

Motivated Attention and Reward in Parenting

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A review of the literature that suggests infant cues hold high incentive value and guide attentional processes.

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SYNOPSIS

Parenting has a significant and lasting impact on child development. From birth, parents must sensitively and appropriately attend to their infant's emotional expressions and vocalizations. Accumulating evidence indicates that these infant cues of emotion attract more attention than equivalent adult cues in parents as well as non-parents. We review this evidence and suggest that infant cues hold high incentive value and elicit motivated attention (i.e., enhanced processing of motivationally relevant stimuli), which in turn promotes approach motivation and thus caregiving responses. Further, we discuss data suggesting that infant cues are salient for non-parents, with increasing motivated attention to infant cues in the transition to parenthood. This increase may depend on interactions between the dopamine reward system and the neuropeptide oxytocin. Therefore, we also explore the human and non-human data that support this association and consider potential sources of variability in motivated attention in parents.

Key words: motivated attention, parenting, motherhood, reward, dopamine, oxytocin

MOTIVATED ATTENTION AND REWARD IN PARENTING

A parental focus on infant needs is crucial for infant survival and well-being. Parental behavior can have a long-term influence on infant development and health (Bornstein, 2002; Swain, Lorberbaum, Kose, & Strathearn, 2007) as well as far-reaching effects on adult behavior, including how parenting methods may pass from generation to generation (Bouvette-Turcot, Bernier, & Meaney, 2013; Van IJzendoorn, 1992). One critical component of parenting is the degree of sensitivity in detecting and responding to infant socio-emotional cues, which may have downstream consequences on parenting behavior (Rutherford & Mayes, 2011). These infant cues may be positive or negative in their valence and include facial expressions and vocalizations that may serve to communicate the infant's inner state and elicit responding from the parent. Critically, we consider the role of motivated attention to infant cues as a potential mechanism that may facilitate preferential orienting in adults towards infants – an effect that may be even more marked in parents. As described below, motivated attention refers to the enhanced processing of motivationally relevant stimuli (Lang, Bradley, & Cuthbert, 1997), which would include infant social and emotional signals. Specifically, we propose that parents preferentially attend to their infant because infant cues are particularly rewarding, and this reward value drives caregiving behavior. Indeed, even potentially aversive cues (e.g., infant cries) appear to be associated with reward and attachment neurocircuitry (Laurent & Ablow, 2012; Strathearn, Fonagy, Amico, & Montague, 2009). Therefore motivated attention forms a critical mechanism through which infant cues become prioritized for processing and consequently guide parental behavior and improve infant outcomes.

Motivated attention is a relatively novel framework within which to consider parental responding to infant cues, and to date has received little empirical investigation. We begin by defining motivated attention before considering behavioral and neurophysiological evidence for motivated attention to infant cues in adults (both parents and non-parents). We draw on behavioral as well as neurobiological studies in human and non-human species that suggest correlates of motivated attention to infant cues. We then consider the evidence that motivated attention to infant cues is especially salient in parents compared to non-parents, and discuss several factors that might underlie this effect. We outline the hypothesis that increases in motivated attention to infant cues during the transition to parenthood may crucially depend on the dopamine reward system and interactions between this system and the neuropeptide oxytocin. Finally, we consider the potential sources of individual differences in motivated attention to infant cues in parents, namely experience in caregiving and maternal psychopathology.

MOTIVATED ATTENTION

Motivated attention refers to the increased processing of motivationally relevant stimuli (Lang et al., 1997). Motivationally relevant stimuli are those that are important to an organism given their relevance to behavior (Downar, Crawley, Mikulis, & Davis, 2002). A stimulus that is evaluated as potentially beneficial is thought to automatically evoke a behavioral tendency to *approach*, whereas potentially harmful or unpleasant stimuli evoke *avoidance* behavior (Chen & Bargh, 1999) - although in complex organisms these behavioral tendencies may be overridden (Lang & Bradley, 2013). Behavioral tendencies to approach or avoid are thought to arise from the activation of one of two motivational systems, *appetitive* and *defensive*, which organize affective and behavioral responses to

environmental cues (Bradley et al., 2003; Lang et al., 1997; Rutherford & Lindell, 2011). The appetitive system is associated with expected reward and is activated in contexts that promote survival, encouraging sustenance, nurturance, and caregiving behaviors (Bradley et al., 2003). In contrast, the defensive system is responsible for managing response to threat (Bradley et al., 2003; Lang et al., 1997). Consequently, we hypothesize that infant cues trigger the appetitive system, evoking an approach response and increasing the motivation to care for and nurture the young.

Relatively aversive infant cues (e.g., infant cries) might also be expected to activate the defensive system. Indeed, there is some evidence that parents and non-parents may rate infant cries as aversive (LaGasse, Neal & Lester, 2005), and insecure-dismissing women demonstrated physiological indices of behavioral inhibition (i.e., avoidance) in response to infant cries and rated cries as more aversive than secure-autonomous women (Ablow, Marks, Feldman, & Huffman, 2013). After the same women became mothers, their attachment style predicted maternal sensitivity to infant cues (see also Strathearn et al., 2009). Despite the potential aversiveness of infant cries and their activation of the defensive system in some women, these cry cues have also been found to elicit activity in brain regions associated with reward processing (Laurent & Ablow, 2011; Lorberbaum et al., 2002). This reward activation may serve a functional purpose in triggering maternal approach behaviors toward the child. Alternatively, whereas the infant cry itself may not be rewarding, the cry may elicit anticipation of reward in soothing the infant and explain the increased reward region activity in the presence of infant cry. Taken together, the activation of appetitive and defensive systems by infant cues reflects the broader conceptualization of this approach-avoidance system in

organizing behavioral responding to emotional stimuli (Lang, Bradley, & Cuthbert, 1990), with a clear potential for individual differences as they relate to the activation of these systems and behavioral outcomes. However, beyond brain and behavioral responding, it has been hypothesized that an approach-avoidance dichotomy could be valuable for understanding psychopathology (Gray, 1982), as well as personality more generally (Carver & White, 1994).

Approach responses to infant cues are present in both parents and non-parents – perhaps as part of a conserved evolutionary system to promote the survival of offspring and young dependents. Critically, the strength of the response may be augmented by hormonal and brain changes triggered by pregnancy and parturition. The degree to which a motivationally relevant stimulus, such as an infant cue, can drive approach or avoidance behavior is termed its *incentive value*. An item with a high incentive value, whether positive or negative, is more motivationally relevant and is therefore more likely to capture attention and drive behavior. Indeed the magnitude of the incentive value of a stimulus predicts the degree to which it captures attention (Hickey & van Zoest, 2012; Theeuwes & Belopolsky, 2012) and sharpens the effects of visual attention by improving its detection (Engelmann, Damaraju, Padmala, & Pessoa, 2009; Engelmann & Pessoa, 2007). This notion of the importance of attentional processes in parenting resonates with prior work suggesting executive functions more generally play a role in parental sensitivity (Chico, Gonzalez, Ali, Steiner, & Fleming, 2014; Gonzalez, Jenkins, Steiner, & Fleming, 2012).

Classically, empirical research probing whether motivationally relevant stimuli modulate attentional processes has focused on anxious populations engaging with

threatening stimuli (Bar-Haim, Lamy, Pergamin, Bakermans-Kranenburg, & Van IJzendoorn, 2007). However, more recent research has identified that reward-linked stimuli also guide attentional processes (e.g., Peck, Jangraw, Suzuki, Efem, & Gottlieb, 2009; Rutherford, O'Brien, & Raymond, 2010). In sum, motivated attention refers to the finding that stimuli with high incentive value attract attention and are preferentially processed (Lang et al., 1997).

ATTENTIONAL BIAS: A BEHAVIORAL MEASURE OF MOTIVATED ATTENTION

Stimuli that elicit motivated attention can have a direct effect on behavior by influencing the speed and direction of basic attentional processes, biasing attention toward motivationally relevant stimuli. *Attentional bias* is defined as either rapid and strong attentional orienting to motivationally relevant stimuli (attentional capture) or delayed disengagement of attention from motivationally relevant stimuli as compared to less-relevant stimuli (Fox, 2002). Attentional bias is typically assessed using a visual probe task (MacLeod, Mathews, & Tata, 1986). This task involves presenting participants with two stimuli (pictures or words) side-by-side on a computer screen. Following the presentation, a target stimulus (the visual probe) appears in one of the locations previously occupied by these stimuli. Participants are instructed to indicate the location of the target as quickly and accurately as possible. When a target is presented in the location of a motivationally relevant stimulus, RTs are typically faster than when the target appears in a location where no motivationally relevant stimulus was presented. This RT difference provides a behavioral index of attentional bias.

How might RT modulation by motivationally relevant stimuli come about in attentional bias studies? Increased attentional bias may occur via a *saliency map* that guides attentional focus (Itti & Koch, 2001), leading to preferential processing of both positive and negative survival-relevant cues (Koster, De Raedt, Goeleven, Franck, & Crombez, 2005; Mogg, Holmes, Garner, & Bradley, 2008; Öhman, Flykt, & Esteves, 2001; Tapper, Pothos, & Lawrence, 2010). A saliency map includes both intrinsically motivating properties of the stimulus and learned associations, such that stimuli that were initially neutral can gain motivational value after repeatedly being associated with a positive or negative outcome. This motivational value modulates perceptual and attentional effects: Associating stimuli with reward influences visual orienting of attention (Rutherford et al., 2010) and produces preferential processing when attentional resources are limited (Raymond & O'Brien, 2009). Increased motivational value therefore leads to a greater prioritization of these stimuli that then biases attention in their direction (Theeuwes & Belopolsky, 2012).

Initial evidence from a visual probe task suggested that adults (males and females) demonstrated an attentional bias toward infant compared to adult face cues when a single infant and adult face were presented simultaneously in experimental trials (Brosch, Sander, & Scherer, 2007). During this visual probe task, target detection was heightened when the infant face and the target to be detected were presented in the left visual field, conferring a right hemisphere processing advantage for face perception (Rossion, Schiltz, & Crommelinck, 2003). Further, there were no differences between male and female participants. Building on this work, another study directly compared attentional engagement by infant cues in mothers and non-mothers using an attentional capture

paradigm including adult and infant emotional faces. In this study, participants searched for blue-eyed target faces amid two brown-eyed distractor faces of the same age (infant or adult) and reported the orientation (tilt) of the target face (Thompson-Booth et al., 2014). Reaction time measured during infant face trials could then be compared to adult face trials. Although both mothers and non-mothers showed slower responses to infant target stimuli vs. adult target stimuli, the slowing was more pronounced in the maternal sample, suggesting greater attentional capture in mothers when viewing infant faces. In keeping with this, Pearson and colleagues examined attentional capture by infant faces in women during late pregnancy (Pearson, Lightman & Evans, 2011). Here attentional engagement was measured using a task in which mothers were instructed to quickly report a peripherally displayed visual stimulus while simultaneously gazing at infant faces showing distressed or non-distressed emotional expressions that were presented in the center of the computer screen. Mothers were slower to disengage attention from distressed relative to non-distressed infant faces to respond to the peripherally presented stimulus, suggesting a stronger attentional bias to distressed infant faces in this sample. Pearson and colleagues (2011) reported that the amount of attentional bias to distressed infant faces measured during pregnancy was associated with later maternal self-reported levels of postpartum bonding with their infant. Taken together, these initial behavioral findings are consistent with motivated attention to infant cues being present in non-parents and in parents to a greater extent. This mechanism is present during pregnancy and may have important implications for parent and child during the postpartum period.

NON-PARENTS: NEUROBIOLOGY OF MOTIVATED ATTENTION

Functional magnetic resonance imaging (fMRI) research has allowed the systematic investigation of the neural correlates of incentive value. Specifically, fMRI has been employed to determine which brain regions are recruited when adults perceive infant cues (e.g., infant facial expressions), and to what extent these brain regions are activated under different experimental conditions (e.g., mothers as compared to non-mothers). It has been well established in non-parent samples that stimuli with high incentive value (e.g., fearful faces, weapons, monetary rewards), relative to neutral stimuli (e.g., neutral faces, household objects), increase activation of key neural regions implicated in the processing of emotion (amygdala; Garavan, Pendergrass, Ross, Stein, & Risinger, 2001), reward (orbitofrontal cortex [OFC] and nucleus accumbens; Knutson & Cooper, 2005; O'Doherty, 2004), and visual and facial information (e.g., striate, extrastriate, and fusiform areas; Bradley et al., 2003; Vuilleumier, Armony, Driver, & Dolan, 2001). In non-parents, there is accumulating evidence that cues such as infant faces may activate the brain's reward systems, likely reflecting their high incentive value and motivating attention toward them (Caria et al., 2012; Glocke et al., 2009). Indeed, the physical characteristics of infant faces may cue greater neural activation, possibly indicating motivated attention to these stimuli. Specific characteristics of infant faces (*baby schema* - e.g., rounder shape, large eyes) elicit greater caregiving desire the more pronounced they are (Lorenz, 1943). Viewing infant faces also leads to heightened neural activation in regions processing visual stimuli, emotion, and reward (Glocke et al., 2009). Further, greater activation in face processing regions (fusiform gyrus) when non-parents viewed infant compared to adult faces has been reported (Caria et al., 2012). The latter study also reported greater activation for infant versus adult faces in regions responsible for motor

preparation (premotor cortex and supplementary motor area) and reward processing (thalamo-cingulate dopaminergic system). Enhanced activation in motor and reward regions could be interpreted as infant cues motivating attention as an outcome of the activation of an appetitive drive (reward) to provide care (motor preparation).

Evidence in support of motivated attention to infant cues in non-parents has also been reported using event-related potentials (ERPs) and magnetoencephalography (MEG). These techniques allow the temporal dynamics of parenting to be investigated, indexing rapid (in the order of ms) neural processes underscoring infant cue perception. MEG offers an additional spatial advantage in localization of the neural response. Increasing stimulus salience is associated with an earlier and greater neural response as measured with these ERP and MEG techniques. Consistent with this, ERP recordings demonstrate greater attentional effects when male and female non-parents view infant faces, with greater attention-related N1 amplitude to infant versus adult faces, although only the N2 was differentiated in females viewing infant and child faces (Proverbio, Riva, Zani, & Martin, 2011). In the latter study, source localization identified regions underscoring this attention-related N2 component, which included the OFC. A related MEG study found that medial OFC activity peaked around 130 ms when non-parents viewed infant faces but not adult faces (Kringelbach et al., 2008). Only at 165 ms after the faces were presented was the same divergence of activity in response to infant and adult faces observed in face processing brain regions. Therefore the medial OFC may be sensitive to the presence of infant faces, modulating activity in fusiform regions for preferential processing of infant stimuli. Taken together, these neuroimaging findings suggest that even in non-parents, infant cues elicit heightened attention relative to adult

cues across a number of paradigms; we propose that this heightened attention provides evidence that infant cues elicit motivated attention.

NEUROBIOLOGY OF ENHANCED PROCESSING OF INFANT CUES IN PARENTS: REWARD

Thus far, the data from studies of non-parents suggest that infant cues form a category of motivationally relevant stimuli that attract and capture attention and preferentially activate brain regions underscoring visual processing and reward. Crucially, the transition to parenthood may serve to enhance this motivated attention, perhaps by increasing the incentive salience of infant cues—an already motivationally relevant class of stimuli—to adults who are now parents. What may shift with parenthood is both the relative intensity of the salience of such stimuli and the valence of the motivation (approach versus withdrawal). Animal studies suggest that the reward response to infant cues is contextualized as part of the developmental process of becoming a mother (the motivated model of mothering; Barrett & Fleming, 2011; Numan, 2006; Rosenblatt & Mayer, 1995). Specifically, maternal motivation toward infant cues may be regulated via the depression of neural systems that promote withdrawal responses and concurrent activation of approach-related neural systems that increase the incentive value of infant stimuli (Numan, 2006). It is hypothesized that this regulation may be driven by hormonal changes during pregnancy and parturition.

Preclinical studies also present findings of maternal brain and behavior consistent with approach-avoidance frameworks presumed to underscore motivated attention in humans. Indeed, the reward-associated neurotransmitter dopamine (DA) has been

implicated in maternal behavior in preclinical research (Afonso, King, Chatterjee, & Fleming, 2009; Afonso, Shams, Jin, & Fleming, 2013). In dams, the ventral tegmental area (VTA) activates in reaction to rat pups (Numan, 2007), and subsequently releases dopamine into the nucleus accumbens (NAcc; Pedersen, Caldwell, Walker, Ayers, & Mason, 1994). NAcc DA levels predict pup licking (Champagne et al., 2004), and increased DA via the administration of a DA uptake inhibitor increases pup-licking behaviors in low-licking rat dams (Champagne et al., 2004). In contrast, virgin rats initially ignore or withdraw from pups, although virgin rats shift from aversion to attraction toward rat pups largely through disinhibition of the medial pre-optic area (MPOA) via the influence of gestational hormones (Barrett & Fleming, 2011; Numan, 2006; Rosenblatt & Mayer, 1995). This disinhibition leads to the activation of key maternal brain regions (e.g., VTA, NAcc, and ventral pallidum) in response to rat pup stimuli (Numan, 2006). Although it is not possible to directly apply these findings to humans, it seems plausible to hypothesize that the hormonal shifts of pregnancy and parturition may also sensitize reward circuitry to infant cues, enhancing motivated attention to infant cues as well as parenting motivation more generally.

Converging neuroimaging studies comparing parents and non-parents also suggest that a neurobiological reorganization may occur during the transition to parenthood in humans that enhances motivated attention to infant cues given the inherent reward value associated with infant cues. ERP evidence comparing parents to non-parents indicates that parents find infant cues more salient and parents are better able to discriminate among different infant emotional expressions (Proverbio, Brignone, Matarazzo, Del Zotto, & Zani, 2006). While viewing infant emotional faces, mothers displayed a

bilateral P110 waveform whereas fathers and non-parents showed exclusively *unilateral* P110 waveforms (Proverbio et al., 2006), suggesting that at very early stages in visual processing, as indexed by the P110, mothers process infant cues differently from fathers and non-parents. Later in processing, parental P300 ERP waveforms are larger in parents than non-parents, and parents' N245 and P300 waveforms (both associated with late visual and attentional processing) show enhanced discrimination between different emotional expressions compared to non-parents. Hence, parents may undergo a neurobiological shift that serves to heighten the salience of infant cues, especially emotional expressions that may be critical to infant survival. Indeed, distress cues were particularly salient, a finding that is supported by fMRI evidence indicating that parents, as compared to non-parents, show stronger activation in limbic brain regions to infant crying compared to infant laughing (Seifritz et al., 2003). Mothers also show activity in the striatum (Laurent & Ablow, 2012) and the orbitofrontal cortex (Lorberbaum et al., 2002) when exposed to infant cry. In sum, the reward system is a critical component of the neurobiological basis of motivated attention to infant cues.

FACTORS THAT MAY INFLUENCE MOTIVATED ATTENTION: OXYTOCIN AND DOPAMINE

One key factor that has been implicated in enhancing motivated attention during the transition to parenthood is oxytocin. Oxytocin (OT) is a neuropeptide that is generally important in social cognition and specifically important in mothering (Donaldson & Young, 2008; Insel, 2010; Pedersen et al., 1994). OT has strong links to the brain's reward and affiliative systems and has been shown to modulate responses to infant cries

in non-parents through intranasal administration (e.g., Riem et al., 2011). Indeed, a replicated finding of intranasal OT administration in a variety of paradigms (e.g., betrayal-of-trust and pairing faces with shocks; c.f., Nave, Camerer, & McCullough, 2015) has shown a decrease in amygdala reactivity, suggesting that OT may influence social interactions (including with infants) by dampening amygdala reactivity, and presumably therefore reducing anxious or negative responding as a consequence (Donaldson & Young, 2008). In keeping with the role of OT in modulating social interactions, correlational evidence suggests that OT is associated with parenting sensitivity in general, and attention to infant cues specifically: Increased OT predicts multiple positive maternal behaviors (e.g., affectionate touch), with greater levels of OT being associated with less gaze aversion and more time gazing at one's infant (Feldman, Weller, Zagoory-Sharon, & Levine, 2007).

The oxytocinergic system also interacts directly with the mesolimbic dopamine reward circuit, priming human brain systems for maternal behavior during pregnancy and the postpartum period (Galbally, Lewis, IJzendoorn, & Permezel, 2011). Evidence from work with mice (Dölen, Darvishzadeh, Huang, & Malenka, 2013) and voles (Olazabal & Young, 2006) implicates increased oxytocin receptor density in the NAcc in both social reinforcement and maternal behavior. Dopamine and oxytocin receptors in the NAcc act together during pair-bond formation in female voles (Liu & Wang, 2003), and similar interactions between the dopamine and oxytocin systems in the NAcc may underlie the reinforcing properties of infant cues in parents. Indeed, higher oxytocin receptor density in the NAcc is positively associated with maternal behavior in voles, and blocking OT in the NAcc interferes with maternal behavior (Olazabal & Young, 2006). Therefore,

oxytocin-dopamine interactions in the NAcc may underlie the increase in rewarding effects of infant stimuli during the transition to parenthood.

Given the apparent role of oxytocin in promoting maternal behavior, it could be hypothesized that impairments in parenting are observed in situations where OT is reduced. Consistent with this hypothesis, in rat dams, impairments in parenting are found following OT gene knockout or OT antagonist administration (Pedersen et al., 1994). In human mothers, diminished nurturance is associated with low-efficiency oxytocinergic alleles (Bakermans-Kranenburg & van IJzendoorn, 2008). However, recent work (e.g., Harari-Dahan, & Bernstein, 2014; Kemp & Guastella, 2010a; 2011) has suggested that the effects of OT in humans may be more complex than simply enhancing social behaviors. OT has been hypothesized to up-regulate social approach motivation while down-regulating social avoidance motivation (the social approach/withdrawal hypothesis; Kemp & Guastella, 2010a; 2011), whereas others have argued that the effect of OT on approach-avoidance responses may not be limited to social stimuli, but may instead enhance personally relevant and emotionally evocative cues (Harari-Dahan & Bernstein, 2014). The increased salience would then induce an approach response. Nevertheless, these more nuanced theories do not contradict the notion that OT may modulate the increased salience of infant cues. Given that infant cues are likely to be emotionally evocative to adults, and particularly personally relevant to parents, OT may act (via the DA reward system) to enhance the salience of infant cues and trigger an approach response. Taken together, the interplay of both OT and DA systems may be important in determining the salience and valence of infant cues to mothers, perhaps through OT

affecting maternal behavior by both increasing the reward salience of infant cues and by reducing amygdala reactivity to their potential anxiety-aversive effects.

FACTORS THAT MAY INFLUENCE MOTIVATED ATTENTION: EXPERIENCE

The transition to parenthood may promote heightened sensitivity to infant cues, but motivated attention to infant cues in adults may be innate, given that increased salience of these cues has been observed in both parents and non-parents in the literature discussed thus far. However, there may be a case for experience and exposure to infant cues in shaping the incentive value of these infant cues over time. For instance, virgin female rats initially show an avoidance response when presented with pups; however, after repeated exposure to the pups for 5-7 days, virgin rats begin to demonstrate more typical maternal behaviors (Numan, 2006; Rosenblatt, 1967).

Additional evidence of the potential effect of experience on motivated attention has been drawn from studies recruiting mothers who are adopting or fostering children. One study found no differences in the neural response to mothers viewing familiar and unfamiliar child faces among biological and non-biological mothers (Grasso, Moser, Dozier, & Simons, 2009). A separate study examined neurophysiological responses to infant cues in foster mothers (Bick, Dozier, Bernard, Grasso, & Simons, 2013). Mothers who foster children represent a unique sample that affords the opportunity to examine experience-based effects of caring for a child in the absence of the immediate hormonal changes related to pregnancy and parturition for that child. In foster mothers, the amplitude of the P300 ERP component was associated with maternal OT levels in

response to a mother's earlier interaction with her infant, but this association changed over time. At the beginning of the relationship (within 2 months of placement), foster mothers' OT production following an interaction with the infant was associated with maternal brain activity in response to infants in general, but not to "their" infant specifically. After 3 to 6 months of fostering, however, foster mothers' OT production in response to an interaction with their infant became associated with the unique P300 amplitude while viewing their "own" infant (Bick, Dozier, Bernard, Grasso, & Simons, 2013). Parental experience with infants may be one reason for an increase in motivated attention to infant cues in parents, which may be modulated by OT (and its associated interactions with other neurobiological systems such as the DA system).

Familiarity with an infant may also increase sensitivity to infant cues. Mothers report more love and pleasant feelings at viewing their own versus another's child photograph (Leibenluft, Gobbini, Harrison, & Haxby, 2004; Noriuchi, Kikuchi, & Senoo, 2008). Additionally, mothers viewing a photograph of their own child compared to an unknown child showed greater activation of in multiple reward regions, including the OFC, striatum, and VTA (Bartels & Zeki, 2004; Nitschke et al., 2004; Noriuchi et al., 2008; Strathearn, Fonagy, & Montague, 2008). Increased activation to own-infant faces and cries relative to unknown infant faces and cries are also seen in brain regions responsive to emotion and empathy, including the amygdala and insula (Leibenluft et al., 2004; Noriuchi et al., 2008; Ranote et al., 2004; Strathearn et al., 2008; Swain et al., 2008). Infant face familiarity does not seem to impact early ERP components in maternal samples, although later ERP components are differentiated by whether mothers are viewing photographs of their own or an unknown infant (Bornstein, Arterberry, & Mash,

2013; Doi & Shinohara, 2012). These converging studies indicate that own-infant cues elicit greater activation in multiple brain regions that may be consistent with enhanced motivated attention to infant cues.

Taken together, this evidence suggests that, although non-parent adults may be biologically primed to assign a high incentive value to infant cues (Caria et al., 2012), exposure to an infant may modulate this value. This increased incentive value to infant cues appears to occur even when pregnancy-related hormonal influences are not present (i.e., in the case of foster parents), suggesting that increased motivated attention and sensitivity to infant cues may also be driven by experience with a particular infant. Thus, experience and/or familiarity may boost the incentive value of cues related to an infant over and above the already-high incentive value of infant cues.

FACTORS THAT MAY INFLUENCE MOTIVATED ATTENTION: PSYCHOPATHOLOGY

We have indicated that overall parents show greater motivated attention to infant cues than non-parents. This section explores the potential for individual differences in motivated attention to infant cues with a focus on psychopathology and its impact on infant cue processing, given that anxiety, depression, and substance abuse are challenges that many mothers contend with (Goodman, 2007; Levine, Oandasan, Primeau, & Berenson, 2003; Wisner, Peindl, & Hanusa, 1996) and that individual differences in mental health status may influence parenting (Gress-Smith, Luecken, Lemery-Chalfant, & Howe, 2012; Manly, Oshri, Lynch, Herzog, & Wortel, 2013).

To date, maternal depression has received the most interest in respect of variation in attentional and neural processing of infant cues. During pregnancy, non-depressed pregnant women show a greater attentional bias (i.e., motivated attention) to distressed compared to non-distressed infant faces than depressed pregnant women (Pearson, Cooper, Penton-Voak, Lightman, & Evans, 2010). In the postpartum period, non-depressed mothers show greater activation in reward (e.g., OFC, striatum) and empathy (e.g., mPFC, right insula) brain regions when listening to their own infant's cry versus a control sound, a differentiation that was absent in depressed mothers (Laurent & Ablow, 2011). Even variability in subclinical levels of depression have been reported as being associated with the neural response to infant faces in mothers and non-mothers (Noll, Mayes, & Rutherford, 2012). However, it is important to note that maternal depression is not always associated with differences in attentional bias to infant faces. In one prior study, attentional bias to infant faces was not found to be associated with self-reported levels of depression symptomatology (Thompson-Booth et al., 2014). Thus, the extent to which depression modulates motivated attention to infant cues should be examined further.

More generally, fMRI data has indicated that activation of the ventral striatum is attenuated more rapidly in depressed versus non-depressed mothers in response to monetary reward (Moses-Kolko et al., 2011), suggesting a more general blunting of rewarding responses in depression beyond the reward associated with infant cues. Anhedonia is a core feature of depression that is defined as the inability to experience pleasure or reward from affectively positive stimuli or situations. Therefore, depressed women may not experience the same level of pleasure from interactions with their infants

as non-depressed women (Leibenluft & Yonkers, 2010). Consistent with this result, social anhedonia measured in neglectful mothers is negatively associated with an ERP marker of motivated attention (the late positive potential, LPP) elicited when viewing infant faces (Rodrigo et al., 2011). Finally, compared to non-substance-using mothers, mothers who use substances show decreased cortical activation in response to emotional infant faces and cries (Landi et al., 2011). The attenuated neural response to infant cues observed in substance-using mothers is thought to reflect that addiction may potentially co-opt the brain's reward system, thus rendering natural rewards even less rewarding (Rutherford, Williams, Moy, Mayes, & Johns, 2011). Given that motivated attention is linked to the incentive salience of a cue, parents who do not experience pleasure in response to infant cues due to anhedonia, other symptoms of depression, or addiction may be less likely to show motivated attention in response to these cues and hence less likely to respond to their infant. In turn, parental decreased attention and responding to their infant may impact the infant's communications and bids for attention as well as response to soothing and other caretaking behaviors.

Emerging evidence suggests that anxiety and stress may negatively impact attention to infant cues. In general, anxiety is associated with diminished attention to positive affective signals (Bradley, Mogg, Falla, & Hamilton, 1998; Bradley, Mogg, & Millar, 2000; Fox, 2002; but for exceptions, see: Bradley, Mogg, White, Groom, & Bono, 1999; Ioannou, Mogg, & Bradley, 2004), which may include infant faces. Depression and anxiety attenuate amygdala activity and reduce positive feelings when mothers viewed their own infant's positive face (Barrett et al., 2011). Consistent with these findings, mothers with high biological stress indicators during a challenging mother-infant task

show attenuated brain activation when listening to their own infants' cry compared to an unknown infant cry, whereas mothers without high stress indicators do not show this discrimination (Laurent, Stevens, & Ablow, 2011). This is a novel area of investigation, and more work is required to understand potential variability in motivated attention to infant cues at both clinical and sub-clinical levels of symptomatology across clinical disorders and in the context of normative processes such as stress reactivity.

LIMITATIONS AND FUTURE DIRECTIONS

The purpose of this review was to discuss literature suggesting that infant cues, compared to equivalent adult cues, hold high incentive value and elicit motivated attention. Notably, most literature discussed here examining parent samples focuses primarily on mothers, which raises important questions regarding the role of paternal motivated attention and whether the mechanisms underlying motivated attention are common across mothers and fathers. The absence of paternal literature has significant implications for the generalizability of this theory of motivated attention to infant cues beyond maternal samples. However, an emerging literature is now documenting the neurobiology of fatherhood (e.g., Mascaro, Hackett, Gouzoules, Lori, & Rilling, 2014), which may facilitate our understanding of whether a comparable mechanism of motivated attention exists in fathers. Critically, as reviewed here, parents (mothers and fathers) are distinct in their neural responses to infant vocalizations when compared to non-parents (Seifritz et al., 2003), suggesting some commonality in infant cue salience regardless of parental gender. Although there is no biological process in men analogous to pregnancy in women that can be hypothesized to spur hormonally induced neurobiological reorganization, the basic appetitive system that is enhanced in mothers is present in all humans, including

fathers (Lang & Bradley, 2013). Fathers also show greater motivated attention to infants than do non-fathers (Proverbio et al., 2006), and fathers evidence an increase in OT levels following the delivery of their child (Gordon, Zagoory-Sharon, Leckman, & Feldman, 2010). More generally, the evidence for gender differences in response to infant cues, in both parents and non-parents, is still in its early stages. Female non-parents perceive infants as more attractive than do men (Hahn, 2012) and show larger and earlier visual processing waveforms to infant cues (Proverbio et al., 2006; 2011). However, gender differences have not been reported in attentional bias tasks employing infant faces (Brosch et al., 2007). Given these inconsistencies in gender effects on motivated attention to infant cues, more research is clearly required in this domain across both parent and non-parent samples.

In the empirical studies presented here providing the impetus for future research, motivation towards infant cues was indexed by reaction time measures and changes in neurophysiological responding. However, these studies did not examine direct changes in motivational states or reward processes as they relate to parenting. Although examining these motivational states may be difficult given that individuals are not always aware of their own motivations (Custers & Aarts, 2010), self-reported changing levels of parental attention towards infant cues have been assessed using semi-structured interviews (Leckman et al., 1999), and could be implemented alongside these behavioral and neurophysiological assessments. Further, an understanding of motivated attention, and the different assessments that can be employed to measure motivated attention, could provide a basis for parenting interventions that focus on increasing attention toward infant cues.

OT appears to play a key role in the link between parenthood and motivated attention to infant cues. Evidence from the animal literature implicates changes in OT receptor density in the brain's reward systems in many of the changes in reactivity to infant cues. In humans, intranasally administered OT (INAOT) enhances the accuracy and speed of detection of subtle emotion displays (Domes, Heinrichs, Michel, Berger, & Herpertz, 2007; Guastella et al., 2010b; Lischke et al., 2012; Schulze et al., 2011) and diminishes attention to angry and sad faces for normative populations (Domes, Steiner, Porges, & Heinrichs, 2013; Ellenbogen, Linnen, Grumet, Cardoso, & Joober, 2012). OT appears to interact with infant cues: one study in a female non-parent sample found the administration of INAOT modulated brain activity in the amygdala, insula, and inferior frontal gyrus when listening to infant cries compared to control sound stimuli (Riem et al., 2011). Future research might compare the impact of INAOT on attention to infant cues in parents and non-parents while being cautious in the design, implementation, and interpretation of such studies given methodological concerns associated with INAOT research (Leng & Ludwig, 2015; Nave et al., 2015).

IMPLICATIONS FOR PRACTICE, APPLICATION, AND THEORY

Responsiveness to infant cues is crucial to both the basic survival of the species and the overall health and well-being of each generation. Adults who respond to infant needs with caregiving behaviors increase the infant's chance of survival and healthy growth and development. Current behavioral evidence indicates that adult humans – both parents and non-parents – show an attentional bias toward infant emotional cues that fits with a broader motivational framework of approach and avoidance. This effect is more

pronounced in parents, although the extent to which there is differentially heightened sensitivity in mothers as compared to father requires further investigation. However, evidence from neuroimaging and animal studies points to brain changes in attentional and reward areas that may underlie this increased sensitivity to infant cues after parenthood. Consequently, this theory of motivated attention to infant cues may have implications for our understanding of the transition to parenthood and the role that attentional processes may play in this developmental stage of adulthood. A motivated attention account provides a theoretical framework through which to understand parenting across families while clearly laying out areas in which more empirical research is needed, such as investigating differences in motivated attention to infant cues in parents and non-parents. The long-term goal of this work is to understand whether targeting motivated attention to infants may facilitate interventions where parenting processes may be compromised.

CONCLUSION

Despite the small number of studies examining attentional processes in parenthood, converging research from preclinical and human neuroimaging modalities suggests that infant cues hold high incentive value such that they guide attentional processes, which facilitate prioritization of these infant cues for processing. Our work, and that of others, is just beginning to systematically investigate the role of motivated attention to infant cues in parenthood. This work will prove valuable for understanding normative variation in motivated attention to infant cues and lead to crucial knowledge about the consequences of psychopathology for responses to infant cues and therefore parenting behaviors and child outcomes.

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