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Origins and development of mirroring mechanisms: A neuroconstructivist framework

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The current review examines models developed to answer questions about the origins and early developmental processes determining the emergence of mirroring mechanisms and considers the debate about the role of the motor system in action understanding. Strengths and points of criticism deriving from existing alternative positions are illustrated. Particular emphasis is put on the neuroconstructivist framework with the aim of evaluating whether the hypotheses driven by this approach are in line with the available evidence. Within the neuroconstructivist framework, a novel model is proposed in which the *direct-matching* and *action reconstruction* viewpoints on action understanding processes can be integrated by assuming a developmental perspective. It is suggested that mirroring mechanisms are shaped by a domain-relevant narrowing process driven by sensorimotor experience and that action understanding can take advantage of both top-down and bottom-up processes, in a multilevel and dynamic fashion.

Originally found in the monkey ventral pre-motor cortex, mirror neurons fire both when an individual performs a goal-directed action (e.g., grasping) and when the same action is perceived as performed by another agent (Di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Fogassi *et al.*, 2005). The activation of the monkey pre-motor cells during observation of others' actions is considered to be evidence that mirror neurons are involved in action understanding processes by representing and internally re-enacting – that is, mirroring-perceived actions (Casile, Caggiano, & Ferrari, 2011). Research on human adults demonstrated that observing another individual performing an action modulates the activity of the observer's motor cortex (e.g., Buccino *et al.*, 2001; Molenberghs, Cunnington, & Mattingley, 2012; Perry & Bentin, 2009), and highlighted the presence of mirror neurons in the human brain through single cell recordings (Mukamel, Ekstrom, Kaplan, Iacoboni, & Fried, 2010; but see Keysers & Gazzola, 2010). Overall, evidence speaks in favour of a human mirror system, being a distributed cortical network, that is activated for action observation and execution.

According to the boldest phylogenetic explanation, mirror mechanisms are a product of genetic evolution and are favoured by natural selection because of their crucial role in understanding and imitating others' actions (Rizzolatti & Arbib, 1998). In this vein, perceptual-motor couplings should be present from birth, thus suggesting that sensori-motor matching mechanisms exist innately in monkey and human brains. Sensory and

motor experiences only have a marginal facilitative role in the development of mirroring mechanisms (Bonini & Ferrari, 2011). Nonetheless, direct neurophysiological evidence of a mirror neuron system in humans at birth is far from being established. The available studies focus almost exclusively on neonatal imitation showing that newborns sponta-neously reproduce tongue and lip protrusion and mouth opening movements up to 24 hr after presentation (Kugiumutzakis, 1999; Meltzoff & Moore, 1977, 1983, 1994). EEG studies with newborn monkeys provided further electrophysiological evidence. Specif-ically, mu rhythm desynchronization over central electrode sites, which is considered a neural marker of sensorimotor cortical activity, was recorded during observation and imitation of facial gestures (Ferrari *et al.*, 2012). Given that neonatal imitation involves cross-modal matching of perceptual and motor information, it was proposed that it might indicate a mirror neuron system that is innately functional soon after birth (Iacoboni & Dapretto, 2006; Lepage & Théoret, 2007; Meltzoff & Decety, 2003). Over the years, the phylogenetic hypothesis gave way to an epigenetic turn, stating the importance not only of strictly genetic mechanisms –that is, phylogenetic natural selection processes – but also of the modality DNA can differently express proteins depending on the environmental influences (at cellular, tissue and organism levels) and the role of learning processes in explaining interindividual variability of mirror responses (Evo-Devo perspective; Ferrari, Tramacere, Simpson, & Iriki, 2013).

The associative learning explanation of action mirroring rejects the idea that mirror mechanisms are genetically inherited, holding that they are a product of sensorimotor experience (Cook, Bird, Catmur, Press, & Heyes, 2014; Heyes, 2010). Specifically, mirror neurons are simple motor neurons activated during action execution. When the activation of motor and visual neurons is simultaneous (i.e., contiguous) and highly probable (i.e., contingent), the association between the motor and visual neurons is strengthened and transforms those motor neurons into mirror neurons (Ray & Heyes, 2011). This occurs, for example, when the perception of an action is frequently associated with the corresponding simultaneous and contingent motor command. The associative hypothesis implies that the perceptual-motor coupling properties of mirror mechanisms result from a domain-general associative learning process (Cook *et al.*, 2014). In this view, evolution only provides humans and other primates with motor and visual neurons and the potential for them to be connected to each other (Heyes, 2010).

In terms of imitation, the associative model suggests that the correspondence problem is solved by exposing an individual to repeated experiences of contiguous and contingent action observations and executions (Ray & Heyes, 2011). Indeed, imitation occurs in a wide variety of species (Range, Viranyi, & Huber, 2007; Whiten, McGuigan, Marshall-Pescini, & Hopper, 2009) and seems limited to those actions with which animals accumulate sensorimotor experience (Catmur, Walsh, & Heyes, 2009).

Studies exploring the role of sensorimotor experience in shaping mirror neuron system activity were carried out both in monkeys and human adults. In human adults, brief periods of sensorimotor experience were able to enhance (Press, Gillmeister, & Heyes, 2007; Wiggett, Hudson, Clifford, Tipper, & Downing, 2012), inhibit (Cook, Dickinson, & Heyes, 2012) and induce (Landmann, Landi, Grafton, & Della-Maggiore, 2011; Press *et al.*, 2012) mirroring activity. Nonetheless, evidence that in adults, sensorimotor experience modulates mirror mechanism activity cannot be directly translated into the idea that the emergence of mirror mechanisms in children is mainly derived from associative processes. Claims based on the study of fully formed adult brains may be inappropriate when applied to the study of the protracted period of development of the neocortex in infancy and childhood. Also, experience acquired in adulthood may determine temporary

changes in cortical functioning, but might be insufficient to generate substantial brain circuit reorganizations, while early experiences, especially if taking place during sensitive periods of development, could trigger long-term rearrangements of the involved brain structures.

Despite growing evidence highlighting the role of active and observational experiences in moulding mirroring mechanisms (Cannon *et al.*, 2015; Hunnius & Bekkering, 2014; Paulus, Hunnius, Van Elk, & Bekkering, 2012), only one study directly examined the effects of a visuomotor training on mirror activity in infancy. Specifically, pre-walking infants were trained to perform stepping movements while observing contingent or non-contingent leg movements. Mu rhythm activity was measured before and after training. The results highlighted that the amount of post-training sensorimotor activation was predicted by the strength of visuomotor contingency during training (de Klerk, Johnson, Heyes, & Southgate, 2015). Nevertheless, no difference was found between pre- and post-training across conditions; thus, the findings might be explained by the infants' previous experience with own leg movement observation and execution (e.g., kicking).

Points of criticism are raised against the associative account. As this position implies that all contingent sensorimotor experiences are learned equally well, some scholars argue that this approach cannot explain why some behaviours are learned more easily than others and why infants tend to imitate human rather than mechanical/non-human actions (Bertenthal, 2014). For example, 18-month-olds successfully imitate a human action, while failing to imitate the same action performed by a mechanical pincer (Meltzoff, 1995). In addition, given the cardinal importance of contingency and contiguity attributed to the associative learning model, some argue that the relatively low level of contingency in mother–infant interactions cannot allow the formation of learned associations (Ferrari *et al.*, 2013). Thus, according to these opposing viewpoints, associative learning does not answer questions about how infants recognize similarities between own and others' actions.

A third alternative explanation of the development of mirror mechanisms is situated within the broader neuroconstructivist framework. Similar to the Evo-Devo explanation, it avoids the idea that a specific set of perceptual and motor neurons are genetically pre-programmed for coding specific actions, and also the hypothesis that trial-and-error learning mechanisms are solely responsible for the development of mirror system. However, different from the Evo-Devo perspective, which tends to confine the role of experience to account for interindividual differences (Ferrari *et al.*, 2013), neuroconstructivism ascribes great value to experience-expectant processes, involving species-specific experiences that result in brain rewiring, which in turn leads to the development of specific neural systems (Greenough, Black, & Wallace, 1987). In this way, higher cognitive functions *become* domain-specific as a result of the ontogenetic development (Karmiloff-Smith, 1998). Thus, in comparison with the Evo-Devo perspective, this view assigns a major emphasis to the gradual tuning of a cortical network to process specific information, evidenced by an increasingly selective cortical response during development – that is narrowing (de Haan, Humphreys, & Johnson, 2002; Johnson, 2011).

Additionally, this model posits the existence of an early experiential canalization process that, by promoting the learning of perception-action couplings, is capable of ensuring the development of the mirror system (Del Giudice, Manera, & Keysers, 2009). Mirror mechanism development is canalized by domain-relevant predispositions of the perceptual-motor system that focus infants' attention towards actions performed by self and others, allowing the development of a specialized system devoted to their immediate understanding. Specifically, pre-specified early predispositions to attend to movements of

specific body parts (i.e., hands and face) (Rochat, 1998; van der Meer, 1997; von Hofsten, 2004) are thought to facilitate the development of a direct matching between executed and observed actions through experience. These predispositions are thought to protect the developing mirroring mechanisms from possible perturbations and to accelerate their developmental process. In contrast to the associative learning explanation, Del Giudice *et al.* (2009) insist on the role of domain-relevant predispositions and experiential canalization. Nonetheless, in agreement with associative learning, these Authors consider Hebbian learning to be a fundamental learning mechanism at the basis of action mirroring. The concept of canalization is acknowledged also by the Evo-Devo perspective, although in this vein it is primarily described at the level of gene-expression modifications, and it is taken into account for explaining the variations observed in mirror neurons properties.

A neuroconstructivist explanation of action mirroring would be in line with recent models of human development (de Schonen, 2002; Karmiloff-Smith, 2006; Westermann *et al.*, 2007). This perspective considers the developmental pathway not to be dependent on fixed genetic specifications or on simple and slow learning associations only, but to gradually emerge from the dynamic interaction between inborn domain-general properties of neural functioning and the structure of the input provided by the species-typical environment. Below we present a set of predictions and interpretations, along with supporting empirical data, that could be offered by the neuroconstructivist view on the development of action mirroring.

Hypothesis 1: Narrowing of mirroring mechanisms

Unlike the empiricist view, which considers experience gained in adulthood and infancy as equally important, neuroconstructivism acknowledges a key role to early inputs, which are responsible for tuning infants' abilities and lead to the progressive formation of domain-specific representations. Indeed, the neuroconstructivist approach to cognitive development considers brain specialization and domain specificity for high level perceptual and cognitive functions to arise from gradual developmental processes, whose only biological constraints are the general properties of neural and body functioning (Westermann *et al.*, 2007). This paragraph summarizes findings supporting a gradual specialization process of the mirror system.

Focusing on neurophysiological data, mu rhythm is an EEG oscillation recorded over sensorimotor scalp areas in the alpha frequency range (adults: 8–13 Hz; infants: 6–9 Hz) attenuating during action production and perception, consistent with the view that it may reflect motor system activation (Muthukumaraswamy & Johnson, 2004). Mu rhythm desynchronization magnitude during action execution and observation undergoes a gradual increase (Marshall & Meltzoff, 2011): 9- and 14-month-olds show a smaller decrease in mu power when observing (5% and 12%, respectively) and performing (10% and 14%, respectively) an action (Marshall, Young, & Meltzoff, 2011; Southgate, Johnson, Osborne, & Csibra, 2009), compared with mu desynchronization magnitude levels recorded in 8-year-old children in response to observing (25%) and performing (60%) an action (Lepage & Théoret, 2006). This developmental increase might reflect an underlying intensification of the neural activity involved in perceptual-motor coupling processes. Crucially, while in adults mu rhythm desynchronization is reported to be specific to central sites (Babiloni *et al.*, 1999), in infants this activity seems more widely distributed across the scalp (Saby, Marshall, & Meltzoff, 2012; van Elk, van Schie, Hunnius, Vesper, & Bekkering, 2008). This supports the notion that the regions involved in mirror

mechanisms in adults are already active in early infancy, although a specific network becomes increasingly localized and tuned with development (Kadosh & Johnson, 2007).

Additional evidence supporting a gradual specialization process comes from studies using surface electromyography (Natale *et al.*, 2014; Turati *et al.*, 2013). These studies demonstrate that motor resonance modulation elicited by the observation of a goal-directed action is lacking at 3 months of age; is evident at 6 months of age, during the observation of the latest phase of the action (i.e., during goal achievement); and precedes the goal of the action at 9 months of age, when the motor system is recruited in an earlier phase of the observed movement (i.e., before goal achievement), similar to what was shown in older children (Cattaneo *et al.*, 2007). These findings point to a gradual process of specialization of mirror mechanisms during the first year of life.

Recent evidence indicating a specific EEG activity response to human action sounds in 7-month-olds (Geangu, Quadrelli, Lewis, Cassia, & Turati, 2015) may also support this claim, especially if supported by future studies that investigate whether the processing of action sounds goes through a narrowing process in the first year of life. As for other auditory social information (i.e., voices, Belin, Zatorre, Lafaille, Ahad, & Pike, 2000), cortical specialization in processing human action sounds may be reflected in an increase in the tuning of the EEG responses to human action versus non-human action sounds.

Indeed, adult studies demonstrate that motor resonance occurs in response to the observation of actions within the observer's motor experience, while for actions like barking motor resonance is absent (Buccino, Binkofski, & Riggio, 2004; Buccino, Lui, *et al.*, 2004). Further studies are needed to directly test the narrowing hypothesis, for example by examining infant action mirroring response to observation of the actions of humans versus other species during the first year of life.

Combined with the ones reviewed above, these expected outcomes would support the hypothesis that action mirroring narrows throughout development, as highlighted for other perceptual domains (e.g., face recognition, language; Scott, Pascalis, & Nelson, 2007). Our idea is that active and observational experiences are responsible for shaping the gradual specialization of mirroring mechanisms (Cannon *et al.*, 2015; Hunnius & Bekkering, 2014; Paulus *et al.*, 2012; Van Elk *et al.*, 2008). Notably, infant understanding of others' actions does not depend on motor or passive experience only, as a variety of social cues such as gaze direction (Woodward, 2003), emotions (Phillips, Wellman, & Spelke, 2002), hand gestures (Woodward & Guajardo, 2002), and motivation to interact with others (Paulus, 2014) are also important in developing the ability to encode action goals.

Hypothesis 2: Constraints on the development of mirroring mechanisms

According to neuroconstructivism, a sequence of interactions between the pre- and post-natal environment and multiple levels embedded in the human body (i.e., cells, tissues and cortical circuits) is considered to drive the reorganizations of the cortical circuits (Johnson, 2011). The outcomes of developmental processes, rather than being inherently pre-specified, are probabilistic, because they are derived from a constellation of organismic and environmental constraints.

What constraints may interact so consistently to shape the emergence of common mechanisms for the specialized processing of others' actions in our species? A first set of constraints may be linked to the gradual development of an infant's own motor repertoire, which, as reviewed above, highly modulates the development of mirroring mechanisms.

An infant's own proprioceptive and sensorimotor experience, as along with limitations in its body movements, might constrain its perception of the surrounding environment, acting as a template that might match perceived actions. This idea might be in line with the associative learning explanation, as it posits that the kind of learning that produces mirror neurons occurs when there is correlated activation of sensory and motor neurons that are responsible for similar actions. Nevertheless, this process might also follow non-associative implicit and probabilistic learning mechanisms, such as statistical learning. This might explain why learning occurs in spite of the high variability of infant interactions with others, action scenes, action movements and so on. Statistical learning is a way of acquiring structure within continuous sensory environments. Initially shown to be involved in word segmentation, it has been demonstrated to be a general mechanism that operates across domains and species (Krogh, Vlach, & Johnson, 2012) and has recently been reported to operate in detecting regularities in action sequences (Monroy, Kaduk, Gerson, Hunnius, & Reid, 2015). Some authors hypothesize that infants' ability to extract regularities from streams of actions might be one of the mechanisms that help them to predict how actions will be executed without necessarily being able to perform those actions (Hunnius & Bekkering, 2014).

On the perceptual side, a second set of constraints may rely on early visual preferences. While the early bias newborns have for looking at faces is established in face processing literature (Johnson & Morton, 1991; Valenza, Simion, Cassia, & Umiltà, 1996), it might be important for developing a mirror system as well (Meltzoff & Moore, 1997). Evidence is accumulating in support of a visual preference for other relevant body parts. After birth, infants spend a great amount of their waking time looking at their own hands (White, Castle, & Held, 1964). Newborns move their hands significantly more when they can watch them (Van der Meer, 1997), and actively attempt to control arm movements to keep their hands visible (Von Hofsten, 2004). Two-day-olds visually discriminate between a hand moving towards or away from the body, looking longer at the hand movement directed away from the body and towards the external world (Craighero, Leo, Umiltà, & Simion, 2011). Additionally, neonates look longer at a biomechanically impossible hand closure compared with a possible one, suggesting that newborns are able to recognize the biomechanical properties of hand movements (Longhi *et al.*, 2015). Overall, these findings speak in favour of an early ability to recognize the hand as a salient body part and to process domain-relevant information related to hand actions.

Notably, it is matter of debate whether such early preferences are due to an inborn sensitivity to the hand shape, or are driven by prenatal sensorimotor experience. During pregnancy, foetuses acquire substantial sensorimotor experience of their hands. The majority of the hand movements of foetuses are directed towards own body parts or the uterine environment (Jakobovits, 2009). Foetuses also show smaller velocity peaks for movements directed towards their eyes and mouth or their twin (Castiello *et al.*, 2010; Zoia *et al.*, 2007). Given the relevance of developmental processes during the prenatal period, disentangling the relative role of genetic predispositions and environmental factors in humans is almost impracticable.

Overall, the evidence highlights that mirroring mechanisms, like other human specialized functions, may not be considered a phenomenon that can be studied by isolating the roles of motor and perceptual constraints and surrounding environment (Clark, 2007). From a developmental perspective, the limited perceptual abilities and motor control of newborns and infants restrict the potential complexity of stimulation available at each developmental stage, but have the advantage of filtering the accessible experiences, thus favouring a gradual increase in progressively complex representations,

as a result of an environment that is perceived as increasingly complex (Westermann *et al.*, 2007). Thus, infants pro-actively explore the environment instead of passively absorbing information (as in the empiricist explanation), selecting the experiences from which to learn and shaping their developmental pathways. Early sensitivities might guide their attention towards information relevant for action understanding, in turn bootstrapping the emerging mirror mechanisms.

Hypothesis 3: Mirroring mechanisms deriving from an experience-expectant process

Neuroconstructivist models about the development of highly specialized functions, such as language and face processing, posit that, rather than acting as independent mechanisms, genetic and environmental factors inextricably interact to cause developmental changes (Kadosh, 2011; Maurer & Werker, 2014). Specifically, it was suggested that the development of specialized human functions should be considered an *experience-expectant* process. This term refers to the development of abilities that (1) are common to all members of the human species, (2) depend on the exposure to certain experiences occurring over limited periods of time – that is, sensitive periods – and (3) rely on initial sensitivities and constraints that prepare infants for learning about aspects of their world that have adaptive significance (Greenough & Black, 1992; Greenough *et al.*, 1987). Experience-expectant processes take advantage of cortical plasticity and allow the fine-tuning of aspects of development that cannot proceed to optimum outcomes as a result of genetic or experiential factors working alone. Experience-expectant processes differ from experience-dependent processes; the latter are like acquiring expertise in adulthood, may contribute to explaining cultural and individual differences and can occur at any time, so that the timing of the experience is not critical for typical development (as in the empiricist explanation).

Is it possible to consider the development of mirror mechanisms to be an experience-expectant process? We can assume that it is adaptive for the human species to possess highly specialized abilities that allow them to immediately understand the actions of others. Although specific motor training in adults may modulate their activity, mirror mechanisms develop in all typically developing human beings, with characteristics specific to our own species compared with other primates (Rizzolatti & Craighero, 2004). Therefore, as for faces or language, it is likely that selection pressures have led to the genetic specification of neural tissue that has the *potential* to become specialized for mirror mechanisms, provided that appropriate and timely experience is available. In contrast to the view that the development of mirror mechanisms is an example of a general-purpose experience-dependent process, we propose that the timing of certain inputs during development is important for the typical development of the mirror system and that alterations occurring during sensitive periods might divert the normal course of its development (Karmiloff-Smith, 1998). Although evidence strongly suggests that both genetic and environmental factors play a role in the development of mirror mechanisms, literature still fails to specify what kind of experience is necessary, and when this experience needs to occur. In the face and language domains, deprivation or alteration of exposure to critical input in specific periods of development strongly affects the typical development of face and language processing (Maurer & Werker, 2014). Our hypothesis predicts that a similar process might also occur in the development of mirror mechanisms. A vital issue for future consideration is that we know very little about the existence of

different sensitive periods that affect the development of mirroring mechanisms in typical and atypical populations. Along this direction, recovery capacity from motor system impairments occurring early in life has been studied in children with congenital cerebral palsy (Buccino, 2014). Further research might explore the effects of impairments in early face recognition and hand gesture discrimination abilities on the typical development of mirror mechanisms. Indeed, Libertus and Needham (2014) recently highlighted the existence of a relationship between face preference and motor development in 3-month-old infants.

Action mirroring and action understanding

It is generally accepted that there is a relationship, independently from its causal direction, between the activation of the motor system during action perception and action understanding (e.g., Southgate, 2013). Also, consistent empirical findings suggest that action mirroring processes are involved in understanding of others' actions (e.g., Cattaneo *et al.*, 2011).

From a developmental perspective, behavioural evidence indicates that the ability to detect and attribute goals to actions gradually emerges during the first year of life (Cannon, Woodward, Gredebäck, von Hofsten, & Turek, 2012; Csibra, 2008; Kamewari, Kato, Kanda, Ishiguro, & Hiraki, 2005; Sommerville & Woodward, 2005). For instance, both 12-month-olds and adults visually anticipate the goal of a manual displacement action, while such ability is lacking in 6-month-olds, who track the observed action in a reactive manner (Falck-Ytter, Gredebäck, & von Hofsten, 2006).

It is thus well demonstrated that, from an early age, infants are capable to interpret the movements of others as goal-directed actions. However, the cognitive mechanisms underlying this ability and how the motor system is activated by simple observation of others' actions are still topics of hot debate, and different explanations have been offered so far. The *direct-matching* hypothesis (Rizzolatti, Fogassi, & Gallese, 2001) posits that an action is directly understood when the observer's motor system resonates in response to the observed action, via an embodied simulation and 'bottom-up' process. Accordingly, some propose that only actions for which infants have previously gathered sensorimotor experience will be interpreted as goal directed (e.g., Sommerville & Woodward, 2005). The *teleological reasoning* hypothesis (Csibra & Gergely, 2007) suggests that motor resonance is the result, rather than the cause, of action understanding. Specifically, the motor system is supposed to be activated by a 'top-down' process in which the observed action is evaluated and reconstructed in terms of goals and subgoals, and subsequently reproduced in the motor system through emulative processes (Csibra, 2007). Finally, within the recently revitalized *ideomotor theories* of cognition, it is proposed that repeated co-occurrence of an action and its effect would tie the activated motor program to the representation of the action effect, in a bidirectional association (Paulus, 2012). Specifically, own action-effect observation would allow the association between a motor code and an action effect. Subsequently, when another person performs a similar action, the perception automatically causes motor resonance as a consequence of the previously established action-effect association (Paulus, 2014). The activated effect representation modulates visual attention and facilitates the processing of corresponding information of a visual scene. Therefore, the role attributed to action mirroring in this model is only that of facilitating the processing of an action visual scene. A full understanding of an action requires higher-level cognitive abilities, such as the processing of intentions as well as the

social implications of the action (Paulus, 2012). In the following section, based on the previously stated hypotheses on action mirroring (i.e., narrowing, experience-expectant processes and constraints on development), we will present an integrative model that combines these apparently competing approaches within a neuroconstructivist developmental perspective.

Towards a neuroconstructivist model of action mirroring and action understanding

Given the inherent complexity of our environment, a powerful cognitive system should take advantage of both 'top-down' and 'bottom-up' processes for the processing of others' actions (Baldwin, 2005). Recent models about adult cognitive functioning state the inadequacy of the top-down versus bottom-up dichotomy and propose integrative frameworks that emphasize not only the role of stimulus- and cognitive-driven activation, but also of the effects of previously acquired experience (Awh, Belopolsky, & Theeuwes, 2012). Indeed, many researchers have suggested that, in human adults, action observation flexibly engages different neural systems, which play different but potentially complementary roles during the observation of actions (Cross *et al.*, 2011; Jeannerod, 2006; Keysers & Gazzola, 2007).

In this light, the neuroconstructivist explanation offers an interesting middle-ground view for interpreting and possibly guiding research on the development of mirroring mechanisms, as the emergence of motor resonance mechanisms that allow the immediate understanding of others' actions may be considered to be the result of a narrowing and experience-expectant process, which is driven by a number of motor and perceptual constraints.

Early predispositions to attend to movements of specific body parts (i.e., hands and faces) together with social motivation to interact with significant other people may help infants to comprehend the complexity they have to deal with after birth, selecting and *constraining* the relevant stimuli to which it is worth focus attention. Also, infants' understanding of the goals of others appears highly affected and *constrained* by the gradual emergence of their own perceptual and motor abilities. Six-month-olds who viewed actions that were more common in their own experience (i.e., feeding actions) visually anticipated the goal of the observed action (Kochukhova & Gredebäck, 2010). If 3-month-olds practiced picking up toys using sticky mittens, they became able to attribute a goal when observing a grasping action (Sommerville, Woodward, & Needham, 2005). Similarly, anticipatory looking behaviour of 6-month-olds in response to grasping actions was found to be related to their skills at reaching for objects (Ambrosini *et al.*, 2013; Daum & Gredebäck, 2011; Kanakogi & Itakura, 2011).

Yet, it is likely that infants first need to process the multiple dimensions of observed movements to construe the meaning of the action they are observing. Observed actions have to be reconstructed based on multiple features, such as familiarity (Gredebäck & Kochukhova, 2010), motivation (Paulus, 2014), efficiency (Southgate & Csibra, 2009), visual (Grossmann, Cross, Ticini, & Daum, 2013), auditory (Paulus *et al.*, 2012), emotional (Phillips *et al.*, 2002) and social cues (Fawcett & Gredebäck, 2013), as well as featural, configural and temporal information sources (Loucks & Sommerville, 2012b), which drive action representations distributed widely over cortical and subcortical areas.

Nonetheless, visuo-motor experience acquired during development together with attunement processes are proposed to shape infant perceptual-motor couplings, so that

the processing of specific actions *becomes* direct and automatized. As a result of a *narrowing process*, the understanding of highly experienced actions may occur bypassing 'top-down' and distributed activation, through the generation of a quicker and direct motor resonance response to perceived actions, made possible by mirror mechanisms (Figure 1). As recognized by Rizzolatti and Sinigaglia (2010), there is no doubt that, in some cases, understanding the motor behaviour of others might require mechanisms different from mirroring. Action understanding is a multilayer process involving different levels of representation, from the goal that drives a given chain of motor acts, to the attitudes (e.g., beliefs, desires) that explain the observed behaviour in terms of its plausible psychological reasons. Different from Rizzolatti and Sinigaglia (2010), we assume a developmental perspective, positing direct-matching mechanisms as gradually emerging from a narrowing process occurring during ontogenetic development. Indeed, narrowing is considered a domain-general process acting upon several knowledge domains (Scott *et al.*, 2007). We suggest that a similar process might subserve the action perception domain too. Specifically, we hypothesize that top-down processes are relevant mechanisms driving infants' understanding of others' actions and that observed actions have to be reconstructed based on identified goals and other significant features early in life. At a later stage, bottom-up mechanisms might start operating in response to those actions that have become familiar as a result of active and observational experiences responsible for the narrowing process.

Indeed, similar to action mirroring, the evidence highlights a gradual process of specialization and tuning of action understanding abilities. While 5-month-olds were shown to attribute goals to non-human agents (Luo & Baillargeon, 2005), 9-month-olds simulated the actions performed by mechanical claws to a lesser extent than those performed by human agents (Boyer, Pan, & Bertenthal, 2011). Fifteen- and 18-month-olds reproduced the outcomes of actions demonstrated by human actors (Meltzoff, 1995) and by human-like agents (Johnson, 2003; Johnson, Booth, & O'Hearn, 2001), but not by mechanical pincers. This developmental trajectory in the processing of actions performed by mechanical devices seems to indicate a progressive tuning towards human actions compared with the actions performed by both human and non-human agents.

A gradual narrowing process was also observed by researchers investigating the sources of information attended to when discriminating between visual actions. Specifically, 4-month-olds discriminated between changes in actions at the featural, configural and temporal information levels, while 10-month-olds and adults differentiated between changes at the featural level only. These findings indicate that younger infants are better able to discriminate between a wider range of action properties than older infants and even adults (Loucks & Sommerville, 2012a,b).

The neural counterpart of this process, which has yet to be thoroughly studied, is possibly reflected by the fact that, while younger infants activate a widespread and non-specific network in response to action observation, later in development-specific and localized regions are selectively activated. In this direction, increased activation of the right inferior frontal-pre-motor region was observed using functional near-infrared spectroscopy in 4-month-olds regardless of the familiarity of the agents (i.e., robot or human) performing an unfamiliar action (Grossmann *et al.*, 2013). Also, as recently outlined, infants' action experience affects early cortical specialization, as the degree of cortical activation, within the posterior superior temporal sulcus, to the perception of manual actions in 4- to 6-month-old infants correlates with their own level of fine motor skills (Lloyd-Fox, Wu, Richards, Elwell, & Johnson, 2015).
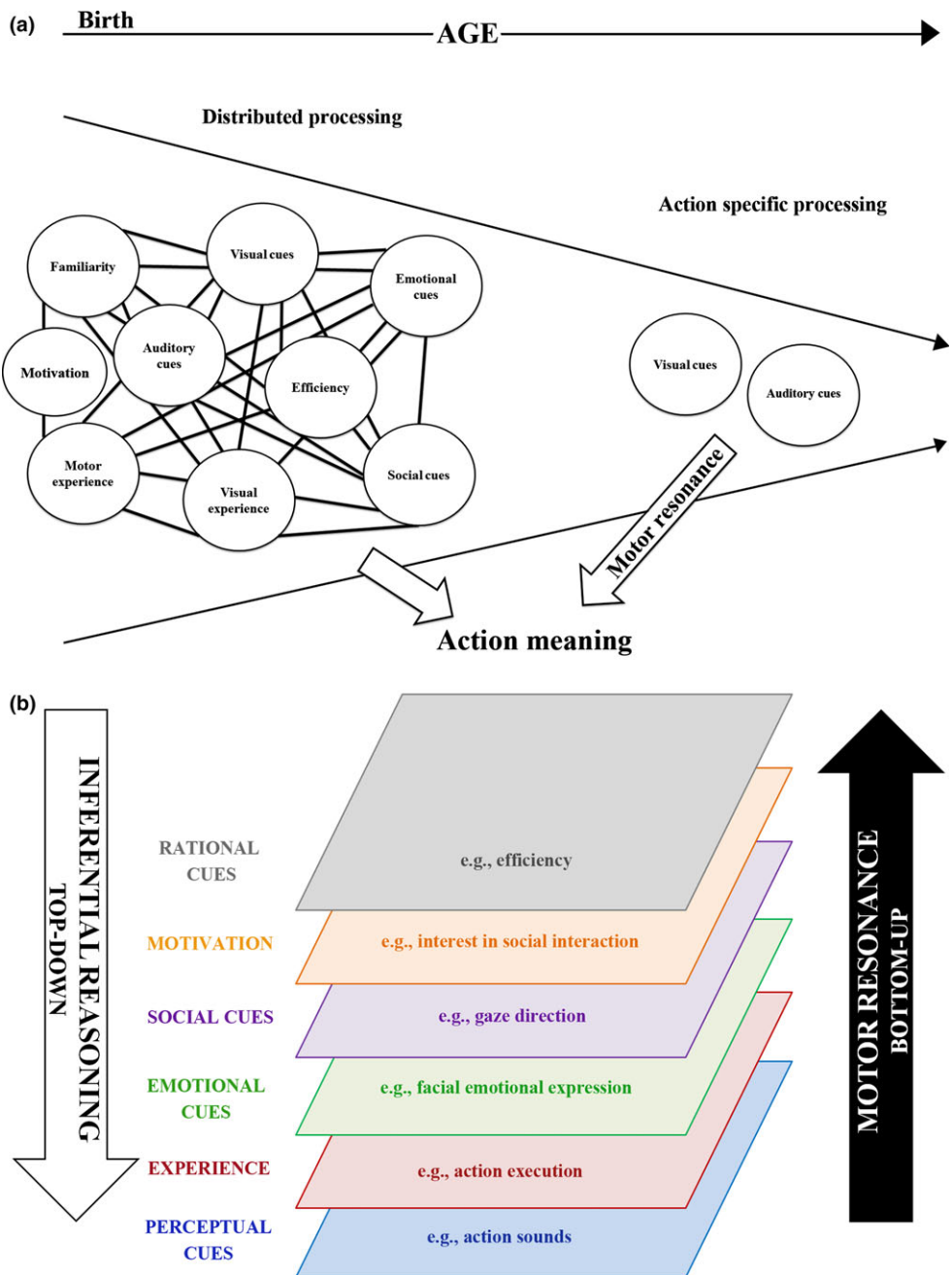
Figure 1. Schematic representation of the proposed integrative model displaying (a) the gradual attunement process (oblique arrows) that shapes mirroring mechanisms during development. Early in life action understanding requires an inferential and distributed processing. Acquired experience and narrowing processes gradually generate a direct motor resonance response. (b) The model posits the existence of a multilayer structure involved in action understanding, which considers the existence of an interplay between higher-level inferential and direct mirroring paths.

Direct activation of mirroring mechanisms does not exclude the involvement of higher cognitive functions at a different level of analysis, because inferential and direct-matching mechanisms should not be considered as mutually exclusive. In line with current views that distributed neural representations underlie domain-specific knowledge (Barsalou, Simmons, Barbey, & Wilson, 2003) and that in adults action observation may flexibly engage different and complementary neural systems (Cross *et al.*, 2011; Jeannerod, 2006; Keysers & Gazzola, 2007), our model states that an action scene might not correspond to a unique representation in our brain, but to a distributed representation of multiple dimensions in different layers, possibly involving the whole organism (Hutto, 2013). Understanding the actions of others may operate at multiple levels in a distributed and dynamic fashion. Thus, it is plausible that 'top-down' inferential processes and 'bottom-up' direct-matching processes interact, exchanging information to understand a given situation. Finally, within a multilevel model, we posit that action understanding can take advantage of different and non-competitive processes and we propose that the direct mirroring and higher-level inferential paths can be adaptively activated according to situational cues, for instance to face highly familiar or never experienced actions, respectively.

Conclusions

Several explanations have been proposed to answer the question about the origins and early developmental processes determining the emergence of mirroring mechanisms, and the debate is even more vigorous about the role of the motor system in action understanding. As a result of the limits and points of criticism deriving from the opposite theoretical frameworks, a novel account has been presented to interpret and possibly guide research on the development of mirroring mechanisms and to offer a middle-ground view on the debate about the development of action mirroring and action understanding capacities. Future research might further investigate the hypotheses put forward, examining the existence of different critical/sensitive periods that affect the development of mirroring mechanisms, possibly depending on the considered motor abilities.

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