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A context-dependent model of resilient functioning after childhood maltreatment—the case for flexible biobehavioral synchrony

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Many children who experience childhood adversity, whether in the form of threat or deprivation, develop adaptive competencies that lead to resilient functioning. Still, research has not succeeded in accurately predicting the level of resilient functioning by any kind of biomarkers, likely because it has sidelined the flexibility inherent in a construct that is situationally and developmentally variable. Whilst recent research acknowledges the importance of redefining resilience in order to reflect its dynamic nature after adversity, evidence for specific behaviors that are developmentally adaptive and dynamic throughout the lifespan is limited. We here propose a model in which resilient functioning is crucially dependent on the individual's capability to flexibly synchronize with and segregate from another's cognitive-affective, behavioral, and physiological states, known as 'biobehavioral synchrony'. Such an adaptive interpersonal skill is rooted in (a) the early caregiving experience and its regulatory effects on an individual's physiological stress reactivity, as well as (b) the development of self-other distinction which can be affected by childhood maltreatment. Bridging the gap between accounts of flexible resilient functioning and the latest thinking in biobehavioral synchrony, we will review behavioral and neurobiological evidence that threat and deprivation in childhood interfere with the development of dynamic, context-sensitive boundaries between self and other, mediated by the (right) tempo-parietal junction (a central neural hub for interpersonal synchronization), which puts the individual at risk for affective fusion or cut-off from others' arousal states. Our proposed model charts a path for investigating the differential effects of maltreatment experiences and mechanisms for intergenerational transmission of non-sensitive caregiving. We conclude with metrics, data analysis methods, and strategies to facilitate flexible biobehavioral synchrony.

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INTRODUCTION

The resilience paradox

Childhood maltreatment, defined as deliberate harm or the failure to prevent harm to individuals under 18 years, is a pervasive risk to development and is associated with psychopathology across the lifespan, affecting up to one in three minors (over 300 million children worldwide [1]). Nonetheless, most children who experience adversity exhibit adaptive functioning that surpasses expectations (resilient functioning, RF [2–5]). Indeed, studies show that the most common response to childhood adversity is predominantly adaptive or competent functioning [5–7], with an estimated two-thirds of individuals experiencing a potentially traumatic event following a resilient trajectory [3].

However, despite advances in our understanding of factors that promote RF after adversity, research has paradoxically not succeeded in accurately predicting positive outcomes based on its likely correlates [7–9]. Reasons for this include: i. the equifinal nature of RF in which many different factors can contribute to positive outcomes (e.g., biological and ecological), ii. oversimplification in

which standard resilience assessments focus only on a small number of predictors (with small effect sizes), and iii. overlooking the importance of situational variability and developmental timing for RF [7–10]. Considering context-dependence in the study of RF prevents the 'fallacy of uniform efficacy' by allowing a specific resilience-promoting behavior to be efficient in one situation and not another, a cost-benefit trade-off that is at the core of almost any resilience promoting trait or behavior [11, 12]. The field of developmental psychology has responded to this criticism by redefining resilience as a skill, a behavioral and neural response that is flexible and adaptable across various situations and developmental stages, moving away from static and binary definitions based on isolated measurements of psychopathology in time [10, 13, 14]. To date, however, mechanistic accounts of the exact biobehavioral mechanisms associated with the dynamic nature of RF are limited.

In this review, we will first provide an overview of the different conceptualizations of RF and highlight the opportunities provided by a definition of RF that is inherently dynamic, i.e., sensitive to situational and developmental variability. We then bridge the gap

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from theoretical accounts of flexible RF to concrete biobehavioral mechanisms, by proposing that the extent to which an individual is able to flexibly align (synchronize) and retract (segregate) themselves from another person's cognitive-affective, behavioral, and physiological state (biobehavioral synchrony), is one such flexible skill that confers RF after childhood adversity. In our model, we suggest that flexible biobehavioral synchrony as an index of RF is crucially dependent (a) on the early caregiving experience and both its regulatory effects on an individual's physiological stress reactivity and interpersonal skills, as well as (b) the development of self-other distinction (SOD), which can be affected by childhood maltreatment. Unifying dynamic resilience accounts and the latest thinking in biobehavioral synchrony, we will review behavioral and neurobiological evidence that threat and deprivation in childhood interfere with the development of dynamic, context-sensitive boundaries between self and other, mediated by the tempo-parietal junction, putting the individual at risk for affective fusion or cut-off from others' affective states and states of arousal. Finally, we present some hypotheses derived from this model about different RF trajectories after childhood adversity and intergenerational transmission of inflexible biobehavioural synchrony, concluding with suggestions for measurement, analyses, and prevention.

RF depends both on context and developmental stage

There is still an ongoing debate on how resilience could be best conceptualized or measured. RF generally refers to an individual who shows healthy and adaptive positive functioning over time in the aftermath of adversity [15-17]. Traditionally, resilience definitions encompassed the presence or absence of psychopathology in childhood [18-20] to more complex indices of socioemotional functioning or individual traits and coping skills in adolescence and adulthood [21, 22]. We here, define RF as 'the capacity of a dynamic system to adapt successfully to disturbances that threaten the viability, the function, or the development of that system' [18, 23]. RF is thus dependent on both, the individual (e.g., neural, hormonal, and genetic make-up) and their environment (social, institutional, and cultural), as well as their interaction (see Ungar [19] for a constructionist view on resilience; see Russo and colleagues [20] for a review of neural, molecular and hormonal RF research and Elbau and colleagues [24] for an overview of genetic RF factors). According to a static conceptualization of RF [25-29], resilience measures often assess basic binary indicators such as academic failure or incarceration [30] or singleand multi-domain composite scores assessing functioning across social and emotional domains [25] (e.g., reaching developmental language milestones [4], but see e.g., Feldman [27] for critique). Whilst static conceptualizations of resilience facilitate measurement, they lack ecological validity and negate both developmental timing and situational variability within which RF occurs [9, 10, 14, 20, 31].

Situational and developmental variability of RF is especially relevant for children who have experienced maltreatment. For example, studies documented more pronounced neurocognitive and behavioral changes depending on maltreatment type, onset, severity, and duration [32-37]. Therefore, RF likely presents differently along the spectrum of adverse experiences, depending on the 'pressure' or allostatic load the system works against [9] (e.g., a child with high maltreatment severity could be considered resilient at a lower threshold of functioning than a child with limited and mild adverse experiences, see [10]). RF is an inherently developmental process that partly unfolds as a function of caregiving from birth [27] and can occur at any stage in life [38], making developmental timing a key variable, too. A child may display RF in one developmental period and domain but not another [7, 16, 39]. Yoon and colleagues [7] strongly support a developmental conceptualization of resilience and have shown that resilience factors vary significantly throughout development, with unique individual, relational, and community protective elements emerging at different stages of life. For example, whilst resilience is primarily linked to caregiver warmth, emotional support, and cognitive stimulation in infancy [4, 40], caregiver well-being, effective parental engagement, as well as individual child characteristics and behaviors, such as child prosocial behavior become crucial for RF after childhood maltreatment in school-aged children [4, 41–43]. Adolescent RF post-adversity still hinges on strong caregiver support [21, 44, 45] including paternal acceptance [46], however, more peer-related activities and school engagement (e.g., involvement in extracurriculars, notably sports), emerge alongside as pivotal factors [21, 44, 45] together with positive attitudes and self-esteem [44, 46, 47]. In adults with childhood maltreatment experiences, RF is closely associated with a sense of community and belonging, encompassing religion, family, and friends [48-51]. Interpersonal strength, positive reframing, acceptance, and optimism are further resilience factors for adults who experienced childhood maltreatment [52-54]. Notably, a supportive family environment remains a strong influencing factor throughout the lifespan [48]. Thus what constitutes RF will look different at each stage of development as the interaction between children and their environment changes. This is why any theory of RF must accommodate the flexibility inherent in dynamic environments.

RESILIENCE IN THE SOCIAL CONTEXT

The importance of social factors for RF has emerged across many studies [55, 56], confirming the significance of social support for the psychosocial development of young adults, who have experienced childhood maltreatment (e.g., [57]). Often, the combination of individual factors (such as gender) and social factors (e.g., maternal and sibling warmth, lower neighborhood crime victimization, greater social cohesion) best predicted whether a victimized individual experienced positive or negative psychosocial and economic outcomes during the transition to adulthood. This highlights the importance of a multidimensional conceptualization [58]. However, the empirical evidence base for mechanistic accounts of how social factors confer resilience after childhood maltreatment is limited and complicated by the use of non-comparable measures of resilience factors and a unidimensional conceptualization of social functioning, which treats structural (i.e., quantitative measures of social integration), functional (i.e., perceived social support), and qualitative indicators (i.e., positive and negative aspects of social relationships) in isolation [56]. Specifically, how close relationships with peers can buffer against the detrimental effects of early adverse childhood experiences remains mechanistically unclear. How can the adaptive advantages conferred by social-affiliative bonds be understood on a neurobiological level? Biobehavioral synchrony emerges as one potential mechanism underlying the resiliencepromoting effects of social connections.

Biobehavioral synchrony refers to the temporal coordination of behavioral and biological responses between two or more interacting individuals [55] and likely embodies the adaptive skills that allow humans to perceive another person's inner arousal state [59]. It may also foster the sharing and regulation of emotions, intensify social affiliation, empathy, and prosocial commitment [60], as well as promote learning [61], and facilitate adjustment to collective actions and group norms [62, 63]. This evolutionary mechanism captures the dynamic and reciprocal interplay between an individual's physiological processes (e.g., heart rate), hormone release, and brain activity alongside observable behaviors like gaze or vocalizations. For instance, during a positive mother-infant interaction, the dyad's heart rates and behaviors (e.g., mutual gaze or touch) might temporarily coordinate [61]. Biobehavioral synchrony plays a crucial role in all human relationships, in parental, romantic, friendship, and stranger

interactions, and 'being in sync' with others has been correlated with improved stress management [64] and superior immune functioning [65], thereby offering a mechanism through which coordinated social actions alleviate stress and bolster resilience.

Based on this evidence, we have formulated a model of RF in which biobehavioral synchrony plays a crucial role in its development as a dynamic and developmentally-adaptive process. We will briefly summarize the different levels on which biobehavioral synchrony can be measured and what we know about biobehavioral synchrony dynamics throughout the lifespan. Biobehavioral synchrony occurs at multiple levels: b Behavioral synchrony, refers to the temporal coordination of observable actions between individuals, such as body movements, eve contact, speech, attention, touch and affect [66-68]. Behavioral synchrony is the most extensively investigated synchrony modality [69] with a major grounding in developmental research, where it is seen as a building block to the formation of attachment [70-73]. Physiological synchrony, mainly refers to the temporal coupling of functions of the autonomic nervous system (e.g., cardiac or electrodermal activity) and can be observed in established or stranger dyads [74-76]. It includes the temporal inter-relatedness of hormonal responses between interacting partners in close relationships: for example highly sensitive (but not less sensitive) mothers' and their toddlers show synchronized cortisol reactivity in response to a laboratory-based challenge [77, 78]. Unsurprisingly, preliminary evidence exists for synchronized oxytocin levels during early parent-infant bonding [79, 80]. Physiological synchrony also varies by context, for example, stressful experimental conditions (e.g., difficult puzzles under time pressure) lead to disrupted parent-child respiratory sinus arrhythmia synchrony (RSA; indexing parasympathetic arousal) compared to less-structured, free-play tasks [81]. Biobehavioral synchrony is also dependent on the caregiver's and child's psychopathological state. For example, in school-aged children, mother-child dyads with a history of maternal depression showed lower RSA synchrony during a negative discussion task (e.g., discussing an issue on which the dyad regularly disagrees), but not during a pleasant, vacation-planning task [80, 82]. In a naturalistic study, less anxious mothers demonstrated greater physiological synchrony with their children throughout the day compared to anxious mothers. They only responded to 'peak' moments in their child's arousal and were better at exhibiting 'stress buffering' behavior, effectively downregulating arousal when the overall arousal level of the dyad was high [83]. Interestingly, a recent meta-analysis showed that synchrony in various physiological systems is related to different outcomes [74]. Whereas overall measures of sympathetic nervous system synchrony were positively associated with favorable relationship outcomes, synchrony in the parasympathetic nervous system was negatively associated with relationship outcomes, indicating that overall high biobehavioral synchrony across different levels should not always be considered as the 'optimal state'. Importantly, biobehavioral synchrony must be considered as a multimodal and flexible mechanism to adapt to changing environmental conditions. Neural synchrony, involves the coupling of neural activity between individuals [84, 85] and is driven by advances in brain imaging technology and a call for a more ecologically valid examination of social interactions [86–89]. Hyperscanning or the simultanoneous assessment of at least two interacting subjects [85, 90] enables scientists to map neural synchrony [85]. The proposed mechanisms of physiological and neural synchrony are associated with engagement and coupling of attentional states [91, 92], mutual prediction and understanding [93-95] emotional and cognitive alignment [96, 97], and co-regulation of arousal states [98, 99]. Gordon and colleagues [100] emphasize the importance of situational and developmental variability in shaping the tendency towards synchrony or segregation within a given social context in their model of flexible multimodal synchrony. Individual traits sensitize individuals to these situational variations. In this manner, the interplay of context and individual differences provides the foundation for adaptable and dynamic synchrony patterns across multiple situations and developmental states, encompassing behavioral, physiological, and neural aspects. In line with this, we suggest that a greater individual capacity to flexibly deploy interpersonal synchrony confers RF, that is tuning in (synchronizing) when it is adaptive and tuning out (segregating) when non-adaptive rather than constant states of alignment.

Biobehavioral synchrony in low- and high-risk dyads

The foundation of biobehavioral synchrony is laid in the last trimester of pregnancy and evolves constantly after birth, where a synchronization of physiological states serves to regulate the infant's emotions [101, 102] and is achieved through the primary caregiver's physical and behavioral attunement to the infant [103]. Positive early relational experiences with primary caregivers, enabled through parental sensitivity, competence, and warmth [4] become important facilitators for the development of the individual skills that are necessary for many RF's, such as emotion and stress regulation, as well as interpersonal skills. It is the extent to which a primary caregiver and infant coordinate and align with one another mentally, behaviorally, and physiologically that confers RF through its regulatory effects on an individual's physiological stress reactivity [72, 104]. Of note, these temporally coordinating events (behaviors, hormones, and peripheralphysiological and brain states) need not occur simultaneously in the interacting dyad but may also include temporally coordinated lagged events. The latter is sometimes referred to as contingency, for example when changes in partner A forward-predict changes in partner B (see [105]) and contrasted against an indirect concurrent (zero-lag) relationship, called synchrony, for example when both partners are in the same state at the same time. In this sense, both synchrony and contingency might impact RF across development. For example, when a caring interaction partner changes their behavior to calm a young person who faces a conditioned and potentially threatening stimulus ('contingency'), this might support the child's ability for extinction learning and thus lower the risk for developing post-traumatic stress symptoms. In a similar vein, if a neglected child's state entrains to the positive emotional state of a caring interaction partner ('synchrony'), this might help to up-regulate the child's affect, broaden attention, and enhance flexibility [106]. Vice versa, a child adapting 'contingently' to a manipulative, abusive caregiver might be just as maladaptive for developing RF as being in concurrent synchrony with a highly impulsive-aggressive caregiver. In both latter cases, moving out of biobehavioural synchrony might bolster RF.

It has been suggested that synchrony has profound effects on social interactions that continue throughout the lifespan [106]. Diminished early synchrony experiences with the primary caregiver can alter neural, emotional, and behavioral development and have significant effects on the child's stress and emotion regulation capacities and social competence [98, 107-109]. In line with this assumption, high-risk dyads (mothers suffering from depression and their infants) were shown to be less synchronous, i.e., had lower levels of gaze and touch synchrony, reduced coordination of affectionate touch with mutual gazing, and diminished maternal behavior [65, 72]. Furthermore, adversity has been associated with altered parent-child synchrony at multiple levels [107-116]. For example, elevated parenting stress has been linked to diminished behavioral synchrony between parents and children aged 3-14 [113]. Higher mother-infant cortisol synchrony was found in dyads from higher-SES compared to lower-SES backgrounds [111]. Mother-preschooler dyads with and without maltreatment experiences differed in within-dyad dynamic concordance in heart rate, such that variations in heart rate in one member of the dyad were associated with subsequent

variations in the other only in those dyads without maltreatment experiences [112]. Hoyniak and colleagues [108] recently reported that adversity, across domains, was associated with decreased parent-child behavioral synchrony and that sociodemographic risk in particular was associated with decreased parent-child neural synchrony in the context of experimentally-induced stress. Collectively, these research findings demonstrate that adversity negatively impacts parent-child synchrony, potentially affecting social reciprocity.

On the behavioral level, childhood maltreatment has been associated with decreased cooperative behavior, more problematic peer relationships, and classroom behaviors such as higher levels of aggression or social withdrawal [117, 118]. On the other hand, maltreatment can be associated with indiscriminate friendliness [119, 120], sometimes also referred to as 'costly altruism' [121], which has recently been included as a diagnostic symptom of Disinhibited Social Engagement Disorder in the DSM-5. In line with this, Keil and colleagues [122] showed that maltreated children showed hyper-cooperativeness toward 9-16year-old peers, which may serve to minimize hostility during initial encounters, but comes at the cost of potential exploitation by others. Given the strong association between cooperative behavior and biobehavioral synchrony [123, 124], the above findings of de- and increased cooperative behavior in young people with maltreatment experiences potentially indicate a diminished capacity for flexible synchronization (fusion, as indicated by hyper-cooperativeness) or segregation (cut-off, indicated by uncooperativeness) from others. This effect seems mediated by physiological arousal as previous research indicates that synchrony encourages greater cooperation mainly when paired with physiological arousal [123]. It is of interest then, that indices of heightened arousal such as decreased RSA [125] have been linked to maltreatment severity [126, 127] and physical abuse specifically whilst indices of decreased arousal (heightened RSA) were linked to maternal neglect history [128, 129]. These findings suggest differential effects of abuse and neglect on mother-child synchrony as is suggested by dimensional models of adversity [130, 131], as well as potential intergenerational transmission pathways of physiological stress management via biobehavioral synchrony [132, 133], in which RSA alterations in parents with their own histories of childhood maltreatment influence synchronous engagement with their offspring [107]. In line with this, parental childhood maltreatment correlates with changes in child interaction quality, possibly mediated by an altered oxytocin system (gauged by plasma levels [134]), and increased insecure attachment patterns, especially from parents who experienced emotional neglect [135]. This influence traverses several pathways, such as parental regulatory behaviors and physiological functions [126, 136], as well as interaction quality affecting attachment formation. Consequently, maltreated parents experiencing both altered levels of arousal and diminished emotion regulation might face challenges in co-regulating with their children in adolescence and adulthood [137].

SOD facilitates dynamic biobehavioral synchrony

Biobehavioral synchrony is mechanistically enabled through the blurring of the Self-Other distinction [SOD, 72, 138–141]. In the postnatal period, the infant relies heavily on the mother's body, and a synchronous 'oneness' emerges between mother and child [142], but the synchrony and 'oneness' that characterizes the early years in normative development is inevitably subject to misalignment and moments of non-synchronous interactions, given that in typical social interactions, "as in any dynamical system, patterns of coordination form and dissipate" [143] (p. 233). In the real world, caregivers are more often unresponsive than responsive to their children (see for a review [144], see also: [62, 145, 146]. Consequently, dyads spend more time in mis-coordinated states that are framed by precious moments of alignment, suggesting an

"optimal midrange level" of behavioral synchrony and contingent interaction [147]. Psychoanalytic and developmental theories emphasize the importance of such match-mismatch cycles for teaching infants how to tolerate moments of non-attunement, how to repair the misunderstandings inherent in human dialog and because they provide vital opportunities to practice distinguishing self from other [142, 148-150]. The child increasingly learns to differentiate their own mental and arousal states from their caregiver through such non-synchronous interactions and their caregivers' ability to both mirror the child's emotional state (contingent mirroring [142, 148]), whilst clearly signaling that they are referring to their infants' mental state (marked mirroring [142, 148]). Gradually, achieving a separate sense of self in relationships with others whilst being able to experience closeness is one of the primary developmental tasks during adolescence [151, 152], as well as a marker of RF across the lifespan [153]. This important individuation can only be achieved if self-other distinction (defined as the capacity to experience a distinct and separate sense of self in relation to others [154]) has been enabled by a complex and dynamic interpersonal synchrony experience [100, 151] resulting in the capacity to respond flexibly to changing contexts throughout the lifespan.

The capacity to distinguish oneself from others emerges around 18-20 months and enables the distinction of one's own body from someone else's (perceptual level), the inhibition of automatic imitation tendencies (action level), representing others' mental states that differ from our own (mental-state level), as well as our ability to empathize with others during incongruent emotional states [155] (see [156] for a detailed discussion of the development of SOD). On the neural level, the increasing ability to distinguish between self and others relies heavily on the right dorsal part of the temporoparietal junction (TPJ), as well as the medial prefrontal cortex [155, 157] (see [158]). Developmentally, TPJ undergoes significant structural and functional maturation at around 3-4 years, corresponding to significant improvements in perspective-taking at this age [159, 160]. Studies using near-infrared spectroscopy (NIRS) during mother-child dyadic interactions have shown that the TPJ is already specialized by 12–14 months of age to process social signals [161] and neural activity increases significantly in the TPJ in response to social stimuli across the first 24 months of life [162].

One common index of SOD is the assessment of the tendency to inhibit automatic imitation of others' actions in experiments where individuals carry out motor responses while observing someone else's congruent or incongruent (i.e., interfering) actions [156]. The degree to which observing incongruent trials interferes with one's own action indexes how well SOD can be maintained. The right TPJ in particular has consistently been involved in upholding SOD, both mentally and behaviorally in imitation of action experiments [155]. Enabling SOD is hypothesized to be achieved through flexible switching between the representations of self and other (or enhance self when relevant / inhibit other, see [163]), enabled by the TPJ's key role in attention reorientation (see e.g., [164, 165]). Interestingly, this overlaps with the central hub in the neural network associated with interpersonal synchronization as identified by Lotter and colleagues [166] in a recent meta-analysis, which included hyperscanning neuroimaging experiments. Across these studies, the most robust brain regional correlates of biobehavioral synchrony were in the right TPJ and left ventral prefrontal cortex. Extending this finding to a developmental population, Morgan and colleagues [167] showed that greater positive affective matching was related to greater synchrony in medial and lateral frontal and temporoparietal regions, confirming that biobehavioral synchrony involves sensory-integrative hubs with functional connections to mentalizing networks and thus overlaps with neural mechanisms of SOD (Fig. 1).

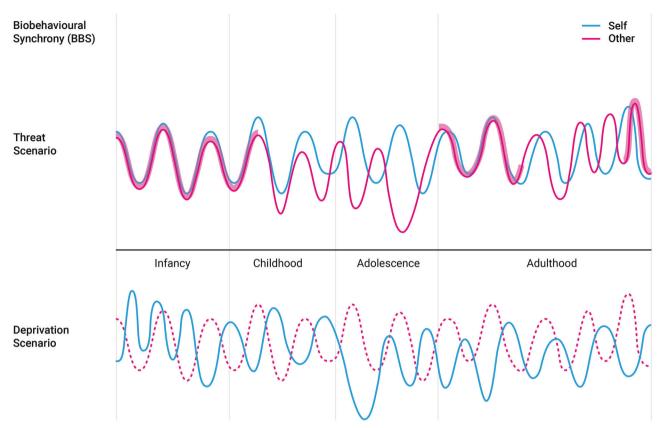


Fig. 1 Flexible biobehavioral synchrony enabled by the maturation of SOD over the lifespan. Figure 1 depicts the trajectories of flexible biobehavioural synchrony and the development of SOD as dynamic processes indexing RF over the lifespan. Strongly coupled synchrony in early infancy, mediated by a blurring of the boundary between the infant (self) and their primary caregiver (other), enabled by sensitive caregiving and co-regulation, which in turn fosters the development of both the infant's stress-coping and interpersonal skills. Beginning in childhood and culminating in later adolescence (when necessary individuation processes take place), positive synchrony alternates increasingly with moments of significant misalignment and uncoupling. These moments of rupture and repair provide the necessary context-dependent experience for the TPJ to master flexible switching between representations of self and other, ultimately establishing the basis for the ability to align (synchronize) and retract (segregate) from another person's mental, and behavioral and physiological arousal state in adulthood in a dynamic and context-sensitive manner.

MALTREATMENT EXPERIENCES IMPACT THE DEVELOPMENT OF A FLEXIBLE INTERPERSONAL SYNCHRONY SYSTEM — A MODEL

In childhood maltreatment, caregiving characterized by abuse and neglect significantly disrupts interpersonal synchrony [107-109, 111-116] and subsequent development of an ability to represent self and others efficiently [168], either because the caregiver was unable to accurately represent the emotional state of the infant (lack of congruency) or because they offered an excess of synchrony by overwhelming the infant with their own emotional states (lack of marking) [142, 148]. Assuming a cascading effect on domains of self-other representation we hypothesize that experiences of maltreatment impact on an individual's capacity to flexibly deploy interpersonal synchrony according to situational and developmental demand, increasing the risk for emotional fusion or cut-off with others and subsequent relational difficulties and stress throughout an individual's life. Such lack of flexible representation of self and others has already been identified as a driving force in different forms of psychopathologies, most comprehensively in borderline personality disorder [168]. Children who have experienced maltreatment, in the form of abuse and neglect, have been found to exhibit changes in SOD and its related domains, including perceptual, action, and mental SOD domains as discussed above. In terms of perceptual SOD for example, a recent study by Machorrinho and colleagues [169] showed that women who experienced intimate partner violence showed decreased levels of body ownership (the feeling of an individual's body as their own) measured via the Rubber Hand Illusion [170] and higher levels of bodily dissociation, even after controlling for symptoms of PTSD and depression. Similarly, Talmon and Ginzburg [171] were able to demonstrate disrupted body boundaries in female students who experienced childhood maltreatment. In line with this, studies have also demonstrated that adults and children with PTSD and experiences of childhood maltreatment show preferences for larger interpersonal distances and aversion of social/affective touch, which is a key promoter of body ownership throughout development [172–174].

With regards to mental SOD, there is evidence that children with maltreatment experiences were delayed or less likely to pass false-belief tasks in experimental studies (ToM [175-177]) and showed an impoverished sense of self, accompanied by a diminished sense of identity [178]. A study by Burack and colleagues [179] has shown that maltreated children and adolescents were less successful in representing others perspectives and delayed in their social perspective-taking development compared to their non-maltreated peers, whilst other studies demonstrated deficits in emotion recognition and identification after childhood maltreatment ("affective ToM" [175]). Testing a specific aspect of SOD, a recent study by Hudson and colleagues [180] found that women with childhood experiences of abuse were less affected by incongruent imitation (inhibiting imitative behavior) suggesting they were less influenced by others' perspectives due to changes in the representation of self and other. These differences in SOD capacity will have important consequences for social interactions throughout the lifespan [168],

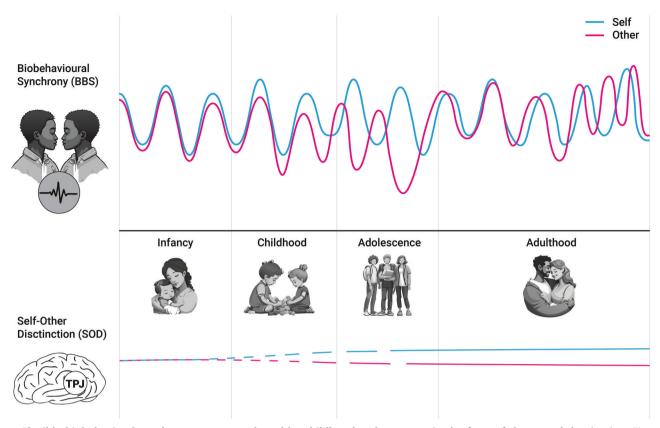


Fig. 2 Flexible biobehavioral synchrony processes altered by childhood maltreatment in the form of threat and deprivation. Figure 2 depicts the hypothesized effects of maltreatment on the development (infancy—childhood) and deployment (adulthood) of flexible biobehavioral synchrony (biobehavioral synchrony). We suggest the potential for threat and deprivation to exert differential effects on biobehavioral synchrony depending on whether (i.) violations of the self–other boundary have occurred that hindered the development of a clear distinction of self from other (e.g., sexual, emotional, and physical abuse), in turn increasing the risk for maladaptive affective merging (fusion) throughout the lifespan or whether (ii.) experiences of blurring of the SOD have been limited which can increase the risk for rigid, inflexible synchrony and potential affective cut-off. We suggest that rigid affective merging and cut-off are exaggerated responses on the continuum of synchrony and segregation.

but even more so during adolescence when the ability to take someone else's perspective is positively related to trusting others and social reciprocity [181]. Given the strong behavioral evidence for the impact of childhood maltreatment on the formation of perceptual, mental, and action SOD it is unsurprising that individuals with maltreatment experiences have shown altered neural activation patterns in key structures supporting biobehavioral synchrony and SOD, i.e., the TPJ, as well as the prefrontal cortex [182-186]. Cracco and colleagues [182] assessed rTPJ activation during spontaneous mentalizing in fMRI in 35 women with histories of childhood physical, sexual, and/or emotional abuse and 31 controls using a false belief task and found reduced activation in rTPJ in the abuse group for false vs true belief conditions and increased functional connectivity between rTPJ and dPFC, suggesting that altered mental SOD can last well into adulthood. Interestingly, these neural circuits involved in both attention and cognitive control were previously shown to be early post-trauma biomarkers of subsequent resilience [187]. Another study showed that childhood abuse was associated with increased resting state functional connectivity between the TPJ and the brainstem, which was driven by the number of types of abuse [183], suggesting a role for brainstem regions in biasing perspective-taking networks after trauma. Recent brain structural evidence also implicates the dorsolateral prefrontal cortex, the medial prefrontal cortex, and the posterior superior temporal sulcus (including TPJ) in higher RF in adolescents [188]. The limited neuroimaging evidence that is predominantly available in adult populations thus suggests that the TPJ's ability to switch in a

flexible manner between the representations of self and others [163] is likely affected by childhood experiences of abuse and neglect. Future neuroimaging studies should extend the investigations of SOD domains to developmental populations (Fig. 2).

A CONTEXT-DEPENDENT AND VALUE-BASED MODEL OF RESILIENCE FACILITATION THROUGH FLEXIBLE BIOBEHAVIORAL SYNCHRONY AFTER MALTREATMENT

In our hypothesized model we have proposed that RF after childhood maltreatment is conferred, at least in part, through flexible biobehavioral synchrony, i.e., the extent to which an individual is able to align with (synchronize), and retract (segregate) themselves from another person's dynamic affective and arousal state depending on its changing adaptive value. We thus suggest that this flexible deployment of synchrony is guided by cost-benefit analyses which are central to almost any resiliencepromoting traits or behaviors [11, 12]. In practice, tuning in and out of someone's affective state could be beneficial in a scenario where one's own mental state is characterized by negative affect and high arousal but the other's by neutral or positive affect and low arousal (regulatory influence), whilst segregation would be adaptive when one's own affective state is neutral or positive and the other's affective state is negative with high arousal (agitatory influence). The level at which this capacity is developed throughout one's life depends crucially on early caregiving experiences. These are influenced by the caregiver's own history of biobehavioral synchrony, the child's biological makeup, socioecological aspects of the caregiver-infant setting, and the adaptive capabilities of other social partners to align and synchronize flexibly. In our model, we propose that childhood adversity in the form of threat (e.g., sexual abuse, physical abuse, and exposure to domestic violence) and deprivation (e.g., emotional and physical neglect) interferes with the effective deployment of flexible synchrony via its main mechanism, SOD. Childhood adversity affects the development of the perceptual and mental SOD in ways that can diminish an individual's ability to uphold the self-other boundary leading to a maladaptive merger (fusion) or rendering it rigid and inflexible (emotional cut-off) to the changing demands of dynamic social interaction, in essence pointing towards exaggerated synchrony and segregation behaviors. During adolescence, in which the brain undergoes significant neuroplastic changes (see [9]) and is particularly sensitive to social experiences outside the family, the ability to flexibly synch and segregate from others might contribute significantly to the quality of adolescents' social experiences and relationships, thereby indirectly impacting RF (see [189]). It is during this developmental period that established SOD is transferred to new (e.g., romantic or peer) relationships, and flexible biobehavioral synchrony capacities might be challenged and reshaped across multiple social contexts. Here, it has to be taken into account that both, biological changes in the individual response system (such as changes in the HPA functioning, development of rTPJ and prefrontal cortex functions), as well as the expansion of the social network might impact and change the flexibility of biobehavioral synchrony during development. Thus, the model proposed here suggests that there cannot be a uniform response to experiences of adversity in childhood as the trajectories of RF will be dependent on both the maltreatment context and the developmental stage in which RF is assessed. However, our model provides a framework within which hypotheses regarding the role of flexible synchrony in RF can be tested. For example, based on the model we outlined here, one testable assumption relates to the effect of early caregiving experiences on the flexible deployment of synchrony based on its context/adaptive value. Individuals who have experienced childhood maltreatment might exhibit less flexible deployment of biobehavioral synchrony in a VR-simulated social contagion experiment as indexed by higher susceptibility to both, negatively and positively valenced emotional contagion as opposed to non-maltreated peers who would be expected to be more susceptible to positive contagion than negative in line with its adaptive value. More nuanced testable assumptions from the model pertain to the influence of maltreatment type on RF through the flexible application of biobehavioral synchrony. Future studies could investigate if a childhood characterized predominantly by neglect is associated with diminished flexibility of biobehavioral synchrony with others in the form of emotional cut-off (i.e., difficulty 'tuning in'), due to the absence of early childhood experiences of 'oneness' and co-regulation. Vice versa, experiences of a breakdown in one's physical and emotional boundaries as is the case in emotional, sexual, and physical abuse could be associated with a diminished flexibility of biobehavioral synchrony in the form of emotional fusion (i.e., difficulty 'tuning out' and distinguishing self from other) as has been suggested in the literature [180]. Importantly, the model allows for testable assumptions to be made about the neurophysiological correlates involved in RF facilitated through flexible biobehavioral synchrony with techniques outlined in more detail below (Fig. 3).

Assessments

For a flexible and active conceptualization of RF we consider the following tools as potentially helpful for future studies (see also Table 1). Given the context- and age-sensitivity of RF, measures of RF should not only focus on the individual itself, but need to consider the environmental context, the significant social relationships, as well as the individual's current life stage including the

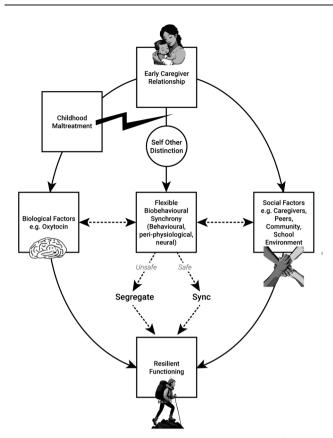


Fig. 3 A context-dependent and value-based model of resilience facilitation through flexible biobehavioral synchrony after maltreatment. Figure 3 shows our proposed model in which RF is crucially dependent on the individual's capability to flexibly synchronize with and segregate from another's cognitive-affective, behavioral, and physiological states, known as 'biobehavioral synchrony'. Such an adaptive interpersonal skill is rooted in i. the early caregiving experience and its regulatory effects on an individual's physiological stress reactivity, as well as ii. the development of SOD which can be affected by childhood maltreatment. Flexible biobehavioral synchrony exerts its effects on RF in direct (i.e., synchrony profiles guided by cost-benefit analyses), as well as indirect ways (e.g., interplay with an individual's neural function and social architecture). Assuming a cascading effect on domains of SOD we hypothesize that experiences of maltreatment impact an individual's capacity to flexibly deploy interpersonal synchrony according to situational and developmental demand (synching or segregating), increasing the risk for emotional fusion or cut-off with others and subsequent relational difficulties and stress throughout an individual's life.

maturation of his/her cognitive and emotional skills. Advancing the study of RF in the light of biobehavioral synchrony thus requires developmental-sensitive assessments of the transactional interactions between person and environment. Several questionnaires for RF have been developed and also adapted to different age groups, including adolescents and whilst some are based on ecological models and include the connectedness and availability of a supportive environment (e.g., family or wider community), questionnaire assessment of RF as a truly interactive process is still scarce. Self-report measures that explicitly assess aspects of social interaction experiences, including aspects of SOD such as "identity fusion" in romantic or close relationships (e.g., the inclusion of other in the self scale) [190] might be helpful. Such assessments should be supplemented by developmentally appropriate experimental assessments of SOD based on the common coding theory, for example through experimental paradigms of inhibition of automatic imitation of others' actions [156]. It is essential to

| Table 1. Implications for measurement tools of RF. | neasurement tools of RF. | | | |
|---|--|---|--|---|
| RF is | Requirements | Questionnaires | Observational measures | Experimental set-ups |
| A flexible and active process Developmentally-dependent Context-dependent | dynamic interplay between the individual and social environment Focus is not on the individual, but is embedded in social networks Repeated, longitudinal assessments Assess SOD Assess flexibility to push into vs. pull out of interpersonal synchrony | • Measure the experienced closeness in pair-bonded relationships • Use questionnaires that assess the quality of social contexts from developmentally relevant ecological domains (e.g., family, peers, school) • Do not rely on a single self-report questionnaire; make use of dyadic questionnaires • Include scales for family and/or community adjustment • Use scales that are developed to capture dynamic adaptations to social | • Assess flexibility rather than aggregate scores during observation, such as in- and out gaze, touch, and motor synchrony • Assess dyadic and group interactions with significant others according to developmental stage • Focus on the quality of context (e.g., coding of sensitivity/hostility during interaction) instead of merely relationship status (e.g., single or stable partnership) | • Include experimental paradigms to assess self—other distinctions (e.g., automatic imitation) according to developmental stage • Consider meta-stable interpersonal synchrony in behavioral, physiological, and neural data • Use ecological momentary assessment strategies • Use micro-coding of interaction behaviors (continuous coding instead of average measures) |

Assessment tools of RF require culturally/community-sensitive, multimodal, and multi-scale assessments across behavioral, physiological, and neural levels

confirm that tools are sensitive to interindividual differences and provide age-specific equivalents in order to validly and consistently capture identical cognitive-affective functions. This necessitates studying measurements tailored to specific ages for consistent concepts over periods, analyzing their associations with other indicators, and bolstering collaboration between labs to standardize testing techniques (see also [191]).

Considering RF in light of the flexible biobehavioral synchrony model also requires assessments of multimodal biobehavioral synchrony paradigms during exemplary interaction situations. For example, assessing RF in the social context of threat might be measurable as the ability to engage in, and synchronize with potentially non-threatening and caring interaction partners, while actively disengaging from interpersonal synchrony in response to an interaction partner sending signals of threat. Assessing RF in the social context of deprivation by contrast might be assessed by flexibility indices of multimodal biobehavioral synchrony in response to different cooperative and emotionally evoking situations.

With respect to data analytic challenges, this conceptualization requires novel and innovative tools for future empirical studies. The current conceptualization of RF calls for advanced statistical techniques to capture these complexities (see also [10] for statistical recommendations according to complexity theory). To account for developmental and context-dependent changes in RF, structural equation modeling which allows the integration of multiple levels of data over time, and Latent Growth Curve Modeling, which captures changes over time, as well as Network Analysis, which examines interrelationships among variables might be promising techniques.

In the past, most studies on biobehavioral synchrony focused on aggregated parameters of synchrony, i.e., the total or average amount or on phases during which the highest level of synchrony is reached, but the current conceptualization of resilience as a dynamic process of engaging in and disengaging from synchrony accordingly requires analyses of such dynamics. This requirement applies across timescales, ranging from biobehavioral synchrony measures in milliseconds to the entire lifespan. For example, methods that are capable of catching sequential biobehavioral synchrony processes, such as Granger causality or partial directed coherence, allow analyses of how one time series influences the time series of another person in multivariate data analyses. It might be particularly promising to analyze whether more resilient subjects more often are leaders or followers when moving into or out of synchrony during different social interaction contexts. Mayo and Gordon [192] recently suggested novel synchrony analyses following the idea of complex dynamical systems. At the core of this model is the concept of meta-stability as a marker of such a flexible interpersonal system. Furthermore, as there is growing evidence that the synchrony of body and mind is distinct and their relationship is dependent on context [193], another methodological challenge concerns the complete multimodal assessment and analysis of multimodal biobehavioral synchrony data. There is evidence that different measures of biobehavioral synchrony follow different time scales, for example, synchronized neural activity was found in a much faster timescale (milliseconds) than behavioral synchrony. It is thus conceivable that such processes might be dynamically linked but need to be analyzed within a multi-level design to reach a better understanding of this complex relationship and how it relates to RF. Finally, according to conceptualizations of resilience as a dynamic and active process, it is also important to assess this process from a life-span perspective.

Implications for prevention programs and targeted interventions

A better understanding of RF within the model of flexible biobehavioral synchrony might also be informative for personalizing programs to foster RF after childhood maltreatment. We suggest that targeting RF in the individual's social context and addressing both, psychological and neurobiological aspects in interacting subjects simultaneously might lead to more effective prevention and intervention programs. As outlined above, we consider that RF benefits if the program moves beyond single subjects but includes significant others, spanning the whole social network or even community level. Here, we will briefly outline some preliminary findings, mainly derived from proof-of-concept studies, based on the model proposed here which might stimulate further clinical trials targeting resilience in the future.

The pivotal role of the rTPJ for biobehavioral synchrony and SOD suggests a potential avenue for neuro-based interventions targeting rTPJ to augment RF. Using transcranial direct current stimulation (tDCS), Santiesteban and colleagues [194] showed that excitatory (anodal) stimulation over the TPJ improved both, the control of imitative tendencies (i.e., distinguishing in favor of selfrepresentations) and visual perspective-taking (i.e., distinguishing in favor of other representations). At the same time, it did not affect social judgments which did not lead to a conflict of self and other representations, thus highlighting the potential for tDCS to be used as a tool to aid SOD also in clinical populations. However, on a more critical note, the evidence for potential enhancement through tDCS is promising but mixed and many tDCS studies have reported no significant enhancing effects on other complex socio-cognitive abilities including theory of mind, empathy, emotion recognition, and joint attention [195-198]. Furthermore, Kohl et al. [199] showed that the rTPJ can also be specifically enhanced by fNIRS-based neurofeedback. Interestingly, while this study showed that reorienting of attention improved after four daily training sessions in healthy adult subjects, no specific effect was found for perspective-taking and SOD. Thus, enhancing TPJ functions does not automatically lead to improved SOD. A remaining question is whether or not the flexibility to push into and segregate from synchrony can be enhanced specifically, either by behavioral training or pharmacologically (e.g., via oxytocin stimulation), via dual brain stimulation (e.g., by simultaneous transcranial altering stimulation (tACS), or via synchronybased physiological or neural neurofeedback.

On the behavioral level, several studies have shown that promising candidates for enhancing biobehavioral synchrony include (i) coordinating or synchronizing body movements [200], (ii) making music together [201] (see also [202], (iii) playing cooperative or interactive games (for a review [203], and (iv) engaging in shared eye contact or joint attention [204] (for a review see [205]). Future research should investigate if such interventions have the potential to stimulate patterns of biobehavioral synchrony which are characterized by rigidity and inflexibility or those characterized by hyper-synchronicity to more flexible and responsive synchrony patterns. This, in turn, could stimulate patterns of adaptive responding in dynamic social interactions in children who have experienced maltreatment.

On the pharmacological level, so far only a few studies demonstrated that maternal chemo-signals might increase biobehavioral synchrony between parents and infants and can also increase biobehavioral synchrony between an infant and an unfamiliar person [206]. Furthermore, the administration of intranasal oxytocin can effectively boost inter-brain synchrony [207] and promote behavioral synchrony in adult participants [208]. Another technique to manipulate biobehavioral synchrony in interacting individuals is to provide ANS-based feedback, for instance, based on heart rate variability. There is preliminary evidence that a dual feedback system may help to increase interpersonal synchrony in a therapeutic setting [209] or promote empathy and social entrainment between two people [210]. Besides heart rate variability, skin conductance has been used to provide (simulated) dyadic feedback [211]. Other studies have provided ANS-based biofeedback based on breathing rhythm [195, 196, 212]. As synchronizing and desynchronizing from arousal and Autonomic Nervous System (ANS) activity during close interactions might be particularly crucial for intergenerational transmission of maltreatment and for RF, such interventional methods are considered particularly promising for future trials.

Furthermore, brain stimulation can be used simultaneously in interacting subjects to directly modulate biobehavioral synchrony on the neural level. In a hyper-tACS protocol, the stimulation can be applied with the same or different frequency and phase. While same-phase-same-frequency stimulation is expected to enhance biobehavioral synchrony, different-phase-same-frequency or different-phase-different-frequency stimulation is expected to reduce biobehavioral synchrony. Modulation of inter-brain synchronization can either impair or improve joint action coordination [213] and thus might be particularly promising for supporting both, pulling into but also segregating from biobehavioral synchrony. Finally, preliminary evidence shows that simultaneous EEG-based neurofeedback can be applied to specifically modulate neural synchrony in interacting subjects. Fewer studies tried to employ neurofeedback based on simultaneous fMRI or fNIRS signals. Although these techniques are still in infancy they are promising candidate methods to personalize and manipulate the neural substrate of RF in interactive contexts.

CONCLUSIONS

In advancing our understanding and the promotion of RF following childhood adversity, it is imperative to delve profoundly into the interplay between ecological factors, particularly the micro-level social dynamic interactions, and individual neurobiological backgrounds. The complexity inherent in resilience research necessitates a bio-convergent approach, bridging the expertise of life sciences and data sciences. By fostering interdisciplinary collaboration, we can overcome the current barriers, enriching our understanding of biobehavioral synchrony, and its pivotal role in RF, especially in the face of early life adversity.

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AUTHOR CONTRIBUTIONS

KK and VP jointly conceived the work, reviewed and interpreted the existing data, and drafted and revised the final manuscript.

COMPETING INTERESTS

The authors declare no competing interests.

ADDITIONAL INFORMATION

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