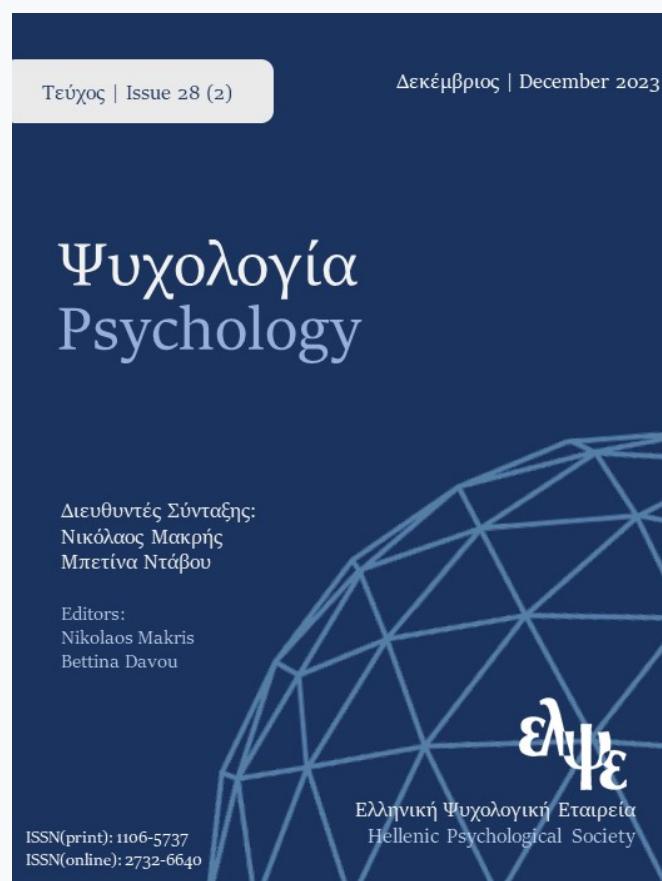


# Psychology: the Journal of the Hellenic Psychological Society

Vol 28, No 2 (2023)

Special Section: Nous: A powerful machine



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doi: [10.12681/psy\\_hps.36229](https://doi.org/10.12681/psy_hps.36229)

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## To cite this article:

Chrysochoou, E. (2023). Biological and cognitive mechanisms and the role of culture in theory of mind development: In need of an integrative, biocultural perspective?. *Psychology: The Journal of the Hellenic Psychological Society*, 28(2), 23-47. [https://doi.org/10.12681/psy\\_hps.36229](https://doi.org/10.12681/psy_hps.36229)

# Biological and cognitive mechanisms and the role of culture in theory of mind development: In need of an integrative, biocultural perspective?

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## KEY WORDS

Biocultural approach,  
Cognitive development,  
Culture,  
Evolutionary theories,  
Lifespan development,  
Mechanisms of development,  
Theory of mind

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## ABSTRACT

The present paper attempts a comprehensive approach to the biological, cognitive, as well as cultural foundations of theory of mind development. A critical analysis and synthesis of contemporary research findings serves as a basis for revisiting key theoretical accounts regarding the nature and development of this valuable sociocognitive faculty. Are the findings best interpreted within frameworks which consider developmental change and individual differences in the domain-general cognitive abilities (executive functions) that may underlie performance on theory of mind tasks (*processing account*)? Or is it more fruitful to discuss the development of theory of mind based on domain-specific mechanisms or capacities: an innate, modular mechanism that is underpinned by neurological maturation (*modularity theories*), or an inborn capacity to form naïve, intuitive theories about the mind, which are then subject to conceptual change as a function of experience (*theory theory account*), or a mechanism that serves simulations of mental states and related attributions (*simulation theories*)? Where possible, biological and neurocognitive processes, and experiential influences are discussed in combination. A disentanglement of general cultural influences from more proximal, social or familial effects on theory of mind development is also attempted. The aim is to highlight the value of an integrative, interdisciplinary approach to its study: a *biocultural perspective* could essentially serve this purpose by shifting attention to the interplay of biological, cognitive, and environmental forces shaping the lifespan dynamics of human theory of mind.

*Theory of Mind* (ToM) refers to an understanding of persons in terms of inner mental states (e.g., knowledge, beliefs, intensions, desires, emotions) that are causally linked with their behaviour (Beaudoin & Beauchamp, 2020; Brizio et al., 2015; Wellman, 2014). Such an understanding is representational, particularly in the case of beliefs and knowledge (i.e. epistemic mental states; see also Flavell & Miller, 1998), and is therefore shaped by idiosyncratic perceptions of the social world (see Sabbagh & Bowman, 2018). A great number of studies have so far examined when and how ToM capacities arise, which mechanisms underlie their development, and to what degree experiential influences shape the timing and sequence of achievements within individuals, as well as differences among them. Most investigations have been cross-sectional so far and have involved young children in behavioural measures of basic ToM capacities (Yu & Wellman, 2022). In particular, the study of children's appreciation that someone may hold a false belief has dominated the field, possibly due to the ease with which relevant tasks could be made natural for use with children (Wellman, 2018b). Parallel lines of research have focused on understandings of diverse desires, beliefs, or access to knowledge, and interpretations of hidden emotions over the early years (e.g., Wellman et al., 2006; Wellman et al., 2011; see also Sabbagh & Bowman, 2018).

*Developmental enough so far?* One might still ask, adopting Willem Koops' critical viewpoint when discussing with Wellman the data on age-related ToM achievements back in the nineties (see Wellman, 2012). Over the last decades, there have been efforts to increase the amount of longitudinal data, regarding childhood at least, since relevant evidence for adolescents or adults remains scarce (see Valle et al., 2015; Wellman, 2018b). Moreover, in cross-sectional studies, researchers have attempted more comprehensive assessments of ToM

capacities to explore the increasingly complex and differentiated understandings of mental life in older children (Devine, 2021; Hughes & Devine, 2015; Osterhaus & Koerber, 2021), and more recently, in adolescents (Bosco et al., 2014; Brizio et al., 2015; Lagattuta & Kramer, 2021; Sebastian, 2015), and adults of different ages (Laillier et al., 2019; Lagattuta et al., 2018; see also Mahy, 2018; Wellman, 2018a). Among more advanced ToM capacities, researchers have mostly focused on complex perspective-taking and higher-order belief understandings (e.g., reasoning about a person's belief regarding someone else's belief, or about someone else's belief regarding the first or a third person's beliefs; in second- and third-order belief tasks, respectively). They have also shed light on the differentiation of justified from unjustified beliefs, and accidental from intentional harms, as well as on the comprehension of non-linear speech (e.g., sarcasm, irony), the interpretation of ambiguous social information, and recognition of social blunders (faux pas), reasoning about people's behaviours in social and moral contexts, or more refined decoding of facial expressions to interpret hidden emotions (see systematic review in Osterhaus & Bosacki, 2022). Emphasis is now placed on the development of age-sensitive ToM measurements and the exploitation of refined statistical methods to test cascades of mental state understandings (e.g., via scaling methods; see Peterson & Wellman, 2019) and ToM trajectories through the lifespan (e.g., via multinomial processing tree model application on data from *continuous* versus *dichotomous* tasks; see work by Coolin et al., 2017 below). A promising line of research is currently being drawn.

In parallel, cross-cultural studies have revealed a significant degree of universality, but also certain variations in early ToM timelines (e.g., Selcuk et al., 2022; Yu & Wellman, 2022; see also Wellman, 2018b). Yet, we still know little about the possible sociocultural modulation of advanced ToM capacities in phases of continuing sensitivity for relevant information processing, such as adolescence or emerging adulthood, or as a function of phase-specific adaptive demands over the course of life (see Bjorklund & Blasi, 2015; Brüne & Brüne-Cohrs, 2006; Valle et al., 2015). Even if mostly cross-sectional, a cumulative amount of behavioural data has allowed researchers to test focal hypotheses regarding the mechanisms that may underlie age-related change and the factors that could explain individual differences in ToM. Recent calls stress the need for more systematic assessments of ToM, over extended age periods and across sociocultural settings, which will serve on the one hand, to disentangle existing theoretical frameworks and on the other, to generate more integrative accounts of ToM development (e.g., Brizio et al., 2015; Devine, 2021; Devine & Lecce, 2021; Saxe, 2013; Sommerville & Decety, 2016; Warnell & Redcay, 2019; Wellman, 2012, 2017, 2018a,b; Yu & Wellman, 2022).

Additionally, studies employing neuroscientific measurements have started to offer valuable insights into the nature and function of the mechanisms driving change and individual variation in ToM. Yet, non-invasive neuroscientific assessments (e.g., EEG or fMRI) are needed to explore the understudied neurocognitive bases of ToM development from early childhood to adolescence and emerging adulthood. There is evidence to suggest that changes in the social brain support change and refinement in ToM throughout these periods (Blakemore, 2012; Blakemore & Mills, 2014; Lagattuta & Kramer, 2021). A lifespan perspective on the neurocognitive underpinnings of ToM is also being prioritized, given the adaptive neuroplastic brain changes observed over adulthood, especially during the silver years (Dunbar, 2003). There are indications, for example, that ToM abilities may function independently from general cognition and remain relatively spared with aging (e.g., Happé et al., 1998; see also Henry et al., 2013), as compensatory mechanisms take action to support older individuals in remaining socially active (e.g., greater reliance on social wisdom; Moran, 2013). The study of the neurocognitive mechanisms driving developmental change in ToM over the lifespan constitutes an exciting work in progress (see Baglio & Marchetti, 2016; Bernstein, 2018; Mahy, 2018; Wellman, 2018b).

Considering the above, the present paper attempts a comprehensive discussion of biological, cognitive, as well as cultural determinants of ToM development. Based on a synthetic-critical review of recent evidence from each line of work, key accounts of ToM development are revisited and discussed. Are the developmental patterns observed better explained when the domain-general resources (e.g., executive functioning – EF; e.g., inhibition, shifting, or working memory) that could support negotiating the demands of ToM assessments are taken into consideration (*processing account*)? Or are they better accounted for by domain-specific views of ToM, suggesting an innate, modular mechanism supported by neurocognitive maturation (*modularity theories*), or an inborn capacity to form naïve, intuitive theories regarding persons' minds, which are then revised via experientially driven conceptual change (*theory theory account*), or mechanisms that specialize in the simulation of others' mental states and related attributions (as *simulation accounts* propose)? Where possible, discussion focuses on the interplay of biological, neurocognitive, and experiential processes underlying ToM development. A disentanglement of general cultural effects from more proximal, that is social or familial, influences on ToM

development is also attempted. It is suggested that an interdisciplinary approach to the study of ToM development (see Beaudoin & Beauchamp, 2020; Bernstein, 2018; Wellman, 2017, 2018b), and the adoption of an integrative, *biocultural* perspective in particular (see Lightfoot et al., 2018), has the potential to serve a deeper examination of universality versus specificity in the developmental, lifespan dynamics of ToM, therefore, enlightening us on the true nature and origins.

### **Recent evidence on the biological and cognitive mechanisms of change in ToM and key developmental accounts revisited**

Recent work regarding the mechanisms underlying developmental change in ToM has inevitably informed discussions of its biological underpinnings and innateness within an evolutionary developmental psychology framework (e.g., Tooby & Cosmides, 2016; Bjorklund, & Blasi, 2015; Buss, 2015; Krill et al., 2007). The capacity to understand others in terms of mental states - most highly developed among humans (Saxe, 2013) - has been regarded as an adaptive response to the increasingly complex social environments of our species over evolutionary time (Brüne & Brüne-Cohrs, 2006). An information processing module that is specialized in understanding mental states is assumed to have been selected in humans, as it reliably produced behaviour that facilitated problem solving in the social setting. For our species in particular, the latter is suggested to regard social cooperation, rather than competition (see Frith & Frith, 2007). As Tomasello suggests, a capacity for social and mental coordination in humans was supported by a species-unique dual shift from motivations of the individual to motivations of joint and collective intentionality, linked to the evolution of *Homo Heidelbergensis* and social life in larger groups of self-aware individuals (see Tomasello, 2018a, 2018b, 2019; see also Tomasello & Gonzalez-Cabrera, 2017).

Tracing the evolutionary origins of ToM through the study of its neural and cognitive underpinnings has led to the suggestion that it might have actually co-evolved with human capacities to monitor motion and imitate behaviour in social environments. Specifically, understanding others' mental states has been found to activate regions in the medial prefrontal cortex, the temporoparietal junction (bilateral), the precuneus (medial aspect of the posterior parietal lobe), and the temporal lobes (see Carrington & Bailey, 2009; Molenberghs et al. 2016; Schurz et al., 2014; Wellman, 2018b). The temporal lobes, for example, are also activated by observation of intentional movements around us, and even, by photographs implying motion (e.g., Brüne & Brüne-Cohrs, 2006). The same regions contain mirror neurons, which are suggested to support our capacity to imitate others' actions as well as to infer action-goal states (e.g., Williams et al., 2001). The evolution of our capacity to simulate others' mental states might be seen as related. There is also evidence to suggest common neural systems (e.g., involving areas in the frontal lobes, as well as sites in the temporal and parietal cortex) employed in the innate foundation of joint attention and sociocognitive mentalizing, with individuals with Autism Spectrum Disorder (ASD), for example, showing a developmental continuity in relevant impairments (Eggebrecht et al., 2018; see also Chan & Han, 2020).

Such evidence, along with data showing maturation of specialized neural networks from infancy to support the emergence of mental state concepts (Leslie, 2005; see also Baillargeon et al., 2010), seem aligned with *modularity* accounts of ToM development. Relevant to Fodor's (1983) modular organization of the human mind, a domain-specific, and neurocognitively *hard-wired* module has also been suggested for mental state reasoning (see Mahy et al., 2014). Evidence that ToM is selectively impaired among mental capacities in individuals with ASD (e.g., Baron-Cohen, 2008) has been approached as consistent with its modular nature (though a domain-general account of mentalizing difficulties in the specific population is discussed below).

In a dominant modularity account, Leslie and colleagues (e.g., German & Leslie, 2000, 2001; Leslie et al., 2004; Scholl & Leslie, 1999, 2001) have related ToM development to the early emergence of a *ToM mechanism*, which matures as early as the second year of life as part of the core architecture of the human brain. Further, age-related performance improvements in behavioural ToM assessments, Leslie and colleagues argue, are due to an inhibitory selection process, which allows increasingly improved coping with relevant (executive) task demands (see also Mahy et al., 2014). In consistence, based on recent EEG evidence, Richardson and Saxe (2017) attributed the emerging success of four-year-olds' on false belief tasks to both maturation of brain regions in the ToM network (the right temporoparietal junction and the dorsomedial prefrontal cortex), as well as online recruitment of regions involved in EF to support task performance. It should be noted, however, that the conceptual continuity of ToM from infancy to childhood remains an open debate. The picture has become less clear recently since meta-analytic evidence pointed to significant variability in the results of earlier studies (e.g.,

Barone et al., 2019), and studies with larger samples and better control conditions have suggested that the reliability of previous findings regarding early ToM capacities at least (e.g., false belief understanding) might be more constrained than previously recognized (see discussion in Poulin-Dubois & Goldman, 2023).

Yet, wouldn't the function of a *hard-wired* ToM module be reflected in a consistent, selective activation of specific brain regions or of a common network across mental reasoning occasions and periods of development? Research evidence does not indicate such clear mapping. Children largely recruit the same brain regions that adults do when reasoning about others' mental states only after six years of age (Richardson & Saxe, 2017). In line, the tempoparietal junction, a brain region that has been related to a ToM module (and ToM reasoning more generally), seems not consistently dedicated to ToM reasoning in the early years; it actually shows increasing selectivity towards late childhood (see Mahy et al., 2014). Moreover, the regions dedicated to ToM and EF do not overlap to a degree that would be consistent with Leslie and colleagues' (German & Leslie, 2000, 2001; Leslie et al., 2004; Scholl & Leslie, 1999, 2001) suggestion for an inhibitory selection process driving ToM improvements during the preschool period; neither would such evidence be aligned with the *processing* account of ToM development, which will be discussed below. Actually, despite a relatively clear mapping of the neural correlates of inhibition in children's and adults' brains (e.g., Durston et al., 2002; Vara et al., 2014), researchers have not consistently related performance improvements in ToM tasks during the preschool years with increased recruitment of a neural region that is specifically dedicated to inhibitory selection, rather than ToM more generally (see Mahy et al., 2014). Further, in the Rothmayr et al.'s (2011) study with young adults, inhibition and false belief assessments recruited both common (bilateral tempoparietal junction included) and distinct neural regions (e.g., bilateral precuneus, or the same areas but in different hemispheres). More generally, we lack studies that examine the innateness and domain-specificity of a mechanism for the meta-representation of mental states as a function of either developmental continuity in the activation of brain networks or adaptive challenges over wider age periods and through the lifespan. As discussed in the following section, evidence from the limited so far cross-cultural investigations suggests a significant degree of universality at least with regard to early ToM developmental patterns. However, certain variation has also been observed across locales in the timing and sequence of early achievements, which could not be easily accounted for by modularity theories of ToM development, unless, as suggested below, culture-gene co-evolution processes are considered.

Within another prominent nativist account, our desires, beliefs, and intention concepts are not introduced into the cognitive system by a mechanism. They are considered parts of a core system of knowledge, which emerges early on in life and equips children with intuitive or *naïve* theories regarding persons' minds (e.g., Gopnik, 1993; Perner, 1995; Wellman et al., 2001). According to this *theory – theory* account, rudimentary theories are revised – as any theory would – when they fail to predict the outcomes observed. Given such conceptual change as a function of experience, children become more efficient in reflecting on and reasoning about the unobserved, inner mental states (e.g., desires, beliefs, goals, intentions), which, based on the *theory's* general principle, constitute the causes of peoples' behaviour (e.g., Wellman, 2014; Wellman & Gelman, 1998). For example, 5-year-olds' success in false-belief tasks (e.g., such as the *Sally-Ann change-of-location* task) is attributed to a conceptual shift in understanding that others' beliefs, which influence their behaviour, might differ from one's own true beliefs (see Wellman et al., 2001).

Could developmental milestones in ToM that pertain to conceptual change be underpinned by neurocognitive maturation? Microgenetic studies have indicated conceptual restructuring of false belief understanding (rather than sudden insight, e.g., Amsterlaw & Wellman, 2006) due to direct experience of prediction-outcome mismatches (Flynn et al., 2004). Interestingly, dopamine has recently been suggested to play a significant role in signaling such mismatches, therefore, catalyzing *theory* change. In a relevant review, Sabbagh (2017) discusses data from studies that have investigated the formation of predictions by participants over a series of trials, as well as the signaling of relevant violations to update predictive mechanisms and recalibrate beliefs. He concludes that dopamine signaling can contribute to such adjustment and anchoring processes related to ToM reasoning. It would be fruitful to test the dopamine – *theory* revision link, within other conceptual change contexts (e.g., regarding notions of number or the learning of science; see Carey, 2009; Kyriakopoulou & Vosniadou, 2020). In parallel, EF has been suggested to facilitate conceptual change by supporting reflection upon the experiences of prediction-outcome mismatches and learning from them (Benson et al., 2013). It is noted that age-related changes in EF have also been related to dopaminergic functioning (Zhang et al., 2015), whereas dopamine-based modulation (of frontal systems in particular) has been associated with the development of executive dysfunction (e.g., in individuals with autism, see Kriete & Noelle, 2015). As will be commented below,

there is cross-cultural evidence to support the conceptual change account. Links have been drawn between factors that can mediate sociocultural influence on early ToM development (e.g., interaction patterns) and genetically-driven functional changes in the brain, which regard dopamine binding; and therefore possibly the signaling of prediction-outcome mismatches.

Viewed from an alternative perspective, evidence relating the neural underpinnings of mentalizing and domain-general cognitive capacities (e.g., EF or working memory; Carlson et al., 2002) has constituted the basis of the *processing* (or *executive*) account of ToM development (see Mahy et al., 2014; Richardson & Saxe, 2017; Sabbagh, 2017). According to the latter, differences in performance on ToM tasks, both within individuals as a function of age as well as among individuals, simply *unmask* variation in the differentiation and efficiency of the higher-order mental abilities that the tasks necessitate (predominantly inhibition). In a recent meta-analysis focusing on the preschool years, Devine and Hughes (2014) concluded on a moderate association between false belief understanding and EF, which was actually evident across cultural contexts. This association was also largely consistent across EF tasks, but not for all types of false belief tasks employed. Moreover, an asymmetrical pattern was observed, with EF predicting false belief understanding, rather than vice versa. On this basis, the researchers suggested a hybrid *expression-emergence* account: the observation of associations between the EF and false-belief domains in early childhood seems task-dependent to a degree, but the emergence of children's ability to reason about mental states seems driven by EF development. Although we lack longitudinal data regarding more advanced phases of development, there is cross-sectional data showing aligned age-related increases in recognition of social transgression (as reflected in a *faux-pas* task) and in inhibition within adolescence and young adulthood (see Meinhart-Injac et al., 2020). Moreover, recent evidence suggests that declines in performance across ToM tasks with aging reflect increasingly compromised EF, rather ToM competence *per se* (in line with Grainger et al., 2018).

Recently, there have been attempts to directly test the processing against the conceptual change account in studies employing more sophisticated methods to tap the lifespan dynamics of ToM development, while efficiently controlling for task-dependent cognitive processing. Past studies have mostly used *dichotomous* tasks, where participants must inhibit one alternative to select the other (e.g., in change-of-location false belief tasks). However, relevant data from older children, adolescents or adults is subject to ceiling effects (see Brizio et al., 2015). In an attempt to overcome such barriers, Coolin et al. (2017) applied a multinomial processing tree model on the data obtained from 3 to 92-year-olds via a *continuous* change-of-location false belief task (the *Sandbox task*). The results were aligned with the processing hypothesis. On the one hand, in line with the developmental trajectories suggested for domain-general cognitive capacities (see De Luca & Leventer, 2010; Best & Miller, 2010), difficulties in suppressing knowledge of the object's actual location (interference parameter) were more pronounced among preschoolers as well as older adults. On the other hand, when accounting for task-specific cognitive processes (interference and memory), age groups did not differ in their capacity to reason about the mental state of a naïve protagonist; neither did mental state reasoning increase across the preschool years (in contrast to the conceptual change hypothesis). Consistent patterns were observed in the case of the memory parameter studied (for the hiding locations). Further use and development of such paradigms can allow testing whether the ToM and EF association remains stable over the course of life, or it increases in specificity from early childhood to adulthood, as a function of EF differentiation.

The processing hypothesis could also be discussed on the basis of evidence regarding structural and functional changes in the brain. With increasing age, ToM reasoning has been suggested to involve an increased amount of cortex, as well as to rely on less diffuse activations (Bowman & Wellman, 2014) and a stronger physical interconnection of the regions in the ToM network, which allow faster and less noisy communication among them (see Richardson & Saxe, 2017; see also Saxe et al., 2009; Wellman, 2018b). Yet, functional shifts of such an extent with age would not be aligned with mere dependence of ToM reasoning on either EF development (or language development, e.g., Baillargeon et al., 2010) or cognitive decline with aging (e.g., Maylor et al., 2002; see also Happé et al., 1998). Indeed, several researchers have shown that EF is only weakly to moderately associated with performance in ToM tasks (see German & Hehman, 2006; Osterhaus & Bosacki, 2022; Vetter et al., 2013; Wang et al., 2016). Moreover, as will be further discussed below, cross-cultural variation in ToM developmental patterns has been found independent of cognitive load. And although the development of inhibitory control - and EF more generally - might be differentially prioritized across cultural settings (e.g., as a function of socialization goals and practices), ToM developments are not differentiated across cultural settings characterized by distinct

EF trajectories (e.g., see evidence regarding inhibitory control and ToM development in children from East Asian and Western cultural settings in Wang et al., 2016; see also Sabbagh et al., 2006).

Experiential effects on ToM development might be better explained in the context of a fourth account. Accumulated experience with age can result in more efficient and automatized perspective taking and evaluative processing, which are central in mental state reasoning, as well as in the enrichment of knowledge and episodic memories pertaining to the self within its social environment. Specifically, according to the *simulation* account (e.g., see Gallese, 2007; Gallese & Sinigaglia, 2011; Goldman, 2006, 2009; Harris, 1992), individuals more accurately attribute mental states to others with age, as they gain direct access to an increasing base of knowledge regarding their own minds, and are therefore facilitated in imagining themselves in others' positions (see also Mahy et al., 2014). This account also suggests domain-specific mechanisms underlying ToM development. Actually, there have been suggestions that the *theory-theory* and *simulation* approaches to ToM development are not necessarily incompatible with each other: interaction patterns observed at a neural level imply an at least partial cerebral implementation of self-perspective in the context of ToM tasks (e.g., Vogeley et al., 2001). Yet, the domain-specific mechanisms suggested by the simulation account are aimed to serve change in mental states' simulations and attributions with age, rather than the adoption and revision of a theory or functional change of a ToM module (see Carruthers, 1996).

Aligned with the specific account would be data showing maturation of specific neural networks - as reflected in the increasing speed and strength of their activation - as well as continuity and consistency in their function across age periods and simulation occasions. Still, as also noted when discussing Leslie and colleagues' modularity account (the *ToM mechanism* hypothesis), research evidence does not indicate such clear mapping. Moreover, Mahy and colleagues (2014) point to two neural systems that might be involved in mental states' simulation: the cortical midline structures, which are suggested to support controlled, evaluative processing regarding the self and others (e.g., see Saxe et al., 2006 for their activation in both self-evaluation and false belief tasks), and the putative mirror neuron system, which activates to the actions, intentions, and emotions of the self or others in both children and adults. On the one hand, these systems have been found to be underactivated in sociocognitive assessments involving individuals with ASD (Dapretto et al., 2006). The *broken mirror* theory of autism (Southgate & Hamilton, 2008) in particular suggests abnormal activation of the frontal and parietal brain regions with mirror neurons (the neural correlates of imitation). On the other hand, such reduced or abnormal activation patterns are not necessarily linked to difficulties in mentalizing via simulation; they might relate to domain-general cognitive deficits (e.g., regarding EF or working memory capacity; see Korkmaz, 2011; Naveh-Benjamin & Cowan, 2023; Ozonoff et al., 2007; see also Wilkinson & Ball, 2012) or to linguistic deficits that characterize the specific population (see Mahy et al., 2014). As noted above, such deficiencies could at least partially account for poorer performance in ToM assessments. Finally, individuals in the spectrum often perform effectively on tests of mental state understanding (see Wilkinson & Ball, 2012). As a result, there have recently been suggestions to move beyond the *broken mirror* theory of autism towards cognitive models that might better account for the poorer social capacities of individuals with ASD (Gerrans & Stone, 2008; see also Wilkinson & Ball, 2012).

Beyond evidence regarding ASD, the simulation account has actually been questioned on the basis of recent neuroscientific data. According to Saxe (2009), evidence shows that co-opted mechanisms (e.g., online activation of one's own motor control systems when observing other's actions, or one's emotional representations when observing corresponding expressions on others' faces) can lead from one individual's mental state (e.g., a belief or desire) to a matching state in an observer. There are also findings indicating that attribution mechanisms support mental state attributions. Yet, as Saxe notes, there is no evidence showing that the latter receive their input from the co-opted simulation mechanisms, nor that shared mechanisms are used for attributing mental states to both the self and the others.

Overall, recent evidence has started to shed valuable light on the evolutionary underpinnings, as well as the neural and cognitive mechanisms explaining age-related change and individual differences in related capacities. Such data remains correlational to its greatest extent, as longitudinal or training studies remain scarce. There are also few studies with non-invasive assessments of ToM-related neural patterns during the early years, or studies adopting a lifespan perspective in the study of ToM (see Bowman & Wellman, 2014; Coolin et al., 2017; Sabbagh et al., 2006; Sebastian, 2015; Warnell & Redcay, 2021). The increasing relevant evidence has started to allow a critical discussion of key theories regarding ToM development. However, as Brizio et al. (2015) note, although innate forces might guide early sociocognitive achievements to a significant degree, individuals may

develop variable sociocognitive profiles with increasing age and accumulated experience, across or even within settings. The section that follows focuses on the sociocultural modulation of ToM timelines, summarizing recent evidence and discussing it within the same developmental accounts. Though this line of research has not yet greatly met with work on the neurocognitive underpinnings of ToM, it is suggested that adopting a more integrative, possibly biocultural, perspective is necessitated to efficiently tap the innateness and universality, or the context-specificity and adaptive variation of human ToM understandings.

### **Recent evidence on the sociocultural modulation of ToM timelines and key developmental accounts revisited**

The value of a cross-cultural approach to the study of ToM development has been stressed from the nineties (e.g., Gopnik & Wellman, 1994), when sharp age trends and absolute, universal patterns were questioned (e.g., Mitchell, 1996; see also Lillard, 1998, 1999). Although relevant data has increased over the last decades, it remains focused on early, rather than more advanced ToM achievements. As with the neuroscientific evidence discussed above, how valuable has cross-cultural research proved in informing us about the nature and development of human ToM, and in disentangling key relevant accounts?

On the one hand, a *theory theory*, conceptual change account, could be seen as consistent with both early competence in understanding others in terms of mental states (e.g., Callaghan et al., 2005; Wellman et al., 2001), and certain modulation of relevant timelines as a function of experience and knowledge acquired (e.g., Gopnik & Wellman, 1992; Perner, 1995; see also Giovagnoli, 2019). Even if a specific, possibly universal set of ToM insights is expected active early on, significant differences among contexts in the social and conversational experiences that pertain to mental states might be translated to accumulated variability in related conceptual change, and therefore ToM progressions (see Wellman et al., 2006; see also Wellman et al., 2001).

In line, research with young children has revealed a certain degree of variation in the timing and sequence of early developmental milestones across locales. For example, slight delays have been observed in false-belief timelines across *non-Western* settings. In a first, influential meta-analysis Wellman et al. (2001) concluded that 3.5-year-old Japanese children were 40% correct in relevant assessments, relative to 50% and 69% reached by peers in the U.S. and Australia respectively. In the Naito and Koyama (2006) study Japanese children also showed prolonged achievement of false-belief understanding, evident at 6-7 years of age. In a more recent meta-analysis of data from studies in China and North America, Liu et al. (2008) concluded on parallel trajectories from below- to above-chance performance in false-belief tasks over the early years, which varied, however, by two or more years across settings. Moreover, Mayer and Träuble (2013) observed no succeeding majority among children in the Polynesian island of Samoa before 8 years, with one third of the 10-13-year-old participants still failing in a change-of-location task. In contrast, children from Canada, Peru, Thailand, and India in the Callaghan et al. (2005) study were found to improve considerably between 3 to 5 years, as is typically the case with *Western* populations. The same age trend was not observed, however, in a fifth sample from Samoa, in consistence with the aforementioned findings regarding this population, whereas Vinden (1996) reported poor false-belief attainment among 4- to 8-year-old children from Peru (Junin Quechua children in the highlands; see also Vinden & Astington, 2000).

Variation in the sequence of early ToM milestones has also been observed across locales. Wellman and colleagues (Wellman et al., 2006; Wellman et al., 2011; see also Wellman, 2012, 2018b) have shown that children from individualistic cultures (e.g., U.S. or Australia) as well as peers from a collectivist context (Chinese) first appreciate diverse desires among individuals (even for the same things), before understanding representational mental states, such as knowledge and beliefs in other people. Still, according to Wellman and colleagues although the second milestone for children from individualistic cultures was understanding diverse beliefs about a situation, and the third concerned appreciation of differences in people's access to knowledge, the opposite sequential pattern was observed among Chinese peers. The milestones that follow were found synchronized, however: children from both individualistic and collectivist settings developed false-belief before hidden emotion understandings (see Wellman, 2012). Similar findings were obtained in a study comparing children from Iran (a collectivist setting) with Australian peers (Shahaeian et al., 2011).

What about cultural influences on more advanced ToM capacities, beyond childhood? Besides the inherent difficulty of cross-cultural investigations, methodological issues have set obstacles to a variety of findings (e.g., inappropriateness of dichotomous tasks for ToM assessments across wider age periods, as discussed above). A recent study by Bradford et al. (2018) involved young adults from both a collectivist setting (Chinese) and

Western contexts (U.K., USA, or Canada) in a computerized task requiring attribution of beliefs to either the self or another person. The groups were not significantly differentiated in terms of performance and the researchers suggested a common mechanism guiding belief understandings across settings, stressing the value of examining its neural signature. Nevertheless, the specific groups were not found to differ on individualism levels. A similar behavioural measure did not differentiate Japanese and American young adults in the Kobayashi et al. (2006) study either. However, a reduced sense of *self* versus *other* distinction was observed among the Japanese participants, consistent with the collectivist nature of their cultural context (see also Wu and Keysar, 2007, for more efficient perspective taking in Chinese versus American young adults). An interesting line of future work could regard recent suggestions for a possibly *biphasic* ToM developmental trajectory: a childhood phase, which is characterized by early prioritization of ToM gains and refinements (e.g., as a function of experientially-driven conceptual change; Peterson & Wellman, 2019), and an adulthood phase, in which accumulated sociocultural effects become gradually evident and individual variation is driven by both external and personal variables (e.g., motivation, lifestyle, sociocognitive stimulation, etc.; see Giovagnoli, 2019).

On the other hand, could performance variation across settings on ToM tasks be better explained by the *processing* account, suggesting masked effects of age-related gains or decline with aging in domain-general cognitive capacities? There are suggestions that the development of EF, and particularly that of inhibitory control can be differentially prioritized across settings as a function of prevalent socialization goals and practices. For example, Asian children have been found to outperform their Western counterparts on EF tasks in the preschool years (e.g., inhibition or set-shifting tasks; e.g., Lewis et al., 2009; Sabbagh et al., 2006) or over childhood and adolescence (e.g., see data regarding 4- to 9-year-olds from Japan and the U.S. in the Imada et al., 2013 study, and 9- to 16-year-olds from China and the UK in the Ellefson et al., 2017 study). On the one hand, as Wellman et al. (2006) note, inhibitory control (and reasoning) capacity would be expected to influence performance more greatly in a knowledge-access rather than a diverse beliefs task. As described above, understanding of access to knowledge has been found prioritized in Eastern relative to Western settings. On the other hand, cultural variation in sequence patterns was found independent of cognitive load in ToM assessments (e.g., the latter was controlled for in the scale tasks employed by Wellman & Liu, 2004). Moreover, if performance improvements in ToM tasks are underlined by growth in domain-general cognitive capacities and the latter has been found prioritized in Eastern (e.g., China, Japan) relative to Western settings (e.g., U.S, U.K.), how could one explain the slight delays described above in children's false-belief understanding within Eastern settings? Unfortunately, relevant discussion can't extend to other non-Western settings that have been the focus of ToM investigations (e.g., the Polynesian island of Samoa, Thailand, India, or Peru, mentioned above). To our knowledge, we lack data comparing domain-general cognitive processing timelines in these contexts relative to Western locales. Available data remains inconclusive. Yet, in line with the conclusion drawn in the previous section, it seems plausible to suggest that age-related change in domain-general cognitive abilities can't fully account for ToM developmental patterns within or across cultural settings.

The modularity account lies somewhere in between: suggesting both a domain-specific module driving ToM understandings, as well as maturational processes underlying related advances. This approach could explain patterns of universality in ToM development, shaped over evolutionary time. Still, would it leave space for experiential effects over the course of life? A ToM module would develop based on innately programmed neurological maturation (see Baron-Cohen, 2008; Leslie et al., 2004; Scholl & Leslie, 2001), with experience triggering its unfolding, yet not altering its nature or function (the latter might only be subject to related brain injury or disorders, e.g., ASD; Gerrans, 2002). However, the psychological mechanism of ToM is suggested to come in two forms: a basic, evolutionarily ancient capacity, which develops early on in humans, and is shared with non-human primates, as well as a meta-representational counterpart, which emerges slowly across human childhood (Rakoczy, 2022), and extends its refinement into adolescence and young adulthood, given accumulated social experience (Giovagnoli, 2019) and related adaptive changes in the social brain (e.g., Blakemore, 2012; Blakemore & Mills, 2014; Lagattuta & Kramer, 2021). Therefore, environmental modulation of this meta-representational capacity would be expected evident over adulthood (e.g., EF; Bardikoff & Sabbagh, 2017; Zelazo & Carlson, 2020; Nguyen et al., 2019). In line, the temporo-parietal junction - a brain region that has not only been related to ToM reasoning, but to a ToM module in particular (see Mahy et al., 2014) - has been found less activated among Japanese young adults, along with a reduced sense of *self* versus *other* distinction that is considered typical of collectivist contexts (Kobayashi et al., 2006). Relevant data covering the course of adulthood would be further informative.

Moreover, culture-gene co-evolution processes might have shaped ToM developmental patterns (Chiao & Blizinsky, 2010; Chudek & Henrich, 2011). Biology is suggested to create the conditions under which culture influences development, further informing and updating in turn its biological underpinnings (see Tomasello, 2019). As Chiao and Immordino-Yang (2013) note, to the extent that (a) social transmission of cultural practices, beliefs, and values results in cultural adaptations of perceptual systems in the brain pertaining to domain-specific mechanisms, and (b) genetic propensities facilitate that transmission, co-opted genetic and cultural selection mechanisms could shape the architecture and function of the mind. From such a viewpoint, besides accounting for universal patterns in ToM development over the early years, modularity accounts could also be regarded as compatible with certain variations in ToM timelines across locales. That is, early on in life, an innate module specialized in mindreading could serve to unite our inherently social, earliest communication attempts with cultural learning to facilitate social interaction and cooperation (Tomasello & Carpenter, 2007; see also Frith & Frith, 2007). In the various forms the latter takes within each setting, it further contributes to the construction of new and the refinement of existing perspectival representations of others' minds throughout development (see also Moll & Tomasello, 2007 for an evolutionary reading of the related *Vygotskian intelligence* hypothesis). This reciprocal process actually feeds the continuous intergenerational creation of culture itself (see Frith & Frith, 2007).

It is noted that such evolution-culture contributions to ToM development could be fruitfully discussed based on general cultural constructs (e.g., collectivism versus individualism societies) or culture-specific pedagogies, rather than in relation to *distal* (e.g., family size or SES) or *proximal* familial influences (e.g., parental practices or goals). Specifically, according to a *general culture hypothesis* (see Hughes et al., 2014), the observed differences in ToM timing and sequence could be accounted for by cultural variation in prevalent values and norms regarding behaviour, and the resulting everyday epistemologies (see also Wang et al. 2016). For example, later prioritization of diverse beliefs understanding in collectivist cultures has been attributed to the greater emphasis placed in such contexts on pragmatic knowledge (Tobin et al., 1989) in daily life (e.g., commenting more on *knowing* vs *thinking* in Chinese, relative to U.S. family or other close settings; see Bartsch & Wellman, 1995; Tardif & Wellman, 2000). Indeed, access to knowledge about shared norms, along with lower levels of tolerance for disagreements and assertions of independent belief (Selcuk et al., 2018; 2022) are prioritized in collectivist settings for social cohesion purposes; on the other hand, the epistemology of individualistic (Western-type) cultures is suggested to be primarily focused on beliefs and their truth or falsity, as well as on independence (e.g., Nisbett & Masuda, 2003; see also Wellman et al., 2006). Culture-specific information processing mechanisms mostly receive input from shared representations pertaining to rules and values regarding social interaction among collectivist contexts; whereas, more localized information processing styles, driven by personal experiences and mental states, are prioritized in individualistic settings (e.g., Naito & Koyama, 2006).

Cultural identity, namely a personal understanding of how the self is defined in relation to the overall cultural group(s) (Kroger, 2006; Schwartz & Pantin, 2006), might also be a variable of interest in future studies. Perceived cultural group membership, interdependence, and reduced prejudice (see Bourhis et al., 1997) have been positively associated with the frequency, as well as the accuracy of mentalizing in both individualistic and collectivist settings (see Rhodes & Wellman, 2017; Selcuk et al., 2022). There is also evidence to suggest that individuals are more likely to simulate the mental states of persons that they perceive as more similar to themselves and that the activation of neural networks involved in ToM reasoning might actually be moderated by such similarity patterns (Mahy et al., 2014). This could be viewed as consistent with the simulation account of ToM presented above, which suggests that individuals rely upon their own psychological states to project and make mental state attributions, and that adults' brains are more specialized than children's in simulating and reasoning about dissimilar versus similar others (Pfeifer et al., 2007; see also Mahy et al., 2014). Yet, evidence directly tapping the interplay of perceived cultural group membership and ToM development remains scarce.

In testing the cultural universality versus specificity of ToM development, attention has also been given to *pedagogical influences*: related to the cultural activity of schooling and related concepts (see Ratner, 1999), or to culturally selected pedagogical methods (e.g., in state schools, see Wang et al., 2016), or merely, to school entrance age and therefore accumulated schooling experience per setting (e.g., Hughes et al., 2014; see also Hughes & Devine, 2015). With regard to the former, there is evidence relating ToM development to children's understanding of the concepts of teaching and learning and their intentionality (see also Frye & Wang, 2008). In turn, an advancing ToM has been suggested to allow children to recognize stimuli as intended to be instructive and better grasp what teachers are attempting to convey (Frye & Ziv, 2005). Actually, besides relying on

observation and implicit learning in everyday settings (a one-way process) to develop mindreading capacities, children can significantly advance explicit ToM understandings via deliberately instructive interaction (a two-way process) that allows space for inquiry, reasoning, and reflection on the process (see Heyes & Frith, 2014). On that basis, pedagogy can be regarded as a mediator in the culture-ToM relation. Actually, as Frith (2008) argues, it was the metacognitive capacity - strongly related to self-consciousness - to recognize stimuli as intended to be instructive that has allowed humans to benefit from cultural learning. And pedagogical experiences have been directly related to human development, rather than to learning *per se*, which can be more generally served by social interaction (e.g., with peers or parents; see a relevant evolutionary reading of the Vygotskian theory in Nardo, 2021).

Shifting the focus to culture-specific pedagogies, in the first cross-cultural investigation regarding middle childhood Wang et al. (2016) suggested that the delay observed in the ToM achievements of a Hong Kong sample was not related to EF development (their performance was similar to that of peers from the UK), but to the application of a *drill-and-practice* pedagogy in the attended state schools. This method emphasizes mindless repetition, instruction following, and behavioural control. In contrast, performance on age-appropriate tests of ToM was higher among peers from the same area or the UK who attended British-type schools. The latter applied an *inquiry-based pedagogy*, providing more opportunities for students to interpret epistemic (e.g., false belief, memories, and knowledge or ignorance) or motivational mental states (e.g., intention, attention) as well as reflect on that process.

Finally, what if the collectivism versus individualism contrast is not serving the study of universality versus specificity in ToM development when viewed in isolation, as it disregards other, *distal* (e.g., family SES, parents' education, family size based on number of siblings, etc.) or *proximal* familial influences (e.g., parental goals and practices, interaction patterns and conversational references to mental states etc.) (Devine, 2021; Devine & Hughes, 2018; Kuntoro et al., 2013, 2017; see also Devine & Lecce, 2021)? In a recent study with 3- to 6.5-year-olds in Turkey, Selcuk et al. (2018) found that a minority of children did not demonstrate the early ToM achievements sequence that is typical of traditional, collectivist societies (e.g., Shahaeian et al., 2014; Wellman et al., 2011), but the pattern observed in individualistic cultures (understanding diverse beliefs before access to knowledge as the second and third milestones respectively). In explaining such variation, researchers pointed to occasional co-existence of individualism and collectivism elements within settings (Turkey included) and corresponding mixtures of reasoning styles (see Selcuk et al., 2018; see also Legare et al., 2012). Yet, could familial influences underlie or interact with general cultural effects in shaping the mixed patterns observed? Family size, for example, has been suggested to relate positively to the opportunities provided to children to encounter diverse beliefs and ideas (see Lewis et al., 1996). In consistence, Selcuk and colleagues found that earlier achievement of diverse beliefs relative to knowledge acquisition in the aforementioned sample was associated with the number of adults in the family - grandparents and other relatives included, as is often the case in more traditional societies like Turkey. Actually, the same sequence pattern was observed in a study of 3-to 5-year-olds growing up in childrearing institutions in Turkey (Etel & Yagmurlu, 2015), where the number of *close others* was also high. Moreover, positive links have been found between early ToM development and the number of siblings, as well as the degree of interaction with them in situations characterized by contrasting mental states (Dunn et al., 1991; Foote & Holmes-Lonergan, 2003). Actually, within both the family and the school setting, pretend play in the preschool period, and increased variation in conversational exposure to mental states as a function of improved language skills in middle childhood constitute important fora for reflecting on different perspectives (e.g., Foley & Hughes, 2021). As language is fundamental to ToM development (see Astington & Baird, 2005; Milligan et al., 2007), the temporal reach of linguistic interaction mechanisms of family influence on ToM development appears an important subject of future research (see De Villiers, 2007; Foley & Hughes, 2021; Hou et al., 2020). Finally, attempting to link neural and experiential underpinnings of early ToM achievements, such interaction patterns could moderate the degree of necessitated ToM revisions, in combination with genetically mediated functional changes in dopamine binding that are suggested to facilitate signaling of prediction-outcome mismatches and trigger conceptual change (see Sabbagh's, 2017 suggestions above).

Nevertheless, although the number of *close others* would be expected to positively correlate with children's exposure to multiple viewpoints early on in development, therefore prioritizing their understanding of diverse beliefs, at least in the aforementioned study by Selcuk et al. (2018) family size was related to lower ToM scores. In attempting to explain this inconsistency, the researchers assumed higher levels of negative affect and stress in multigenerational, crowded households, which could in turn negatively influence mental state understandings.

Yet in the same study, family size was negatively related to SES as well. There have been suggestions that children from disadvantaged backgrounds might be at risk of delayed ToM development, as a result of poorer nutrition and higher levels of stress, more authoritarian parenting practices, reduced levels of mental state talk and elaborated causal reasoning as a function of parental educational level, or lack of appropriate materials to support quality interactions (see Devine & Hughes, 2018; Selcuk & Yucel, 2017; Selcuk et al., 2022). Regarding these possible SES-related moderators of early ToM development, links have been drawn, for example, between the latter and parental mind-mindedness (Devine & Hughes, 2018; Laranjo et al., 2014) or conversational exposure to mental state terms within the family setting (Mayer & Träuble, 2013; Ruffman et al., 2002). However, such exposure has been found negatively related to parenting goals of strict obedience and mastery of impulse control (Chasiotis et al., 2006). Though not the direct focus of the present review, it seems that complex familial dynamics, often through psychological language and verbalization of epistemic cognition (see Astington & Baird, 2005; Bosacki, 2021), can shape early ToM achievements to a degree and mediate general cultural influences on ToM timelines. Longitudinal research across cultural settings could directly test these effects.

Summing up, evidence from an increasing number of cross-cultural investigations points to universality as well as certain sociocultural modulation of early ToM developments. We lack evidence regarding cumulative experiential effects on advanced mindreading capacities with increasing age, as well as their possible interaction of ToM development with psychosocial development more generally (e.g., perceived social or cultural group membership, or identity development more broadly), and other personal (e.g., motivation, lifestyle) or external factors (sociocognitive stimulation etc.). The evidence offered over the last decades has set grounds for revisiting and discussing key ToM development accounts – though we seem far from a clear disentanglement. The latter could be facilitated by the development of a more comprehensive account of sociocultural ToM antecedents and determinants: encompassing generalized cultural effects (e.g., growing up in individualistic versus collectivist societies), culture-specific pedagogical influences (e.g., related to the roles of instruction and learning, or pedagogical methodology), as well as familial influences (e.g., from SES and family size to parental practices and mental state talk patterns). In parallel, as suggested below, the study of the culture-biology interplay in ToM development needs to be prioritized. Since prevalent mental state talk and interaction patterns, as well as exposure to variable or contrasting mental states within the sociocultural setting seem to assert influence over ToM development, future work could attempt studying them in combination with related functional changes in the brain with age and accumulated experience, including those pertaining to dopamine binding and its role in *theory change*.

### ***A theory of ToM in development: in need of a more integrative biocultural perspective?***

Over the last decades, parallel lines of systematic research have offered valuable information about the evolutionary underpinnings of ToM capacities, as well as the neural and cognitive mechanisms explaining change with age, and the social and cultural factors influencing developmental trajectories and individual variation in related capacities. After an initial focus on the emergence of mental state understandings (particularly regarding epistemic states, e.g., false-belief understanding) in earlier phases of development, researchers have started attempting comprehensive behavioural assessments of more advanced ToM achievements within adolescence and adulthood (e.g., Bosco et al., 2014; Brizio et al., 2015; Lagattuta & Kramer, 2021; Laillier et al., 2019; Lagattuta et al., 2018; Sebastian, 2015; see also Mahy, 2018; Wellman, 2018a). Still, evidence mostly stems from cross-sectional and correlational studies, with longitudinal data having increased lately, but mostly regarding early ToM developments. The neurocognitive underpinnings of ToM have mostly been studied in adults, due to the difficulty of involving children in relevant measurements (though non-invasive techniques are promising in that respect), and the lack of assessments that can reliably capture the increasing complexity of mindreading from childhood to adolescence and adulthood (e.g., Brizio et al., 2015; Coolin et al., 2017; Warnell et al., 2019). A promising line of research is currently focusing on the interplay of biological and cognitive mechanisms driving change in ToM over the lifespan (see Apperly et al., 2009; Baglio & Marchetti, 2016; Bernstein, 2018; Mahy, 2018; Wellman, 2018b). On the other hand, several recent studies aim at a deeper understanding of experiential influences on ToM development, again mostly focusing on early ToM achievements so far. Cross-cultural investigations are fewer and have discussed general cultural influences (e.g., everyday epistemologies pertaining to norms and values in collectivist versus individualistic contexts), culture-specific pedagogical patterns (related to the cultural activity of schooling and related concepts, or to culturally-selected pedagogical methods), or

familial influences (from family size and SES to parental practices and conversational patterns pertaining to mental states within the home setting) (see Devine, 2021; Selcuk et al., 2018, 2022; Wang et al., 2016; Wellman, 2012; Wellman et al., 2006).

The present paper attempted to present, analyze, and synthesize recent data from these lines of research, and, where possible, use conclusions as a basis for revisiting key accounts of ToM development. That is, either those suggesting that developmental and individual differences in domain-general cognitive capacities (e.g., executive functions - EF - such as inhibition) underlie the observed variation in ToM performance (within or among individuals), or alternative, domain-specific viewpoints on ToM development. Among the latter, discussion has focused on suggestions for an innate, modular ToM mechanism that is supported by neurocognitive maturation (*modularity* theories), for an inborn capacity to form intuitive theories regarding persons' minds, which are then revised via experientially driven conceptual change (*theory-theory* account), or for mechanisms that specialize in the simulation of others' mental states and related attributions (*simulation* accounts).

Specifically, based on frontier research, we have started to gain valuable insights into the neural and cognitive mechanisms driving developmental change in ToM. Maturation of specific brain regions (e.g., the dorsal medial prefrontal cortex, the right temporoparietal junction, or the precuneous) seems related to ToM reasoning. Actually, in line with the function of a *hard-wired* ToM module very early in life, there are suggestions for specialized neural networks supporting the emergence of mental state concepts from infancy already (Leslie, 2005; see also Baillargeon et al., 2010). Yet, there is also evidence for significant increases in neural selectivity with increasing age (Carrington & Bailey, 2009; Molenberghs et al. 2016; Sabbagh et al., 2009; Schurz et al., 2014; Warnell & Redcay, 2021; Wellman, 2018b), and we still lack strong evidence pointing to a consistent and selective activation of specific brain regions or of a common network across mental reasoning occasions and periods of development. In parallel, cross-cultural data suggests a significant degree of universality, as well as certain variation in early ToM achievements - evidence regarding advanced ToM capacities remains scarce. Such variation could not be accounted for by modularity theories of ToM development, suggesting *hard-wired* ToM mechanisms; unless, as suggested above, culture-gene co-evolution processes constitute the basis of discussion, along with data on general culture or culture-related pedagogical effects (rather than familial influences; see Chiao & Blizinsky, 2010; Chudek & Henrich, 2011).

Developmental change in cognitive processing has been related to improvements in performance on ToM tasks not only within the related *processing* account, but also within certain modularity accounts. Leslie and colleagues (e.g., German & Leslie, 2000, 2001; Leslie et al., 2004; Scholl & Leslie, 1999, 2001), for example, have related early ToM development to the emergence of a ToM mechanism in the second year of life, as part of the core architecture of the human brain. Yet, they have attributed further performance improvements in ToM assessments to a gradually improving inhibitory selection process (see also Mahy et al., 2014). Inhibitory control efficiency, as part of EF, has received great attention within the *processing* account of ToM development: domain-general cognitive capacities, such as inhibitory control, shifting or working memory, have been suggested to moderately (e.g., Devine and Hughes, 2014; Grainger et al., 2018; Meinhart-Injac et al., 2020) or even fully account (e.g., Coolin et al., 2017) for age-related changes in performance on ToM tasks. Still, the extent of ToM-related structural and functional changes in the brain with increasing age does not seem compatible with mere dependence of mental state reasoning on either EF (or language; e.g., Baillargeon et al., 2010) trajectories or cognitive decline with aging (e.g., Maylor et al., 2002; see also Happé et al., 1998). Neither are the observed functional shifts in the brain fully aligned with EF developmental patterns (see Oh & Lewis, 2008; Sabbagh et al., 2006) or EF variation among individuals as well as across locales (e.g., Wang et al., 2016; Sabbagh, 2017). Nevertheless, as discussed above, domain-general processing capacities are seriously considered in a currently unraveling, promising line of work: attempts are made to develop age-sensitive ToM measurements and refined statistical methods to test cascades of mental state understandings (e.g., via scaling methods; see Peterson & Wellman, 2019) and ToM trajectories through the lifespan (e.g., via multinomial processing tree model application on data from *continuous* versus *dichotomous* tasks; see Coolin et al., 2017).

A great amount of evidence has been supportive of the *theory-theory* account of ToM development, though, recently suggesting a certain degree of conceptual change facilitation by neurocognitive maturation. Dopamine binding in particular has been assigned a critical role in the signaling of prediction-outcome mismatches and has therefore been suggested to facilitate theory revision (see Sabbagh, 2017). In parallel, age-related changes in dopaminergic functioning have been related to EF (Zhang et al., 2015; see also Kriete & Noelle, 2015); the latter

has been assumed to support reflection upon the experiences of prediction-outcome mismatches, as well as learning from them in the context of experientially driven conceptual change (Benson et al., 2013). In line, there is evidence suggesting certain experiential effects on early ToM timelines at least (Wellman et al., 2006, 2011; see also Wellman, 2012, 2018b). Links have also been drawn between possible mediators of sociocultural influence on ToM development (e.g., interaction patterns) and genetically-driven to a degree, functional changes in the brain with age, which regard dopamine binding – therefore, possibly, the signaling of prediction-outcome mismatches in a theory revision framework.

Finally, evidence remains inconclusive regarding the *simulation* account, which relates ToM development to domain-specific mechanisms that serve improvements in mental states simulations and attributions with increasing age - rather than to the adoption and revision of a theory, or functional change in a ToM module (see Carruthers, 1996; Mahy et al., 2014). On the one hand, the account has been questioned by behavioural (e.g., regarding ASD) as well as neuroscientific evidence. As noted, for example, though there is evidence to suggest the function of co-opted attribution and simulation mechanisms, we lack data confirming that the former receive their input from the latter, or evidence showing that shared mechanisms are used for attributing mental states to both the self and the others (see Saxe, 2009). On the other hand, recent data relating ToM to sociocultural development could be accounted for by simulation theories. As discussed above, perceived cultural group membership, interdependence, and reduced prejudice have been positively related to the frequency, as well as the accuracy of mentalizing in both individualistic and collectivist settings (see Rhodes & Wellman, 2017; Selcuk et al., 2022). It seems that individuals are more likely to simulate the mental states of persons that they perceive as more similar to themselves. Such similarity patterns have actually been suggested to moderate the activation of neural networks involved in ToM reasoning (see Mahy et al., 2014). Would these patterns be dependent on identity development (e.g., of its social-cultural dimensions), and would they become more robust with increasing age and accumulated sociocultural experience? A question to be examined. Overall, even if progressing in parallel channels so far, research on the neural and cognitive mechanisms driving ToM development and its sociocultural determinants has started to set the grounds for a more fruitful discussion of key ToM accounts; the *theory theory*, the *processing*, the *modularity*, and *simulation* accounts discussed above. However, we seem far from a decisive disentanglement. It is suggested that focusing further on the biology-culture interplay in ToM development, has the potential to contribute to the evaluation of existing accounts, shedding valuable light into the nature and origins of this valuable sociocognitive faculty, its developmental prioritization – universal or culture-specific – as well as the sources of individual variation in ToM (e.g., trait-like, and relatively stable after the early phases of development, maturation-dependent and unfolding at different rates, or subject to accumulated sociocultural experience; see Sabbagh, 2017; see also Devine, 2021). From such a *biocultural* perspective, experiential influences (social-cultural) on ToM development might be moderated by maturational processes (e.g., dopamine-based modulation of frontal systems; see Sabbagh, 2017) and dynamically interact with other aspects of sociocognitive (e.g., moral) or personality development (see Kriete & Noelle, 2015; Zhang et al., 2015; Kroger, 2006; Schwartz & Pantin, 2006). This dynamic might not necessarily shape continuous or monophasic ToM trajectories. There have been suggestions, for example, for a childhood ToM phase, which quickly leads to basic developmental achievements, possibly as a function of innate forces, and an adulthood phase, in which changes or refinements of ToM are subject to greater idiosyncratic as well external modulation (see Giovagnoli, 2019) via neuroplastic brain adaptations (Bardikoff & Sabbagh, 2017; Zelazo & Carlson, 2020; Nguyen et al., 2019). Such biocultural interplay might better account for developmental and individual variation in ToM.

While currently high in the research agenda, lifespan investigations of ToM, in particular, remain limited in number (e.g., Coolin et al., 2017; Giovagnoli, 2019; Lagattuta & Kramer, 2021; Laillier et al., 2019; see also Apperly et al., 2009), and discussion of relevant developmental patterns seems patchy (Wellman, 2018a; see also Baglio & Marchetti, 2016; Bernstein, 2018; Mahy, 2018). Yet, such a perspective could offer valuable information regarding the prioritization, as well as the determinants of ToM capacities, as a function of phase-specific challenges. If contextual factors are considered in combination, then recognizable patterns might appear even faster in the overall ToM *puzzle* (see also Blakemore & Mills, 2014; Devine & Lecce, 2021; Kilford et al., 2016).

To move the field forward and reveal the true antecedents of ToM development, we need more data from training, as well as longitudinal studies, covering extended age ranges. We also need evidence, even if cross-sectional, from studies attempting more comprehensive assessments of ToM capacities (e.g., see Osterhaus & Bosacki, 2022). Although increasing in number, the available meta-analyses have by necessity focused on the

most widely studied early ToM achievements (Wellman & Liu, 2004) - predominantly, on false belief understanding (e.g., Devine & Hughes, 2014; Liu et al., 2008; Wellman et al., 2001; Wellman & Yu, 2022). Future investigations should consider capacities that have received less research attention in the early years (e.g., those regarding diverse desires or access to knowledge, or interpretations of hidden emotions), as well as more advanced capacities (from higher-order false belief and nonliteral speech to the decoding of facial expressions and the recognition of social blunders - faux pas; see Osterhaus & Bosacki, 2022). They should also aim at better disentangling the roles of EF mechanisms in lifespan ToM development, equally focusing on shifting and working memory updating (Miyake et al., 2000), along with the better-studied inhibition function, and more comprehensively assessing dimensions of the latter (i.e. response inhibition versus resistance to distractor or to proactive interference; see Friedman & Miyake, 2004). More systematic investigations of the ToM - EF interplay during childhood (e.g., see systematic review by Economacou et al., 2023) as well as adulthood (e.g., Apperly et al., 2009) are necessitated. Evidence suggests individual differences in EFs that are heritable to a degree improve and refine as a function of neurocognitive maturation by late adolescence, but remain sensitive to environmental influence even during adulthood (Friedman et al., 2016). This line of research can, more generally, offer valuable insight into human cognitive architecture (see discussion in Friedman & Miyake, 2017).

An expansion of the developmental scope of research is necessitated to capture the dynamics of lifespan ToM development (see Brizio et al., 2015; Devine & Hughes, 2014; Saxe, 2013); that is, both its early underpinnings and its conscious refinement within purposive adult development (see Aldwin, 2014). In that direction, it seems pertinent to shift focus from the study of mental state understandings in lab-based, culture-free interaction contexts (Brizio et al., 2015), to ToM reasoning processes driving decisions and actions in real-life social situations, along with affect and cognition (e.g., pertaining to episodic memory representations) or self-related processing (see Laillier et al., 2019). We need more ecological, contextualized assessments to better grasp the interplay of mechanisms and factors shaping variation in ToM understandings across age periods (e.g., see interactive neuroscientific paradigms in Warnell & Redcay, 2021). Knowledge more generally, not only regarding others' minds, has long been regarded neural in form, but inherently social in content; therefore, subject to sociocultural modulation. And since our thoughts, feelings, and actions are seen as social even when we are alone (see Clancey, 1997), an advancing capacity to perceive and process information regarding persons' minds serves not only social fine-tuning (Frith, 2008), but in essence the development of self-consciousness.

Considering the unfolding paradigm changes in developmental science, including shifts from developmental contextualism (age- or history-graded and non-normative influences) to developmental biocultural co-constructivism (see Baltes & Smith, 2004; Baltes et al., 2006; Lightfoot et al., 2018), and from reductionism to the study of interacting sources of change over time (e.g., Aldwin, 2014), the interdisciplinary study of the biocultural architecture of lifespan ToM development - by psychologists, neuroscientists, anthropologists, philosophers - seems imperative and timely. It will unavoidably set both conceptual and methodological challenges. Since the extent to which biology and culture contribute to the refinement and differentiation of cognitive capacities remains open to discussion, attention should be paid to avoid overgeneralizing differences across contexts. Moreover, while coping with the inherent difficulty of cross-cultural investigations, scientists will be invited to test meta-models of ToM through advanced, novel paradigms and analytical approaches. They will be required to further exploit non-invasive assessments of neurocognitive functioning in early phases of development (see Warnell & Redcay, 2021), and develop paradigms that allow assessments over the lifespan (e.g., continuous tasks; see Coolin et al., 2017 above). Methodological innovations predicated on the idiographic nature of intra-individual change in ToM will also be required (see Aldwin, 2014; Lerner et al., 2021). Still, for highly auspicious research domains such as ToM, interdisciplinary investigations are worth prioritizing: they have the potential to better capture its development, as encompassing multiple levels (neurobiological, cognitive, sociocultural; see Li, 2003), and as occurring within different time scales (i.e. human phylogeny, lifespan ontogeny, or even, moment-to-moment microgenesis) (see Lightfoot et al., 2018; Massimini & Delle Fave, 2000). Could the adoption of a *biocultural* perspective serve this purpose, setting grounds for the development of the more integrative - if not unifying - theory of ToM that we still lack?

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# Βιολογικοί και γνωστικοί μηχανισμοί και ο ρόλος του πολιτισμού στην ανάπτυξη της θεωρίας του νου: Αναγκαία μια ενοποιητική, βιοπολιτισμική οπτική;

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## ΛΕΞΕΙΣ-ΚΛΕΙΔΙΑ

Βιοπολιτισμική προσέγγιση,  
Γνωστική ανάπτυξη,  
Δια βίου ανάπτυξη,  
Εξελικτικές θεωρίες,  
Θεωρία του νου,  
Μηχανισμοί ανάπτυξης,  
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## ΠΕΡΙΛΗΨΗ

Στο παρόν άρθρο επιχειρείται μια περιεκτική προσέγγιση των βιολογικών, γνωστικών, καθώς και πολιτισμικών βάσεων ανάπτυξης της θεωρίας του νου. Η κριτική ανάλυση και σύνθεση σύγχρονων ευρημάτων αξιοποιείται ως βάση επανεξέτασης βασικών θεωρητικών προτάσεων για τη φύση και την ανάπτυξη της πολύτιμης αυτής κοινωνικογνωστικής ικανότητας. Ερμηνεύονται καλύτερα τα ευρήματα στα πλαίσια προσεγγίσεων που λαμβάνουν υπόψη αναπτυξιακές αλλαγές και ατομικές διαφορές σε γνωστικές λειτουργίες γενικού πεδίου (εκτελεστικές λειτουργίες) που ενδέχεται να διέπουν τις επιδόσεις σε έργα θεωρίας του νου (προσέγγιση επεξεργασίας); Η μήπως είναι πιο γόνιμη η συζήτηση της ανάπτυξης της θεωρίας του νου στη βάση εξειδικευμένων μηχανισμών ή ικανοτήτων (ειδικού πεδίου): ενός έμφυτου, αρθρωτού μηχανισμού, που υποστηρίζεται από τη νευρολογική ωρίμανση (θεωρίες σπονδυλωτής διάρθρωσης του νου) ή μιας εγγενούς ικανότητας διαμόρφωσης αφελών, διαισθητικών θεωριών για το νου, οι οποίες υπόκεινται σε διεργασίες εννοιολογικής αλλαγής βάσει της εμπειρίας (θεωρία της θεωρίας), ή ενός μηχανισμού που εξυπηρετεί προσομοιώσεις νοητικών καταστάσεων και σχετικές αποδόσεις (θεωρίες προσομοιώσης); Όπου αυτό είναι εφικτό, βιολογικές και νευρογνωστικές διεργασίες και επιδράσεις εμπειριών συζητούνται συνδυαστικά. Επιχειρείται επίσης ο διαχωρισμός γενικών πολιτισμικών επιρροών από εγγύτερες, κοινωνικές ή οικογενειακές επιδράσεις στην ανάπτυξη της θεωρίας του νου. Στόχος είναι να επισημανθεί η αξία μιας ενοποιητικής, διεπισημονικής προσέγγισής της: μια βιοπολιτισμική οπτική θα μπορούσε να υπηρετήσει αυτόν τον σκοπό ουσιαστικά, στρέφοντας την προσοχή στην αλληλεπίδραση των βιολογικών, γνωστικών και περιβαλλοντικών παραγόντων που διαμορφώνουν τη δυναμική της δια βίου ανάπτυξης της θεωρίας του νου στον άνθρωπο.