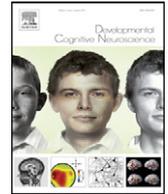




Contents lists available at ScienceDirect

Developmental Cognitive Neuroscience

journal homepage: <http://www.elsevier.com/locate/dcn>



Review

Putting together phylogenetic and ontogenetic perspectives on empathy

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ARTICLE INFO

Article history:

Received 10 January 2011
Received in revised form 2 May 2011
Accepted 13 May 2011

Keywords:

Evolution
Affective neuroscience
Developmental psychology
Developmental neuroscience
Empathy
Attachment
Prosocial behavior
Self-awareness

ABSTRACT

The ontogeny of human empathy is better understood with reference to the evolutionary history of the social brain. Empathy has deep evolutionary, biochemical, and neurological underpinnings. Even the most advanced forms of empathy in humans are built on more basic forms and remain connected to core mechanisms associated with affective communication, social attachment, and parental care. In this paper, we argue that it is essential to consider empathy within a neurodevelopmental framework that recognizes both the continuities and changes in socioemotional understanding from infancy to adulthood. We bring together neuroevolutionary and developmental perspectives on the information processing and neural mechanisms underlying empathy and caring, and show that they are grounded in multiple interacting systems and processes. Moreover, empathy in humans is assisted by other abstract and domain-general high-level cognitive abilities such as executive functions, mentalizing and language, as well as the ability to differentiate another's mental states from one's own, which expand the range of behaviors that can be driven by empathy.

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Abbreviations: ACC, anterior cingulate cortex; AIC, anterior insular cortex; dACC, dorsal anterior cingulate cortex; aMCC, anterior medial cingulate cortex; dlPFC, dorsolateral prefrontal cortex; ERP, event-related potentials; fMRI, functional magnetic resonance imaging; HPA, hypothalamic–pituitary–adrenal axis; IFG, inferior frontal gyrus; IPS, intraparietal sulcus; MEG, magnetoencephalography; mPFC, medial prefrontal cortex; MPOA, medial preoptic area; OFC, orbitofrontal cortex; PAG, periaqueductal gray; SMA, supplementary motor area; SPL, superior parietal lobule; STS, superior temporal sulcus; TPJ, temporoparietal junction; vmPFC, ventromedial prefrontal cortex; VTA, ventral tegmental area.

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doi:10.1016/j.dcn.2011.05.003

Please cite this article in press as: Decety, J., Svetlova, M., Putting together phylogenetic and ontogenetic perspectives on empathy. *Dev. Cogn. Neurosci.* (2011), doi:10.1016/j.dcn.2011.05.003

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1. Introduction

The social brain and its development is a topic that is getting increasing attention in contemporary science. In recent years, developmental neuroscience has begun to bring new insights into how the social mind develops (De Hann and Gunnar, 2009; Munakata et al., 2004; Killen and Smetana, 2008; Saxe and Pelphrey, 2009; Zelazo and Paus, 2010). In particular, noninvasive functional neuroimaging techniques that allow to chart neural activity while individuals perceive and respond to particular social stimuli, have begun to provide neural signatures for a variety of socioemotional and cognitive processes, such as the development of mentalizing (Brunett et al., 2009; Saxe et al., 2004), moral reasoning (Decety et al., in press), facial emotion processing (Lobaugh et al., 2006), social perspective-taking (Van den Bos et al., 2010), social exclusion (Masten et al., 2010), ostracism (Crowley et al., 2010), emotion regulation (Pulman and Pelphrey, 2010), and empathy (Decety and Michalska's, 2010). While investigations of the neuro-cognitive mechanisms underlying socioemotional processing are not sufficient for answering complex theoretical questions about the developing mind, neuroscientific investigations are informative, and even essential, when based on existing behavioral evidence and targeted at specific research-driven questions. In this paper, because of its paramount importance in various aspects of our social life, we focus on one socioemotional ability, empathy.

The ability to perceive, share and understand others' affective states is crucial for successfully navigating the social world. Broadly defined as empathy-related responding (Eisenberg and Eggum, 2009), this set of socioemotional competences underlies some of the most meaningful human interactions, from bonding between mother and child to complex prosocial behaviors (Batson, 2009), all essential for survival. There are signs of early development of empathy-instigated behavior. For instance, very young children attempt to alleviate the distress of others and show empathic concern well before they are able to articulate their understanding verbally (Zahn-Waxler et al., 1992). Deficits in socioemotional processing, especially the lack of empathy, are related to such neurodevelopmental disorders as psychopathy (Blair, 2005) and other clinical conditions that involve social impairment and aggression such as conduct disorder (Cheng et al., in press) and disruptive behavior disorder (De Wied et al., 2010). It has been suggested that aggressive behavior can arise from abnormal processing of affective information, resulting in a deficiency in experiencing fear, empathy, and guilt, which,

Box 1: Key concepts

- Altruism refers to prosocial behaviors that benefit the recipient at a cost to the donor.
- Attachment is an innate biological system promoting proximity seeking between an infant and a specific attachment figure in order to increase the likelihood of survival.
- Emotional contagion is an automatic response resulting in similar emotion being aroused in the observer as a direct result of perceiving the expressed emotion of another.
- Empathy is as an affective response stemming from the understanding of another's emotional state or condition similar to what the other person is feeling or would be expected to feel in the given situation.
- Empathic concern (also called sympathy) is an other-oriented emotional response congruent with the perceived welfare of someone in need.
- Emotion regulation is the ability to respond to the ongoing demands of an emotional experience in a manner that is socially tolerable and sufficiently flexible to permit spontaneous reactions.
- Mentalizing (also called theory of mind) is the ability to explain, predict, and interpret behavior by attributing mental states such as desires, beliefs, intentions and emotions to oneself and to other people.
- Personal distress is an aversive self-focused reaction to the expression of another's negative emotion, often leading to avoidance behavior.
- Prosocial or helping behavior refers to actions that are intended to help or benefit another individual or group of individuals.

in normally developing individuals, inhibits acting out violent impulses (Davidson et al., 2000).

The construct of empathy is particularly complex and is applied to various phenomena which cover a broad spectrum, ranging from feelings of concern for other people, experiencing emotions that match another individual's emotions, knowing what the other is thinking or feeling, to blurring the line between self and other (Batson, 2009; Decety, 2010a, 2011; Decety and Jackson, 2004; Hodges and Klein, 2001; Shamay-Tsoory, 2009). Uniting these views is the notion that empathy is a fundamental building block for positive growth and development (see Box 1 for key concepts used in this paper). Far from considering empathy as a unitary function, we will argue that it subsumes a variety of neurobiological systems and partially dissociable social, emotional and cognitive sub-

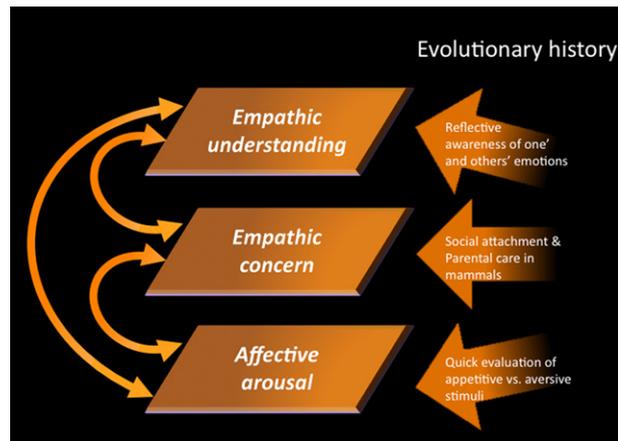


Fig. 1. Human empathy subsumes a number of interacting and partially dissociable neurobiological systems each having a unique evolutionary history. The interaction between emotional awareness, empathic concern and affective arousal operate on a series of nested evolutionary processes, which are intertwined with social, contextual and motivational contingencies. While empathic understanding, which encompasses self/other awareness, is probably specific to humans, empathic arousal and empathic concern are shared in common with other primates and mammals. Thus human empathy depends on ancient systems for intersubjectivity, rooted in attachment to kin and care for their well-being. However, layered on top of this, the cognitive abilities that are unique to our species – language, meta-representation and executive function – interact with more ancient systems and expand the range of behaviors that can be driven by empathy.

systems that operate in parallel fashion. In addition, these different subsystems have their own evolutionary history and neurobiological underpinnings (see Fig. 1).

In our view human ontogeny cannot be understood without its relation to evolutionary history, and it is not helpful to contend that the components that matter for empathy are inborn or that they develop at such-and-such a particular age. Rather, it is essential to consider empathy within a neurodevelopmental framework that recognizes both the changes and the continuities in social and emotional understanding from infancy to adulthood within a phylogenetic perspective on how the social brain has evolved.

The paper begins with examining how empathy has evolved in the context of parental care in mammalian species, and what neurobiological mechanisms and systems underlie its operation. Next we discuss how empathy develops in humans from birth to adulthood, combining theory and empirical research from developmental science and affective neuroscience. We stress the importance of the maturation of the prefrontal cortex and its reciprocal connection with the limbic system and development of a sense of self to account for more complex forms of cognitive abilities such as mentalizing and language that interact with our older abilities (intersubjectivity and motivation to care for others). Compared to other species, humans indeed exhibit more advanced and flexible levels of empathy, tied to self-awareness and perspective-taking. These new levels of information processing provide both greater understanding of others' affective and mental states and flexibility in behavioral responses. While it is tempting to propose that empathy develops on a continuum from implicit/intuitive and non-verbal to explicit/reflexive and verbalizable, several evolutionarily conserved adaptations illustrate that the social brain has evolved by accretion. Rather than replacing older structures with newer ones, evolution is a patchwork of additions. These additions are

integrated with older elements, but do not replace them and do not necessarily control them (Konner, 2010). For that reason, the various situational and interpersonal variables that impact the processes involved in empathy and its behavioral outcomes such as prosocial behavior and inhibition of aggression occur at different levels of neurobiological organization.

2. Evolutionary roots of empathy

For empathy to have evolved it must have had major survival benefits. Empathy increases the inclusive fitness of organisms by enhancing survival in a variety of ways (e.g., providing increased defense against predators) and it serves to bond individuals to one another, especially mothers to offspring (Plutchik, 1987). Most models of empathy agree that helping behavior is motivated by other-oriented affective states that evolved in the context of parental care and pair bonding (Hrdy, 2009). Recently, Batson (2011) has argued that the effects of parental nurturance on reproductive fitness are much more focused, direct and straightforward than the effects of inclusive fitness. Sober and Wilson (1998) have distinguished evolutionary altruism (behavior by one organism that reduces its reproductive fitness relative to the reproductive fitness of one or more organisms) from psychological altruism (a motivational state with the ultimate goal of increasing another's welfare), without a necessary connection between these two concepts. Once the empathic capacity evolved, following the principle of motivational autonomy (i.e., motivation for a given behavior becomes disconnected from its ultimate goals), it could be applied outside the parental-care context (De Waal, 2008). Moreover, empathy in humans is assisted by other abstract and domain-general high-level cognitive abilities such as executive functions, language, and perspective-taking, which enhance and expand the range of behaviors that can be driven by empathy. When

people send money to distant earthquake victims in Haiti, or petition to support a bill that would contribute to curb the violence in Darfur, empathy reaches beyond its context of evolutionary origins, extending beyond inclusive fitness benefits among kin. Humans are special in the sense that they can feel empathic concern for a wide range of others in need, even dissimilar others or members of different species (Lamm et al., 2010).

A major development in the evolution of mammals was placentation, internal development of the fetus and protracted care after birth to ensure infant survival to reproductive age. MacLean (1985) proposed that empathic concern emerged in concert with the evolution of mammals, which gave rise to new classes of behaviors, including parenting, attachment, and play, that support dependent juveniles and the extended embryonic plasticity of their brains. The development of this behavioral triad may have depended on the evolution of the thalamocingulate division of the limbic system, a derivative from early mammals. This division is, in turn, geared in with the prefrontal cortex that, in humans, may be inferred to play a key role in familial acculturation. When mammals developed parenting behavior, the stage was set for increased exposure and responsiveness to emotional signals of others, including signals of pain, separation, and distress. Indeed, parenting involves the protection and transfer of energy, information, and social relations to offspring (Harris, 2007). In mammals, empathic concern has evolved from a set of mechanisms that promotes parental care of offspring, and not just from shared experience with or perceived similarity to an individual in need. The human social brain, like all other mammalian brains, is fundamentally built upon ancient emotional and motivational value systems that generate affective states as indicators of potential fitness trajectories. While one needs to be cautious regarding the forms of behaviors in the animal kingdom that have been interpreted as evidence of empathy and concern (see Silk, 2007), basic affective states – and the neural mechanisms to support them – are homologous in all mammals (Panksepp, 1998). The study of comparative neuroanatomy makes clear that behaviors motivated by emotion arousal evolved earlier than those driven by complex cognitive capacities. The highly interconnected regions of the brainstem, basal ganglia, and limbic system antedated expansion of the neocortex.

Over millions of years of evolution, efficient and manifold neurobiological mechanisms have evolved for differentiating hostile from hospitable stimuli and for organizing adaptive responses to these stimuli (Norris et al., 2010). This integrated set of neural systems is genetically hardwired to enable animals to evaluate and readily respond to threatening or nurturing, unpleasant or pleasant, appetitive or aversive stimuli using specific response patterns that are most adaptive to the particular species and environmental condition. The architecture of this affect system maps onto the neural circuitry of the brainstem and that of limbic system, which includes the hypothalamus, the parahippocampal cortex, amygdala, and several interconnected areas (septum, basal ganglia, nucleus accumbens, anterior insular cortex (AIC), and retrosplenial cingulate cortex), and underlies rapid and pri-

oritized processing of affective signals. The limbic system also projects to the orbitofrontal cortex (OFC) and anterior cingulate cortex (ACC), which are involved in the evaluation and regulation of emotion, as well as decision-making. Moreover, aversive and appetitive stimuli are processed by partially independent neural circuitry with distinct subregions of the OFC and striatum (Kringelbach and Rolls, 2004). The functional separability between positivity and negativity is also supported by the opposing roles for dopamine and acetylcholine in the striatum in the control of GABA output systems for approach and avoidance (Hoebel et al., 2007).

Basic affective circuits emerged much earlier in brain evolution than higher cognitive capacities. This enables mammalian species to care for offspring sufficiently long so that the offspring, too can, reproduce. As such, a species' genetic legacy is associated with the ability to perceive and respond to emotional expressions of hunger, pain, distress or fear. Such signals are primary and powerful stimuli that call for parental care. Without doubt, some aspects of emotional connectedness, empathy and even concern are present in other non-human animals (Cheney and Seyfarth, 1985; De Waal, 2011). Emotion contagion constitutes a phylogenetically ancient and basic form of intraspecies communication that has been documented in many vertebrate species (Hatfield et al., 1994). Rats that had learned to press a lever to obtain food would stop doing so if their action is paired with the delivery of an electrical shock to a visible neighboring rat (Church, 1959), suggesting that they perceive a conspecific's pain as aversive. Interestingly, this simple process of emotional contagion appears to be context-specific and modulated by social relatedness. For example, a study with rodents demonstrated that when exposed to a cagemate, but not a stranger, that is displaying pain behavior, sensitivity to noxious stimuli increases in the observing mouse (Langford et al., 2006). Similarly, female mice show more freezing behavior when exposed to the pain of a close relative than when exposed to the pain of a more distant relative, suggesting that it serves an adaptive function (Jeon et al., 2010). To investigate whether such pain-related behavior can serve the function of soliciting social approach, Langford et al. (2010) tested test mice in various dyadic or triadic conditions, including restrained mice – some in pain via intraperitoneal injection of acetic acid – and test mice free to approach or avoid the jailed mice. Results showed a sex-specific effect whereby female, but not male, test mice approached a familiar same-sex conspecific in pain more frequently than an unaffected familiar or unfamiliar, but affected, conspecific. Furthermore, the frequency of contact by the test mouse was negatively correlated with the pain behavior of the restrained mouse, suggesting that proximity of a familiar unaffected conspecific may have analgesic properties. An experiment in which peripheral skin temperature was measured in chimpanzees while they were viewed emotionally laden video reported a decrease of skin temperature, indicative of negative sympathetic nervous system arousal, when subjects viewed videos of conspecifics injected with needles or videos of the needles themselves, but not videos of a conspecific chasing the veterinarian (Parr, 2001). Thus, when chimpanzees per-

ceive meaningful emotional stimuli, they are subject to physiological changes similar to those observed during fear in humans, that is, to the dispositional effects of emotional contagion (Hatfield et al., 2009). Recent empirical studies on ape empathic reactions and prosocial behavior demonstrate that they have an appreciation of the other's situation (Warneken et al., 2007). Consolation in chimpanzees reduces behavioral measures of stress in recipients of aggression, and was found to occur more frequently between individuals with more valuable relationships (Fraser et al., 2008). Of course, this does not mean that chimpanzees have a social-cognitive understanding of the situation and of their affective state in relation to the affective state of others, since emotion contagion is a self-focused process that does not necessarily involve a distinction between self- and other-generated affective states. It occurs without conscious awareness. Gomez (2004) raised the idea that non-human primates can represent overt mental states such as attention and intention, whereas covert mental states such as knowing and beliefs remain out of reach.

Overall, what the studies with non-human animals, including rodents, clearly indicate, is that a link between affective connectedness and prosocial behavior does not need to access a meta-representational level or conscious awareness. Non-human animals clearly possess at least one of the essential underlying components of empathy: the ability to be affected by, and share, the emotional state of another.

3. Caregiving, social attachment and empathy

For all mammals, and especially humans, adaptive neurobehavioral mechanisms have evolved to provide support and protection of the vulnerable infant. Of all the types of attachment mammalian babies form, none is more powerful than that between babies and their mothers. Although little is known about the neurobiological circuits that underpin parental care in humans, there is substantial degree of conservation across mammalian species. The animal data on maternal care and nurturance suggest an approach-avoidance model of maternal responsiveness. Efferent circuits from the medial preoptic area (MPOA) of the hypothalamus regulate the consummatory and appetitive aspects of maternal behavior. In contrast, and amygdala-hypothalamus circuit depresses maternal behavior by activating an aversion system (Numan and Sheehan, 1997). Hormonal events of late pregnancy, in particular rising estrogen and prolactin levels and declining progesterone levels, act on brain mechanisms to either decrease fear/aversion of infant-related stimuli or increase attraction/approach toward infant-related stimuli.

Social attachment serves intrinsically important regulatory functions of security, nurturing and distress alleviation. The neural systems supporting attachment include multi-sensory processing and complex motor responses as well as cognitive processes that link sensory inputs to motor output, including attention, memory, social recognition, and motivation (Insel and Young, 2001). A functional network involving preoptic areas of the hypothalamus, ventral septum, diencephalic and mid-

Box 2: Oxytocin and sociality

Oxytocin is a nine amino acid peptide primarily synthesized in hypothalamic neurons and transported down axons of the posterior pituitary for secretion into blood, but also released within the brain. Receptors are found in many limbic and brainstem structures such as the amygdala and reward pathways (nucleus accumbens and ventral pallidum). Oxytocin has many physiological influences on behavioral states, emotions, and the autonomic nervous system (for a review, see Carter and Porges, 2011) including:

- Decreasing fear and anxiety.
- Increasing tolerance to stressful stimuli.
- Allowing immobility without fear.
- Inducing maternal attachment.
- Anti-nociceptive effects by reducing pain sensitivity and delaying withdrawal latency.
- Down-regulating the HPA axis.
- Association with the functions of the parasympathetic component of the autonomic nervous system.
- Involvement in formation of trust and generosity.
- Regulating emotional states including approach-avoidance reactions.
- Enhancing empathy and mind reading in humans.

In general, oxytocin seems to enable animals to overcome their natural avoidance of proximity and to inhibit defensive behavior, thereby facilitating approach behavior (Heinrichs et al., 2009). While it is becoming increasingly clear that neuropeptides and their receptors are important mediators of social behaviors, and that comparative studies are a powerful approach for social neuroscience, the translational bridge between findings in animal and human neurobiology need to be built with careful consideration of species differences, based on evolutionary adaptations (Insel, 2010).

brain systems (Panksepp, 1998) may change somewhat in phylogeny with more contribution of paralimbic areas, as evidence suggests that in primates, ACC and nucleus accumbens are increasingly critical for attachment and maternal behavior (Watt, 2000). In mammals, neuropeptides regulating attachment, particularly oxytocin, opioids, and prolactin, are relevant for regulating empathic responsiveness. Oxytocin facilitates maternal behavior and is capable of increasing positive social behaviors and both oxytocin and social interactions reduce activity in the HPA axis (Carter, 1998). Secretion of hormones of the HPA axis (cortisol, corticosterone or adrenocorticotrophic hormones) follow separation from the attachment figure and HPA activity tends to decline upon reunion. Oxytocin's targets are widespread and include the hypothalamus, amygdala, hippocampus, brainstem, heart, uterus, and regions of the spinal cord that regulate the autonomic nervous system, especially the parasympathetic branch (Carter et al., 2008).

While the HPA modulatory effects of oxytocin are species-specific, in recent years, a number of studies have clearly reported its special implications for social cognition and empathy in humans (see Box 2). In particular, its application via nasal spray reduces responses to social

stress (Heinrichs et al., 2003). Oxytocin can increase mutual trust, and this effect is not due to a general increase in the readiness to bear risk. On the contrary, oxytocin specifically affects an individual's willingness to accept social risks arising through interpersonal interaction (Kosfeld et al., 2005). Intranasal administration of oxytocin, compared to placebo, reduces amygdala activation and modulates its coupling with brainstem regions that are involved in automatic fear reactivity (Kirsch et al., 2005). Another study showed that a single dose of intranasally administered oxytocin is sufficient to cause a substantial increase in the affective mind reading ability on a test relying on the detection of subtle affective facial expressions (Domes et al., 2007). There is evidence that a naturally occurring genetic variation of the oxytocin receptor relates to both empathy and stress profiles. This was discovered in a study that tested how a polymorphism (rs53576) of the oxytocin receptor relates to empathy and stress reactivity (Rodrigues et al., 2009). Compared with individuals homozygous for the G allele of rs53576 (GG), individuals with one or two copies of the A allele (AG/AA) exhibited lower behavioral and dispositional empathy. Furthermore, AA/AG individuals displayed higher physiological and dispositional stress reactivity than GG individuals, as determined by heart rate response during a startle anticipation task and an affective reactivity scale.

All these results concur with animal research suggesting a critical role of oxytocin in prosocial behavior and reactivity to social stress. It has also been proposed that the interaction between oxytocin and dopamine enhances the reward of social encounters, promoting the motivation to engage in social interactions, increasing the probability of approach and decreasing the probability of withdrawal (Insel and Young, 2001). Research on human parenting behavior suggests that networks of highly conserved hypothalamic–midbrain–limbic–paralimbic–cortical circuits act in concert to support aspects of parent response to infants, including emotion, attention, motivation, empathy, decision-making and other mental capacities that are required to navigate the complexities of parenting (Swain et al., 2007). In particular, infant stimuli activate basal forebrain regions, which regulate brain circuits that handle specific nurturing and caregiving responses and activate the brain's more general circuitry for handling emotions, motivation, and attention – all of which are crucial for effective parenting. A handful of functional magnetic resonance imaging (fMRI) studies have examined the neuro-hemodynamic response to emotionally charged infant stimuli. In keeping with MacLean's thalamo-cingulate hypothesis of maternal behavior in humans, it has been found that mothers listening to infant cries show increased activity in the medial thalamus, AIC, subgenual ACC, and OFC, as well as structures important for maternal behavior, such as the midbrain, hypothalamus, dorsal and ventral striatum, and septal regions (Lorberbaum et al., 2002). Another study examined gender- and parental status-dependent differences in the brain response pattern to infant brief 6-s vocalizations (crying and laughing) by male and female participants (Seifritz et al., 2003). Women but not men, independent of their parental status, showed neural deactivation in the ACC, as indexed by

decreased blood oxygenation level-dependent signal, in response to both infant crying and laughing. The response pattern changed fundamentally with parental status. Parents showed a vocalization-specific pattern of response, with greater activation by infant crying than laughing. Nonparents, on the other hand, showed greater response to infant laughing than crying. This differential neural activation pattern was found in the amygdala, the ACC, the AIC, the ventral prefrontal cortex, and the right temporoparietal junction (TPJ), areas that represent elements of an attentional network regulating cognitive and emotional processes. Notably, nonparents activated the amygdala in response to baby cries, but parents did not. In a similar vein, Swain (2008) reported regions of relative activation in a group of first-time mothers at 2–4 weeks postpartum, which included midbrain, basal ganglia, cingulate, amygdala, and insula. Interestingly, given the same stimuli at 3–4 months postpartum, amygdala and AIC activations were not observed in this same group of mothers. Instead, mPFC and hypothalamic activations were observed, which may reflect a change in brain responses as the parent–infant relationship develops.

4. Empathy and attachment are interdependent

Human infants are biologically predisposed to seek out and maintain attachment, which builds on a highly conserved set of behaviors found among all primates (Hrdy, 2009). Attachment has been defined as an innate biological system promoting proximity seeking between an infant and a specific attachment figure in order to increase the likelihood of survival to a reproductive age (Sroufe, 2000). Attachment cannot survive without empathy in the sense that the caregiver must necessarily be empathic with the infant. A number of studies have shown a mediational relationship between attachment style and empathy, and have indicated that children with secure attachment histories will be more responsive to the needs of others (Weinfield et al., 2010). There is also solid behavioral evidence demonstrating that attachment security provides a foundation for empathic concern, caregiving and forgiveness. For instance, results from a series of studies that examined the causal effect of chronic and contextual activation of attachment security on reactions to others' need (Mikulincer et al., 2001), indicate that attachment security priming facilitates empathy responses toward others' plight, even when the individuals are not aware of the manipulation (subliminal priming). Furthermore, the sense of security led participants to adopt a more empathic attitude not only to close relationship partners, but also to non-intimate others. Conversely, emotional distress, which may be induced from affective arousal interferes with empathic concern in depleting attentional and cognitive resources that could be used to attend to others' need and to provide adequate care to alleviate their suffering (Eisenberg and Eggum, 2009). This shows that affective arousal does not necessarily lead to prosocial behavior and concern for the well-being of others. Affect regulation linked to attachment security plays a crucial role in the motivation to help by reducing personal distress and avoidance behaviors. Individuals who were evaluated as avoidant are less likely to forgive, and this rela-

tionship is mediated by a lack of empathy (Burnette et al., 2009). Empathy and pain perception interact with attachment styles. Individuals' responses to psychological pain are moderated by attachment style (Cassidy et al., 2009). A recent study investigated whether the presence of others and perceived empathy (defined as participants' knowledge of the extent to which observers felt they understood and shared their pain) can modulate subjective and autonomic responses to physical pain; and whether these influences can be explained by individual traits of pain coping and social attachment (Sambo et al., 2010). The effects of social presence and empathy on pain ratings depended on individual differences in attachment style. Higher scores on attachment anxiety predicted higher pain ratings in the low-empathy than in the high-empathy condition; and higher scores on attachment avoidance predicted lower pain ratings in the alone condition than in the presence of others.

Mothers with secure attachment show increased activation of mesocorticolimbic reward brain regions including the ventral striatum, on viewing their own infant's smiling and crying face, whereas insecure/dismissing mothers showed greater insular activation in response to their own infant's sad faces (Strathearn et al., 2009). Furthermore, they showed an increased peripheral oxytocin response while interacting with their infants, which was positively correlated with activation of oxytocinergic and dopamine associated reward processing regions of the brain.

These functional neuroimaging data represent the first forays into the study of gender- and experience-dependent modulation of brain responses to infant distress signals. It would be interesting to see how measures of parenting behaviors and parent–infant interaction might be reflected in these changing brain activations as parent–infant attachment develops. Successful recognition and evaluation of infant vocalizations are critical for bonding mechanisms and for offspring well-being and survival. Thus, the modulation of responses by experience seems to represent an adaptive mechanism that can be related to reproductive fitness.

5. Parental care is rewarding

While it is a fact that parental nurturance has evolved because it provides obvious survival benefits to offspring, it is equally important to emphasize that caring is rewarding to the parents. Increased evidence supports the idea that parental care is addictive and includes elements of both dopamine and enkephalin signaling that are the trademarks of activation of the reward pathways (Gammie, 2005). The endogenous opioids are well known to influence social bonding and affiliative behavior. Opioids mediate the rewarding properties of social affiliation, specifically opioids are released during social contact and this release is rewarding (Maestripieri, 2010). There is a wealth of studies on maternal behavior across a range of species that reveal a direct effect of oxytocin on dopamine release within the mesocorticolimbic dopamine system. Pup suckling is a robust stimulus for activating the mesocorticolimbic system. This dopaminergic pathway from the ventral tegmental area (VTA) to the accumbens (NAcc) and pre-

frontal cortex system is involved in reward seeking and may help to strengthen the pup–dam bond, as indicated by fMR scans in rats showing that in lactating dams, addiction and reward brain regions show much greater activation with pups rather than with cocaine as a stimulus but that this effect is reversed in virgin females (Ferris et al., 2005). Mother rats that exhibit consistently increased pup licking and grooming (LG) (i.e., high LG mothers) by comparison with low LG mothers show increased oxytocin expression in the medial preoptic area (mPOA) and the paraventricular nucleus of the hypothalamus and increased projections of oxytocin-positive cells from both mPOA and paraventricular nucleus of the hypothalamus to the VTA. Further, direct infusion of oxytocin into the VTA increased the dopamine signal in the NAcc. Finally, high compared with low LG mothers show greater increases in dopamine signal in the NAcc during bouts of pup LG, and this difference is abolished with infusions of an oxytocin receptor antagonist directly into the VTA which are consistent with previous reports of oxytocin–dopamine interactions in the establishment and maintenance of social bonds (Shahrokh et al., 2010).

In humans too, the hormones of pregnancy prime the mesolimbic DA projection to the NAcc as well as upregulation of receptors for oxytocin and opioids in the ventral striatum/NAcc (Broad et al., 2006). This undoubtedly predisposes the brain reward system to forming mother–infant bonds at birth. However, caring behaviors in humans extend to non-kin and are reinforced both by endogenous reward (dopamine system) and positive social feedback from others. Behavioral and functional neuroimaging studies have begun to demonstrate that being nice and caring for others makes us feel good via the release of dopamine through the projection of neural pathways from the brain stem to the NAcc. The fronto-mesolimbic reward network is engaged to the same extent when individuals receive monetary rewards and when they freely choose to donate money to charitable organizations (Moll et al., 2006). Furthermore, medial orbitofrontal–subgenual and lateral orbitofrontal areas, which play key roles in more primitive mechanisms of social attachment and aversion, mediate decisions to donate or to oppose societal causes. Another study reported that the mere presence of observers increased donation rates and significantly affected activity in the striatal regions (Izuma et al., 2010).

The neural mechanisms and underlying endocrinology that developed originally in the service of parental nurturance in the mammalian species continued to evolve in more complex social groups extending to others in groups of closely related individuals and even to strangers. This evolution of generalized parental nurturance is accompanied by an increase in the plasticity and flexibility provided by the prefrontal cortex, which led in turn to a heightened capacity for learning in social environments, and came to operate at the cultural level.

6. How empathy develops in humans

It is usually considered that empathy emerges during the second year of life, as the child comes to a greater awareness of the experiences of others, and that it develops

in the context of a social interaction. While the reflective awareness of one's own and others' emotions and intentions is a key characteristic of the experience of human empathy, more reflexive, intuitive aspects of empathy are available to infants. Both evolutionarily and developmentally, advanced forms of empathy are preceded by and grow out of more elementary ones, such as the capacity to send and respond to emotional signals.

6.1. *Sharing affects with others*

Not surprisingly, given the adaptive value of emotional contagion, human infants are biologically predisposed to affectively resonate with basic affective – positive and negative – states of others. Emotional contagion occurs when the vocal, facial and gestural cues of one individual generate a similar state in the perceiver. Newborns' contagious crying in response to others' cries has generated much theoretical debate in developmental psychology (Simmer, 1971; Sagi and Hoffman, 1976; Geangu et al., 2010). In particular, the question of interest for researchers is whether this reaction involves any, even if rudimentary, understanding that the source of distress lies within another person. Hoffman (1984) hypothesized that infants may interpret the sounds of others' cries as their own and thus engage in early primary circular reactions by continuing to cry. However, subsequent experiments have shown that infants exhibit more distress in response to others' cry than to the recording of their own cry. Of special interest, a study by Martin and Clark (1987) tested 1-day-old babies' reactions the crying of an 11-month-old, the newborn's own crying, and a baby chimp's cry. Not only did they replicate Simmer's results that infants cry in response to other infant cries, but more interestingly they also showed that newborns responses were peer- and species-specific, and that they were able to discriminate their own and other infants' cries (for a replication, see Dondi et al., 1999).

These studies indicate that newborn infants show rudimentary signs of emotion contagion. This is possible because brainstem auditory pathways are functioning before birth as shown by auditory-evoked responses, and even premature infants have a functional auditory system (Aslin et al., 2008). These results also suggest that there is some modicum of self–other distinction already functioning soon after birth. This does not imply any self-consciousness or self-awareness. Rather, it is an implicit sense of self as an agentive entity in the environment, which Neisser (1991) coined as the ecological self. This implicit sense of self develops from birth, prior to an explicit manifestation of self-knowledge in the second year, when this sense of self is discriminated from the sense of others (Rochat and Striano, 2000). For example, infants distinguish between perceptual events that are self-generated or not self-generated as demonstrated by one study that tested whether newborn infants within 24 h of birth discriminate between double touch stimulation specifying themselves, and external (one way) tactile stimulation indicating non-self objects, as measured via the robust rooting response manifest by healthy infants from birth (Rochat and Hespos, 1997).

Mimicking certain facial expressions has been demonstrated in a variety of studies. For example, the matching of certain facial movements such as tongue thrusting or mouth opening has been demonstrated in neonates (Field et al., 1982; Meltzoff and Moore, 1977). By 10 weeks of age, infants respond differently to three maternal affect expressions when the presentation is simultaneously facial and vocal – joy, anger, and sadness, and can mirror joy and anger expressions (Haviland and Lelwica, 1987).

Research with adults indicates that the mere visual perception (without a task) of emotionally salient stimuli elicit activation in the brainstem, thalamus, amygdala, hippocampus, insula and somatosensory cortex (Winkielman et al., 2011). Importantly, the brainstem, which handles primitive components of emotion and arousal, as well as all inborn reflexes such as crying and suckling and regulates basic homeostatic functions, is the most highly developed area of the brain at birth (Joseph, 2000). Whether emotional contagion necessarily produces the relevant emotional experience in the receiver or simply primes core affect mechanisms (valence and approach/avoidance) is not well established, given the difficulty of obtaining accurate and reliable online measures of specific emotions. In addition, smiling, screaming and crying can be produced from brainstem stimulation even with complete forebrain transection (Zhang et al., 1994), and thus it may be more appropriate to see these reactions in newborns as reflexive affective arousal than as true emotions. This issue is also relevant to the growing appeal to mirror neurons which posits that the perception of facial expression of emotion automatically triggers activity in brain regions involved in experiencing similar emotions (Van der Gaag et al., 2007).

Does mimicry facilitates emotional recognition and understanding? In fact, there is little evidence in support of the notion that individuals attribute the specific emotion that they are feeling to the facial expression of their interaction partners. For example, a study investigated whether emotion recognition accuracy is associated with either facial mimicry or shared affect or both (Blairy et al., 1999). The results confirmed that observers spontaneously mimic facial expressions, and that the decoding of facial expressions is accompanied by shared affect. However, no evidence was found that emotion recognition accuracy or shared affects are mediated by mimicry, whether spontaneous or voluntary. What research suggests instead, is that mimicry may lead to empathy and prosocial behavior via the associated increase in similarity – it fosters feelings of rapport between interaction partner – and not via an increase in understanding of the other's emotional state (Hess et al., 1999). Furthermore, affiliation between two interacting partners is moderated by the situational similarity of the affiliate, regardless of the emotional reaction of the affiliate (Gump and Kulik, 1997). These results are also consistent with other empirical research showing that facial movements alone carry simple affective information (whether the face should be approached or avoided), which is insufficient for perception of emotion, and context needs to be conjointly encoded to make more specific inference about an individual's emotion (Barrett and Kensinger, 2010).

Thus, newborns come to the world equipped with neural functions that subserve basic and vital functions, which with rapid maturation with the forebrain allows them in the first few months of life to engage in face-to-face protoconversation with caregivers, essential for mutual regulation of emotional engagement (Trevarthen, 1979), and paves the way to intersubjective transactions between self and other. This primary intersubjectivity is not something that we leave behind as we mature. During the lifespan we continue to rely on our perceptual access to others' affective expressions to pick up information about what others are feelings (Gallagher, 2009). This is indeed the case as indicated by research using measures of facial electromyography (EMG) which showed that viewing facial expressions triggers distinctive patterns of facial muscle activity similar to the observed expression, even in the absence of conscious recognition of the stimulus (Dimberg et al., 2000). In one study, participants were exposed very briefly (56 ms) to pictures of happy or angry facial expressions, while EMG was recorded from their face (Sonnby-Borgstrom et al., 2003). Results demonstrate facial mimicry despite the fact that participants were unaware of the stimuli. A study conducted with school-age boys demonstrated that angry and happy facial stimuli spontaneously elicit different EMG response patterns (De Wield et al., 2006). Angry faces evoked a stronger increase in corrugator activity than happy faces, while happy faces evoked a stronger increase in zygomaticus activity than angry faces. Another study examined the relationship between facial mimicry and self-reported mood upon exposure to static facial expressions of anger and happiness in participants who were categorized as either high or low empathizers, and found that the high-empathy participants produced greater facial mimicry than the low-empathy participants (Sonnby-Borgstrom et al., 2003). However, another study did not find any relation between emotion recognition performance and participants' tendency to mimic dynamic displays of emotions (Hess and Blair, 2001). Selective facial EMG responses were detected in participants presented with movie clips of morphed (non-natural) expressions of happy and angry facial expression, but no correlation between the intensity of facial mimicry and dispositional empathy level was observed (Achaibou et al., 2008). This motor resonance may be based on the mirror neuron system, which from electroencephalographic (EEG) studies seems to be already functioning in infants as young as 6 months (Nystrom, 2008, but see Blair, 2011; Blair and Fowler, 2008, and Decety, 2010b for critical evaluations of the contribution of the mirror neuron system to empathy).

In concert with these implicit tendencies to react to others' emotional expressions, precursors of self- and other-understanding are thought to gradually develop in the course of early social interactions, as the infant monitors the other's behavior as well as the other's reactions to his or her own behavior – a process that by the end of the first year gives rise to a new, “interpersonal self” (Neisser, 1993; Moore, 2006). The tendency to match others' affective states may be a part of this process, as in doing so with a caregiver, the infant elicits a shared affective experience that further fosters reciprocal interactions.

With regard to affective sharing, studies of pain perception in others are of particular relevance, as unlike other bodily sensations, pain is a reliable source of distress, and its expression by facial expressions or cries provides a strong signal for eliciting empathy and concern in others. A growing number of functional neuroimaging studies have reliably documented an overlap in activation in the neural network underlying the affective-motivational dimension of pain processing, which reflects the perceived unpleasantness of a painful event and involves the ACC and AIC during the perception or imagination of other people in pain and the first-hand experience of pain (e.g., Bird et al., 2010; Botvinick et al., 2005; Jackson et al., 2005, 2006; Singer et al., 2004; for a meta-analysis, see Lamm et al., 2011). Furthermore, numerous functional MRI and MEG investigations, that used facial expression and stimuli depicting body parts being injured, have reported significant signal change not only in the regions implicated in the affective dimension of pain, but also in the somatosensory cortex/posterior insula, a region involved in the sensory-discriminative dimension of pain (Akitsuki and Decety, 2009; Benuzzi et al., 2008; Bufalari et al., 2007; Cheng et al., 2007, 2008; Jackson et al., 2006; Lamm and Decety, 2008; Lamm et al., 2007a,b, 2010; Moriguchi et al., 2007; Zaki et al., 2007).

It is worth noting that vicariously instigated activations in the pain matrix are not necessarily specific to the emotional experience of pain, but may be related to other processes such as negative stimulus evaluation, attention to noxious stimuli, somatic monitoring, and the selection of appropriate skeletomuscular defensive movements. Several EEG and fMRI studies have documented extremely similar patterns of responses to nociceptive and non-nociceptive stimuli suggesting that multimodal neural activity (i.e., the activity of neurons that respond to a range of stimuli, regardless of their sensory modality) could explain a large part of the pain matrix (Iannetti and Mouraux, 2010). Thus, shared neural representations in the affective-motivational as well as in the sensory-discriminative aspects of the pain matrix between perceiving others in pain and experiencing it might be associated with more general survival mechanisms such as the detection and reaction to salient potentially threatening sensory inputs which usually elicit withdrawal reactions when exposed to danger and threat (Decety, 2010b, 2011; Yamada and Decety, 2009).

6.2. Developmental changes in perceiving the pain of others

Until recently, relatively limited knowledge existed on the neurobiological changes during the normal development of empathy from early childhood to adulthood. One cross-sectional developmental fMRI study tested participants ranging from 7 to 40 years of age while they watched short video clips depicting people being physically injured by accident or intentionally by another individual (Decety and Michalska's, 2010). Behavioral ratings collected after scanning indicated a gradual decrease in the subjective evaluation of pain intensity for both painful situations (accidental versus intentional) across age, with

younger participants rating them as significantly more painful than did older participants. An interesting developmental finding was that the younger the participants, the more strongly the amygdala, posterior insula and medial OFC (interconnected regions involved in subjective affective and bodily state processing) were recruited when they watched others in painful situations. A significant negative correlation between age and degree of neuro-hemodynamic response was found in the posterior insula. In contrast, a positive correlation was found in the anterior portion of the insula. A posterior-to-anterior progression of increasingly complex re-representations in the human insula is thought of as providing a foundation for the sequential integration of the individual homeostatic condition with one's sensory environment, and motivational condition (Craig, 2003). The posterior insula receives inputs from the ventromedial nucleus of the thalamus that is highly specialized to convey emotional and homeostatic information, and serves as a primary sensory cortex for each of these distinct interoceptive feelings from the body. Thus, the fact that in response to others' physical distress, younger participants recruited the posterior portion of the insula in conjunction with the amygdala and medial OFC more than adults did may speak to the children's tendency to be aroused by the perception of others' distress in a more direct sense, leading to experiencing more discomfort associated with a visceral response to a potential threat, whereas adult participants tend to use more abstract secondary representations of pain when perceiving others in pain.

Another interesting finding from Decety and Michalska's (2010) neurodevelopmental study is that greater signal change with increasing age was found in the prefrontal regions involved in cognitive control and response inhibition, such as the dorso-lateral prefrontal cortex (DIPFC) and inferior frontal gyrus (Aron et al., 2004; Swick et al., 2008). This pattern of age-related change may be seen as reflecting frontalization of regulatory capacity, providing top-down modulation of emotion processing, especially on the amygdala reactivity to aversive stimuli (Hariri et al., 2000; Yurgelun-Todd, 2007). Similarly, age-related change was observed in the OFC in response to the pain inflicted by another: activation in that region shifted from its medial portion in younger participants to the lateral portion in older participants (Fig. 2). The OFC has intrinsic networks that are defined on the basis of their cortico-cortical connections and also connections with other parts of the cerebral cortex and subcortical structures, including the mediodorsal nucleus of the thalamus, sensory areas, virtually all limbic structures including the amygdala and brainstem, subserving distinct functions (Ongur and Price, 2000).

Since the medial part of OFC is involved in regulating motor and visceral responses and its lateral part is involved in executive control of emotion reactivity (Hurliman et al., 2005), this pattern of developmental change is indicative of a gradual shift from the monitoring of somatovisceral responses in young children (consistent with their tendency to process others' pain information at a proprioceptive level) to a more cognitive evaluative level associated with executive control

of higher-order emotion processing in older participants.

In a second fMRI study, a large sample of 126 individuals between the age of 4 and 37 years were scanned while viewing visual scenarios depicting intentional harm and accidental harm to people (Decety et al., in press). At the whole group level (irrespective of age), the perception of intentional harm was associated with increased signal in the amygdala, periaqueductal gray (PAG), insula, ventromedial prefrontal cortex (vmPFC) and right posterior STS/TPJ. While participants' rating of empathic distress (how sad they felt for the person who was hurt and how upset they were) did not vary with age, there were significant developmental changes in the neural response. The younger the participants, the stronger the activity in amygdala, PAG and insula when they viewed intentional harm versus accidental harm, whereas the older the participants the higher the activity in the vmPFC. Functional connectivity analysis showed a significant difference between the early childhood group and the adult group in the connectivity between the vmPFC and amygdala reflecting increased functional integration between these two regions in adults.

The early engagement of the amygdala, PAG, insula, and medial OFC during the perception of others' distress is consistent with the timing of their structural architecture maturation. These reciprocally interconnected regions, which underlie rapid and prioritized processing of emotion signals and are involved in affective arousal and somatovisceral resonance, come online much earlier in ontogeny than other neural structures such as the dorsal and lateral vmPFC, which become progressively specialized for the evaluation of social stimuli, and undergo considerable maturation during childhood (Decety, 2010a; Leppanen and Nelson, 2009; Luna and Sweeney, 2004; Paus, 2011). These latter regions of the prefrontal cortex are vital for more advanced forms of empathy linked with perspective-taking and mentalizing.

Overall, the neurodevelopmental pattern of activation and functional connectivity in response to viewing others in distress supports the notion that the development of affective processing from childhood to adulthood is accompanied by reduced activity within brainstem and limbic affect processing systems and increased involvement of other prefrontal systems (Killgore and Yurgelun-Todd, 2007). These progressive and regressive patterns of age-related activity changes reflect the phylogeny of different developmental trajectories – from reflex-like responses and somatovisceral resonance to increasing evaluative control of the cortex associated with awareness of one's emotions and those of others.

6.3. *The role of self-awareness in the development of empathy*

The emergent capacity for self-awareness is closely linked to the development of more advanced forms of empathy. Having a clear sense of self may have evolved to solve two kinds of adaptional problems: (1) the self is the repository of the social feedback we receive from others, and is thus a major influence guiding adaptive interpersonal strategies; (2) the self is also useful because it allows

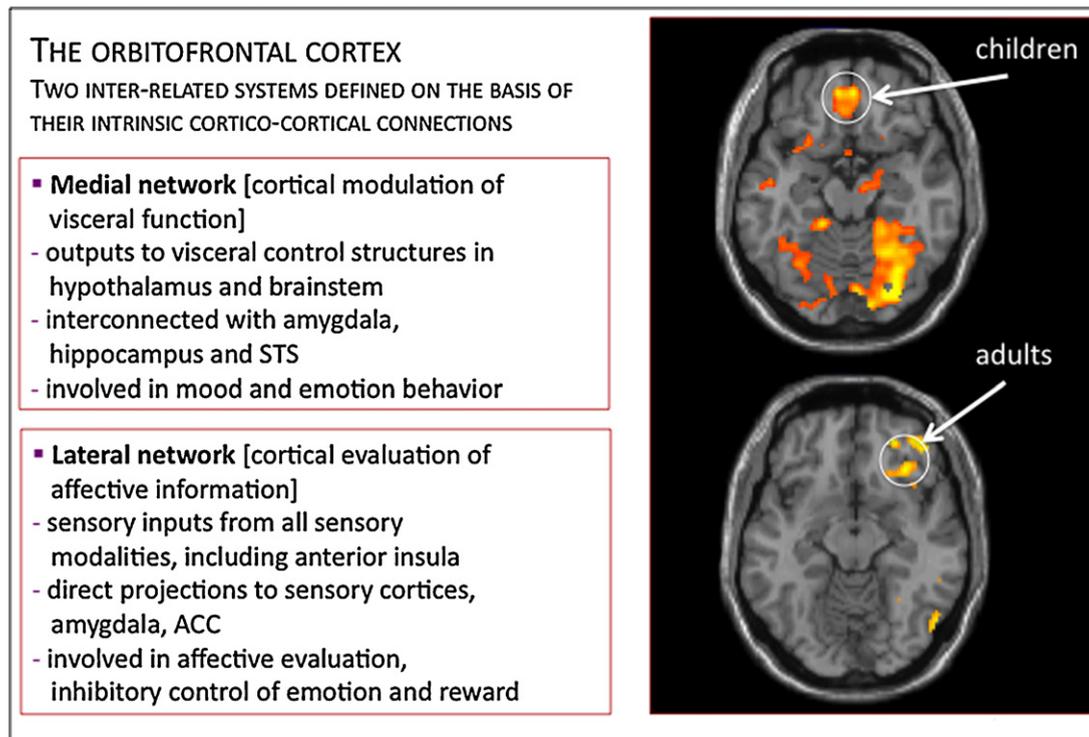


Fig. 2. The orbitofrontal cortex and its role in empathy. On the left, a brief summary of two inter-related neural circuits and their contribution to the processing of affective information (Hurliman et al., 2005). On the right, the shift in neuro-hemodynamic activation in the ventromedial prefrontal cortex across age in 57 participants aged from 7 to 40 years when they are shown video clips depicting an individual being intentionally injured by another. A significant negative correlation ($r = -43$, $p < 0.001$) between age and degree of activation was detected in the medial portion of the orbitofrontal cortex ($x 10$, $y 50$, $z -2$), while a significant positive correlation ($r = 0.34$, $p < 0.01$) was found in the lateral portion of the orbitofrontal cortex ($x 38$, $y 48$, $z -8$). Interestingly, the spatial organization of neurons (spacing distance in minicolumns) in this region of the prefrontal cortex differs significantly between humans and apes, and this unique increase in the distance between minicolumns takes place after the age of 2 (Semendeferi et al., 2010). Adapted from Decety and Michalska's (2010).

us to model and understand the subjective worlds of others (Forgas and Williams, 2003). Whether the emergence of an integrated self–other representational system has occurred relatively recently (during the course of the last 2 million years of human evolution) and only exists in a handful of species such as chimpanzees, elephants and bottlenose dolphins, or has evolved along a continuum so it can be found in different forms in other species is still a matter of debate (see Gallup, 1985; Lauwereyns et al., 2010; Povinelli et al., 2000).

By the time of their first birthday, human children acquire several new social–cognitive abilities that point to their nascent understanding of themselves and others as independent psychological agents. They are able to follow the attention of others by looking where others are looking (joint attention), use others' reactions to novel objects to form their own attitudes toward these objects (social referencing), and attempt to imitate what others are doing with novel objects (imitative learning) (Carpenter et al., 1998). By the beginning of the second year, objective self- and other-awareness has begun to form – a phenomenon that, according to a number of scholars, is a fundamental prerequisite for the transition from emotional arousal and self-distress to more sophisticated empathic responsiveness and perspective-taking abilities (Decety and Meyer, 2008; Kagan, 1981; Moore, 2007; Nichols et al., 2009;

Thompson et al., 1997). When witnessing another's distress, children's prosocial interventions take a variety of forms, including sharing, helping, and comforting behaviors (Svetlova et al., 2010; Zahn-Waxler and Radke-Yarrow, 1990; Zahn-Waxler et al., 1992).

Empathy-related responding presents several challenges for someone who has just started to form a concept of self and others. To experience the full-blown experience of empathy the child must know that another's distress is a part of the other's subjective experience, different from the child's own. In the middle of the second year, this sort of self–other differentiation becomes evident with the emergence and development of mirror self-recognition (Brooks-Gunn and Lewis, 1984; Nielsen et al., 2006), verbal indices of self- and other-knowledge such as use of personal pronouns, self-conscious reactions to the attention of others, etc. (Bullock and Lutkenhaus, 1990; Kelley et al., 2000; Lewis and Ramsay, 2004).

Experimental studies that have examined associations between self and other awareness and empathy-related responding in the second year of life have found that mirror self-recognition was related to empathy toward distressed adults (Johnson, 1982), although this relationship might have been more pronounced earlier but not later in the second year (Zahn-Waxler et al., 1992); in one study, mirror self-recognition related to prosocial behavior but

relations with emotional, empathic responses were weak (Bischof-Köhler, 1991). A more recent study, designed to clarify these inconsistencies and to use a broader measure of self–other understanding, examined the associations between 12- and 24-month-olds' empathy and various indices of early self-awareness such as expressions of pride, possession, and references to self, as well as children's emotion understanding, in addition to the classic test of mirror self-recognition (Nichols et al., 2009). The results revealed that children with more advanced self- and other-awareness were more empathically responsive to a distressed peer (above and beyond age and empathic disposition). When their empathy-related responding was broken down into expressions of empathic concern and personal distress, individual differences in children's self-awareness specifically predicted expressions of concern; the model predicting their personal distress was not significant. Thus, during the second year of life – a period of important transition in the development of inter-subjectivity – understanding oneself as an independent psychological entity appears to be a critical factor in the ability to represent others' feelings and care about them.

Age-related developments revealed by these and other studies of empathic and prosocial responsiveness in toddlers are also quite consistent. In a study of development of concern for others, Zahn-Waxler et al. (1992) found that rates of expressions of empathy and sympathy toward a distressed adult increased significantly between 13 and 24 months of age, and that reactions of personal distress were gradually replaced by more constructive, action-oriented patterns. Comparing responses of 12-, 18-, and 24-month-olds to a distressed peer, Nichols et al. (submitted for publication) found that 12-month-olds were neither interested nor concerned about the crying peer, 18- and 24-month-olds showed higher levels of social interest in the peer, and 24-month-olds exhibited greater empathy, concern, and prosocial responsiveness toward the distressed peer than any of the younger ages. In a study of helping behavior in 1- and 2-year-olds, Svetlova et al. (2010) found that whereas 1-year-olds readily helped an adult in action-based situations which required inferring the adult experimenter's goals, they had great difficulty knowing how to help when the situation involved the adult's negative emotions. Two-year-olds were more responsive, and required less communicative cues from adults, in both action-based and emotion-based situations, suggesting that by that age children are able to read emotional cues of others and generate appropriate empathy-related responses. Another study explored affective perspective-taking ability in toddlers, and found that by 2 years of age, toddlers begin to be able to make appropriate judgments about others' emotional reactions even without explicit emotional cues (Vaish et al., 2009).

Thus, the second year of life is the period of great advances in self–other awareness and the time when emotional empathy develops and conscious concern for others first emerges. The process of developing more mature forms of empathy-related responding goes in waves and circles; and even though as adults we probably never return to the experience of neonatal non-conscious contagious crying, we may continue to experience the rest of the range

of empathy-related reactions, including affective arousal and personal distress.

How are these processes instantiated at the neural level? Both fMRI experiments and studies of patients with brain injury provide converging evidence for the importance of the medial prefrontal cortex (mPFC) in self-awareness. A number of studies have reported activation of the mPFC and posterior cingulate cortex (PCC) when individuals reflect on their own personal characteristics as compared with thinking about others (D'Argembeau et al., 2010; Northoff et al., 2006). Only one developmental study compared the hemodynamic response to self- and social knowledge retrieval between school-age children and adults (Pfeifer et al., 2007). The authors found significant differences in the pattern of activation between children and adults – greater in magnitude and larger spatial extent in children in the mPFC, which was interpreted as resulting from a lack of automaticity in children's self-knowledge retrieval, as well as reflecting greater neural efficiency in adults (resulting in decreases in magnitude and/or spatial extent with development). It is important to note that several studies do not find any specific changes in the mPFC for self-processing (Yaoi et al., 2009) and interpretation of these findings is still debated (e.g., Cacioppo and Decety, 2011; Legrand and Ruby, 2009).

The right inferior parietal cortex at the junction with the right TPJ is thought to play a pivotal role the distinction between self-generated actions and actions generated by others (Blakemore and Frith, 2003; Farrer et al., 2003, 2004; Ruby and Decety, 2001). Repetitive transcranial magnetic stimulation of the right inferior parietal cortex disrupts self–other discrimination, but not when applied to the left homologous region (Uddin et al., 2006). This region has also been implicated in studies of empathy as well as studies of conceptual (Ruby and Decety, 2003), emotional perspective-taking (Ruby and Decety, 2004) and theory of mind (Decety and Sommerville, 2003; Saxe and Wexler, 2005). The right TPJ is considered as a critical hub within the ventral attention network that supports the detection of behaviorally relevant stimuli. It is therefore plausible that this region is implicated in higher level cognitive processing such as mentalizing and empathic understanding where complex expectation and inferences have to be integrated for generating an adaptive response (Decety and Lamm, 2007).

Overall, humans are quite distinct in possessing an impressive degree of self-awareness and second-order representations, and this ability start to develop around the second year of life. This representational system confers distinct evolutionary advantages because it makes sophisticated interactions with other conspecifics more predictable and manageable. Ultimately, this allows people to empathize with others, understand their emotional states, and predict their behaviors with more flexibility. However, the most beneficial aspect of self-awareness is the ability to reflect on the thoughts, intentions and emotions of others. In addition, the cognitive processes and neural circuitry that underpin self-awareness are similar to those implementing theory of mind (Leslie, 1987; Wimmer and Perner, 1983) also termed mentalizing (Frith and Frith, 1999).

6.4. Mentalizing and empathy

While the relationship between theory of mind and empathy has yet to be established, the two constructs partly overlap. The full-blown capacity of human empathy is more sophisticated than the mere automatic resonance of the target's affective state. Indeed, empathy is both about sharing the emotional state of others and understanding it in relation to oneself. Mentalizing underlies the ability to explain, predict, and interpret actions and speech by attributing mental states – such as beliefs, desires, intentions, and emotions – to oneself and to other people (Astington and Hughes, 2011; Wimmer and Perner, 1983). While some building blocks of theory of mind are present in our ape relative (Premack and Woodruff, 1978), the ability to explicitly represent representations as representations (meta-representation) is specific to humans (Leslie, 1994; Stone and Gerrans, 2006; Suddendorf, 1999). The important condition for mentalizing is the intersubjective awareness that others' subjective internal states may be similar or may differ from our own (Frith and Frith, 1999). The abilities to conceptualize and reflect on our own and other's emotions and to appreciate that these can differ are central to socioemotional competence. In developmental psychology research, children are considered to possess theory of mind when they are able to understand that a person's beliefs motivate his or her actions, even when those beliefs conflict with reality and/or the child's own beliefs (Wellman et al., 2001). Mentalizing follows a developmental course over the first 5 years of life that includes apparent transitions and transformations. The most significant transition occurs between the ages of 3 and 4 marked by the passing of tests involving object transfer problems, with most children achieving full competency in this ability by age five. The false belief task has been the most widely used test of children's theory of mind.

Although theory of mind is a very specific construct, it is useful to take it into account when considering the development of empathy-related responding. If children before the age of 3 or 4 have a difficulty sorting out conflicting information about their own and another's mental states, it must be challenging for them to deal with others' emotional states if they are significantly different from the children's own states and/or difficult to read from the situation. In fact, research shows that at the early school age, similarity between the perceiver and the victim of distress is still an important factor in empathy: for example, in a study in which 6- and 7-year-old boys and girls observed slide-sequence stories about other boys and girls in different emotional states, they had a stronger vicarious emotional response to children of their own gender (Feshbach and Roe, 1968). Mentalizing abilities continue to be a source of variability in empathic and prosocial responsiveness in early adolescence. For instance, children who are better at reconciling conflicting emotional cues also exhibit more helping behaviors (Carlo et al., 1991). The transition between childhood and adolescence is also marked by an important development that is believed to be related to a combination of self-concept development, growth of perspective-taking abilities and moral reason-

ing: the ability to empathize with a generalized group of others (Fabes et al., 1999).

Functional neuroimaging studies have consistently identified a circumscribed neural network reliably underpinning the understanding of mental states, using various tasks such as cartoon strips, stories and interactive games, that links the mPFC, pSTS/TPJ, and temporal poles/amygdala (e.g., Brunet et al., 2000; Choudhury et al., 2009; Frith and Frith, 2006). Of particular interest, one fMRI study investigated the overlap in the neural response to empathy and mentalizing using a non-verbal task in which participants had to make inferences about either the mental or emotional state of the story protagonists (Vollm et al., 2006). Results showed that both mentalizing and empathy depend on the activation of similar brain networks involved in social perception, namely the mPFC, OFC, pSTS/TPJ and temporal poles. These areas form the basis for making inferences about the mental states of others. However, the appreciation of the other's emotional states required the additional engagement of emotional networks, particularly the parahippocampal gyrus and amygdala.

A few neuroimaging studies have investigated the neurodevelopment of mentalizing. In one such study, children aged 6–11 years were scanned while they listened to sections of a story describing a character's thoughts compared to sections of the same story that described the physical context (Saxe et al., 2009). Signal increase was found in the mentalizing network, including the mPFC. Further, change in response selectivity with age was observed in the right TPJ, which was recruited equally for mental and physical facts about people in younger children, but only for mental facts in older children. Results from a study with 4-year-old children showed that individual differences in EEG alpha activity localized to the dorsal mPFC and the right TPJ were positively associated with children's mentalizing performance, which suggests that the maturation of dorsal mPFC and right TPJ is a critical constituent of preschoolers' explicit theory of mind development (Sabbagh et al., 2009). Support for age-related changes in brain response associated with mentalizing is also provided by an fMRI study in which adolescents and adult volunteers were scanned as they read sentences describing situations in which social (such as guilt and embarrassment which require an awareness of other people's mental states in relation to ones' own) or basic emotions would be felt (Brunett et al., 2009). Regions underlying mentalizing, including the mPFC, pSTS, and the anterior temporal poles, showed greater activity in social relative to basic emotions in both age groups. However, when activity was compared between age groups, it was found that adolescents activated the mPFC more strongly than did adults for social relative basic emotions. Functional connectivity analyses further demonstrated stronger connectivity in the adolescents between mPFC and pSTS during social relative to basic emotion than did the adults, suggestive of developmental changes in functional integration within the mentalizing system (Brunett and Blakemore, 2009). Direct evidence for the implication of the mPFC in accurate identification of interpersonal emotional states was documented in a study in which adults participants were requested to rate how

they believe target persons felt while talking about autobiographical emotional events (Zaki et al., 2009).

Understanding the social context in which distress is inflicted to others is associated with activation of the neural network underpinning mentalizing, as demonstrated by a study that compared patterns of brain activation while 7- to 11-year-old children observed video clips depicting painful situations occurring by accident and painful situations intentionally caused by another individual (Decety et al., 2008). Since pain is the result of a type of social interaction in the latter situation, its recognition is likely to involve not only the affective arousal elicited by its perception but also the cognitive evaluation of the social interaction. Results showed that attending to painful situations caused by accident is associated with activation of several regions of the pain matrix, including the aMCC, AIC, PAG, and somatosensory cortex. Interestingly, when children observed one person intentionally harming another, regions that are consistently engaged in mental state understanding and affective evaluation (mPFC, rTPJ, OFC and amygdala) were additionally recruited (Fig. 3). Further, increased functional connectivity was found between the mPFC and the frontoparietal supramodal attention network, as well as the right TPJ, when children viewed painful situations intentionally caused by another individual relative to situations where pain occurred accidentally. Post-scan debriefing indicated that children expressed more concern for people who have been harmed intentionally than for people who have been harmed accidentally. Regression analysis computed between intentional harm and pain ratings showed a significant cluster of activation in the aMCC, a region that implements a domain-general process that is integral to negative affect, pain and cognitive control (Shackman et al., 2011). Together, these data demonstrate the impact of social context on the neural response to the perception of others' distress, and the role of mentalizing in the appraisal processes in understanding social interaction.

In sum, children's mind reading abilities that interact with emotion circuits are implemented in a network of regions that include the mPFC, right pSTS/TPJ, and posterior cingulate cortex. That network supports rather complex cognitive processes that may be unique to humans, and these areas (especially the prefrontal cortex) follows an extremely protracted developmental course, with age-related changes continuing well into adolescence (Casey et al., 2005; Luna and Sweeney, 2004). Importantly, several prefrontal cortex territories such as the ACC, OFC and vmPFC play a critical role in the functional integration between cognition and emotion important for sophisticated and adaptive empathic responses. Mentalizing is also strongly associated with processes important for executive function, including emotion regulation. Age-related changes in mPFC and its functional connectivity with limbic regions and TPJ may represent increased regional specialization or efficiency within integrated neural circuits.

6.5. Emotion regulation and empathy

There is solid evidence that self-regulatory processes play an important role in empathy-related responding. Individuals who are well-regulated are unlikely to be

overwhelmed by their negative emotion when witnessing another person in distress or need. The fact that humans have evolved powerful social cognitive abilities assisted by episodic memory, language, future planning, and meta-representation brings both adaptive benefits and costs. As indicated by developmental work of Eisenberg and colleagues, in addition to stemming from affective arousal and emotional contagion, emotional distress may also arise from purely cognitive processes such as perspective-taking or memory retrieval (Eisenberg and Eggum, 2009). There are individual differences associated with dispositional variables and propensity to enact prosocial behaviors that are mediated by emotion regulatory processes. Prosocial children tend to be well-regulated and low in impulsivity, whereas personal distress has been associated with low regulation in children and adults (Eisenberg and Fabes, 1998).

Both emotional arousal and self-regulation are jointly influenced by the early maturation of attentional systems that enable progressively consistent voluntary control and the capacity to disengage from emotionally arousing events (Rothbart, 2007). Intrinsic self-regulatory processes begin to emerge with the growth of attentional control and simple forms of self-soothing, and concurrently the extrinsic regulation of emotion manifested by the caregiver's responsiveness to the infant's emotion expressions (Thompson, 2011). In addition, neurobiological systems involved in stress regulation, including the HPA axis, are functional at birth and mature rapidly during the early years in ways that help account for declining emotional lability and permit greater self-control (Gunnar and Quevedo, 2007). By the time infants have formed attachment relationships to one or a few caregivers, the presence and history of responsiveness of the attachment figure both influences whether infants exhibit cortisol increases to stressors and whether behavioral distress correlates with these increases (Gunnar and Donzella, 2002). The social modulation of physiological stress responses not only lay the foundation for the development of emotion regulation competencies but continue to influence HPA activity in adolescents and adults by providing a buffer against stress and have a positive impact on measures of health and well-being (DeVries et al., 2003; Heinrichs et al., 2003).

The ways in which mentalizing and emotion regulation abilities interact in predicting patterns in children's empathy-related responding have been studied extensively by Eisenberg and colleagues (Eisenberg et al., 1989, 1994). One of their studies compared adults' and 2nd- to 5th-graders' empathic reactions to others' distress, as well as their tendency to help the victims. The measures included self-reported reactions to a video of injured characters – children and adults – as well as the subjects' facial expressions and heart rates recorded while they were watching the video (age of the characters matched to the age of the participants). Importantly, for both the self-reports and the physiological measures, the researchers looked separately at expressions of self-focused personal distress versus empathic concern about the others. Consistent with earlier findings in adults (Batson et al., 1987), self-reported and facial expressions of concern predicted helping. Children's self-reports of personal distress and

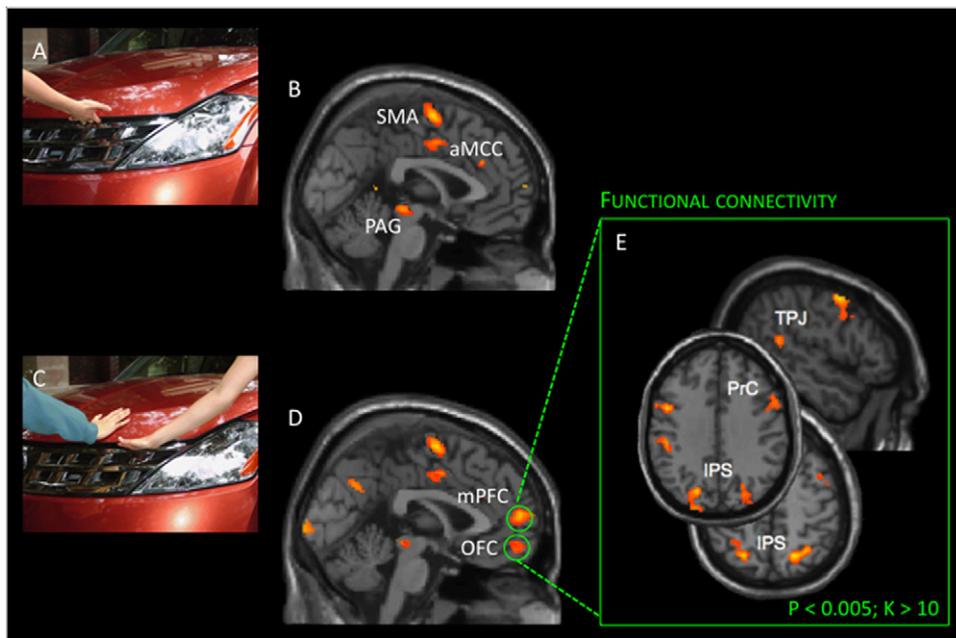


Fig. 3. Intention understanding and neural processing of others' distress. When children (age between 7 and 11 years) are shown short video clips (2.2 s) depicting harmful situations that occur accidentally and non intentionally (like in A), the neural regions involved in processing nociceptive/aversive information such as the anterior midcingulate cortex (aMCC), anterior insula (not shown), thalamus, somatosensory cortex (not shown), supplementary motor area (SMA) and periaqueductal gray (PAG) are activated (B). When the videos depict harmful actions intentionally done by another individual (C), in addition to the network that processes aversive information, neuro-hemodynamic signal increase is detected in the amygdala (not shown), medial prefrontal cortex (mPFC) and orbitofrontal cortex (OFC) (D). Besides, both mPFC and OFC increase their effective connectivity with the fronto-parietal attention network (E), which consists of the superior precentral sulcus (PrC), superior intraparietal sulcus (IPS) and the temporo-parietal junction (TPJ). This network plays a critical role in reorienting attention to salient stimuli in the environment and is functionally connected with the neural system underpinning mentalizing (Corbetta and Shulman, 2002). Adapted from Decety et al. (2008).

empathic concern were not related to their prosocial behavior (possibly suggesting children's immature abilities to self-reflect or to accurately report their experiences). However, physiological measures, in particular children's facial display of personal distress were negatively related to their helping behavior. Other developmental studies, using various measures of empathy-related responsiveness, have confirmed that children's increased empathic concern is positively correlated with other-oriented behavior (Eisenberg and Eggum, 2009).

It has been shown that empathic concern is strongly related to effortful control, with children high in effortful control showing greater concern (Rothbart et al., 1994), as indicated by a number of developmental studies which reported that individual differences in the tendency to experience sympathy versus personal distress vary as a function of dispositional differences in individuals' abilities to regulate their emotions. Some aspects of emotion regulation are functionally linked to the development of executive functions and meta-cognition. Improvement in inhibitory control correlates with increasing meta-cognitive capacities (Zelazo et al., 2004), as well as with maturation of prefrontal regions, which underlie working memory and inhibitory control (Tamm et al., 2002). Regions of the prefrontal cortex that are most consistently involved in emotion regulation include the ventral and dorsal aspects of the prefrontal cortex, as well as the dorsal ACC through their reciprocal connections with

limbic areas (Ochsner and Gross, 2005). Importantly, ventromedial areas of the prefrontal cortex develop relatively early, and are actively implicated in the control of affective states, whereas lateral prefrontal cortical regions develop relatively late and are principally involved in higher executive functions (Philips et al., 2008). Prefrontal cortex maturation, which continues well into adolescence, is associated with an increase in children's ability to activate areas involved in emotional control and exercise inhibitory control over their thoughts, attention, and actions. This maturation also allows children to use verbalizations to achieve self-regulation of their feelings (Diamond, 2002). Language provides children with an additional, socially appropriate means of communicating about their needs, with enhanced ability to understand their own and others' emotional lives (Cole et al., 2010). Verbalization of feelings can help reduce distress and can improve physical and psychological well-being. Language development contributes to the early development of skillful emotion regulation. But these two systems, affect and speech, have different evolutionary and developmental histories. Expressions of affect are present from birth whereas speech develops during the first 3 years and onward. As children begin to speak, their verbal and non-verbal expressions are sequential rather than simultaneous (Bloom and Capatides, 1987). By preschool age preschoolers animate their verbal exchanges with emotional expressions (Gamer and Lemerise, 2007) and are able to exert some control over spontaneous neg-

ative emotional expression (Cole, 1986). Then by middle childhood children understand how and when to regulate the display of emotion depending both on social experiences, through which they learn the rules of interpersonal behavior, and on cognitive capacity, necessary for children to anticipate how they will be perceived by others (Gnepp and Hess, 1986).

Several empirical studies have now demonstrated that affective language dampens amygdala response (e.g., Lieberman et al., 2007) and facilitates exposure-related attenuation of autonomic reactivity to aversive stimuli (Tabibnia et al., 2008). It is therefore likely that different and widely distributed neural circuits may be differentially involved in emotion regulation at different ages. Developmental neuroimaging work indicates that as a child matures into adolescence, there is a shift in response to emotional events from using more limbic-related anatomic structures, such as the amygdala, to using more frontal lobe regions to control and regulate emotional responses (Killgore and Yurgelun-Todd, 2007). Thus, not only may there be less neural activity related to the regulation of cognition and emotion in younger individuals, but the neural pattern itself is likely to differ.

Overall, children are most likely to experience empathy and concern if they are prone to at least moderate levels of affective arousal combined with adaptive emotional regulation that are context dependent. Neurobiological systems and circuits that are relevant to emotion regulation progressively mature from early years to adolescence with constant influences from supportive social interaction.

7. Flexibility in empathic responsiveness

Empathy is not automatic or reflexive, and various social and contextual factors moderate its induction and expression. It would not be adaptive to respond with care and to extend one's empathic concern to all. Empirical work with non-human animals (e.g., Langford et al., 2010) and humans has shown that empathy can be moderated by how the target individual is perceived, including how similar (Batson et al., 2005), or likable that person is (e.g., Kozak et al., 2006), and by group membership (e.g., Yabar et al., 2006), which impacts information processing on the different components of empathy such as affective arousal, emotion understanding and motivation to care (Echols and Correll, 2011). Recent neuroimaging studies have documented that the neural network associated with the perception of others' distress is modulated by various social, contextual, and interpersonal factors. For instance, one fMRI study demonstrated that empathic arousal is moderated early in information processing by a priori attitudes toward other people (Decety et al., 2009). Participants were significantly more sensitive to the pain of individuals who had contracted AIDS as the result of a blood transfusion as compared to individuals who had contracted AIDS as the result of their illicit drug addiction (sharing needles), as evidenced by significantly higher pain and empathy ratings and significantly greater hemodynamic activity in areas associated with pain processing (i.e., AIC, aMCC, PAG). Another fMRI study found evi-

dence for a modulation of empathic neural responses by racial group membership (Xu et al., 2009). Notably, the neural response in the ACC to perception of others in pain decreased remarkably when participants viewed faces of racial out-group members relative to racial in-group members. Furthermore, activity in the pain matrix network was enhanced when people viewed their loved ones in pain compared to strangers (Cheng et al., 2010) and reduced if the person in pain has been unfair in a prior interaction (Singer et al., 2006). To the extent to which empathic understanding promotes empathic concern and helping behavior, one might expect perceivers to experience reduced concern for out-group victims as well. Recent research provides support for this hypothesis. Soccer fans in one study observed either another fan of their favored team (in-group) or a rival team (out-group) experiencing painful shocks (Hein et al., 2010). Participants showed increased empathic understanding for in-group than out-group targets, reporting higher pain ratings and showing greater activation in the anterior insula for in-group targets. Participants also reported feeling more empathic concern for in-group targets, and they were more likely to volunteer to help by sharing the pain of in-group than out-group targets. Moreover, the difference in anterior insula activation when viewing in- versus out-group members in pain predicted the group difference in helping behavior. Another neuroimaging study demonstrated that, in sport context, the failures of an in-group member are painful, whereas those of a rival out-group member give pleasure – a feeling that may motivate harming rivals (Cikara et al., 2011).

Individuals' personal context also modulates affective arousal, as demonstrated by two functional neuroimaging studies showing that physicians do not react to the pain of others in the same way as non-physicians do. One study compared the neuro-hemodynamic response in a group of physicians and a group of matched control participants while they viewed short video clips depicting faces, hands and feet being pricked by a needle (painful situations) or being touched by a Q-tip (non-painful situations). The results demonstrated activation of the pain matrix in the controls when they attended to the painful situations relative to the non-painful ones. A different pattern of signal increase was detected in the physicians when they watched painful procedures (Cheng et al., 2007). Cortical regions underpinning executive function and self-regulation (dlPFC and mPFC) and executive attention (precentral, superior parietal and TPJ) were found to be activated, and unlike in the control group, no signal increase was detected in the pain matrix. A second study recorded event-related potentials (ERPs) from physicians and matched controls as they were presented with the same visual stimuli (Decety et al., 2010). The results showed early N110 differentiation between pain and no pain, reflecting negative arousal, over the frontal cortex as well as late P3 over the centro-parietal regions in the control participants. In contrast, no such early ERP response was detected in the physicians, which indicates that affect regulation has very early effects, inhibiting the bottom-up processing of negative arousal from the perception of painful stimuli.

At what age and how much social experience is necessary for such modulatory effects on empathic arousal and prosocial motivation are important questions for future developmental studies, given that in-group versus out-group processes have an impact on the social brain quite early. There is evidence from ERPs measures that infants tune their visual neural representations to environmentally salient stimuli experienced starting from 6 to 9 months of age (Scott and Monesson, 2010), and that 5-year-old children quickly come to categorize other people along dimensions that are both perceptually available to infants and socially salient to adults such as age, gender, race languages and accents (Kinzler et al., 2009). These social preferences are likely to be the product of evolutionary adaptations that served as predictors of group membership.

8. The added value of integrating evolution and developmental science

The concept of empathy and emotion-related behaviors reflect the end product of interactions among multiple neural systems that become well integrated over the course of phylogeny and ontogeny. Nevertheless, it is important to remember that underlying empathy and prosocial behaviors are many converging processes, including attention, processing affective stimuli, attachment, understanding the causes of emotions in relation to oneself and others, regulating one's own emotional arousal, and motivation to help. These systems operate in parallel and are highly influenced by social contexts and learning.

At birth, perceptual systems are wired to be sensitive to information from the social environment. Humans are born with the neural circuitry that implements core affect (that can be described by hedonic valence and arousal), and binds sensory and somatovisceral information to create meaningful representations that can be used to safely navigate the world (Duncan and Barrett, 2007). Cortico-limbic circuits that evaluate and regulate responses to psychosocial stress rapidly develop after birth with constant influences from caregivers. These mechanisms are the product of the long evolution of the mammalian brain and are critical in helping the infant to assess the overall valence of social stimuli. While the intensity of emotional reactions to others' affect may asymptote at a relatively young age and has a significant biological contribution particularly relying on reciprocal connections between the brainstem, ACC, vmPFC and amygdala, the ability to understand others' emotional states gradually increases with age and maturation of language, executive function and mentalizing abilities. This is crucial for decoding confounded emotions, interpreting situational regulators of affect, and understanding "unexpressed" affect. The complexity and interconnectivity of neural systems implicated in socioemotional processing and empathy contributes to multiple aspects of processing and feedback circuitry (Fig. 4). Sensory cortices, brainstem, amygdala, insula, and OFC are highly interconnected regions that operate in a parallel fashion. As a result, individuals may be concurrently experiencing an emotion, perceiving a continually changing stream of potentially relevant emotional infor-

mation, propagated by contextual or language interaction with another person, and regulating a behavioral response depending on motivation, social relationship, and prior experience. Each process feeds both forward and backward to other stages and types of processing (Wismer Fries and Pollak, 2009), which become progressively integrated as they mature.

Part of the developmental process may consist of acquiring more elaborated and complex empathy/concern-related behaviors – more occasions that evoke affect and buffer against such evocation – as well as better abilities at distancing, distracting, display, and avoidance patterns (More, 1990). With age and increased maturation of the prefrontal cortex and its reciprocal connections with limbic structures, in conjunction with input from interpersonal experiences that are strongly modulated by various contextual and social factors such as in-group versus out-group processes, children and adolescents become sensitive to social norms regulating prosocial behavior and accordingly, may become more selective in their responses to others.

From an evolutionary perspective, it seems reasonable to argue that females evolved to be more empathetic than males because mothers need to be more sensitive to the needs of their infants (see Text Box 3). After all, the only parent guaranteed to be present at birth, that directly invests time and energy resources for in utero development and equipped to provide initial post-natal feeding through lactation, is the mother.

It is important to note that there are large cultural differences in how much fathers engage in direct care of infants. It has been suggested that time spent in proximity with pregnant women and their infants and the act of caring for babies render men more nurturing (Hrdy, 2009). While endocrinological transformation during pregnancy, birth and lactation are far more pronounced in mothers than in fathers, men as well as women can be physiologically altered by exposure to babies. For instance, circulating levels of prolactin increase in experienced fathers holding their second-born infant against their chest (Delahunty et al., 2007). Lower male testosterone levels are associated with pair bonding and parental care (Gray and Campbell, 2009). Research shows that fathers with lower testosterone levels are more sympathetic and feel a greater need to respond to infant cries and that those with higher prolactin levels feel more positive (Storey et al., 2000). Fathers with more prior interactive experience caring for infants (usually from having had a previous baby) have lower testosterone levels and higher prolactin levels than do fathers having their first baby (Fleming et al., 2002). These findings illustrate how social experiences can induce hormonal changes and facilitates the expression of paternal behavior.

Finally, empathy may not always be adaptive. The benefits of empathy appear obvious as it often motivates caring and prosocial actions toward others, and its impairment can be associated with callous lack of regard for others, like in the case of psychopathy. Too much empathy, however, may be detrimental to the self. For instance, the medical profession has a longstanding struggle to achieve an appropriate balance between empathy and clinical distance (Halpern, 2001). In clinical contexts, empathy is challeng-

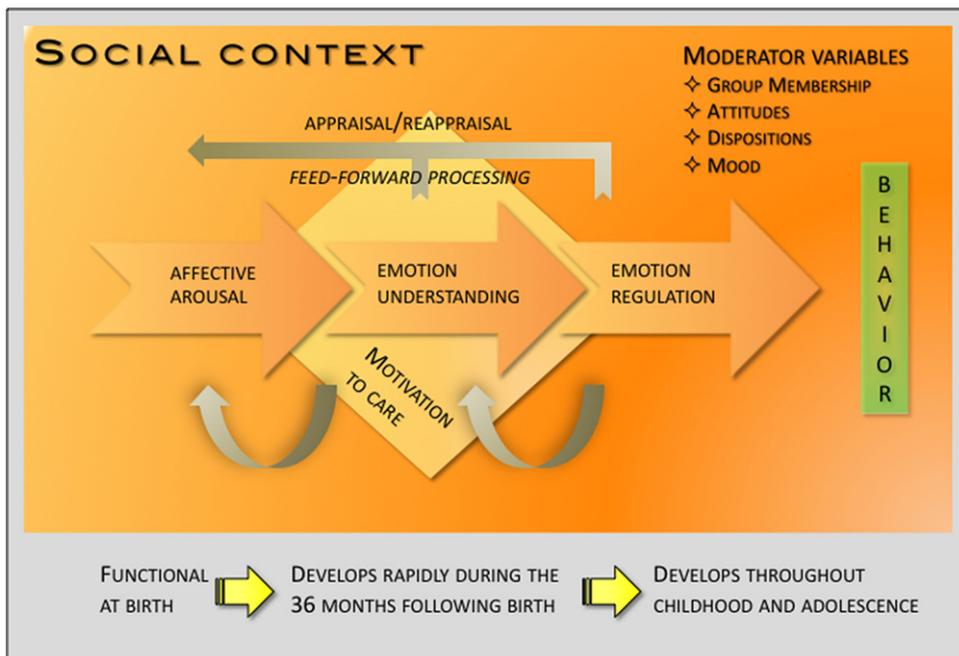


Fig. 4. Schematic illustration of the macro information processing components involved in development of human empathy. These different components are intertwined and contribute to different aspects of the experience of empathy. They feed both forward to other stages of processing thereby enhancing flexible and appropriate behavioral responses. These components are continuously and mutually influential in the course of emotion responding and are contextually embedded. 1 – Affective arousal is the first component in place in development. It has evolved to differentiate hostile from hospitable stimuli and organize adaptive responses to these stimuli. This component refers to the automatic discrimination of a stimulus – or features of a stimulus – as appetitive or aversive, hostile or hospitable, pleasant or unpleasant, threatening or nurturing. Subcortical circuits including brainstem, amygdala, hypothalamus, hippocampus, striatum, and OFC are the essential neural components of affective arousal. The amygdala and OFC with reciprocal connection with the pSTS underlie rapid and prioritized processing of emotion signals. 2 – Emotion understanding develops later, and begins to be really mature around the age of 2–3. This component largely overlaps with mentalizing-like processing and draws on the mPFC, posterior superior temporal sulcus/TPJ and vmPFC as well as executive functions. Reciprocal connectivity between posterior STS and mPFC allows the child to entertain several perspectives and a decoupling mechanism between first-person and second-person information. 3 – Emotion regulation, which enables the control of emotion, affect, drive, and motivation, begins to emerge with simple forms of self-soothing and extrinsic regulation in caregiver responsiveness to the baby's emotional expressions. The dlPFC, ACC, and vmPFC through their reciprocal connections with the amygdala, hypothalamus, brainstem play a primary role in self-regulatory processes. The sympathetic-adrenomedullary (SAM) and hypothalamic–pituitary–adrenocortical (HPA) systems are centrally modulated by limbic brain circuits that involve the amygdala, hippocampus, and orbital/medial prefrontal cortex. Both SAM and HPA are functional in newborns and mature significantly during the early years in ways. 4 – Motivation to care that produces prosocial motivation arises from a set of biological mechanisms that evolved to promote parental care and attachment. The neural underpinnings are found in subcortical systems (especially the medial preoptic area, hypothalamus and striatum) as well as neuropeptides regulating attachment particularly prolactin, oxytocin, opioids, and prolactin have relevance for regulating empathic responsiveness. Emotional experience is always continuously influenced by appraisal processes. Thus empathy is not a passive affective resonance phenomenon with the emotions of others. Rather, goals, intentions, context and motivation play feed-forward functions in how emotions are perceived and experienced. From this model, it is clear that empathy and concern for others are implemented by a complex network of widely distributed, often recursively connected, interacting subcortical and cortical circuits as well as autonomic and neuroendocrine processes implicated in affiliative behaviors.

ing because doctors and nurses are dealing with the most emotionally distressing situations – illness, dying, suffering in every form. This painful reality may take its toll on medial practitioners in leading to compassion fatigue, burn out, professional distress, and result in a low sense of accomplishment and severe emotional exhaustion (Gleichgerrcht and Decety, 2011).

A surfeit of empathy might also be seen in patients with internalizing disorders such as anxiety and depression (O'Connor et al., 2007). Zahn-Waxler (2000) has described the presence of an early developmental pathway where too much empathy as well as guilt can place individuals at risk for later depression. High empathy in children is a risk factor for later depression if they are over-involved and distressed with unregulated negative affect (Klimes-Dougan and Bolger, 1998).

A better understanding the complex relationship between empathy, prosociality and mental health variables will gain from adopting a developmental system view to investigate how components mature in reciprocal interaction between biology and socialization. We are indeed biologically predisposed to be emotionally connected with others and care for them, and various socializing and biological factors shape the way empathy develops in both adaptive and maladaptive ways.

9. Conclusions

Drawing from multiple sources of data can help paint a more complete picture of the phenomenological experience of empathy and prosocial behavior, as well as an understanding of the development and interaction

Box 3: Sex differences in empathy

Given the multi-level construct of empathy, one may expect gender differences for different neurobiological systems involved in emotion sensitivity and concern. Research indicates that females compared to males:

- Are more accurate and sensitive in labeling facial expressions of emotion (Montagne et al., 2005).
- Have better memory for highly emotional events (Canli et al., 2002).
- Are faster at consciously recognizing both positive and negative emotions from facial cues (Hampson et al., 2006).
- 14- to 36-month-old girls score higher in empathic concern as measured by expressions of apparent concern, including facial, vocal, or gestural–postural expressions, for victim of physical injury, and this difference is stable with age (Knafo et al., 2008; Zahn-Waxler et al., 1992). But see Bandstra et al. (2011) for a lack of sex differences in response to an individual in pain or an individual experiencing sadness.
- Studies using questionnaires indicate that, for all ages, girls score significantly higher in empathy and prosocial behavior (e.g., Garaigordobil, 2009). However, the results from self-report questionnaires measures of dispositional empathy are inconsistent and are influenced by social desirability and positive self-presentation (Batson, 2011; Eisenberg and Lennon, 1983). Neuroimaging studies with children (e.g., Decety and Michalska's, 2010; Decety et al., in press) and adults (Lamm et al., 2011 for a recent meta-analysis) that used the empathy questionnaires measures in search of correlation with brain response to the perception of others in pain does not support any reliable nor meaningful relationship between empathy disposition, gender differences and neural processing (Decety, 2011). An illustration of this inconsistency, a study that included 91 participants (51 males) reported that while women participants gave more intense self-report ratings of fear and disgust to IAPS pictures, no sex differences in overall brain activity (measured with fMRI) was found during the viewing of these two aversive picture conditions (Schienle et al., 2005).
- Quantitative meta-analyses on 65 neuroimaging studies of emotion processing showed that women more frequently activate midline limbic structures, including the subcallosal anterior cingulate, thalamus, and midbrain, whereas males showed more activation in left inferior frontal and posterior cortex (Wager et al., 2003).
- Administration of testosterone in female leads to a significant impairment in the ability to infer emotions, intentions, and other mental states from the eye region of the face (Van Honk et al., 2011).

between the respective physiological mechanisms that drive the phenomena. The multiple components of empathy are continuously and mutually influential in the course of social interactions and are contextually embedded. And as they mature, they become progressively integrated. Further, studying subcomponents of more complex psychological constructs like empathy can be particularly

useful from a developmental perspective, because only some of its components or precursors may be observable in children. Developmental studies can provide unique opportunities to see how the components of the system interact in ways that are not possible in adults where all the components are fully mature and operational (De Hann and Gunnar, 2009). Until quite recently, research on the development of empathy-related responding from a neurobiological level of analysis has been relatively sparse. We believe that integrating this perspective with behavioral work can shed light into the neurobiological mechanisms underpinning the basic building blocks of empathy and concern and their age-related functional changes.

The relations between emotion, empathic concern and prosocial behavior operate on a series of nested evolutionary processes, which are intertwined with social and motivational contingencies. An important lesson that we learned from evolution and ontogeny is that motivation to care and help others in need does not require access to the meta-representational level to occur. (see Fig. 1).

Affective and developmental neuroscience studies of empathy and related processes reviewed above offer an interesting new angle for developmental psychologists studying these phenomena. Despite some limitations of neuroimaging methods, the precise biological markings that they provide for psychological processes may be considered a valuable tool for exploring the developmental timing of these processes and the various social factors that influence them. It seems that the most productive course of action for investigating developmental processes with neuroimaging is to first identify brain mechanisms of specific psychological computational processes in adults and then design experiments for use with children, so that the resulting brain activation patterns can be precisely classified as pertaining to one or the other psychological process. This is especially valuable when behavior alone is not sufficient for explaining what mechanisms govern it cognitively.

Finally, an integrated view of the development of empathy and its neurobiological underpinnings has enormous potential for improving our understanding of children who are at risk for socioemotional difficulties, which will likely help inform interventions. The capacity for empathy may indeed be altered by a variety of causes, including genetic factors, hormonal and neuroendocrine responses, that result from complex reciprocal interactions between physiological systems and social environment. Excellent illustrations are provided by the work on child maltreatment on the reactivity of the HPA axis (Tarullo and Gunnar, 2006) and the development of emotion understanding (Perlman et al., 2008).

Acknowledgement

The writing of this paper was supported by a grant (BCS-0718480) from the National Science Foundation to Jean Decety.

References

- Achaibou, A., Pourtois, G., Schwartz, S., Vuilleumier, P., 2008. Simultaneous recording of EEG and facial muscle reactions during spontaneous emotion mimicry. *Neuropsychologia* 46, 1104–1113.

- Akitsuki, Y., Decety, J., 2009. Social context and perceived agency modulate brain activity in the neural circuits underpinning empathy for pain: an event-related fMRI study. *NeuroImage* 47, 722–734.
- Aron, A.R., Robbins, T.W., Poldrack, R.A., 2004. Inhibition and the right inferior frontal cortex. *Trends in Cognitive Sciences* 8, 170–177.
- Aslin, R.N., Clayards, M., Bardhan, N.P., 2008. Mechanisms of auditory reorganization during development: from sound to words. In: Nelson, C.A., Luciana, M. (Eds.), *Handbook of Developmental Cognitive Neuroscience*. MIT Press, Cambridge, pp. 97–116.
- Astington, J.W., Hughes, C., 2011. Theory of mind: self-reflection and social understanding. In: Zelazo, P.D. (Ed.), *Oxford Handbook of Developmental Psychology*. Oxford University Press, New York.
- Bandstra, N.F., Chambers, C.T., McGrath, P.J., Moore, C., 2011. The behavioral expression of empathy to others' pain versus others' sadness in young children. *Pain* 152, 1074–1082.
- Barrett, L.F., Kensinger, E.A., 2010. Context is routinely encoded during emotion perception. *Psychological Science* 21, 595–599.
- Batson, C.D., 2009. These things called empathy: eight related but distinct phenomena. In: Decety, J., Ickes, W. (Eds.), *The Social Neuroscience of Empathy*. MIT press, Cambridge, pp. 3–15.
- Batson, C.D., 2011. *Altruism in Humans*. New York, Oxford University Press.
- Batson, C.D., Fultz, J., Schoenrade, P.A., 1987. Distress and empathy: two qualitatively distinct vicarious emotions with different motivational consequences. *Journal of Personality* 55, 19–39.
- Batson, C.D., Lishner, D.A., Cook, J., Sawyer, S., 2005. Similarity and nurturance: two possible sources of empathy for strangers. *Basic and Applied Social Psychology* 27, 15–25.
- Benuzzi, F., Lui, F., Duzzi, D., Nichelli, P.F., Porro, C.A., 2008. Does it look painful or disgusting? Ask your parietal and cingulate cortex. *Journal of Neuroscience* 28, 923–931.
- Bird, G., Silani, G., Brindley, R., White, S., Frith, U., Singer, T., 2010. Empathic brain responses in insula are modulated by levels of alexithymia but not autism. *Brain* 133, 1515–1525.
- Bischof-Köhler, D., 1991. The development of empathy in infants. In: Lamb, M.E., Keller, H. (Eds.), *Infant Development: Perspectives from German Speaking Countries*. Erlbaum, Hillsdale, NJ, pp. 245–273.
- Blair, R.J.R., 2005. Responding to the emotions of others: dissociating forms of empathy through the study of typical and psychiatric populations. *Consciousness and Cognition* 14, 698–718.
- Blair, R.J.R., 2011. Should affective arousal be grounded in perception-action coupling? *Emotion Review* 3, 109–110.
- Blair, R.J.R., Fowler, K., 2008. Moral emotions and moral reasoning from the perspective of affective cognitive neuroscience: a selective review. *European Journal of Developmental Science* 2, 303–323.
- Blairy, S., Herrera, P., Hess, U., 1999. Mimicry and the judgment of emotional facial expressions. *Journal of Nonverbal Behavior* 23, 5–41.
- Blakemore, S.-J., Frith, C.D., 2003. Self-awareness and action. *Current Opinion in Neurobiology* 13, 219–224.
- Bloom, L., Capatides, J.B., 1987. Expression of affect and the emergence of language. *Child Development* 58, 1513–1522.
- Botvinick, M., Jha, A.P., Bylsma, L.M., Fabian, S., Solomon, P., Prkachine, K.M., 2005. Viewing facial expressions of pain engages cortical areas involved in the direct experience of pain. *NeuroImage* 25, 312–319.
- Broad, K.D., Curley, J.P., Keverne, E.B., 2006. Mother-infant bonding and the evolution of mammalian social relationships. *Philosophical Transactions of the Royal Society, Biological Sciences* 361, 2199–2214.
- Brooks-Gunn, J., Lewis, M., 1984. The development of early visual self-recognition. *Developmental Review* 4, 215–239.
- Brunet, E., Sarfati, Y., Hardy-Bayle, M.C., Decety, J., 2000. A PET investigation of attribution of intentions to others with a non-verbal task. *NeuroImage* 11, 157–166.
- Brunett, S., Blakemore, S.-J., 2009. Functional connectivity during a social emotion task in adolescents and in adults. *European Journal of Neuroscience* 29, 1294–1301.
- Brunett, S., Bird, G., Moll, J., Frith, C., Blakemore, S.-J., 2009. Development during adolescence of the neural processing of social emotion. *Journal of Cognitive Neuroscience* 21, 1736–1750.
- Burnette, J.L., Davis, D.E., Green, J.D., Worthington, E.L., Bradfield, E., 2009. Insecure attachment and depressive symptoms: the mediating role of rumination, empathy, and forgiveness. *Personality and Individual Differences* 46, 276–280.
- Bufalari, I., Aprile, T., Avenanti, A., Di Russo, F., Aglioti, S.M., 2007. Empathy for pain and touch in the human somatosensory cortex. *Cerebral Cortex* 17, 2553–2561.
- Bullock, M., Lutkenhaus, P., 1990. Who am I? Self-understanding in toddlers. *Merrill-Palmer Quarterly* 36, 217–238.
- Cacioppo, J.T., Decety, J., 2011. Social neuroscience: challenges and opportunities in the study of complex behavior. *Annals of the New York Academy of Sciences* 1224, 162–173.
- Canli, T., Desmond, J.E., Zhao, Z., Gabrieli, J.D.E., 2002. Sex differences in the neural basis of emotional memories. *Proceedings of the National Academy of Sciences USA* 99, 10789–10794.
- Carlo, G., Knight, G.P., Eisenberg, N., Rotenberg, K.J., 1991. Cognitive processes and prosocial behaviors among children: the role of affective attributions and reconciliations. *Developmental Psychology* 27, 456–461.
- Carpenter, M., Nagell, K., Tomasello, M., 1998. Social cognition, joint attention, and communicative competence from 9–18 months of age. *Monographs of the Society for Research in Child Development* 4, 255–263.
- Carter, C.S., 1998. Neuroendocrine perspective on social attachment and love. *Psychoneuroendocrinology* 23, 779–818.
- Carter, C.S., Grippo, A.J., Pournajafi-Nazarloo, H., Ruscio, M.G., Porges, S.W., 2008. Oxytocin, vasopressin and sociality. *Progress Brain Research* 170, 331–336.
- Carter, C.S., Porges, S.W., 2011. The neurobiology of social bonding and attachment. In: Decety, J., Cacioppo, J.T. (Eds.), *The Oxford Handbook of Social Neuroscience*. Oxford University Press, New York, pp. 151–163.
- Casey, B.J., Tottenham, N., Liston, C., Durston, S., 2005. Imaging the developing brain: what have we learned about cognitive development? *Trends in Cognitive Sciences* 9, 104–110.
- Cassidy, J., Shaver, P.R., Mikulincer, M., Lavy, S., 2009. Experimentally induced security influences responses to psychological pain. *Journal of Social and Clinical Psychology* 28, 463–478.
- Cheney, D.L., Seyfarth, R.M., 1985. The social and non-social world of non-human primates. In: Hinde, R.A., Perrett-Clermont, A., Stevenson, J. (Eds.), *Social Relationships and Cognitive Development*. Oxford University Press, Oxford, pp. 23–40.
- Cheng, Y., Hung, A.Y., Decety, J. Dissociation between affective sharing and emotion understanding in juvenile psychopaths. *Development and Psychopathology*, in press.
- Cheng, Y., Chen, C.Y., Lin, C.P., Chou, K.H., Decety, J., 2010. Love hurts: an fMRI study. *NeuroImage* 51, 923–929.
- Cheng, Y., Yang, C.Y., Lin, C.P., Lee, P.R., Decety, J., 2008. The perception of pain in others suppresses somatosensory oscillations: a magnetoencephalography study. *NeuroImage* 40, 1833–1840.
- Cheng, Y., Lin, C., Liu, H.L., Hsu, Y., Lim, K., Hung, D., Decety, J., 2007. Expertise modulates the perception of pain in others. *Current Biology* 17, 1708–1713.
- Choudhury, S., Charman, T., Blakemore, S.-J., 2009. Mentalizing and development during adolescence. In: De Haan, M., Gunnar, M.R. (Eds.), *Handbook of Developmental Social Neuroscience*. Guilford, New York, pp. 159–174.
- Church, R.M., 1959. Emotional reactions of rats to the pain of others. *Journal of Comparative and Physiological Psychology* 52, 132–134.
- Cikara, M., Botvinick, M.M., Fiske, S.T., 2011. Us versus them: social identity shapes responses to intergroup competition and harm. *Psychological Science* 22, 306–313.
- Cole, P.M., 1986. Children's spontaneous control of facial expression. *Child Development* 57, 1309–1321.
- Cole, P.M., Armstrong, L.M., Pemberton, C.K., 2010. The role of language in the development of emotion regulation. *Child development at the intersection of emotion and cognition*. In: Calkins, S., Bell, M.A. (Eds.), *Child Development at the Intersection of Emotion and Cognition, Human Brain Development*. American Psychological Association, Washington, DC, US, pp. 59–77.
- Corbetta, M., Shulman, G.L., 2002. Control of goal-directed and stimulus-driven attention in the brain. *Nature Neuroscience Reviews* 3, 201–215.
- Craig, A.D., 2003. Interoception: the sense of the physiological condition of the body. *Current Opinion in Neurobiology* 13, 500–505.
- Crowley, M.J., Wu, J., Molfese, P.J., Mayes, L.C., 2010. Social exclusion in middle childhood: rejection events, slow-wave neural activity, and ostracism distress. *Social Neuroscience* 5 (5–6), 483–495.
- D'Argembeau, A., Stawarczyk, D., Majerus, S., Collette, F., Van der Linden, M., Salmon, E., 2010. Modulation of medial prefrontal and inferior parietal cortices when thinking about past, present, and future selves. *Social Neuroscience* 5, 187–200.
- Davidson, R.J., Putnam, K.M., Larson, C.L., 2000. Dysfunction in the neural circuitry of emotion regulation – a possible prelude to violence. *Science* 289, 591–594.
- De Hann, M., Gunnar, M., 2009. *Handbook of Developmental Social Neuroscience*. Guilford Publications, New York.
- De Waal, F.B.M., 2008. Putting the altruism back into altruism: the evolution of empathy. *Annual Review of Psychology* 59, 279–300.

- De Waal, F.B.M., 2011. Empathy in primates and other mammals. In: Decety, J. (Ed.), *Empathy: From Bench to Bedside*. MIT press, Cambridge.
- De Wied, M., Van Boxtel, A., Zaalberg, R., Goudena, P.P., Matthys, M., 2006. Facial EMG responses to dynamic emotional facial expressions in boys with disruptive behavior disorders. *Journal of Psychiatric Research* 40, 112–121.
- De Wied, M., Gispens-de Wied, C., van Boxtel, A., 2010. Empathy dysfunction in children and adolescents with disruptive behavior disorders. *European Journal of Pharmacology* 626, 97–103.
- Decety, J., 2010a. The neurodevelopment of empathy in humans. *Developmental Neuroscience* 32, 257–267.
- Decety, J., 2010b. To what extent is the experience of empathy mediated by shared neural circuits? *Emotion Review* 2, 204–207.
- Decety, J., 2011. Dissecting the neural mechanisms mediating empathy. *Emotion Review* 3, 92–108.
- Decety, J., Lamm, C., 2007. The role of the right temporoparietal junction in social interaction: how low-level computational processes contribute to meta-cognition. *The Neuroscientist* 13, 580–593.
- Decety, J., Jackson, P.L., 2004. The functional architecture of human empathy. *Behavioral and Cognitive Neuroscience Reviews* 3, 71–100.
- Decety, J., Meyer, M., 2008. From emotion resonance to empathic understanding: a social developmental neuroscience account. *Development and Psychopathology* 20, 1053–1080.
- Decety, J., Michalska's, K.J., 2010. Neurodevelopmental changes in the circuits underlying empathy and sympathy from childhood to adulthood. *Developmental Science* 13, 886–899.
- Decety, J., Echols, S.C., Correll, J., 2009. The blame game: the effect of responsibility and social stigma on empathy for pain. *Journal of Cognitive Neuroscience* 22, 985–997.
- Decety, J., Michalska, K.J., Akitsuki, Y., 2008. Who caused the pain? A functional MRI investigation of empathy and intentionality in children. *Neuropsychologia* 46, 2607–2614.
- Decety, J., Michalska, K.J., Kinzler, K.D., 2011. The contribution of emotion and cognition to moral sensitivity: a neurodevelopmental study. *Cerebral Cortex*, Epub ahead of print.
- Decety, J., Sommerville, J.A., 2003. Shared representations between self and others: a social cognitive neuroscience view. *Trends in Cognitive Sciences* 7, 527–533.
- Decety, J., Yang, C.Y., Cheng, Y., 2010. Physicians down regulate their pain empathy response: an event-related brain potential study. *NeuroImage* 50, 1676–1682.
- Delahunty, K.M., McKay, D.W., Noseworthy, D.E., Storey, A.E., 2007. Prolactin responses to infant cues in men and women: effects of parental experience and recent infant contact. *Hormones and Behavior* 51, 213–220.
- DeVries, A.C., Glasper, E.R., Detillion, C.E., 2003. Social modulation of stress responses. *Physiology & Behavior* 79, 399–407.
- Diamond, A., 2002. Normal development of prefrontal cortex from birth to young adulthood: cognitive functions, anatomy, and biochemistry. In: Stuss, D.T., Knight, R.T. (Eds.), *Principles of Frontal Lobe Function*. Oxford University Press, New York, pp. 446–503.
- Dimberg, U., Thunberg, M., Elmehed, K., 2000. Unconscious facial reactions to emotional facial expressions. *Psychological Science* 11, 86–89.
- Domes, G., Heinrichs, M., Michel, A., Berger, C., Herpertz, S.C., 2007. Oxytocin attenuates amygdala responses to emotional faces regardless of valence. *Biological Psychiatry* 62, 1187–1190.
- Dondi, M., Simion, F., Caltran, G., 1999. Can newborns discriminate between their own cry and the cry of another newborn infant? *Developmental Psychology* 35, 418–426.
- Duncan, S., Barrett, L.F., 2007. Affect is a form of cognition: a neurobiological analysis. *Cognition and Emotion* 21, 1184–1211.
- Echols, S., Correll, J., 2011. It's more than skin deep: empathy and helping behavior across social groups. In: Decety, J. (Ed.), *Empathy: from Bench to Bedside*. MIT press, Cambridge.
- Eisenberg, N., Eggum, N.D., 2009. Empathic responding: Sympathy and personal distress. In: Decety, J., Ickes, W. (Eds.), *The Social Neuroscience of Empathy*. MIT press, Cambridge, pp. 71–83.
- Eisenberg, N., Fabes, R.A., 1998. Prosocial development. In: Damon, W., Eisenberg, N. (Eds.), *Handbook of Child Psychology*. Fifth ed. John Wiley & Sons, New York, pp. 701–778.
- Eisenberg, N., Fabes, R.A., Miller, P.A., Fultz, J., Shell, R., Mathy, R.M., et al., 1989. Relation of sympathy and personal distress to prosocial behavior: a multimethod study. *Journal of Personality and Social Psychology* 57, 55–66.
- Eisenberg, N., Fabes, R.A., Murphy, B., Karbon, M., Maszk, P., et al., 1994. The relations of emotionality and regulation to dispositional and situational empathy-related responding. *Journal of Personality and Social Psychology* 66, 776–797.
- Eisenberg, E., Lennon, R., 1983. Sex differences in empathy and related capacities. *Psychological Bulletin* 94, 100–131.
- Fabes, R.A., Carlo, G., Kupanoff, K., Laible, D., 1999. Early adolescence and prosocial/moral behavior I: the role of individual processes. *Journal of Early Adolescence* 19, 5–16.
- Farrer, C., Franck, N., Frith, C.D., Decety, J., Jeannerod, M., 2003. Modulating the experience of agency: a PET study. *NeuroImage* 18, 324–333.
- Farrer, C., Franck, N., Frith, C.D., Decety, J., Damato, T., Jeannerod, M., 2004. Neural correlates of action attribution in schizophrenia. *Psychiatry Research: Neuroimaging* 131, 31–44.
- Ferris, C.F., Kulkarni, P., Sullivan, J.M., Harder, J.A., Messenger, T.L., Febo, M., 2005. Pup suckling is more rewarding than cocaine: evidence from functional magnetic resonance imaging and three-dimensional computational analysis. *Journal of Neuroscience* 25, 149–156.
- Feshbach, N.D., Roe, K., 1968. Empathy in six- and seven-year-olds. *Child Development* 39, 133–145.
- Field, T.M., Woodson, R., Greenberg, R., Cohen, D., 1982. Discrimination and imitation of facial expressions by neonates. *Science* 218, 179–181.
- Fleming, A.S., Corter, C., Stallings, J., Steiner, M., 2002. Testosterone and prolactin are associated with emotional responses to infant cries in new fathers. *Hormones and Behavior* 42, 399–412.
- Forgas, J.P., Williams, K.D., 2003. The social self. In: Forgas, J.P., Williams, K.D. (Eds.), *The social Self; Cognitive, Interpersonal and Intergroup Perspectives*. Psychology Press, New York, pp. 1–18.
- Fraser, O.N., Stahl, D., Aureli, F., 2008. Stress reduction through consolation chimpanzees. *Proceedings of the National Academy of Sciences USA* 105, 8557–8562.
- Frith, C.D., Frith, U., 1999. Interacting minds – a biological basis. *Science* 286, 1692–1695.
- Frith, C.D., Frith, U., 2006. The neural basis of mentalizing. *Neuron* 50, 531–534.
- Gallagher, S., 2009. Two problems of intersubjectivity. *Journal of Consciousness Studies* 16, 289–308.
- Gallup, G.G., 1985. Do minds exist in species other than our own? *Neuroscience & Biobehavioral Reviews* 9, 631–641.
- Gamer, P.W., Lemerise, E.A., 2007. The roles of behavioral adjustment and conceptions of peers and emotions in preschool children's peer victimization. *Development and Psychopathology* 19, 57–71.
- Gammie, S.C., 2005. Current models and future directions for understanding the neural circuitries of maternal behaviors in rodents. *Behavioral and Cognitive Neuroscience Reviews* 4, 119–135.
- Garaigordobil, M., 2009. A comparative analysis of empathy in childhood and adolescence: gender differences and associated socio-emotional variables. *International Journal of Psychology and Psychological Therapy* 9, 217–235.
- Geangu, E., Benga, O., Stahl, D., Striano, T., 2010. Contagious crying beyond the first days of life. *Infant Behavior and Development* 33, 279–288.
- Gleichgerricht, E., Decety, J., 2011. The costs of empathy among health professionals. In: Decety, J. (Ed.), *Empathy: from Bench to Bedside*. MIT Press, Cambridge.
- Gnepp, J., Hess, D.L., 1986. Children's understanding of verbal and facial display rules. *Developmental Psychology* 22, 103–108.
- Gomez, J.C., 2004. Apes, Monkeys, Children, and the Growth of Mind. Harvard University Press, Cambridge, MA.
- Gray, P.B., Campbell, B.C., 2009. Human male testosterone, pair-bonding, and fatherhood. In: Ellison, P.T., Gray, P.B. (Eds.), *Endocrinology of Social Relationships*. Harvard University Press, Cambridge, pp. 270–293.
- Gump, B.B., Kulik, J.A., 1997. Stress, affiliation, and emotional contagion. *Journal of Personality and Social Psychology* 72, 305–319.
- Gunnar, M., Donzella, B., 2002. Social regulation of the cortisol levels in early human development. *Psychoneuroendocrinology* 27, 199–220.
- Gunnar, M., Quevedo, K., 2007. The neurobiology of stress and development. *Annual Review of Psychology* 58, 145–173.
- Halpern, J., 2001. *From Detached Concern to Empathy: Humanizing Medical Practice*. Oxford University Press, New York, NY.
- Hampson, E., van Anders, S.M., Mulin, L.L., 2006. A female advantage in the recognition of emotional facial expressions: test of an evolutionary hypothesis. *Evolution and Human Behavior* 27, 401–416.
- Hariri, A.R., Bookheimer, S.Y., Mazziotta, J.C., 2000. Modulating emotional responses: effects of a neocortical network on the limbic system. *Neuroreport* 11, 43–48.
- Harris, J., 2007. The evolutionary neurobiology, emergence and facilitation of empathy. In: Farrow, T.F.D., Woodruff, P.W.R. (Eds.), *Empathy in Mental Illness*. Cambridge University Press, Cambridge, pp. 168–186.
- Hatfield, E., Cacioppo, J.T., Rapson, R.L., 1994. *Emotional Contagion*. Cambridge University Press, Cambridge.

- Hatfield, E., Rapson, R.L., Le, Y.C., 2009. Emotional contagion and empathy. In: Decety, J., Ickes, W. (Eds.), *The Social Neuroscience of Empathy*. MIT Press, Cambridge, MA, pp. 19–30.
- Haviland, J.M., Lelwica, M., 1987. The induced affect response: 10-week-old infants' response to three emotional expressions. *Developmental Psychology* 23, 97–104.
- Hein, G., Silani, G., Preuschoff, K., Batson, C.D., Singer, T., 2010. Neural responses to ingroup and outgroup members' suffering predict individual differences in costly helping. *Neuron* 68, 149–160.
- Heinrichs, M., Baumgartner, T., Kirschbaum, C., Ehlert, U., 2003. Social support and oxytocin interact to suppress cortisol and subjective responses to psychosocial stress. *Biological Psychiatry* 54, 1389–1398.
- Heinrichs, B.V., von Dawans, B., Domes, G., 2009. Oxytocin, vasopressin, and human social behavior. *Frontiers in Neuroendocrinology* 30, 548–557.
- Hess, U., Blairy, S., 2001. Facial mimicry and emotional contagion to dynamic emotional facial expressions and their influence on decoding accuracy. *International Journal of Psychophysiology* 40, 129–141.
- Hess, U., Philippot, P., Blairy, S., 1999. Mimicry: facts and fiction. In: Philippot, P., Feldman, R., Coats, E.J. (Eds.), *The Social Context of Nonverbal Behavior, Studies in Emotion and Social Interaction*. Cambridge University Press, New York, pp. 213–241.
- Hodges, S.D., Klein, K.J.K., 2001. Regulating the costs of empathy: the price of being human. *Journal of Socio-Economics* 30, 437–452.
- Hoebel, B.G., Avena, N.M., Rada, P., 2007. Accumbens dopamine-acetylcholine balance in approach and avoidance. *Current Opinion in Pharmacology* 7, 617–627.
- Hoffman, M.L., 1984. Interaction of affect and cognition in empathy. In: Izard, C.E., Kagan, J., Zajonc, R.B. (Eds.), *Emotions, Cognition and Behavior*. Cambridge University Press, New York, pp. 103–131.
- Hrdy, S.B., 2009. *Mothers and Others*. Harvard University Press, Cambridge.
- Hurliman, E., Nagode, J.C., Pardo, J.V., 2005. Double dissociation of exteroceptive and interoceptive feedback systems in the orbital and ventromedial prefrontal cortex of humans. *Journal of Neuroscience* 25, 4641–4648.
- Iannetti, G.D., Mouraux, A., 2010. From the neuromatrix to the pain matrix (and back). *Experimental Brain Research* 205, 1–12.
- Insel, T.R., 2010. The challenge of translation in social neuroscience: a review of oxytocin, vasopressin, and affiliative behavior. *Neuron* 65, 768–779.
- Insel, T.R., Young, L.J., 2001. The neurobiology of attachment. *Nature Reviews Neuroscience* 2, 129–136.
- Izuma, K., Saito, D.N., Sadato, N., 2010. Processing of the incentive for social approval in the ventral striatum during charitable donation. *Journal of Cognitive Neuroscience* 22, 621–631.
- Jackson, P.L., Meltzoff, A.N., Decety, J., 2005. How do we perceive the pain of others? A window into the neural processes involved in empathy. *NeuroImage* 24, 771–779.
- Jackson, P.L., Brunet, E., Meltzoff, A.N., Decety, J., 2006. Empathy examined through the neural mechanisms involved in imagining how I feel versus how you feel pain. *Neuropsychologia* 44, 752–761.
- Jeon, D., Kim, S., Chetana, M., Jo, D., Ruley, H.E., Lin, S.Y., Rabah, D., Kinet, J.P., Shin, H.S., 2010. Observational fear learning involves affective pain system and Ca(v)1.2 Ca²⁺ channels in ACC. *Nature Neuroscience* 13, 482–488.
- Johnson, D.B., 1982. Altruistic behavior and the development of the self in infants. *Merrill-Palmer Quarterly* 28 (3), 379–388.
- Joseph, R., 2000. Fetal brain & cognitive development. *Developmental Review* 20, 81–98.
- Kagan, J., 1981. *The Second Year: Emergence of Self-Awareness*. Harvard University Press, Cambridge, MA.
- Kelley, S.A., Brownell, C.A., Campbell, S.B., 2000. Mastery motivation and self-evaluative affect in toddlers: longitudinal relations with maternal behavior. *Child Development* 71, 1061–1071.
- Killien, M., Smetana, J., 2008. Moral judgment and moral neuroscience: intersections, definitions, and issues. *Child Development Perspectives* 2, 1–6.
- Killgore, W.D.S., Yurgelun-Todd, D.A., 2007. Unconscious processing of facial affect in children and adolescents. *Social Neuroscience* 2, 28–47.
- Kinzler, K.D., Shutts, K., DeJesus, J., Spelke, E.S., 2009. Accent trumps race in guiding children's social preferences. *Social Cognition* 27, 623–634.
- Kirsch, P., Esslinger, C., Chen, Q., Mier, D., Lis, S., Siddhanti, S., Gruppe, H., Mattay, V.S., Gallhofer, B., Meyer-Lindenberg, A., 2005. Oxytocin modulates neural circuitry for social cognition and fear in humans. *Journal of Neuroscience* 25, 11489–11493.
- Klimes-Dougan, B., Bolger, A.A., 1998. Coping with maternal depressed affect and depression: adolescent children of depressed mothers and well mothers. *Journal of Youth and Adolescence* 27, 1–15.
- Knafo, A., Zahn-Waxler, C., van Hulle, C., Robinson, J.L., Rhee, S.H., 2008. The developmental origins of a disposition toward empathy: genetic and environmental contributions. *Emotion* 8, 737–752.
- Konner, M., 2010. *The Evolution of Childhood*. Belknap Press, Cambridge, MA.
- Kosfeld, M., Heinrichs, M., Zak, P.J., Fischbacher, U., Fehr, E., 2005. Oxytocin increases trust in humans. *Nature* 435, 673–676.
- Kozak, M., Marsh, A., Wegner, W., 2006. What do I think you're doing? Action identification and mind attribution. *Journal of Personality and Social Psychology* 90, 543–555.
- Kringelbach, M.L., Rolls, E.T., 2004. The functional neuroanatomy of the human orbitofrontal cortex: evidence from neuroimaging and neuropsychology. *Progress in Neurobiology* 72, 341–372.
- Lauwereyns, J., Rajala, A.Z., Reininger, K.R., Lancaster, K.M., Populin, L.C., 2010. Rhesus monkeys (*Macaca mulatta*) do recognize themselves in the mirror: implications for the evolution of self-recognition. *PLoS ONE* 5 (9), e12865.
- Lamm, C., Decety, J., 2008. Is the extrastriate body area (EBA) sensitive to the perception of pain in others? An fMRI investigation. *Cerebral Cortex* 18, 2369–2373.
- Lamm, C., Batson, C.D., Decety, J., 2007a. The neural basis of human empathy: effects of perspective-taking and cognitive appraisal. *Journal of Cognitive Neuroscience* 19, 42–58.
- Lamm, C., Decety, J., Singer, T., 2011. Meta-analytic evidence for common and distinct neural networks associated with directly experienced pain and empathy for pain. *NeuroImage* 54, 2492–2502.
- Lamm, C., Nusbaum, H.C., Meltzoff, A.N., Decety, J., 2007b. What are you feeling? Using functional magnetic resonance imaging to assess the modulation of sensory and affective responses during empathy for pain. *PLoS ONE* 12, e1292.
- Lamm, C., Meltzoff, A.N., Decety, J., 2010. How do we empathize with someone who is not like us? *Journal of Cognitive Neuroscience* 2, 362–376.
- Langford, D.J., Crager, S.E., Shehzad, Z., Smith, S.B., Sotocinal, S.G., Levenstadt, J., et al., 2006. Social modulation of pain as evidence for empathy in mice. *Science* 312, 1967–1970.
- Langford, D.J., Tuttleb, A.H., Brown, K., Deschenes, S., Fischer, D.B., Mutso, A., Root, K.C., Sotocinal, S.G., Stern, M.A., Mogil, J.S., Sternberg, W.F., 2010. Social approach to pain in laboratory mice. *Social Neuroscience* 5, 163–170.
- Legrand, D., Ruby, P., 2009. What is self-specific? Theoretical investigation and critical review of neuroimaging results. *Psychological Review* 116, 252–282.
- Leppanen, J.M., Nelson, C.A., 2009. Tuning the developing brain to social signals of emotions. *Nature Reviews Neuroscience* 10, 37–47.
- Leslie, A., 1987. Pretence and representation: the origins of "theory of mind". *Psychological Review* 94, 412–426.
- Leslie, A.M., 1994. Pretending and believing: issues in the theory of ToMM. *Cognition* 50, 211–238.
- Lewis, M., Ramsay, D., 2004. Development of self-recognition, personal pronoun use, and pretend play during the second year. *Child Development* 75, 1821–1831.
- Lieberman, M.D., Eisenberger, N.I., Crockett, M.J., Tom, S.M., Pfeifer, J.H., Way, B.M., 2007. Putting feelings into words: affect labeling disrupts amygdala activity to affective stimuli. *Psychological Science* 18, 421–428.
- Lobaugh, N.J., Gibson, E., Taylor, M.J., 2006. Children recruit distinct neural systems for implicit emotional face processing. *Neuroreport* 17, 215–219.
- Lorberbaum, J.P., Newman, J.D., Horwitz, A.R., Dubno, J.R., Lydiard, R.B., Hamner, M.B., Bohning, D.E., George, M.S., 2002. A potential role for thalamocingulate circuitry in human maternal behavior. *Biological Psychiatry* 51, 431–445.
- Luna, B., Sweeney, J.A., 2004. The emergence of collaborative brain function: fMRI studies of the development of response inhibition. *Annals of the New York Academy of Sciences, USA* 1021, 296–309.
- MacLean, P.D., 1985. Brain evolution relating to family, play, and the separation call. *Archives of General Psychiatry* 42, 405–417.
- Maestripietri, D., 2010. Neurobiology of social behavior. In: Platt, M.L., Ghazanfar, A.A. (Eds.), *Primate Neuroethology*. Oxford University Press, New York, pp. 359–384.
- Martin, G.B., Clark, R.D., 1987. Distress crying in neonates: species and peer specifically. *Developmental Psychology* 18, 3–9.
- Masten, C.L., Eisenberger, N.I., Pfeifer, J.H., Dapretto, M., 2010. Witnessing peer rejection during early adolescence: neural correlates of empathy for experiences of social exclusion. *Social Neuroscience* 5 (5–6), 496–507.
- Meltzoff, A.N., Moore, M.K., 1977. Imitation of facial and manual gestures by human neonates. *Science* 198, 75–78.

- Mikulincer, M., Gillath, O., Halevy, V., Avihou, N., Avidan, S., Eshkoli, N., 2001. Attachment theory and reactions to others' needs: evidence that activation of the sense of attachment security promotes empathic responses. *Journal of Personality and Social Psychology* 81, 1205–1224.
- Moll, J., Krueger, F., Zahn, R., Pardini, M., de Oliveira-Souza, R., Grafman, J., 2006. Human fronto-mesolimbic networks guide decisions about charitable donation. *Proceedings of the National Academy of Sciences* 103, 15623–15628.
- Montagne, B., Kessels, R.P.C., Frigerio, E., de Haan, E.H.F., Perrett, D.I., 2005. Sex differences in the perception of affective facial expressions: do men really lack emotional sensitivity? *Cognitive Processing* 6, 136–141.
- Moore, C., 2006. *The Development of Commonsense Psychology*. Lawrence Erlbaum Associates Publishers, Mahwah, NJ, US.
- Moore, C., 2007. Understanding self and others in the second year. In: Brownell, C.A., Kopp, C.B. (Eds.), *Socioemotional Development in the Toddler Years: Transitions and Transformations*. Guilford Press, New York, pp. 43–65.
- More, B.S., 1990. The origins and development of empathy. *Motivation and Emotion* 14, 75–79.
- Moriguchi, Y., Decety, J., Ohnishi, T., Maeda, M., Matsuda, H., Komaki, G., 2007. Empathy and judging other's pain: an fMRI study of alexithymia. *Cerebral Cortex* 17, 2223–2234.
- Munakata, Y., Casey, B.J., Diamond, A., 2004. Developmental cognitive neuroscience: progress and potential. *Trends in Cognitive Sciences* 8, 122–128.
- Neisser, U., 1991. Two perceptually given aspects of the self and their development. *Developmental Review* 11, 197–209.
- Neisser, U., 1993. The self perceived. In: Neisser, U. (Ed.), *The Perceived Self: Ecological and Interpersonal Sources of the Self-Knowledge*. Cambridge University Press, Cambridge, MA, pp. 3–21.
- Nichols, S.R., Svetlova, M., Brownell, C.A., 2009. The role of social understanding and empathic disposition in young children's responsiveness to distress in parents and peers. *Cognition, Brain, Behavior* 13 (4), 449–478.
- Nichols, S.R., Svetlova, M., Brownell, C.A. A peer in need: the development of empathic responsiveness to peers over the second year of life. *Developmental Psychology*, submitted for publication.
- Nielsen, M., Suddendorf, T., Slaughter, V., 2006. Mirror self-recognition beyond the face. *Child Development* 77, 176–185.
- Norris, C.J., Gollan, J., Bertson, G.G., Cacioppo, J.T., 2010. The current status of research on the structure of the evaluative space. *Biological Psychology* 84, 422–436.
- Northoff, G., Heinzel, A., de Greck, M., Bermpohl, F., Dobrowolny, H., Panksepp, J., 2006. Self-referential processing in our brain: a meta-analysis of imaging studies on the self. *NeuroImage* 31, 440–457.
- Numan, M., Sheehan, T.P., 1997. Neuroanatomical circuit for mammalian maternal behavior. *Annals of the New York Academy of Sciences* 807, 101–125.
- Nystrom, P., 2008. The infant mirror neuron system studied with high density EEG. *Social Neuroscience* 3, 334–347.
- O'Connor, L.E., Berry, J.W., Lewis, T., Mulherin, K., Crisostomo, P.S., 2007. Empathy and depression: the moral system on overdrive. In: Farrow, T.F.D., Woodruff, P.W.R. (Eds.), *Empathy in Mental Illness*. Cambridge University Press, Cambridge, pp. 49–75.
- Ochsner, K.N., Gross, J.J., 2005. The cognitive control of emotion. *Trends in Cognitive Sciences* 9, 242–249.
- Ongur, D., Price, J.L., 2000. The organization of networks within the orbital and medial prefrontal cortex of rats, monkeys and humans. *Cerebral Cortex* 10, 206–219.
- Panksepp, J., 1998. *Affective Neuroscience: The Foundations of Human and Animal Emotion*. Oxford University Press, New York.
- Parr, L.A., 2001. Cognitive and physiological markers of emotional awareness in chimpanzees (*Pan troglodytes*). *Animal Cognition* 4, 223–229.
- Paus, T., 2011. Brain development during childhood and adolescence. In: Decety, J., Cacioppo, J.T. (Eds.), *The Oxford Handbook of Social Neuroscience*. Oxford University Press, New York, pp. 293–313.
- Perlman, S.B., Kalish, C.W., Pollak, S.D., 2008. The role of maltreatment experience in children's understanding of the antecedents of emotion. *Cognition and Emotion* 22, 651–670.
- Pfeifer, J.H., Lieberman, M.D., Dapretto, M., 2007. I know you are but what am I?: neural bases of self- and social knowledge retrieval in children and adults. *Journal of Cognitive Neuroscience* 19, 1323–1337.
- Phillips, M.L., Ladouceur, C.D., Drevets, W.C., 2008. A neural model of voluntary and automatic emotion regulation: implications for understanding the pathophysiology and neurodevelopment of bipolar disorder. *Molecular Psychiatry* 13, 833–857.
- Plutchik, R., 1987. Evolutionary bases of empathy. In: Eisenberg, N., Strayer, J. (Eds.), *Empathy and its Development*. Cambridge University Press, New York, pp. 37–46.
- Povinelli, D.J., Bering, J.M., Giambrone, S., 2000. Toward a science of other minds: escaping the argument by analogy. *Cognitive Science* 24, 509–541.
- Premack, D., Woodruff, G., 1978. Does the chimpanzee have a theory of mind? *Behavioral and Brain Sciences* 1, 515–526.
- Pulman, S.B., Pelphrey, K.A., 2010. Regulatory brain development: balancing emotion and cognition. *Social Neuroscience* 5 (5–6), 533–542.
- Rochat, P., Hespos, S.J., 1997. Differential rooting response by neonates: evidence for an early sense of self. *Early Development & Parenting* 6, 105–112.
- Rochat, P., Striano, T., 2000. Perceived self in infancy. *Infant Behavior & Development* 23, 513–530.
- Rodrigues, S.M., Saslow, L.R., Garcia, N., John, O.P., Keltner, D., 2009. Oxytocin receptor genetic variation relates to empathy and stress reactivity in humans. *Proceedings of the National Academy of Sciences* 106, 21437–21441.
- Rothbart, M.K., 2007. Temperament, development, and personality. *Current Directions in Psychological Sciences* 16, 207–212.
- Rothbart, M.K., Ahadi, S.A., Hershey, K.L., 1994. Temperament and social behavior in childhood. *Merrill-Palmer Quarterly* 40, 21–39.
- Ruby, P., Decety, J., 2001. Effect of the subjective perspective taking during simulation of action: a PET investigation of agency. *Nature Neuroscience* 4, 546–550.
- Ruby, P., Decety, J., 2003. What you believe versus what you think they believe? A neuroimaging study of conceptual perspective taking. *European Journal of Neuroscience* 17, 2475–2480.
- Ruby, P., Decety, J., 2004. How would you feel versus how do you think she would feel? A neuroimaging study of perspective taking with social emotions. *Journal of Cognitive Neuroscience* 16, 988–999.
- Sabbagh, M.A., Bowman, L.C., Evraire, L.E., Ito, J.M.B., 2009. Neurodevelopmental correlates of theory of mind in preschool children. *Child Development* 80, 1147–1162.
- Sagi, A., Hoffman, M.L., 1976. Empathic distress in newborns. *Developmental Psychology* 12, 175–176.
- Sambo, C.F., Howard, M., Kopelman, M., Williams, S., Fotopoulou, A., 2010. Knowing you care: effects of perceived empathy and attachment style on pain perception. *Pain* 151, 687–693.
- Saxe, R., Pelphrey, R., 2009. Introduction to a special section of developmental social cognitive neuroscience. *Child Development* 80, 946–951.
- Saxe, R., Carey, S., Kanwisher, N., 2004. Understanding other minds: linking developmental psychology and functional neuroimaging. *Annual Review of Psychology* 55, 87–124.
- Saxe, R., Wexler, A., 2005. Making sense of another mind: the role of the right temporo-parietal junction. *Neuropsychologia* 43, 1391–1399.
- Saxe, R.R., Whitfield-Gabrieli, S., Pelphrey, K.A., Scholz, J., 2009. Brain regions for perceiving and reasoning about other people in school-aged children. *Child Development* 80, 1197–1209.
- Schienze, A., Schafer, A., Stark, R., Walter, B., Vaitl, D., 2005. Gender differences in the processing of disgust- and fear-inducing pictures: an fMRI study. *Neuroreport* 16, 277–280.
- Scott, L.S., Monesson, A., 2010. Experience-dependent neural specialization during infancy. *Neuropsychologia* 48, 1857–1861.
- Seifritz, E., Esposito, F., Neuhoff, J.G., Luthi, A., Mustovic, H., Dammann, G., von Bardeleben, U., Radue, E.W., Cirillo, S., Tedeschi, G., Di Salle, F., 2003. Differential sex-independent amygdala response to infant crying and laughing in parents versus nonparents. *Biological Psychiatry* 54, 1367–1375.
- Semendeferi, K., Teffer, K., Buxhoeveden, D.P., Park, M.S., Bludau, S., Amunts, K., Travis, K., Buckwater, J., 2010. Spatial organization of neurons in frontal pole sets humans apart from great apes. *Cerebral Cortex*, Epub ahead of print.
- Shackman, A.J., Salomons, T.V., Slagter, H., Fox, A.S., Winter, J.J., Davidson, R.J., 2011. The integration of negative affect, pain and cognitive control in the cingulate cortex. *Nature Review Neuroscience* 12, 154–167.
- Shahrokh, D., Zhang, T.Y., Diorio, J., Gratton, A., Meaney, M.J., 2010. Oxytocin-dopamine interactions mediate variations in maternal behavior in the rat. *Neuroendocrinology* 151, 2276–2286.
- Shamay-Tsoory, S., 2009. Empathic processing: its cognitive and affective dimensions and neuroanatomical basis. In: Decety, J., Ickes, W. (Eds.), *The Social Neuroscience of Empathy*. MIT press, Cambridge, pp. 215–232.
- Silk, J.B., 2007. Empathy, sympathy, and prosocial preferences in primates. In: Dunbar, R.I.M., Barrett, L. (Eds.), *The Oxford Handbook of Evolutionary Psychology*. Oxford University Press, New York, pp. 115–128.

- Simmer, M.L., 1971. Newborn's response to the cry of another infant. *Developmental Psychology* 5, 136–150.
- Singer, T., Seymour, B., O'Doherty, J., et al., 2004. Empathy for pain involves the affective but not the sensory components of pain. *Science* 303, 1157–1161.
- Singer, T., Seymour, B., O'Doherty, J.P., Stephan, K.E., Dolan, R.D., Frith, C.D., 2006. Empathic neural responses are modulated by the perceived fairness of others. *Nature* 439, 466–469.
- Sober, E., Wilson, D.S., 1998. *Unto Others: The Evolution and Psychology of Unselfish Behavior*. Harvard University Press, Cambridge.
- Sonnby-Borgstrom, M., Jonsson, P., Svensson, O., 2003. Emotional empathy as related to mimicry reactions at different levels of information processing. *Journal of Nonverbal Behavior* 27, 3–23.
- Sroufe, L.A., 2000. Early relationship and the development of children. *Infant Mental Health Journal* 21, 67–74.
- Stone, V.E., Gerrans, P., 2006. What's domain-specific about theory of mind? *Social Neuroscience* 1 (3–4), 309–319.
- Storey, A.E., Walsh, C.J., Quinton, R.L., Wynne-Edwards, K.E., 2000. Hormonal correlates of paternal responsiveness in new and expectant fathers. *Evolution and Human Behavior* 21, 79–95.
- Strathearn, L., Fonagy, P., Amico, J., Montague, P.R., 2009. Adult attachment predicts maternal brain and oxytocin response to infant cues. *Neuropharmacology* 13, 2655–2666.
- Suddendorf, T., 1999. The rise of the metacognition. In: Corballis, M.C., Lea, S. (Eds.), *The Descent of Mind: Psychological Perspectives on Hominid Evolution*. Oxford University Press, London, pp. 218–260.
- Svetlova, M., Nichols, S., Brownell, C., 2010. Toddlers' prosocial behavior: from instrumental to empathic to altruistic helping. *Child Development* 81, 1814–1827.
- Swain, J.E., 2008. Baby stimuli and the parent brain: functional neuroimaging of the neural substrates of parent–infant attachment. *Psychiatry* 5, 28–36.
- Swain, J.E., Loberbaum, J.P., Kose, S., Strathearn, L., 2007. Brain basis of early parent–infant interactions: psychology, physiology, and in vivo functional neuroimaging studies. *Journal of Child Psychology and Psychiatry* 48, 262–287.
- Swick, D., Ashley, V., Turken, A.U., 2008. Left inferior frontal gyrus is critical for response inhibition. *BMC Neuroscience* 9, 102e.
- Tabibnia, G., Lieberman, M.D., Craske, M.G., 2008. The lasting effect of words on feelings: words may facilitate exposure effects to threatening images. *Emotion* 8, 307–317.
- Tamm, L., Menon, V., Reiss, A.L., 2002. Maturation of brain function associated with response inhibition. *Journal of American Children and Adolescent Psychiatry* 41, 1231–1238.
- Tarullo, A.R., Gunnar, M.R., 2006. Child maltreatment and the developing HPA axis. *Hormones and Behavior* 50, 632–639.
- Thompson, R.A., 2011. Emotion and emotion regulation: two sides of the developing coin. *Emotion Review* 3, 53–61.
- Thompson, C., Barresi, J., Moore, C., 1997. The development of future-oriented prudence and altruism in preschoolers. *Cognitive Development* 12, 199–212.
- Trevarthen, C., 1979. Communication and cooperation in early infancy. A description of primary intersubjectivity. In: Bullowa, M. (Ed.), *Before Speech: The Beginning of Human Communication*. Cambridge University Press, London, pp. 321–347.
- Uddin, L.Q., Molnar-Szakacs, I., Zaidel, E., Iacoboni, M., 2006. rTMS to the right inferior parietal lobule disrupts self–other discrimination. *Social Cognitive and Affective Neuroscience* 1, 65–71.
- Vaish, A., Carpenter, M., Tomasello, M., 2009. Sympathy through affective perspective taking and its relation to prosocial behavior in toddlers. *Developmental Psychology* 45, 534–543.
- Van den Bos, W., van Dijk, E., Westenberg, M., Rombouts, S.A.R.B., Crone, E.A., 2010. Changing brains, changing perspectives: the neurocognitive development of reciprocity. *Psychological Science*, Epub ahead of print.
- Van der Gaag, C., Minderaa, R., Keyesers, C., 2007. Facial expressions: what the mirror neuron system can and cannot tell us. *Social Neuroscience* 2, 179–222.
- Van Honk, J., Schutter, D.J., Bos, P.A., Kruijt, A.-W., Lentjes, E.G., Baron-Cohen, S., 2011. Testosterone administration impairs cognitive empathy in women depending on second-to-fourth digit ratio. *Proceedings of the National Academy of Sciences* 108, 3448–3452.
- Vollm, B.A., Taylor, A.N.W., Richardson, P., Corcoran, R., Stirling, J., McKie, S., Deakin, J.F.W., Elliott, R., 2006. Neural correlates of theory of mind and empathy: a functional magnetic resonance imaging study in a nonverbal task. *NeuroImage* 29, 90–98.
- Wager, T.D., Phan, K.L., Liberzon, I., Taylor, S.F., 2003. Valence, gender, and lateralization of functional brain anatomy in emotion: a meta-analysis of findings from neuroimaging. *NeuroImage* 19, 513–531.
- Warneken, F., Hare, B., Melis, A.P., Hanus, D., Tomasello, M., 2007. Spontaneous altruism by chimpanzees and young children. *PLoS Biology* 5 (7), e184.
- Watt, D.F., 2000. The centrencephalon and thalamocortical integration: neglected contributions of periaqueductal gray. *Emotion and Consciousness* 1, 93–116.
- Weinfield, N.S., Srouffe, L.A., Egeland, B., Carlson, E., 2010. Individual differences in infant–caregiver attachment. In: Cassidy, J., Shaver, P.R. (Eds.), *Handbook of Attachment*. The Guilford Press, New York, pp. 78–101.
- Wellman, H.M., Cross, D., Watson, J., 2001. Meta-analysis of theory of mind development: the truth about false belief. *Child Development* 72, 655–684.
- Wimmer, H., Perner, J., 1983. Beliefs about beliefs: representation and constraining function of wrong beliefs in young children's understanding of deception. *Cognition* 13, 103–128.
- Winkelman, P., Berridge, K., Sher, S., 2011. Emotion, consciousness, and social behavior. In: Decety, J., Cacioppo, J.T. (Eds.), *The Oxford Handbook of Social Neuroscience*. Oxford University Press, New York, pp. 195–211.
- Wisner Fries, A.B., Pollak, S., 2009. Emotion processing and the developing brain. In: Coch, D., Fisher, K.W., Dawson, G. (Eds.), *Human Behavior, Learning, and the Developing Brain*. Guilford, New York, pp. 329–361.
- Xu, X., Zuo, X., Wang, X., Han, S., 2009. Do you feel my pain? Racial group membership modulates empathic neural responses. *Journal of Neuroscience* 29, 8525–8529.
- Yabar, Y., Johnston, L., Miles, L., Peace, V., 2006. Implicit behavioral mimicry: investigating the impact of group membership. *Journal of Nonverbal Behavior* 30, 97–113.
- Yamada, M., Decety, J., 2009. Unconscious affective processing and empathy: an investigation of subliminal priming on the detection of painful facial expressions. *Pain* 143, 71–75.
- Yaoi, K., Osaka, N., Osaka, M., 2009. Is the self special in the dorsomedial prefrontal cortex? An fMRI study. *Social Neuroscience* 4 (5), 455–463.
- Yurgelun-Todd, D., 2007. Emotional and cognitive changes during adolescence. *Current Opinion in Neurobiology* 17, 251–257.
- Zahn-Waxler, C., 2000. The development of empathy, guilt, and internalization of distress: implications for gender differences in internalizing and externalizing problems. In: Davidson, R.J. (Ed.), *Anxiety, Depression, and Emotion*. Oxford University Press, New York, pp. 222–265.
- Zahn-Waxler, C., Radke-Yarrow, M., 1990. Origins of empathic concern. *Motivation and Emotion* 14, 107–130.
- Zahn-Waxler, C., Radke-Yarrow, M., Wagner, E., Chapman, M., 1992. Development of concern for others. *Developmental Psychology* 28, 126–136.
- Zaki, J., Ochsner, K.N., Hanelin, J., Wager, T.D., Mackey, S.C., 2007. Different circuits for different pain: patterns of functional connectivity reveal distinct networks for processing pain in self and others. *Social Neuroscience* 2, 276–291.
- Zaki, J., Weber, J., Bolger, N., Ochsner, K., 2009. The neural bases of empathic accuracy. *Proceedings of the National Academy of Sciences* 106, 11382–11387.
- Zhang, S.P., Davis, P.J., Bandler, R., Carrive, P., 1994. Brainstem integration of vocalization: role of the midbrain periaqueductal gray. *Journal of Neurophysiology* 72, 1337–1356.
- Zelazo, P.D., Craik, F.I., Booth, L., 2004. Executive function across the life span. *Acta Psychologica* 115, 167–183.
- Zelazo, P.D., Paus, T., 2010. Developmental neuroscience: an introduction. *Social Neuroscience* 5 (5–6), 417–421.