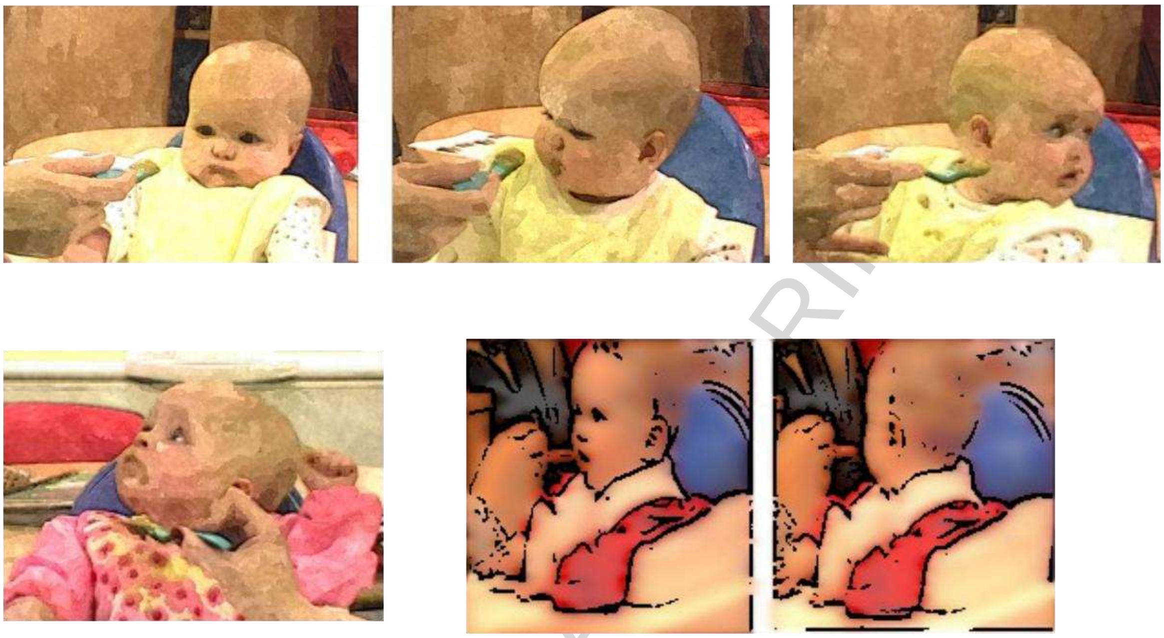

Figure 2

Figure 3

A B C D E

Figure 4

A B C

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Highlights:

- Infants signal appetite through their interest or disinterest in food
- Infants use rapid and transient facial expressions to signal liking
- They use subtle or potent gestures, bodily movements and vocalisations to express wanting
- Video capture and behavioural coding of infant communication and caregiver responses reveal the dynamic nature of mealtime interactions.
- Responsiveness to infant communication can promote self-regulation