



Review article

Developmental trajectory of interpersonal motor alignment: Positive social effects and link to social cognition

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ARTICLE INFO

Keywords:

Interpersonal motor alignment
Mimicry
Synchrony
Automatic imitation
Action observation
Social cognition
Development
Adolescence

ABSTRACT

Interpersonal motor alignment is a ubiquitous behavior in daily social life. It is a building block for higher social cognition, including empathy and mentalizing and promotes positive social effects. It can be observed as mimicry, synchrony and automatic imitation, to name a few. These phenomena rely on motor resonance processes, i.e., a direct link between the perception of an action and its execution. While a considerable literature debates its underlying mechanisms and measurement methods, the question of how motor alignment comes about and changes in ontogeny all the way until adulthood, is rarely discussed specifically. In this review we will focus on the link between interpersonal motor alignment, positive social effects and social cognition in infants, children, and adolescents, demonstrating that this link is present early on in development. Yet, in reviewing the existing literature pertaining to social psychology and developmental social cognitive neuroscience, we identify a knowledge gap regarding the healthy developmental changes in interpersonal motor alignment especially in adolescence.

1. Scope, definitions and why study interpersonal motor alignment

In our everyday social lives, we unconsciously and automatically align our behavior to the people around us. We define this interpersonal alignment as the reciprocal matching of behavior, posture, facial or vocal expression to the interaction partner. We propose to review the development of interpersonal motor alignment appearing as synchrony, mimicry or automatic imitation, the former two being ubiquitous in daily social life. We focus on interpersonal motor alignment that is automatic, spontaneous and mostly unconscious, as opposed to interpersonal coordination that is intentional and conscious, such as in cooperative tasks.

Synchrony refers to the temporally matched behaviors of interaction partners. Through temporal motor matching, it allows precise prediction of interactive behavior (Hove and Risen, 2009; Launay et al., 2016; Wiltermuth and Heath, 2009). Synchrony may include verbal and non-verbal communicative, as well as emotional behaviors (Leclère et al., 2014). In this review we focus on studies investigating the temporal and rhythmic matching of topographically isomorph and dynamic behaviors, such as during dance, but will also touch upon rhythmic vocal and musical synchrony, such as during singing and drumming. While

synchrony refers to simultaneous motor behavior, mimicry refers to the matching of behavior occurring with a slight temporal delay, of the order of 3–5 seconds (Chartrand and Bargh, 1999). This phenomenon has also been coined the *Chameleon-effect* (Chartrand and Bargh, 1999), alluding to the way chameleons change their colour to fit their environment. Automatic imitation on the other hand, is, with the exception of the kids' play "Simon says" that is prominent in different cultures and languages, mainly used as an experimental paradigm in cognitive psychology/neuroscience to assess underlying mechanisms of motor alignment (Brass et al., 2000). Automatic imitation is most often instantiated in a stimulus-response compatibility (SRC) paradigm (e.g., Brass et al., 2000; Kilner et al., 2003), in which observing an irrelevant movement interferes with target movement execution. If the irrelevant action matches the target movement, response execution is facilitated, while a mismatch requires inhibition of the perceived action representation to execute the target response and thus impairs execution. This paradigm has the advantage of high experimental controllability, implementation as a within-subject, repeated measures design and suitability for neuroscientific investigations, with, for example functional magnetic resonance imaging (fMRI) (e.g., Brass et al., 2005; Brass et al., 2009), electroencephalography (EEG) (e.g., Deschrijver et al., 2017; Rauchbauer et al., 2018), transcranial magnetic stimulation

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<https://doi.org/10.1016/j.neubiorev.2020.07.032>

Received 13 February 2020; Received in revised form 19 June 2020; Accepted 27 July 2020

Available online 09 August 2020

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(TMS) (e.g., Catmur et al., 2011; Catmur et al., 2007; Mengotti et al., 2013; Sowden and Catmur, 2015) or transcranial direct current stimulation (e.g., Santiesteban et al., 2012). In the developmental literature the majority of studies refer to the effect of motor interference between target movement and task-irrelevant simultaneous movement as “motor interference task”. In this article we use motor interference interchangeably with automatic imitation. Also, experimentally, automatic imitation is evidenced by recordings of brain activity in motor neuronal circuits during passive observation of others’ actions, without the task requirements of response execution, which we will review as action-observation studies, a special case of instantiation of interpersonal motor alignment.

These phenomena, synchrony, mimicry, automatic imitation and action observation, are thought to rely on motor resonance processes, i.e. a direct link between the execution and perception of an action (for review see Rizzolatti and Craighero, 2004). The perception-action link is modulated by the action repertoire and proficiency of the observer (Calvo-Merino et al., 2004) and is also presumably involved in action understanding and learning.

The investigation of the perception-action link is tightly related to discussions on the mirror neurons system. These neurons originally discovered in monkey’s ventral premotor cortex (F5) fire on observation and execution of the same action (for review see Rizzolatti and Craighero, 2004). A human mirror network has also been proposed (e.g., Brass and Heyes, 2005; Catmur et al., 2007; Keysers and Gazzola, 2010; Mukamel et al., 2010), which may provide a direct matching between our interacting partner’s actions and our own motor programs and thereby support motor resonance. While a mirror mechanism as a basis for action understanding has been criticized (Hickok, 2009), there is evidence for its participation in understanding actions in one’s own motor repertoire. This can occur even for recognition of actions performed by a different species, while behaviors outside one’s repertoire (e.g., barking) are instead mapped onto the visual and not the motor system (Buccino et al., 2004).

Yet motor resonance might not be the sole support for interpersonal motor alignment, which most often implies a tight temporal coupling between the interaction partner’s and one’s own movement. It may also involve brain mechanisms related to temporal processing (see e.g., Coull et al., 2011; Merchant et al., 2013), for detecting timing of events and rhythmic properties. There is a tight relationship between these brain circuits and neural networks implicated in motor processes, as evidenced also by the fact that action facilitates time estimation in adults and children (Monier et al., 2019). In particular, the striatum and the supplementary motor area have been shown to be involved in perceiving time as well as in producing timed motor actions, rhythmic sequences and coordination of motor actions (Coull et al., 2011; Merchant et al., 2013), and are thus likely to play a key role in interpersonal motor alignment. Yet, the interactions between motor resonance mechanisms and temporal processing may differ between synchrony, mimicry and automatic imitation given their specific reliance on precise timing.

From a developmental perspective, interpersonal motor alignment is tightly linked to the ongoing discussion of the origins of the human mirror mechanisms. Debated accounts range from completely innate mechanisms evolved through selection pressure (Meltzoff and Moore, 1997), to a sole product of associative sensorimotor learning (Keysers and Perrett, 2004; Oostenbroek et al., 2016), and experience (Catmur et al., 2007; Catmur et al., 2009; Heyes, 2011; Heyes et al., 2005; Ray and Heyes, 2011) with mixed-accounts in between (Farmer et al., 2018; Quadrelli and Turati, 2015). While it is not our goal to contribute directly to this discussion, we argue that a critical review of the literature on the development of interpersonal motor alignment and its link to the construction of social abilities across the lifespan is currently lacking in this debate. Yet, including developmental aspects not just at the beginning of life, but at all ages until adulthood, may advance apprehension of the underlying mechanisms of interpersonal motor

alignment. Considering the positive effects of interpersonal (motor) alignment, a deeper insight into its underlying processes at different stages of development across the lifespan, may offer a more nuanced, targeted insight.

1.1. Interpersonal motor alignment in adult studies

Synchrony and mimicry both have been suggested to promote positive social behaviors. Joint singing, for instance, has positive, and fast, “ice-breaking” (Pearce et al., 2015) effects on social bonding (Pearce et al., 2015; Weinstein et al., 2016). The accelerated positive effects of joint singing may be product of multimodal motor synchronization of laryngeal muscles and respiration patterns and the production and perception of the same sounds (Good and Russo, 2016). Relatedly, synchronized activation during joint laughter (Dunbar et al., 2011), physical activity, such as dance (Tarr et al., 2016) and rowing (Cohen et al., 2010), leads to similar cohesive group effects. Group synchrony may reinforce a group’s cooperative tendency (Reddish et al., 2013). A group moving together may become a collective social unit (Good and Russo, 2016) through boundary loss and getting into a “we”-mode (McNeill, 1997). But apart from (inter)active motor alignment, already the mere observation of interpersonal coordination enhances the perception of commitment to joint action (Michael et al., 2016), rapport (Miles et al., 2009), a feeling of unity (Lakens, 2010; Lakens and Stel, 2011), and of a shared goal and cohesiveness (Ip et al., 2006).

In line with this, mimicry has been suggested to enhance liking, social cohesion and prosocial behavior towards the interaction partner (Chartrand and Lakin, 2013; Chartrand et al., 2005; Duffy and Chartrand, 2015; Van Baaren et al., 2009). Prosociality after being mimicked may be enhanced towards the mimicking confederate, but moreover extends to an unknown experimenter and to charities (Duffy and Chartrand, 2015; Van Baaren et al., 2004; Van Baaren et al., 2009), as well as strangers on a street (Fischer-Lokou et al., 2011). Mimicry has thus been suggested to act as a “social glue” that may have an evolutionary function for establishing and maintaining social relations (Lakin et al., 2003) or to regain inclusion into a group (Lakin et al., 2008).

While some reports suggest that interpersonal motor alignment is enhanced towards in-, as compared to out-group members (e.g. Bourgeois and Hess, 2008; Yabar et al., 2006), studies show that the positive effects of interpersonal motor alignment extend to intergroup relations. Enhanced synchrony with an out-group member may reduce intergroup boundaries and support closeness (Miles et al., 2011), which may be mediated by an increased perception of interpersonal similarity through the display of interpersonal synchrony (Rabinowitch and Knafo-Noam, 2015; Valdesolo and DeSteno, 2011; Valdesolo et al., 2010). Likewise, mimicry increases sympathy, closeness and the perception of harmonious interaction with an virtual avatar posing as an out-group member (Hasler et al., 2014). Synchronous and mimicry behavior may enhance perceived self-other overlap between self-generated and other-produced movements. A constant matching between interactive movements may enforce an overlap in the shared representations of perception and execution of an action. This self-other overlap may lead to social cohesion (Lang et al., 2017; Tarr et al., 2014), extending also to out-group members and contribute to overcoming group boundaries. The positive intergroup effects of interpersonal motor alignment have also been demonstrated using the tightly controlled automatic imitation tasks (Gleibs et al., 2016; Marsh et al., 2016; Rauchbauer et al., 2015; Rauchbauer et al., 2016).

It has been suggested that automatic imitation measures covert (Cracco et al., 2018; Cracco and Brass, 2019; Heyes, 2011), and to some extent overt, imitation (Cracco and Brass, 2019), but this has recently been a matter of debate (cf. Cracco and Brass, 2019; Ramsey, 2018). While mimicry and automatic imitation may not be correlated (Genschow et al., 2017), being mimicked may reduce inhibitory mechanisms of automatic imitation (Rauchbauer et al., 2020), potentially indicating an interrelationship between the two phenomena. In any

Table 1
 Experimental studies on interpersonal motor alignment on infants. Systematic search of studies on interpersonal motor alignment in infants (age < 30 months) The table shows references with authors and year of publication, the type of interpersonal motor alignment (IMA), main findings and method used; * denotes studies mentioned in the text, EEG = electroencephalography, (f)NIRS = (functional) near-infrared spectroscopy, EMG = electromyography, n = number of participants (in the final sample of analyzed data).

Authors	IMA	Main finding	Method	Age in months, sample size
*Cannon et al., 2015	Action observation	Mu suppression (posterior sites) correlated with motor skills.	EEG	8–10 months, n = 21
*Carpenier et al., 2013	Mimicry	Being mimicked increases help to experimenter and stranger	Behavior	18 months, n = 48
*Cirelli et al., 2014	Synchrony	More helping towards an adult moving in synchrony than asynchronously or a stranger	Behavior	14 months, n = 48
*Cirelli et al. (2016)	Synchrony	Prosocial effect of synchrony transfers to affiliate	Behavior	14 months, n = 48
*Debnath et al., 2019	Action observation	Mu suppression at central location and connectivity central-occipital	EEG	9 months, n = 46
de Klerk et al., 2015	Action observation	Mu suppression independent of experience (walking)	EEG	7–9 months, n = 31
*de Klerk et al., 2019a	Mimicry (face and hand)	More facial mimicry in infants whose mother imitate more; no correlation for hand mimicry	Behavior, EMG	4 months, n = 27
de Klerk et al., 2019b	Mimicry (face)	More mimicry and temporal cortex activity for videos of same-language (compared to foreign) speaking actor	fNIRS, EMG	11 months, n = 55
de Klerk et al., 2018	Mimicry	Facial mimicry increases with direct gaze; associated with superior temporal activity.	fNIRS, EMG	4 months, n = 60
Fawcett and Liszkowski, 2012	Mimicry	Being mimicked or mimicking spontaneously increases play initiation with adults	Behavior	18 months, n = 32
Filippi et al., 2016	Action observation	Mu suppression predicts subsequent goal imitation	EEG	6–8 months, n = 36
*Grossmann et al., 2013	Action observation	Premotor and temporal cortex activation when watching human and robot-like movements	fNIRS	4 months, n = 15
Isomura and Nakano, 2016	Mimicry	Mimicry only for audio-visual (but not unimodal) stimuli (emotional face)	Behavior, EMG	4–5 months, n = 15
*Jones, 2007	Mimicry – Automatic imitation	Encouraged imitation of parents actions appears slowly with age. dependent on behavior	Behavior	6–20 months, n = 162
Kaiser et al., 2017	Mimicry	Face mimicry dependent on emotion in 7 m. old; likely to include evaluative processes	Behavior, EMG	4 months, n = 27; 7 months, n = 24
*Langeloh et al., 2018	Action observation	Mu suppression stronger for unusual than usual actions	EEG	12 months, n = 42
*Lloyd-Fox et al., 2015	Action observation	Temporal cortex activation correlates with fine motor skills (grasp and lift)	fNIRS	4–6 months, n = 24
*Marshall and Meltzoff, 2011	Action observation	Mu suppression(fronto central) when watching live actions	EEG	14 months, n = 38
*Montiroso et al., 2019	Action observation	Mu suppression (frontal parietal) when watching live actions	EEG	14 months, n = 33
*Oostenbroek et al., 2016	Imitation	No spontaneous initiation face and hand movements	Behavior	Newborn – 2months, n = 106
Pratt et al., 2015	Synchrony	Mother child synchrony in face to face interaction associated with stress reduction depending on temperament.	Behavior	4–6 months, n = 132
*Rayson et al., 2016	Action observation	Mu suppression (central; bilateral) when watching videos of facial movements	EEG	30 months, n = 17
*Reid et al., 2011	Action observation	Mu suppression only when observing actions that engage the child.	EEG	14 months, n = 10
Ruysschaert et al., 2013	Action observation	Mu suppression for live but not video stimuli.	EEG	18–36 months, n = 34
*Saby et al., 2012	Action observation	Mu suppression greater for actions that match action just executed by the infant	EEG	14 months, n = 16
Saby et al., 2013	Action observation	Motor activity during execution and observation, more in live setting than video	EEG	14 months, n = 32
*Shimada and Hiraki, 2006	Action observation	Being mimicked increases tool-use learning by observation.	fNIRS	6–7 months, n = 13
*Somogyi and Esseily, 2014	Mimicry	Mu suppression starting before onset of observed movement.	Behavior	16 months, n = 48
*Southgate et al., 2009	Action observation	Mu suppression stronger for extraordinary actions	EEG	9 months, n = 15
*Stapel et al., 2010	Action observation	12 months-old but not 9 months old prefer social character (but not object) that have moved synchronously with them	EEG	12 months, n = 12
*Tunçgenç et al., 2015	Synchrony	Spontaneous imitation more likely when watching peers than older children or adults	Behavior	9 months, n = 41; 12 months, n = 40
Upshaw et al., 2016	Action observation	Mu suppression during observation related to grip strength	EEG	12 months, n = 12
Vacaru et al., 2019	Mimicry (face)	Spontaneous mimicry of face pictures. Effect of attachment style, not inhibitory control	Behavior, EMG	3 months, n = 42
*Virji-Babul et al., 2012	Action observation	Mu suppression when watching videos of reaching, walking or object motion	EEG	4–11 months, n = 14
*Wairayn et al., 2013	Action observation	Mu suppression for object-directed and mimicked actions	EEG	18–30, n = 17
*Yoo et al., 2015	Action observation	Mu suppression during observation of grasp-with-tool actions.	EEG	9 months, n = 26; 12 months, n = 34
*Zmyj et al., 2012	Imitation	Spontaneous imitation more likely when watching peers than older children or adults	Behavior	14 months, n = 36

Table 2
 Experimental studies on interpersonal motor alignment on children and pre-adolescents. Result from a systematic search of studies indexed on Pubmed on interpersonal motor alignment in children (age 2.5–12 years). The table shows references with authors and year of publication, the type of interpersonal motor alignment (IMA), main findings and method used; * denotes studies mentioned in the text, AON = action observation network, EEG = electroencephalography, ERP = event-related brain potential, (f)NIRS = (functional) near-infrared spectroscopy, EMG = electromyography, n = number of participants (in the final sample of analyzed data).

Authors	IMA	Main finding	Method	Age in years, sample size
Berchio et al., 2014	Action observation	Ventral and dorsal fronto-parietal circuits recruited at different time	EEG (ERP, high density)	10, n = 12
*Bernier et al., 2013	Action Observation	Mu suppression in most children (hand actions); correlated to face imitation abilities	EEG	5–7, n = 19
*Biagi et al., 2016	Action observation	Same network as in adults but more variability	fMRI	7–15, n = 12
*Brunsdon et al., 2020	Action observation	Increases mu and beta suppression with age throughout adolescence	EEG	10–86, n = 301
Bryant and Cuevas, 2019	Action observation	Mu, but not beta, suppression for observation of tool use; independent of experience	EEG	3–6, n = 21
Bureau et al., 2014	Synchrony	Greater dyadic synchrony with mother during free play. Linked to attachment quality	Behavior	3.5–4 n = 107
*Cochin et al., 2001	Action observation	Mu suppression left central theta band. No age effect	EEG	2–8, n = 30
Deschamps et al., 2015	Action observation	Mimicry of all expressions (face)	EMG	6–7, n = 27
*Eismond et al., 2017	Action observation	No age effect for mu suppression when watching or doing hand drawing	EEG	4–14, n = 53
Endeijck et al., 2017	Action observation	Mu and beta power increase watching action videos; correlated with peer cooperation	EEG	4.5, n = 29
*Fecteau et al., 2004	Action observation	Mu desynchronization over sensorimotor cortex during observation (live) and execution	Subdural electrodes	3, n = 1
*Good and Russo, 2016	Synchrony	Group singing enhances prosociality	Behavior	7, n = 50
*Grosbras et al., 2007	Action observation	Functional connectivity within AON related to resistance to peer influence	fMRI	10, n = 46
Helt et al., 2010	Mimicry	Contagious yawning frequency increases until 4	Behavior	1–15, n = 186
*Kajume et al., 2013	Action observation	Ventral premotor activity during observation and imitation of hand actions	fNIRS	9–13, n = 6
*Kirschner and Tomasello, 2009	Synchrony	Higher synchrony with adult drummer than with drumming machine	Behavior	2.5–4.5, n = 36
*Kirschner and Tomasello, 2010	Synchrony	Joint singing or dancing enhances helping behavior	Behavior	4–5, n = 96
Kleinspehn-Ammerlahn et al., 2011	Synchrony	Better (instructed) synchrony with age and with an older partner	Behavior	5, n = 18; 12, n = 18
*Lepage and Théoret, 2006	Action observation	Mu suppression for observation (live) and execution object-directed actions. No age effect	EEG	4.5–11, n = 18
Liao et al., 2015	Action observation	Mu (6–9 Hz) and beta (15–18Hz) suppression when watching mother's action	EEG	3.5, n = 11
Lust et al., 2019	Action observation	Mu suppression stronger during observation to imitate vs in order to detect oddball	EEG	9–13, n = 15
*Marshall et al., 2010	Automatic Imitation	Interference (motor contagion) stronger when observing a peer than an adult.	Behavior	4, n = 25
Martineau et al., 2008	Action observation	Mu suppression in central, frontal and temporal locations	EEG	5–7.5, n = 14
*Martineau and Cochon, 2003	Action observation	Decrease theta power in theta frequency band when watching videos human movement	EEG	2.5–7.5, n = 34
Meyer et al., 2011	Action observation	Mu and beta suppression during observation while engaged in a joint action game	EEG	3, n = 7
*Morales et al., 2019	Action observation	Similar network as in adults. Less activation anterior parietal	fMRI	7–10, n = 21
Nishimura et al., 2018	Action observation	Mu suppression during observation weaker than in adults and less in allocentric compared to egocentric configuration	EEG	8–12, n = 28
Nobusako et al., 2018	Automatic imitation	Effect of congruency on trajectory when drawing on tablet in front of experimenter; No age effect	Behavior	1.5–7, n = 42
Oberman et al., 2008	Action observation	Mu (8–13 Hz) for familiar and stranger hand actions	EEG	8–12, n = 13
*Oberman et al., 2013	Action observation	Mu suppression during observation (not execution) gets stronger with age	EEG	6–17, n = 51
*Ohnishi et al., 2004	Action observation	Same network as observed in adult studies	fMRI	7–10, n = 11
O'Sullivan et al., 2018	Automatic imitation	Correct movement and reaction time effects (live). No age effect	Behavior	3–7, n = 72
*Rabinowitch and Knafo-Noam, 2015	Synchrony	Child-child synchronous rhythmic interaction increases feeling of closeness	Behavior	8–9, n = 148
*Rabinowitch and Meltzoff, 2017a	Synchrony	Synchronous and asynchronous sway increases sharing	Behavior	4, n = 162
*Rabinowitch and Meltzoff, 2017b	Synchrony	Synchronization during swing sway increases cooperation and give behavior	Behavior	4, n = 162
*Reindl et al., 2018	Brain synchrony	Parent-child prefrontal synchrony during cooperative game; predictive of performance	fNIRS hyperscanning	5–9, n = 33
Ruysschaert et al., 2014	Action observation	Mu (9Hz) suppression during observation of goal directed and pantomime movement	EEG	2–5.5, n = 19
*Saby et al., 2011	Automatic Imitation	Observed movement interference on line tracing depends on expectancy on biological motion	Behavior	4–5, n = 61
*Shaw et al., 2011b	Action observation	Same network as in adults studies. Small gender-dependent age effects in intensity and extent	fMRI	10–13 (longitudinal), n = 65
*Shaw et al., 2011a	Action observation	Gender dependent effect of emotion depicted in the observed action on AON activity	fMRI	10–13 (longitudinal), n = 65
Simpson and Carroll, 2014	Automatic imitation	Great difficulty (60 % correct) in performing action different from experimenter	Behavior	3–4, n = 24
Su et al., 2020	Synchrony – Action Observation	Less synchrony with experimenter in children. No age difference for brain activity: STS for observation. Right STS, IPL and IFG for synchronized behavior.	fNIRS, Behavior	10, n = 17; 22, n = 15
*Tuncgenç and Cohen, 2018	Synchrony	More helping behavior after synchronous play	Behavior	4–6 n = 4 × 19
*van Schaik et al., 2016w	Automatic Imitation	More interference for out-group adult	Behavior	4–6, n = 65
van Schaik and Humnius, 2016v	Mimicry	More mimicry (head and hand movement) of videos of in-group adults	Behavior	3, n = 25; 4–6, n = 40

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Table 2 (continued)

Authors	IMA	Main finding	Method	Age in years, sample size
Van Schaik and Hunnius, 2018	Mimicry	No mimicry when watching storytelling videos of experimenters with positive or negative interaction	Behavior	5, n = 20
Vink et al., 2017	Synchrony	More postural sway synchrony in pairs of children with higher popularity	Behavior	9–13, n = 392
Xavier et al., 2018	Synchrony	Improvement with age in instructed synchronization of movement and posture with virtual character	Behavior	6–19, n = 38
*Yu and Kushnir, 2014	Mimicry & Imitation	Only 2 years old are influenced by mimicry for subsequent imitation tasks	Behavior	Exp 1: 2 & 4, n = 36 Exp 2: 2, n = 12

case, automatic imitation tasks allow investigators to test a variety of modulatory factors in controlled settings using both behavioral and neuroscientific methods. Thereby they have provided evidence that interpersonal motor alignment is modulated by social context, like group membership (Gleibs et al., 2016; Marsh et al., 2016; Rauchbauer et al., 2015; Rauchbauer et al., 2016), social contagion and group size (Cracco and Brass, 2018a, 2018b), eye-contact (Marsh et al., 2016; Wang et al., 2011), and emotional facial stimuli (Butler et al., 2016) (see also for meta analyses: Cracco et al., 2018). They may also have the potential to contribute to identifying the factors that link interpersonal motor alignment and positive social behaviors.

Divergent accounts suggest that increased social closeness and helping behavior may either rely on topographically isomorphic body movements (Majdandžić et al., 2016), whereas other reports suggest a role of perceived contingency (i.e., predictive relationship) of one’s own and the interaction partner’s movements, rather than on their similarity (i.e., topographic isomorphism) (Catmur and Heyes, 2013). Yet again, other accounts suggest that social affiliation may not only be linked to high contingency, but also high contiguity (i.e., temporal proximity) of movements (Dignath et al., 2018) and effector matching (Sparenberg et al., 2012).

Moreover, both synchronous movements and exertion have been shown to induce beneficial social effects (Tarr et al., 2015). Similarly, the choice of control condition in a mimicry or synchrony induction could potentially influence social-cognitive variables. While prominent studies on mimicry have used control conditions without any movement (e.g., Chartrand and Bargh, 1999; Van Baaren et al., 2004), other studies have used Anti-Mimicry conditions (Dalton et al., 2010; Finkel et al., 2006; Kühn et al., 2010; Rauchbauer et al., 2020). In an Anti-Mimicry control condition, the confederate’s movements will be topographically misaligned to the participant’s, as compared to the Mimicry condition in which they are aligned. A control condition without movement may itself evoke negative social effects due to perceiving the interaction partner uninterested and passive. Conversely, an Anti-Mimicry condition may also induce positive effects itself in case of perceived temporal contingency (Catmur and Heyes, 2013) or high exertion (Tarr et al., 2015) of movements. Thus, the mechanisms by which mimicry and synchrony may induce positive social-cognitive effects may not be entirely clear yet and lead to divergent results. As such, it has recently been suggested that being mimicked by topographically isomorph postures as compared to an Anti-Mimicry condition, does not influence experienced social cohesion with the confederate, measured with a rating scale (Rauchbauer et al., 2020). Thus, there are certain contradictions in the literature of interpersonal motor alignment, which may require in-depth analysis. To date it remains unclear as to which conditions and mechanisms may give rise to which positive social-cognitive effects via synchrony or mimicry. For example, while mimicry seems to evoke a kind of generalized prosociality, synchronous behavior may rather evoke directed prosociality (Cirelli, 2018). However, some studies have demonstrated that also synchrony induces generalized prosocial behavior (Reddish et al., 2014; Reddish et al., 2016).

The aforementioned studies rely only on adult populations. Yet, interpersonal motor alignment is pertinent throughout ontogeny and may play an important part of a healthy social life, as a building block for higher social cognition, including empathy. Indeed inter-individual differences in experience of and ability for interpersonal motor alignment early in infancy is associated with empathic abilities in adolescence as well as with the ability to engage in intimate relationships across the lifespan (Feldman, 2007b, 2007c), suggesting a protective buffering role against psychosocial maladjustment. The “motor theory of empathy” suggests that human mirror mechanisms may mediate the understanding of others’ intentions and feelings (Rizzolatti and Fadiga, 2008) and that empathy may originate from the perception-action link (Jacoboni, 2009; Leslie et al., 2004). As such, action understanding may play a role in feeling emotions and empathizing with others (Carr et al., 2003). Yet, this theory has also been criticized,

Table 3
Experimental studies on interpersonal motor alignment on adolescents (13–17 years). Result from a systematic search of studies indexed on Pubmed on interpersonal motor alignment in adolescents. The table shows references with authors and year of publication, the type of interpersonal motor alignment (IMA), main findings and method used; * denotes studies mentioned in the text, EEG = electroencephalography, EMG = electromyography, fMRI = functional magnetic resonance imaging, IFG = inferior frontal gyrus, MTG = middle temporal gyrus, SMG = supramarginal gyrus, n = number of participants (in the final sample of analyzed data).

Authors	IMA	Main finding	Method	Age in years, sample size
Arduzzi et al., 2014	Mimicry (face)	More spontaneous mimicry of videos of facial expressions of peers	Behavior, EMG	15–19, n = 20
*Bevilacqua et al., 2019	Brain synchrony	No correlation between student-student and student-teacher synchrony and memory retention	EEG hyperscanning	16–18, n = 12
*Brunsdon et al., 2020	Action observation	Increases mu and beta suppression with age throughout adolescence	EEG	10–86, n = 301
*Cook and Bird, 2011	Automatic imitation	Congruency effect similar to adults; modulated by social priming in adults only.	Behavior	13, n = 34 Adults n = 56
*Dikker et al., 2017	Brain synchrony	Intersubject brain-to-brain synchrony in classroom modulated by closeness and shared attention.	EEG hyperscanning	17–18, n = 12
Fitzpatrick et al., 2016	Synchrony	Spontaneous phase entrainment with parent during pendulum swing	Behavior	12–16, n = 9
Fourie et al., 2020	Action observation	AON activity stronger with age and higher for communicative gestures in IFG and MTG	fMRI	9.5–17, n = 16
Gordon et al., 2020	Automatic imitation	Strong effect, modulated by block congruency rate	Behavior	14–24 n = 50
*Oberman et al., 2013	Action observation	Mu suppression during observation but not executions increases with age	EEG	6–17, n = 51
Pokorny et al., 2015	Action observation	Same network as in adults studies. Effect of object presence in IFG and SMF	fMRI	9–17, n = 18
Xavier et al., 2018	Synchrony	Improvement with age in instructed synchronization of movement and posture with virtual character	Behavior	6–19, n = 38
*Wadsworth et al., 2017	Imitation	Online Instructed imitation of hand postures; AON activity except in STS	fMRI	8–17, n = 15

arguing that contrary to previously mentioned findings, empathy does not necessarily involve the activation of the mirror neuron system (MNS) (De Vignemont and Singer, 2006), or that its involvement may depend on the specific form of empathy (Baird et al., 2011).

Regardless of this debate, studies show that right after birth, social contingencies in the form of multimodal responses by the mother to the infant’s signals, and contingency detection on the side of the infant, aid to form reliable reciprocal interactions. Synchronous interactions, starting with caregiver-infant interactions, may provide a buffer against psychosocial maladjustment, shape empathic capacities in adolescents and lay the basis for engagement in intimate relationships across the lifespan (Feldman, 2007b, 2007c). Therefore, it is important to integrate the ontogenetic dimension while building accounts of these functions during typical and atypical developments.

In the next sections we review existing behavioral and neuroimaging research on synchrony, mimicry and automatic imitation in infants, children and adolescents. For this we conducted a systematic search on Pubmed (<https://pubmed.ncbi.nlm.nih.gov/>; as of 15 May 2020), presented in Tables 1–3, and analyzed the main findings. Keywords included (Infant OR Development) AND (Mimicry OR Synchrony OR Automatic Imitation OR Action Observation) AND (experiment OR EEG OR fMRI OR fNIRS OR EEG). Then results were filtered to select only the studies that focused on interpersonal motor alignment as we have circumscribed above, in particular excluding experiments on instructed or delayed imitation. We also excluded studies that concerned only atypical populations or provided only qualitative data. This list, while probably not exhaustive due to limitations of the search algorithm, provides a panorama of the state of the research in this domain so far. We analyzed the main findings with regards to the nature of interpersonal motor alignment and its relationships with other social behaviors, on the one hand, and its neural mechanisms, on the other hand, at different ages.

2. Investigation of interpersonal motor alignment, its positive social effects and link to social cognition during infancy, childhood and adolescence

2.1. Synchrony

Humans may be biologically prepared for coordinated interaction due to their responsiveness to rhythmical information and build-in tendency to detect contingencies (Feldman, 2007b). A recent review suggests that the establishment of interpersonal synchrony in reciprocal interactions is supported by adults’ rhythmical information to their infants (Markova et al., 2019). These rhythms are often spontaneously displayed by caregivers in the form of affective touch or singing to aid the infant’s affect regulation (Provasi et al., 2014). The caregiver’s adaptive signals to the newborn’s behavior form social contingencies, which the infant readily detects. These interpersonal mechanisms appearing in the first months of life may be multimodal precursors for synchronous interactions, including, apart from movements, vocalizations, gaze, touch, affect, position or proximity to each other. As the infant grows, the time lag between behavior and response diminishes and social contingencies develop into synchronous behaviors (Feldman, 2007b, 2007c). A longitudinal study points towards crucial positive long-term effects of socially contingent and synchronous interactions. Affective synchrony in mother-infant interaction from three and nine months of age predicted self-regulatory capabilities in two, four- and six-year olds. The same study also found that synchronous mother-infant interactions at three months of age predicted empathic abilities in thirteen-year old adolescents (Feldman, 2007a).

Apart from interactions with their primary caregiver, 12- and 14-month-old infants already use interpersonal movement information to guide social expectations. As such they attend to and interpret interpersonal synchronous and asynchronous behavior in a socially meaningful way (Cirelli, 2018; Fawcett and Tunçgenç, 2017). They seem to

prefer synchronously moving partners and show spontaneous helping behavior towards them and their affiliates (Cirelli et al., 2014; Cirelli et al., 2016; Tunçgenç et al., 2015). Even more so, when observing asynchronous dyadic interactions, infants believe the interaction partners to be nonaffiliates (Cirelli et al., 2018). This suggests that they can infer third-party affiliation on the basis of synchrony (Cirelli, 2018; Fawcett and Tunçgenç, 2017).

Synchrony, as a social signal per se, may be a cue for self-similarity from the beginning of life on (Leclère et al., 2014; Xavier et al., 2016), increasing prosocial behavior and encouraging empathy and affiliation (for review see Cirelli, 2018). In four-year-old children, synchronous interactions of only three minutes may already lead to enhanced peer cooperation. In children of eight to nine years of age they enhance closeness and feelings of similarity (Rabinowitch and Knafo-Noam, 2015; Rabinowitch and Meltzoff, 2017a). These positive effects extend from synchrony in direct interaction to joint music making and rhythmic synchrony. Children synchronize drumming with higher accuracy in a social condition, which elicits cooperative behavior and fairness (Kirschner and Tomasello, 2009, 2010; Rabinowitch and Meltzoff, 2017a). Also cooperative singing with peers, as reported for adults (Pearce et al., 2015), increases group cooperation in children of seven to eight years more than art or competitive games (Good and Russo, 2016). Furthermore, the positive effects of synchronous singing have been reported to contribute to feelings of social inclusion in refugee children (Marsh, 2017; Marsh and Dieckmann, 2017). This suggests, that singing in synchrony, just as moving in synchrony (Tunçgenç and Cohen, 2016) or joint music making (Marsh, 2012, 2017), may support the establishment of a collective group membership by forging intergroup bonds.

In summary, synchronous behaviors can be observed, in different forms, throughout infancy and childhood (for a list of experimental studies on interpersonal motor alignment in developmental population see Tables 1–3). First mainly restricted to caregivers, they extend to peer relations and can also be recognized in other dyads during observation. In all cases the ability to engage in synchronous behavior has positive prosocial outcomes especially with regards to interpersonal affiliation, similarly to what we have discussed in adults.

2.2. Mimicry, conscious and automatic imitation

Interpersonal motor alignment in neonates has been evidenced by seminal studies showing imitative hand opening and mouth protrusion movements (Meltzoff and Moore, 1997). This finding has led to an ongoing debate on whether spontaneous imitation is innate or not (e.g., Anisfeld, 1996; Jones, 2017; Kennedy-Costantini et al., 2017; Keven and Akins, 2017; Libertus et al., 2017; Meltzoff, 2017; Meltzoff et al., 2018; Oostenbroek et al., 2016). Alternatively, it has been suggested that imitation is learned through an associative learning sequence (Catmur et al., 2009), Hebbian learning (Keysers and Perrett, 2004) and correlated sensorimotor experiences, forming perception-action couplings through interaction with the primary caregiver (de Klerk et al., 2019a). As mentioned above, it is not our aim to contribute to this discussion in the present article, but rather to summarize facts about interpersonal motor alignment and their social correlates at different ages.

A large corpus of work shows that, during the first two years of life, infants faithfully imitate adults actions or just their goal (social or instrumental) in a variety of contexts (Yu and Kushnir, 2014). Children of pre-school age imitate not only causally relevant, but also irrelevant actions (i.e. sequences of movements that are not necessary to achieve the desired goal). This “over-imitation” (e.g., Nielsen and Blank, 2011; Over and Carpenter, 2012, 2013), may be an important learning mechanism to acquire cultural expertise. It seems to also have social reasons, such as the identification with a model and the social group in general. It may occur through social pressure (Over and Carpenter, 2012), but can also be used to overcome in-group ostracism (Over and

Carpenter, 2009; Watson-Jones et al., 2016). The dual role of imitation, for social learning and for establishing group cohesion is supported by studies showing that 14-month-olds are more likely to imitate communicative gestures and familiar actions performed by same-age infants, than when they are performed by older children and adults (Zmyj et al., 2012). Nevertheless, in a context when they are presented with a novel object, they are more likely to reproduce the action that they have seen an adults perform on this object (Zmyj et al., 2011). This suggests that infants and toddlers may more likely align their behavior to that of an adult role-model in a learning context. In an affiliative context though it seems that children would preferentially imitate their peers, potentially to enhance group cohesion. Similarly, having been mimicked by an adult, 14–18-month-olds learned better by observation (Somogyi and Esseily, 2014), and were more prone to help this adult (Over and Carpenter, 2013). This prosocial behavior can also extend to a stranger (Carpenter et al., 2013). This suggests that being mimicked may evoke a generalized prosociality (Cirelli, 2018).

The positive effects of interpersonal motor alignment throughout development are not only shown during imitation, mimicry and synchrony, but also in the more experimental environment of automatic imitation. In motor interference tasks, children are asked to perform straight lines in a vertical or horizontal movement on a tablet computer screen using a stylus, while an interaction partner performs a congruent or incongruent drawing movement (Marshall et al., 2010; Saby et al., 2011; van Schaik et al., 2016v). Using this task, automatic imitation was increased in four- to six-year-olds when interacting with an out-group member (van Schaik et al., 2016). This suggests, in line with adult studies (Rauchbauer et al., 2016), that even during automatic imitation the regulation of interpersonal motor alignment may be used to overcome intergroup differences. Also, 4-year-old children show a greater motor interference effect in interaction with peers, rather than adults (Marshall et al., 2010), in line with the studies mentioned above on imitation (Zmyj et al., 2012, 2011). Thus, already during childhood, group membership seems to influence the perception-action link. This is also demonstrated in a study with children of four and five years of age in which automatic imitation is modulated according to animacy beliefs of an interaction puppet (Saby et al., 2011). Yet, a recent meta-analysis suggested that automatic imitation may not be sensitive to animacy beliefs (Cracco et al., 2018).

Group membership may influence interpersonal motor alignment via top-down modulation. For instance, it has been suggested that during conscious imitation neural activity in a wide range of brain areas, and not only early visual areas, is modulated by the race of the model (Losin et al., 2012). This may be driven by socially learned associations concerning race, rather than self-similarity (Losin et al., 2014). This seems in line with motivational theories of automatic imitation, such as the social top-down response modulation account (STORM; Wang and Hamilton, 2012). These accounts suggest that the motivation to affiliate (the wish to be liked by the interaction partner) may increase imitation. This has also been suggested to influence mimicry, via a strengthened the perception-action link (Chartrand et al., 2005; Lakin and Chartrand, 2003; Lakin et al., 2008). Group membership may be one salient social factor activating affiliative motivation. High motivation to affiliate with the in-group has been shown to moderate the influence of group membership during imitation (Genschow and Schindler, 2016). Other studies have found higher imitation for out-group members, which could suggest affiliative motivation for appeasement (Rauchbauer et al., 2015, Rauchbauer et al., 2016). Contrary to these studies conducted in adult samples, social modulation of automatic imitation may be absent in adolescents. While automatic imitation has been observed to the same level as in adults in adolescents, no modulation by pro-social priming has been observed (Cook and Bird, 2011). This would indicate that the adaptability and social function of interpersonal motor alignment is still fine tuning in adolescence.

Apart from Cook and Bird (2011) and as pointed in the previous

sections, to this date, investigation of interpersonal motor alignment in adolescence is scarce (see Table 3). This may be due to the assumption of social cognitive maturity by mid-childhood (Blakemore and Mills, 2014), leading to a wealth of studies of interpersonal motor alignment during child- and adulthood, but skipping the period of adolescence.

Yet, adolescence is an important social transition period, with ongoing brain development. This absence of studies warrants conclusions of social effects of adolescent interpersonal motor alignment and encourages further investigation of its potential positive effects. This is especially the case since adolescence is a period of enhanced importance of the peer group, sensitivity for social acceptance and rejection, as well as continuing structural and functional brain development (for review see Blakemore and Mills, 2014; Grosbras et al., 2007; Mills et al., 2016). A more in-depth investigation of interpersonal motor alignment during adolescent interaction could inform on healthy adolescent social cognitive development. This could have implications with respect to psychopathology with a prevalent onset in adolescence like conduct disorder, social anxiety or schizophrenia. As these disorders have been associated with altered brain development, it is also paramount to link those observations to knowledge about subserving brain organisation and its development. In the next section we review studies using neuroscientific methods to investigate brain correlates of interpersonal motor alignment across development.

3. Brain correlates of interpersonal motor alignment and the action-observation network

3.1. Brain correlates of interpersonal motor alignment in adult populations

The neural correlates of interpersonal motor alignment have been investigated in adults in three different categories of studies. First, the regulation of automatic imitative tendencies, second, motor resonance phenomena investigated via action observation studies, and third, synchronized brain activity. Here we give only a brief overview of some adult studies that have used various neuroscientific methods, as our aim is to focus on the developmental aspect. This section illustrates that, although neural correlates of interpersonal motor alignment have been investigated broadly, both with respect to experimental paradigms and research methods, as a whole the corpus evidence converges to show that specific brain circuits and mechanisms are involved in the alignment of behaviors during interaction.

Automatic imitation tasks have been used to assess brain regions specifically involved in the control of imitative tendency. Functional magnetic resonance imaging (fMRI) studies indicate the engagement of prefrontal (inferior frontal and medial prefrontal) and parieto-temporal regions when subjects imitate a movement (Carr et al., 2003) or perform a motor interference task (e.g., Brass et al., 2005; Mengotti et al., 2013; Rauchbauer et al., 2015). Patients with frontal lobe lesions tend to over-imitate, which suggests the existence of specific mechanisms to control this function (Brass et al., 2003). Non-invasive brain stimulation studies also show that disruption in inferior frontal regions interferes with imitation of simple finger movements (Heiser et al., 2003). Moreover, stimulating posterior regions in the parietal opercular region (Mengotti et al., 2013) or temporo-parietal junction (Sowden and Catmur, 2013) impedes the ability to repress the automatic tendency to imitate.

Motor resonance phenomena, tightly linked to automatic imitation, can also be revealed in passive action observation tasks that do not require explicit control over imitation. Already observing other people's actions consistently engages a set of brain regions to a greater extent than watching other categories of visual movement. This "Action Observation Network" (AON) encompasses the human mirror neuron system, which, alongside fronto-parietal regions and temporal cortices, is also engaged during action execution (Caspers et al., 2010; Grosbras et al., 2012). Thus, it contains an implicit "motor resonance" system, coupled with a mechanism to inhibit actual movement. This is also

evidenced in indirect electrophysiological measures of brain activity using electro- or magneto-encephalography (EEG and MEG), which show the same signature of brain activity, namely a decrease in power in mu (8–13 Hz), and often also beta (15–20 Hz), frequency bands over the motor cortex (central electrodes) for both action execution and observation (for review see Marshall and Meltzoff, 2011). Experiments in non-human primates indicate that the mu rhythm would reflect activity of motor and mirror neurons (Bimbi et al., 2018).

In addition, interpersonal synchrony has been associated to inter-brain synchrony, which has been measured directly during hyperscanning that is data recorded using neuroscientific methods, such as EEG or fMRI, simultaneously on multiple partners engaged in interpersonal motor alignment. Simultaneous EEG recordings in a dyad showed enhanced correlation in the theta and beta frequencies across brains during the execution of simple coordinated finger or hand movements (Dumas et al., 2010; Yun et al., 2012). In cooperative settings, inter-brain activity coherence was also demonstrated using near-infrared spectroscopy (NIRS) (Cui et al., 2012; Funane et al., 2011). Cooperative or affiliative behavior in economic games (Astolfi et al., 2014; De Vico Fallani et al., 2010), as well as in more ecological situations like flight behavior cooperation in professional pilots (Toppi et al., 2016) and interaction in romantic partners (Kinreich et al., 2017) was furthermore predicted by different patterns of brain-to-brain synchrony (most often in theta range and frontal cortex). In the same vein, it has been suggested that the greater the coupling between speakers' and listeners' brains, the greater the understanding between partners in communication (Stephens et al., 2010). A recent study showed a causal effect of neural synchrony on behavioral synchrony by entraining the motor activity of two individuals at the same time with transcranial alternating current stimulation: in-phase 20 Hz stimulation facilitated the establishment interpersonal movement synchrony in a joint finger tapping task (Novembre et al., 2017). Describing inter-brain coupling throughout development is a key part of gaining full understanding of these mechanisms. Yet, developmental brain imaging studies have been mainly concerned with single subjects set ups, only a few implementing dual scanning paradigms.

Next, we review the main findings in infants and toddlers, primarily using electro-encephalography (EEG) and functional near-infrared spectroscopy (fNIRS), and then turn to studies involving children and adolescents, which are mainly using fMRI. Table 1–3 present a more complete list of developmental studies involving the different sorts of interpersonal motor alignment in these populations.

3.2. Brain correlates of interpersonal motor alignment and action observation in infants and toddlers

Experiments using EEG or fNIRS have described components of the action observation network present very early on in infancy (see Table 1). Desynchronization of the equivalent of the mu rhythm in infants (6–9 Hz over central cortex) (Marshall and Meltzoff, 2011), has been reported in 4–11-month-olds when seeing adults walking (Virji-Babul et al., 2012). Similarly, 9-month-old infants show mu rhythm desynchronization while they observe actors performing reach and grasp movements (Debnath et al., 2019; Southgate et al., 2009). This was also reported in 9- and 12-month-olds observing tool use (Yoo et al., 2015), and in 18–36 month-olds watching actors pantomime actions without an actual object present (Warreyn et al., 2013). Moreover, mu rhythm desynchronization has been shown in 12-month olds observing unusual movements depending on the use of objects (e.g., bringing a phone to the mouth compared to a cup) (Stapel et al., 2010) and in 12–14 month olds depending on the unexpected use of effectors for the action (e.g., while having the hands free, using the head to turn on a lamp) (Langeloh et al., 2018). Mu desynchronization in 30-month-old infants during observation of facial movements furthermore suggests an already functioning mirror mechanism of facial expressions during early stages of development (Rayson et al., 2016).

Desynchronization in the motor cortex in the frequency range of 8–12 Hz for both execution and observation of drawing actions has been confirmed in a 36-month-old child with pre-surgical cortical electrodes implantation using intracranial recording (Fecteau et al., 2004). Using fNIRS, Shimada and Hiraki (2006) showed that 6–7 months infants who passively observed objected directed hand-arm actions engaged, although to a lesser extent, the same brain regions that when they manipulated the object themselves (Shimada and Hiraki, 2006). Thus, these studies converge to indicate an overlap between action execution and observation very early on in development. The relevance of automatic motor system engagement during passive action observation for studying interpersonal motor alignment is further supported by studies showing that motor resonance in 14-month-old infants is enhanced in an interaction context compared to the direct copying of adults' gestures. This points towards a stronger mirror resonance mechanism during interaction already in infants (Reid et al., 2011; Saby et al., 2012).

Yet, the automatic engagement of neural mirror mechanism may depend on experience (for review see Marshall & Meltzoff, 2014). This is reflected in studies showing that 4-month-olds show the same response to movements performed by an artificial agent or by a human (Grossmann et al., 2013). Furthermore, studies have reported that the degree of mu desynchronization during action observation is cumulatively correlated with motor skills according to experience (e.g. grasping (Cannon et al., 2015) or crawling (van Elk et al., 2008)). As such, stronger mu- and beta-desynchronization have been observed in 14- to 16-month-olds watching videos of other infants crawling, as compared to seeing them walking, for which they hadn't developed rich experience yet (van Elk et al., 2008). Interestingly, similar findings have also been reported in very young macaques who exhibit signs of EEG desynchronization in sensorimotor cortices during grasping observation in the first two weeks of life, increasing as a function of rudimentary grasp development (Festante et al., 2018). These findings are compatible with a narrowing processing dependent on motor experience (Lloyd-Fox et al., 2013). However, these results are contradicted by a study, showing that sensorimotor activation in response to videos of someone walking is present even for infants (4–11 months old) who don't yet walk. This could suggest that visual familiarity with an action is sufficient to drive motor resonance, without direct implication for behavior (Virji-Babul et al., 2012). In the same vein, Shimada and Hiraki (2006) showed that motor engagement during action observation in 6-month-olds was larger for live than video-taped stimuli, the latter being supposedly less familiar at this age. Alternatively, some authors have suggested that the relationship between motor competencies and motor resonance might be more apparent in older than younger infants (12-month-old compared to 9 month olds) (Yoo et al., 2015). In addition, experience beyond specific action execution skills may also be important. As such, general early life history may have an impact on the degree of interpersonal brain resonance. Fourteen-month-old preterm infants show mu suppression during action observation only in the right parietal regions, whereas full term infants showed the effect in a bilateral fronto-parietal network. Yet, no difference between groups was observed for action execution (Montirosso et al., 2019).

Another line of research has looked at interpersonal neural synchrony during infant social interactions. For instance, Leong et al. (2017) showed that phase-locking of brain activity between infants and parents was related to communication features, like direct gaze or duration of vocalizations. This finding could be interpreted as a mechanism for aligning the periods of higher sensory receptivity between interpersonal partners (Giraud and Poeppel, 2012) and facilitate learning. Recently, some studies have used dual fNIRS scanning to look at correlation in brain activity between infant and parent. The strength of association between parent and child activity in prefrontal regions was increased when they were engaged in cooperative as compared to independent behavior (Miller et al., 2019). Thus, some mirror like

mechanisms seem to be present in the brain early in life and well established in the first two years potentially supporting learning, as well as sensorimotor and socio-emotional development. More data is needed to draw stronger conclusions, however, in particular with respect to their link to the positive social effects described in the first section.

3.3. Brain correlates of action observation in children and adolescents

Most often data from infant populations are directly compared to adult studies, leading to discontinuity in the literature with respect to changes later in development. The reason for this may be that the methods and questions are often different when studying older children and adolescents. For these age groups most investigation has focused on action observation paradigms, which can give first insights into the perception-action link underlying interpersonal motor alignment during these years of development (see Tables 2 and 3).

A handful of studies have investigated motor activity during observation of others in older children and young adolescents using the mu suppression index, confirming findings from infants and adult studies. Eismont and colleagues (2017) reported desynchronization of the mu rhythm (taking into account the differences in dominant mu frequencies at different age ranging from 6–13 Hz) over central electrodes in children aged 4–14 years, during execution, observation and imitation of arm movements, with a stable effect across ages. Similar effects were also reported from other research groups, in 2-, 4-, 5-, and 11-year-olds respectively (Cochin et al., 2001; Lepage and Théoret, 2006; Martineau and Cochin, 2003). Extending these results, Bernier and colleagues, while showing similar effects in 5–7 year-olds, demonstrated that the strength of the interpersonal motor resonance effect was correlated with a measure of facial imitation abilities (Bernier et al., 2013). Altogether these EEG studies demonstrate a signature of the engagement of children's own motor system when they observe actions from others that may be stable during childhood.

Nonetheless pulling data from five different studies Oberman and colleagues (2013) concluded that mu suppression might indeed decrease with age (between 6 and 17). This is consistent with the report of Cheng and colleagues who observed higher mu suppression in 3- to 9-year-old children compared to adults (Cheng et al., 2014). Yet, this is inconsistent with other reports of weaker suppression in 8–12 year old children compared to adults, especially when watching movements from an allocentric perspective (Nishimura et al., 2018), or of an increase from 10 to adulthood (Brunsdon et al., 2020). More data from adolescents would be needed to ascertain this developmental trajectory. Other modulating factors such as attention and engagement with the stimulus, for example due to affiliation should also be investigated. Interestingly, Cheng and colleagues reported that contrary to adults, mu suppression in children was not modulated by the emotional content (painful or not) of the observed videos. This is in line with a study that used transcranial magnetic stimulation of motor cortex in combination with electromyography to measure motor resonance, and showed that contrary to adults, motor resonance was not modulated by emotion in 17 year olds (Salvia et al., 2016).

The presence of motor activity during action observation is confirmed using other methodologies. In a small sample of pre-adolescents (age 9–13), Kajume and colleagues used fNIRS and reported increased activity, compared to a baseline control, in the inferior-frontal / pre-motor regions when participants observed or imitated object-directed actions (Kajume et al., 2013). A handful of fMRI studies also confirm that children and adolescents, similarly to adults, recruit the AON when observing object-directed hand actions (Biagi et al., 2016; Ohnishi et al., 2004; Shaw et al., 2011a, 2011b). When comparing the activity in the AON directly between children (7–15) and adults, Biagi and colleagues (2016) observed less lateralization to the left in children. This is partly consistent with a longitudinal study showing decreasing activity with age in the right parietal cortex during action observation (although mainly in males) (Shaw et al., 2011b).

Assessing both action execution and observation suggests that the extent of shared activation, reflecting mirror activity, would increase from child- (age 7–10) to adulthood (Morales et al., 2019). Structurally also, areas in the AON, as well as other regions of the social brain, undergo developmental changes throughout adolescence (Mills et al., 2016). Moreover, the activation of the mirror system or the AON is modulated by personal and social factors in development. For instance, children and adolescents (age 9–15) with autism showed higher precentral and middle temporal activity in an action simulation task (i.e., when simulation is necessary to solve a problem), than age-matched control participants (Wadsworth et al., 2017). For passive observation of emotional actions, adolescents with a higher resistance to peer pressure show more coordinated brain activity in the right dorsal pre-motor and the left dorsolateral prefrontal cortex, than adolescents with low resistance to peer pressure. Thus, the propensity to withhold social peer pressure seems related to neural interaction when observing emotional actions (Grosbras et al., 2007). Indeed, the AON seems to be modulated by the emotional connotation of the observed action, with higher activity in fronto-parietal regions and additional supramarginal medial prefrontal and amygdala activity for angry as compared to emotionally neutral hand movements (Grosbras et al., 2007; Shaw et al., 2011b). This emotional modulation is however expressed differently in boys and girls across development. At the age of 10 and 11.5 years, both girls and boys show a common level of activity in the AON during observation of angry hand movements, specifically in the posterior parietal cortex, extending into the parieto-occipital junction, the fusiform gyrus, cerebellum, right inferior parietal lobule (IPL), dorsal pre-motor cortex (PMC), intraparietal sulcus (IPS) and orbito-frontal cortex (OFC). Yet, by the age of 13, the same male participants showed higher engagement of a “socioemotional” network than the AON, as compared to their female counterparts. This network comprised brain regions of the so-called social brain, specific to the processing of emotional actions including the temporo-parietal junction, the orbitofrontal cortex and the insula. This suggests that male adolescents around the age of thirteen years do not recruit action observation, but rather socioemotional processes when observing angry hand actions (Shaw et al., 2011a). These findings are paralleled by observations of structural brain development: adolescents with a higher degree of resistance to peer influence show higher interregional correlation of cortical thickness between nodes of the AON (Paus, Toro, et al., 2008). This underlines that the importance of the peer group on behavior could be related to brain development of areas related to social cognition.

Another line of investigation looked directly at interindividual brain synchrony in social settings, using dual-functional fNIRS in naturalistic interactions between caregivers and their children of preschool (mean age of five years) (Nguyen et al., 2020) and school age (five to nine years of age) (Reindl et al., 2018). High neural synchrony between children and caregivers correlated positively with behavioral reciprocity, predicted problem-solving success (Nguyen et al., 2020) and cooperative performance (Reindl et al., 2018). It has thus been suggested that neural synchrony may be a biomarker for interaction quality between a child and the caregiver, representing a neural mechanism for emotional connection linked to the development of adaptive emotion regulation. In a study on adolescents (17 and 18 years), Dikker et al. (2017) used portable EEG devices in a highschool classroom and observed that general measures of synchrony in the group (i.e., coherence between responses in multiple brain areas) were highly correlated with the level of engagement and enjoyment reported by students. Furthermore, they showed that, as in adults, social priming through engagement in eye contact increased interbrain synchrony within student pairs. Nonetheless, in another study with the same protocol, Bevilacqua and colleagues (2019) reported that the level of “interbrain synchrony” was not related to memory retention. Research in this direction should be pursued to explore to what extent interpersonal neural synchrony relates to interpersonal alignment and to social facilitation at different stages of development.

In particular, the continuing development brain areas important for social processing during adolescence suggests interpersonal motor alignment as a potential connective element between the two networks for healthy adolescent development. This could furthermore inform maladaptive development, for example in autism spectrum disorder (ASD) and psychopathologies, such as schizophrenia, social anxiety and depression, whose onsets often fall into adolescence (Paus, Keshavan, et al., 2008). Adolescence, as a formative transition period from child-, to adulthood, may be the optimal period to intervene and prevent psychopathologies (Eldreth et al., 2013)

4. Implications: the importance of studying interpersonal motor alignment in healthy development, including adolescence

As we hope to have demonstrated, interpersonal motor alignment is an important social signal for the establishment and maintenance of relationships and group cohesion throughout development. Even more so, the lack of coordinated interactions starting already at birth may lead to persistent difficulties throughout life in domains of social and emotional development, as well as self-regulation and the capacity for intimate relationships (Feldman, 2007b, 2007c). We contend that this importance of interpersonal motor alignment continues throughout development, extending from early relations with primary caregivers to family and peer relationships. Especially during adolescence, given the reorientation of the social focus to peers and away from family members, social contingencies and interpersonal behavioral alignment with peers may come into focus.

Reliable reciprocated interpersonal motor alignment throughout childhood and adolescence could contribute to strengthen the link between functional and structural brain development in areas related to the social brain and the AON and thereby enhance social and emotional resilience during adolescence. This is underlined by findings showing that socially contingent and synchronous interactions between caregivers and infants predict adolescent empathic abilities (Feldman, 2007a). But also, adolescents with higher resistance to peer influence show higher cortical thickness between nodes of the AON (Paus, Toro, et al., 2008) and highly coordinated brain activity in areas related to action perception and decision making (Grosbras et al., 2007). Conversely, unreliable alignment with peers or the family could augment feelings of social rejection and stress, in a period already marked by heightened sensitivity to peer rejection (Sebastian et al., 2010).

Social stressors such as (cyber-) bullying (Crick et al., 2001), social exclusion (Crone and Konijn, 2018) and enhanced risk-taking behavior (Chein et al., 2011; van Oosten and Vandenbosch, 2017v) peak during adolescence. Moreover, adolescence, as a time of substantial neurobiological and behavioral changes, confers a vulnerability for certain types of psychopathologies (Paus, Keshavan, et al., 2008). Continuing interpersonal motor alignment throughout adolescence may strongly support the establishment and maintenance of resilience and coping mechanisms. Yet research in this domain is critically lacking.

Indeed, as demonstrated throughout this article, reliable reciprocity through interpersonal motor alignment has positive social and emotional effects, which are, with the exception for action observation, underinvestigated during adolescence. Yet, especially its potentially strengthening effects of interpersonal motor alignment through mimicry and synchronous behavior on the connection between the AON and other brain regions implicated in social cognition, may have beneficial effects on adolescent resilience. This remains to be investigated, but interpersonal motor alignment programs to strengthen social resilience during adolescence and intervention programs targeting adolescents’ psychological or psychiatric problems could be envisioned. This could be implemented, in (online) video games and social media to strengthen healthy adolescent development through interpersonal motor reciprocity. Implementation on social media, via videoconferencing tools or on- or offline video games, may help reaching out to adolescents and making interventions more accessible to them. Yet,

while this idea is attractive, technical limitations, such as delays of timing due to different internet connections, may hinder smooth interaction and impede mechanisms mediating positive effects. Aiming to overcome this problem, several software programs have been suggested for musicians and to sing together¹. Social media and videoconferencing tools allow adolescents to stay connected, even in the face of isolation. This could be observed recently during social isolation in the wake of the COVID-19 pandemic, when two third of American teenagers reported using video chat to stay connected with their peers². This makes this avenue worth pursuing.

5. Conclusion

This is the first integrative review of interpersonal motor alignment and its positive social functions from a developmental perspective. It highlights the importance of reliable interpersonal motor alignment for healthy social development and especially points towards the need to extend this research to adolescence, a period of enhanced social sensitivity. Indeed, although interpersonal motor alignment may link social cognition to cognitive control and may have an important role in healthy adolescent interactions, it is still underinvestigated during adolescence. Moreover, since adolescence is a time of substantial neurobiological and behavioral changes, it may confer a psychopathological vulnerability. Studying interpersonal motor alignment as one of the links between social cognition and cognitive control may inform motor therapies for prevention and recovery and aid healthy adolescent development.

Acknowledgements

This work was supported by the Fondation pour la Recherche Médicale (FRM, SPF20171039127) to BR, the grants from the Agence Nationale de la Recherche (ANR, France) ANR-14-ACHN-0023 and ANR-11-IDEX-0001-02) to MHG and benefited from the grants ANR-16-CONV-0002 (ILCB), ANR-11-LABX-0036 (BLRI) and the Excellence Initiative of Aix-Marseille University (A*MIDEX).

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¹ See for example: <https://ccma.stanford.edu/software/jacktrip/>; <https://blog.smule.com/go-live-using-livejam-on-smule/>; <https://www.jamkazam.com/>; <https://audiomovers.com/>; <http://lcon.sourceforge.net/>; <https://github.com/gisogrimm/ovbox>; https://en.wikipedia.org/wiki/Telematic_performance

² <https://www.statista.com/statistics/1115305/technology-used-by-teens-stay-connected-during-coronavirus-pandemic-usa/>

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