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Moral learning and decision-making across the lifespan

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Abstract

Moral learning and decision-making are crucial throughout our lives from infancy to old age. Emerging evidence suggests that there are important differences in how we learn and decide in moral situations, and these may be underpinned by co-occurring changes in the use of model-based values and theory of mind. Here, we review the decision neuroscience literature on moral choices and moral learning considering four key concepts. These concepts are learning and experiencing moral emotions, learning and deciding about other's moral character, moral learning and deciding for others, and moral influence and contagion. We focus on recent behavioural and neuroimaging findings using a value-based decision-making framework, showing how mathematical models of decision-making can be used to determine the computational mechanisms underlying these concepts, uncover their neural correlates, and ultimately provide a mechanistic account of morality across the whole lifespan.

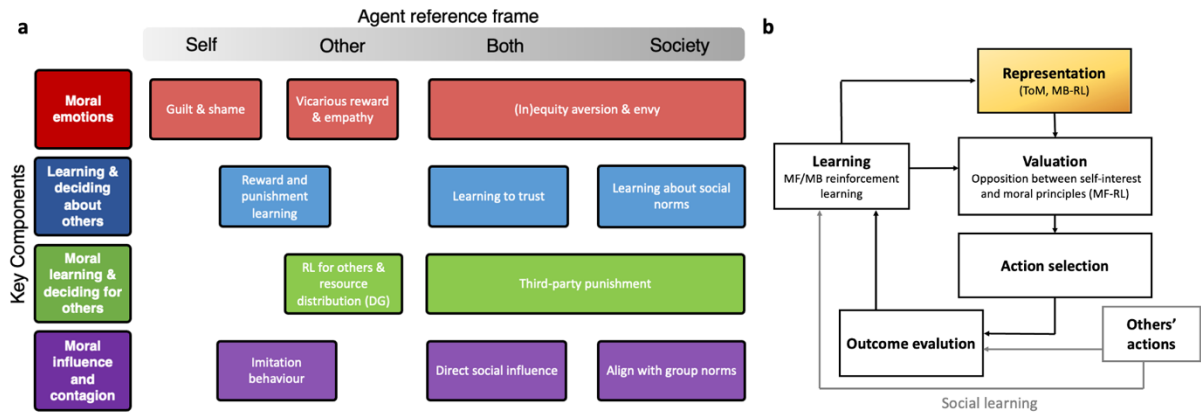
Keywords: Moral, decision-making, lifespan, computational, learning, brain

Introduction

1
2 The question of what makes humans moral has been of interest to philosophers, psychologists,
3 economists, and sociologists for centuries. At a basic level, we can define morality as the set of norms
4 and values subscribed to by a social group to guide its actions in terms of good and bad (Crockett 2013;
5 DeScioli & Kurzban 2009; Qu et al. 2022; Tomasello & Vaish 2013). A key question is how and when
6 such morality develops, and does it differ across our lifespan? In addition, research has begun to focus
7 on using mathematical computational models of value-based learning and decision-making to link
8 cognition, behaviour and neural activity (Crockett 2013; Qu et al. 2022). How can we use this framework
9 to understand the development of learning and decision-making in a moral context, and are some of
10 the foundational components of these models apparent from infancy to old age?

11
12 Some have argued that infants are born with an innate moral sense (Bloom & Wynn 2016; Hamlin 2013;
13 Wynn et al. 2018) whereas others emphasise the role of the social environment more strongly in the
14 acquisition of morality (Dahl & Paulus 2019). However, the extent to which we are moral is multifaceted
15 and may indeed differ across our whole lifespan from infancy to older age (Cutler et al. 2021a; Mayr &
16 Freund 2020). Here we argue that to understand the unique interaction of development on morality it
17 may be crucial to take such a lifespan perspective and to do so within a value-based framework of
18 reinforcement learning (**Figure 1, RL sidebar**). In parallel, the basic mechanisms of moral learning and
19 decision-making likely depend on cognitive processes that also differ with age, such as model-based
20 learning and theory of mind (**Figure 2**). Understanding how these related processes develop and
21 change can bring us insights into the dynamic fluctuations of basic building blocks of morality across
22 our lives.

23
24 We suggest that four key components underlie morality from infancy to older adulthood. There are likely
25 other processes important for moral learning and decision-making. Yet, these four components provide
26 a framework to draw parallels across age. The first component is learning and experiencing moral
27 emotions. How do we learn and experience emotions such as guilt, envy and empathy? The second
28 concept is learning and deciding about other's moral character. How do we learn moral norms, and how
29 do we decide whether others have abided by them? The third concept is moral learning and deciding
30 for others. How do we learn to be prosocial and make decisions that help and avoid harming other
31 people, and how do we punish other people when they violate norms? Finally, how do others' moral
32 norms influence ourselves, through moral influence and contagion. We consider each of these concepts
33 in turn to provide a taxonomy of moral decision-making that can be relevant throughout our lives.



42
43 **Figure 1. Lifespan framework for moral learning and decision-making. (a)** We propose four key
44 components underlie morality from infancy to older adulthood. These components provide a framework
45 to draw parallels across ages that can provide new insights into the fundamental nature of morality. We
46 suggest that outside of these four components, we should also consider the agent reference frame, i.e.
47 whether moral choices are about or for self, other, both, or society. **(b)** A conceptual framework
48 describing the computations involved in moral decision-making that can be separated into distinct
49 components. The first consists of the representations of the moral dilemma that encompass the moral
50 principles or norms involved as well as the mental states and intentions of others (Theory of Mind: ToM).
51 Then, individuals evaluate each possible action by weighing the personal benefit against the
52 consequences for others. Third, individuals select the action that maximizes their utility following moral
53 principles and moral norms. Fourth, they evaluate the outcome based on the consequences of their
54 moral action and based on other's reactions to it, these outcomes are often experienced as moral
55 emotions. Finally, a learning signal is used to update individuals' model of the world (Model-based
56 reinforcement learning: MB-RL), and the expected value of specific actions (Model-free reinforcement
57 learning: MF-RL). Note that learning from the consequences of others' actions is ubiquitous and can
58 lead to updates of our world model and the direct expectation of outcomes of actions. Abbreviations:
59 DG, Dictator Game, RL, reinforcement learning
60
61

62 Learning and experiencing moral emotions

63 Moral emotions are those emotions that underpin our capacity for morality (Tangney et al. 2007). These
64 may include guilt, envy and empathy. The onset of moral emotions coincides with the development of
65 the ability to distinguish self from others (**Figures 1b & 2**). These emotions can further be grouped as
66 positive (e.g., pride) or negative (e.g., guilt, envy) (Bastin et al. 2016). One common characteristic of
67 negative moral emotions is that they occur when individuals break social norms, which are internalized
68 as values. Moral emotions may serve to regulate moral behaviour, helping individuals to follow social
69 norms. The development of moral emotions such as envy allows us to experience disadvantageous
70 inequity aversion, where we disfavour unfair allocations of value. How and when these processes
71 develop and differ across the lifespan is therefore essential to understand. In the following sections, we
72 consider the development of moral emotions from infancy to old age.

73 *Moral emotions in infancy and childhood*

74
75 From our first days, we rapidly develop abilities in visual, motor and auditory domains (Tierney & Nelson
76 2009). This is well-established. However, our propensity for moral emotions is much less well
77 understood. Some have argued that infants are born with a sense of morality that provides a foundation
78 for the rest of life (Bloom & Wynn 2016; Hamlin 2013; Wynn et al. 2018). Given the challenges with
79 reliably measuring infant emotions and behaviour, several studies have sought to understand if infants
80 experience moral emotions through observational studies. Here we focus on moral emotions including
81 guilt, fairness and empathy which have been examined the most extensively in this age group.
82
83

84 The literature on when guilt emerges is somewhat mixed. One seminal study suggested that 8-year-
85 olds were more likely to experience guilt than 4-year-olds. And this effect was replicated in various
86 studies around the world (Krettenauer et al. 2008). Other studies have suggested that guilt and shame
87 may develop early in life in toddlers. For example, in the broken toy paradigm (Cole et al. 1992) a child
88 believes they have broken an adult's favourite toy. Infants display more guilt and shame (as rated by
89 observers) to this event than in contexts where they simply engage in free play (Cole et al. 1992).

90

91 In parallel, the transition from infancy to childhood is associated with development in the complexity of
92 our understanding of inequity. Inequity aversion is where people consider their own material self-interest
93 but also the resources of others (Fershtman et al. 2012). Children aged 4 show disadvantageous
94 inequity aversion to unequal divisions of resources (Blake & McAuliffe 2011; Fehr et al. 2008; McAuliffe
95 et al. 2013; Sheskin et al. 2014). Researchers have also examined childhood facial expressions in
96 response to unfairness at receiving less than a peer. In this context, 3 to 5-year-olds respond with
97 negative emotional expressions when receiving less but neutral to positive expressions when they
98 receive more (House et al. 2012; LoBue et al. 2011).

99

100 As we transition from infancy to childhood a sense of self and other distinction emerges that supports
101 the development of empathy, the capacity to vicariously experience the affect and cognition of other
102 people, beyond simply experiencing emotional contagion (Decety & Holvoet 2021; Frick & Kemp 2021;
103 Lockwood 2016). Indeed, theoretical accounts suggest that when emotional contagion is experienced
104 with self-other distinction it may be conceptualised as empathy (Decety & Meyer 2008; Lockwood 2016).
105 These cognitive and affective changes are likely underpinned by structural and functional brain
106 maturation (Decety & Michalska 2010; Mills & Tamnes 2020). In turn, such developmental processes
107 support more complex value-based and decision-making architecture. For example, recent work
108 suggests that children aged 5-6 can infer the cost-benefit utility of others' competencies and preferences
109 (Jara-Ettinger et al. 2016).

110

111 Finally, children increase their understanding of intentional vs. unintentional harm to guide behaviour
112 (Amsterdam 1972; Steinbeis 2016). When the self rather than another person is the source of harm or
113 help, 4- to 6-year-olds can attribute negative emotions to transgressors who violate social norms
114 unintentionally (Nunner-Winkler & Sodian 1988). This contrasts with before this age where there is little
115 distinction between intentional and unintentional harm (Nunner-Winkler & Sodian 1988). With
116 developing architecture of moral emotions including self-other distinction, understanding intentional vs
117 unintentional harm, inference regarding costs and benefits, and co-occurring brain maturation, this sets
118 the scene for further complexity of moral emotions in the transition to adolescence.

119

120 *Moral emotions in adolescence*

121

122 As children transition to adolescence, they increase their self-awareness and become more
123 preoccupied with their peers. Subsequently, they may feel moral emotions like guilt and shame more
124 often and more deeply (Zeman et al. 2006). In adolescence, moral emotions of guilt and fairness have
125 been frequently studied with economic games, specifically the Dictator, Trust, and Ultimatum Games
126 (DG, UG, TG) (Fett et al. 2014; Güroğlu et al. 2014; Güroğlu et al. 2009; van den Bos et al. 2010).
127 According to the Fehr-Schmidt inequity aversion model, two parameters govern the utility of resources
128 that are split by two parties (Fehr & Schmidt 1999). This first one is guilt, expressed as the utility
129 attributed to giving up on one own pay-off to achieve a more equal outcome. The second is envy, which
130 expresses how one dislikes unequal outcomes in the advantage of the other leading to disadvantageous
131 inequity aversion described above.

132

133 In the DG, participants are asked to divide money or points between him or herself and another player.
134 In this game any non-zero offerings are examples of guilt. Recent evidence shows that, in context of
135 different variations of the DGs, social contextual factors such as the target of giving increasingly

136 influence adolescent decision-making. For example, Guroglu et al., 2014 showed that with increasing
137 age adolescents start to differentiate their sharing behavior between different types of peers in their
138 classroom. Later studies also showed that the extent to which adolescents differentiate between others
139 depends on their level of perspective-taking (van de Groep et al. 2020). Moreover, a recent study
140 showed that donations to charity increased across adolescence, indicating an increasing interest in
141 societal goals (Spaans et al. 2023). Finally, self-report studies have shown adolescents prone to
142 experiencing guilt were more likely to show higher levels of prosocial behaviour and lower levels of
143 aggression (Roos et al. 2013; Stuewig & McCloskey 2005; Zeman et al. 2006). Taken together these
144 results suggest a shift from a model-free (outcome-based) towards a model-based (rule/norm-based)
145 decision-strategy, in which adolescents take the perspective of others, and society increasingly into
146 account.

147

148 A similar developmental pattern is seen in context of the UG, specifically, the mini-UG. Here the
149 proposer only has two options, an unfair and an alternative offer. The alternative is either an equal split
150 or another unfair offer. When the first player proposed an unfair offer (8/2) when the alternative was fair
151 (5/5), players of all ages rejected unfair offers. But when the first player had no alternative (8/2 vs. 8/2),
152 the number of times participants accepted an unfair offer increased with age, indicating an increase in
153 taking intentions into account (Gummerum & Chu 2014; Güroğlu et al. 2009). A developmental
154 neuroimaging study further revealed an age-related increase inactivation in the dorsolateral prefrontal
155 cortex (dlPFC) and Temporo-Parietal Junction (TPJ), which correlated with the increased sensitivity to
156 others intentions (Güroğlu et al. 2011). In sum, these results highlight that self-regulation (dlPFC) and
157 perspective taking (TPJ) become more important processes in adolescent moral decision-making.

158

159 Finally, empathy involves both feeling others pain and sharing their joy (Lockwood 2016). The response
160 to vicarious rewards, rewards received by others, provides a fundamental insight into the value placed
161 on the welfare of others, is considered a necessary foundation for empathizing (Bird & Viding 2014),
162 and may contribute to a learning signal that enforces morality. Several studies have focused on neural
163 activity in response vicarious rewards in adolescence. In these studies, it was observed that
164 adolescents showed ventral striatum activity when gaining rewards themselves, but also when their
165 best friends gained rewards. Furthermore, this effect was larger for participants who reported higher
166 friendship quality but was absent for unknown others (Braams et al. 2014). The same pattern of results
167 – increased striatal activity for close others- was replicated by a study that focused on adolescents'
168 family members. In adolescence, there is a well-established link between empathy, increased prosocial
169 behavior and moral judgement (Eisenberg et al. 1995, 2005; Eisenberg-Berg & Mussen 1978).

170

171 *Moral emotions in adulthood*

172

173 A recent approach, mostly developed in adolescents and adults, has been to combine economic games
174 (DG, UG, trust game), or new moral tasks (Rutledge et al. 2016; van Baar et al. 2019), with
175 computational modelling and model-based fMRI to study the neurocomputational mechanisms
176 underlying moral emotions. Using this approach, empathy, guilt and its anticipation, envy and other
177 moral emotions, have been defined using computational models (Fehr & Schmidt 1999; Qu et al. 2022).
178 These models formalize people's sensitivity to weigh personal benefits against the moral cost of
179 violating internalized moral norms, such as harming others. Moral emotions emerge at the time of the
180 decision when self/other interests are weighed (i.e. expected value) or at the time of outcome when
181 (un)expected harms/benefits concerning self and others are revealed (i.e. experienced value). For
182 example, empathy is associated with a higher rate of learning about actions that result in beneficial
183 outcomes for other people as well as the neural drivers of prosocial learning in the subgenual anterior
184 cingulate cortex (Lockwood et al. 2016).

185

186 Adults not only show inequity aversion to self-other distributions that disfavor them (i.e.
187 disadvantageous inequity), they are also averse to unequal distributions that benefit them (i.e.

188 advantageous inequity) (Gao et al. 2018; Nihonsugi et al. 2015). Disadvantageous-inequity aversion
189 has been linked to negative moral emotions such as envy (Blake et al. 2015; Fehr & Schmidt 1999),
190 and engages the amygdala and posterior part of the insula (Feng et al. 2021; Gao et al. 2018). In
191 contrast, when manipulating the social context in which the resource allocation occurs, advantageous
192 inequity has been associated with social and mentalizing-related processes, involving the dIPFC,
193 anterior insula and dorsomedial prefrontal cortex (Gao et al. 2018). This social context manipulation
194 allowed researchers to dissociate the psychological and neural processes of payoff and inequity by
195 modulating the salience of inequity but not the salience of absolute payoff. When causing pain to a
196 coplayer (guilt context), adults cared more about advantageous inequity and became more tolerant of
197 the disadvantageous inequity, compared with other conditions. Moreover, the dorsal anterior insula may
198 modulate cognitive processes that generate expectancy for norm compliance, whereas ventral anterior
199 insula could be linked to aversive emotions associated with inequality aversion that generate motivation
200 for norm enforcement (Bellucci & Dreher 2020; Bellucci et al. 2018).

201
202 Guilt is closely related to inequity aversion because it both signals and constitutes the obligation of
203 moral violators to balance the inequity created by their moral transgression (Gong et al. 2019). Guilt
204 has been conceptualized as anticipation of a negative emotional state associated with the violation of
205 personal moral rules, social standards or another's expectations (Chang et al. 2011). Recent models of
206 guilt-aversion provide a precise quantification of the amount of guilt anticipated as the result of a given
207 decision (Gong et al. 2019). According to these models, one's aversion to the possibility of experiencing
208 future guilt prompts morally aligned decisions to minimize guilt anticipation. Guilt has been associated
209 with activity in the ventral anterior cingulate cortex, posterior temporal regions and precuneus in adults
210 (Bastin et al. 2016).

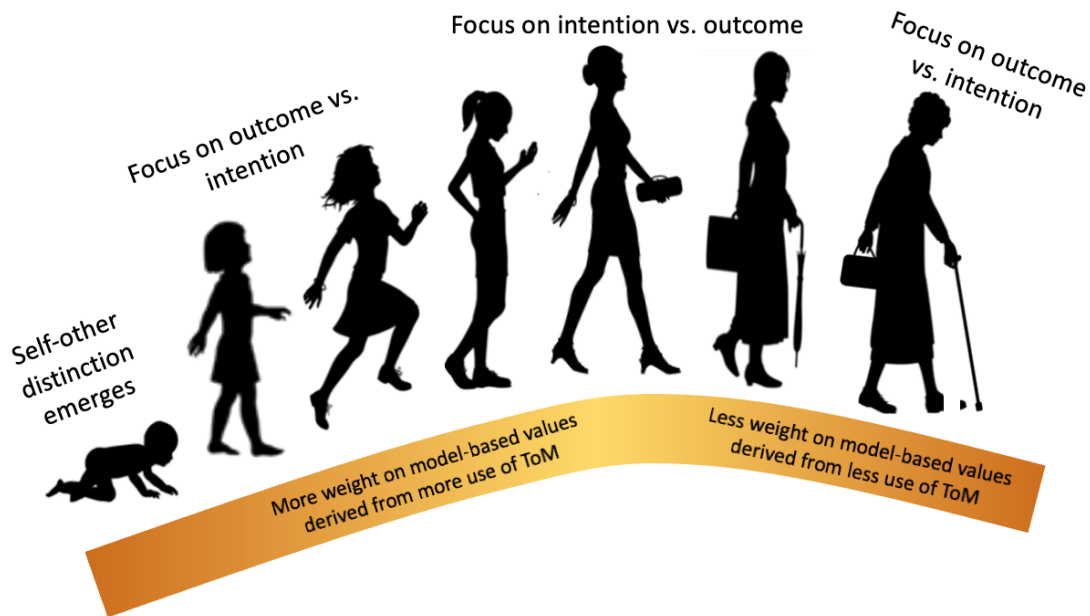
211
212 Shame has been associated with activity in the dIPFC, posterior cingulate cortex and sensorimotor
213 cortex (Bastin et al. 2016). A difference between shame and guilt is that shame is a self-oriented emotion
214 while guilt is other-oriented. This difference has important consequences on empathy for other people:
215 while guilt tends to increase the empathic concern towards other people, empathic responses seem to
216 be disrupted by the self-oriented distress associated with shame (Tangney et al. 2007). For example,
217 the experience of guilt or inequity is strongly predictive of altruism (Gong et al. 2019; Hu et al. 2021a;
218 Seara-Cardoso et al. 2016), suggesting that variability in the emotional impact of inequality on well-
219 being can explain heterogeneity in altruistic behaviour (Rutledge et al. 2016). Similarly, adults are more
220 likely to reverse ranks and reduce inequality when a social hierarchy is perceived as unfair (Foncelle et
221 al. 2022). These findings indicate that moral emotions related to inequity aversion, guilt and shame
222 guide individuals when making moral decisions weighing considerations between oneself and others
223 and that moral emotions can be accounted mechanistically using a neurocomputational approach.

224 225 *Moral emotions in older adulthood and ageing*

226
227 By older adulthood, changes still occur in what may be considered moral emotions: empathy, guilt,
228 pride, and inequity aversion. Of course, at the basic level ways moral emotions remain consistent.
229 However, it is widely documented that older age is associated with higher levels of emotional well-being
230 (Charles & Carstensen 2010) and lower rates of anxiety and major depressive disorder (Blazer 2003;
231 Charles & Carstensen 2010; Fields et al. 2022), at least cross-sectionally. These increases in positivity
232 occur despite decreased cognitive and physical capacity (Murman 2015). So how do our moral
233 emotions change with senescence? When measuring emotional responses to inequity, older adults
234 have been suggested to show greater aversion to inequity and an outcome bias that is insensitive to
235 others' intentions (Margoni et al. 2021, 2023). In general older adults, aged 65+, are thought to rely
236 more on outcomes than intentions (Margoni et al. 2021, 2023), consistent with a reduced use of theory
237 of mind and model-based reasoning (**Figure 2**). This is despite possibly age-related differences in
238 generosity, discussed later (Bailey et al. 2013; Cutler et al. 2021a; Mayr et al. 2024; Mayr & Freund
239 2020).

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Studies also suggest that the emotional and affective aspects of empathy remain stable or increase in later adulthood (Beadle & de la Vega 2019; Beadle et al. 2012; Ze et al. 2014), although see (Chen et al. 2014). This is based on self-reported empathic responses to specific scenarios. Other work in an effort-based decision-making context has shown that both young (aged 18-35) and older (aged 60- 80) adults feel equally positive when they help another person, and these feelings of positivity drive cost-benefit analyses of their effortful helping (Lockwood et al. 2021).



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Figure 2. Moral learning and decision-making across the lifespan are underpinned by changes in the weight and influence of model-based values and the use of theory of mind (ToM). Self-other distinction emerges in infancy and supports the development of more complex moral emotions. A focus on the outcome vs. intentions of others' social decisions fluctuates from childhood to adulthood and old age and co-occurs with a different reliance on model-free and model-based learning. Model-based learning ability is highest in early to late adulthood and has a lower influence in childhood and older adulthood. In parallel, the use of theory of mind for moral decision-making increases from later childhood to adulthood before being used less in older age. These fluctuations in the reliance on model-based values and theory of mind could be critical for understanding moral learning and decision-making across the lifespan.

Learning and deciding about other's moral character

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With the foundational architecture of moral emotions, the next step is to be able to learn and decide about the moral character of other people. Do we view others as behaving prosocially or antisocially? Are they trustworthy or not? Do we engage in punishment of those who have committed transgressions? Several experimental approaches have been developed to assess how we learn and decide about moral character, and these differ substantially from infancy to older adulthood. In infancy, most studies have used looking time experiments, and in adolescents and adults, complex economic games with multiple trials and computational models of behaviour have been deployed. Here we review how the ability to learn and decide about other's moral character differs from infancy to older adulthood within a value-based decision-making framework.

Learning and deciding about other's moral character in infancy and childhood

One crucial aspect of morality is the ability to reason about value-based decisions. In pre-verbal infants,

276 this can be measured using looking-time experiments where gaze at expected and unexpected events
277 is taken as a proxy for reasoning about differences between them. Studies have compared preferences
278 for actors that behave prosocially to antisocially and suggested that infants will attend more to a
279 prosocial character (Hamlin et al. 2007; Ziv & Sommerville 2017). A systematic review of 27 experiments
280 reported that 67% showed infants preferred a prosocial actor (Holvoet et al. 2016). This preference was
281 present as early as 5 months. Failure to replicate these effects or demonstrate developmental
282 differences in older infants may be due to definitions surrounding the social cues needed to capture
283 prosocial behaviour. They may also be related to unique developmental trajectories and individual
284 differences amongst infants. Moreover, looking time measures have also faced methodological
285 challenges of being as unable to truly reveal infants' preferences (Tafreshi et al. 2014).

286

287 In childhood, when more complex methodologies can be used, studies show that from around age 6
288 moral character information influences children's evaluations of moral transgressions (Cameron et al.
289 2022), and children will engage in costly punishment to enforce fairness norms (McAuliffe et al. 2015).
290 With co-occurring development in theory of mind and model-based reasoning (**Figure 2**) children's
291 moral judgements become more intricate and incorporate notions of intent, causality and future
292 repercussions (Cushman et al. 2013). This enables the development of more sophisticated forms of
293 moral judgement in the transition to adolescence. Such changes support the ability to decide about
294 others moral character, and eventually act upon these judgements when we decide to punish others in
295 the case of third-party punishment (TPP) discussed in further detail in the following section, learning
296 and deciding for others.

297

298 *Learning and deciding about other's moral character in adolescence*

299

300 As discussed previously, adolescents increasingly start to involve the intentions of others in their
301 judgement of others moral behaviour, rather than focussing solely on the consequences or outcomes
302 (Gummerum & Chu 2014; Güroğlu et al. 2009; van den Bos et al. 2011). However, the moral character
303 of others is often not based on single events but instead may emerge over a series of interactions or
304 observations. As such, judgement of moral character may rely on very basic learning mechanisms
305 already present in infancy. Indeed, in the past decade several studies have provided evidence for the
306 hypothesis that learning social values or learning in social context relies on basic value-based learning
307 mechanisms that are already in place at an early age (Hofmans & van den Bos 2022; Lockwood &
308 Klein-Flügge 2021).

309

310 As adolescents mature, there is a notable improvement in the capacity to optimally integrate recent
311 outcomes into value estimates. Many studies also applied reinforcement learning models (**RL sidebar**)
312 that have separate learning rates for positive and negative events, capturing sensitivities to rewards
313 and punishments. Whereas initial studies suggested that younger adolescents may be more sensitive
314 to negative outcomes and young adults put more weight on positive outcomes (Van den Bos et al.
315 2012), this pattern was not robustly replicated (Nussenbaum & Hartley 2019). Instead, the overall
316 picture of developmental changes in learning rates suggests that the optimization of these rates may
317 be fine-tuned to the specific learning context, and that it is this adaptive ability that increases with age.
318 A study in a large sample of adolescents aged 9-18 (n=742) showed that in tasks where the absence
319 of response is optimal for some stimuli, and therefore can be distinguished from reward learning,
320 adolescents' learning from punishment improves with age, whereas learning rates from reward remain
321 stable (Pauli et al. 2023). Finally, other studies that have focused on more complex tasks have shown
322 that model-based contributions to learning increase across adolescence (Bolenz et al. 2017, 2019;
323 Decker et al. 2016; Nussenbaum et al. 2020) which is modulated by increased cognitive abilities
324 (Nussenbaum et al. 2020; Potter et al. 2017).

325

326 Most developmental studies on moral character have focused on learning whom to trust in an iterative
327 version of the TG, where the participants play multiple rounds as the trustee with partners (real or fictive)

328 that differ in their level of trustworthiness. Consistent with previous studies on RL and social
329 preferences, these studies have revealed that with age adolescents trust and trust evaluation of others
330 becomes more pronounced (Fett et al. 2014; Sijtsma et al. 2023; van den Bos et al. 2012; Westhoff et
331 al. 2020). Whilst there are very few changes in adapting to non-trustworthy partners there is an
332 improvement in learning to trust a trustworthy partner (Sijtsma et al. 2023; Westhoff et al. 2020), most
333 likely due to the decreasing sensitivity to rejection. Furthermore, Lee et al. showed that older
334 adolescents are more likely to adapt their behaviour based on experience rather than the prior
335 information they received about the moral quality of others (Lee et al. 2016). Therefore, older
336 adolescents become better at updating the model they have of the other player. Finally, Fett et al.,
337 (2014) also indicated that these changes were paralleled by increased brain activation in regions linked
338 to social and self-regulation, such as the TPJ, posterior cingulate and the precuneus. The activation of
339 these networks further supports the idea that with age the learning processes may become more model-
340 based (**Figure 2**) and that adolescents spend more time forming and updating a model of the other
341 player.

342

343 *Moral learning and decision making about others moral character in adulthood*

344

345 *Moral choices about others*

346

347 By adulthood, people make complex trade-offs between self and other harm and studies have examined
348 the neural mechanisms underlying these computations. For example, when people trade off self-
349 monetary gains/losses against moral costs/benefits concerning others (Qu et al. 2019, 2020) or when
350 they weigh pain to themselves and others (Crockett et al. 2015, 2017). In these paradigms, the notions
351 of moral cost and harm aversion are important to explain trade-offs between moral and monetary values
352 (Crockett et al. 2017; Qu et al. 2019, 2020). These computations reflect specific features of the choice
353 options (e.g. amount of money donated to a bad cause and to oneself, or, the difference in the quantity
354 of money and number of electric shocks) to their underlying decision values.

355

356 When making choices that weigh moral against monetary cost/benefit, areas of the brain involved in
357 valuation are engaged (Qu et al. 2022). In one study, a trade-off between moral cost and self-monetary
358 benefit engaged the lateral PFC and the anterior insula (Qu et al. 2019). In contrast, a decision value
359 signal encoding the difference between self-monetary cost and compliance with one's moral values (i.e.
360 moral benefit) engaged the ventral putamen. This is consistent with distinct brain systems for treating
361 violations of moral norms as aversive outcomes on one hand, and another system treating compliance
362 with moral rules as a rewarding outcome. The right TPJ, dlPFC, anterior insula have also been reported
363 to be engaged in encoding moral values (Ugazio et al. 2019). In particular, the lateral PFC responds
364 more strongly when harming others for a small relative to a larger profit (Crockett et al. 2017), to moral
365 norm violations (Chang & Koban 2013; Ruff et al. 2013) and computes variables of moral utility (Bellucci
366 et al. 2019; Sai et al. 2021; Speer et al. 2020) or weighs differences between honesty and self-interest
367 (Dogan et al. 2016; Greene & Paxton 2009; Zhu et al. 2014).

368

369 The neural bases of another type of dishonest behavior, corruption behavior, has also been investigated
370 (Hu et al., 2021; 2022). When a power-holder decides to accept or reject a bribe, they consider two
371 types of moral cost brought by taking bribes: the cost of conniving with a fraudulent briber, encoded in
372 the anterior insula, and the harm brought to a third party, represented in the rTPJ. These moral costs
373 were integrated in the vmPFC and the dlPFC was selectively engaged to guide anti-corrupt behaviors
374 when a third party would be harmed. Understanding the neurocomputations engaged in moral tradeoffs
375 in adults is not only useful at a mechanistic and fundamental level, AI-based anticorruption tools may
376 also benefit from these recent computational models (Köbis et al. 2022).

377

378 *Moral learning about others in adults*

379

380 Three types of moral learning phenomenon have been described at the neurocomputational level in
381 adults when learning a new set of moral rules, when learning the moral character of strangers, and
382 when learning the moral character of others (Qu et al. 2022). First, when learning a new set of moral
383 rules/norms, a RL model showed that a PE is encoded in brain regions engaged in moral choices,
384 including the vmPFC/mOFC, the anterior insula and the striatum. The ability to learn moral norms, such
385 as criminal laws and religious commandments has also been investigated (Cushman et al. 2017; Siegel
386 et al. 2018, 2019). Second, when learning the moral character of strangers through observation of their
387 actions, a few studies in adults have identified a brain system including the rTPJ and caudate nucleus.
388 This network responds with variables evolving with the impression of agents' moral character and
389 according to the way they shape subsequent moral judgments (Bellucci et al. 2019; Fouragnan et al.
390 2013). The rTPJ is associated with a PE signal updating the impressions of others' morality (Park et al.
391 2020) while caudate nucleus activity has been associated with updating others' trustworthiness
392 (Fouragnan et al. 2013). Third, learning about the moral characters of others has also been explained
393 by an asymmetric Bayesian updating mechanism in which beliefs about the morality of bad agents are
394 more uncertain than beliefs about the morality of good agents (Siegel et al. 2018, 2019). Together, these
395 studies indicate that different forms of learning processes can be formalized by different types of PE:
396 norm PE, PE about harmful outcomes occurring to others, and PE by observation of other's moral
397 actions.

398

399 *Learning and deciding about moral character in ageing*

400

401 Studies on judgement and decision-making in older adults have suggested that there are age-related
402 shifts in affective processing and deliberative judgment, that may be key to understanding differences
403 in moral judgment. As mentioned previously, positivity biases may increase in age and the influence of
404 executive functioning and theory of mind may reduce due to age-related decline. These shifting lifespan
405 patterns could underpin differences between young and older adults in moral judgements, although
406 paradigms such as the harm aversion paradigm used in young adults (Contreras-Huerta et al. 2020;
407 Crockett et al. 2015) are yet to be used in older samples. Using simple tasks of moral judgment, one
408 study reported that older participants relied less on intentions and more on outcomes compared to
409 younger participants (Margoni et al. 2018), reminiscent of earlier developmental differences. Intriguingly,
410 these age-related differences were associated with a decline in older adults' theory of mind abilities
411 (**Figure 2**). Indeed, there is debate as to whether this outcome-to-intention shift seen in children and
412 older adults is reflective of a fundamental conceptual change (Cushman et al. 2013) an improvement
413 in theory of mind abilities and model-based reasoning (Margoni et al. 2018).

414

415 A longitudinal study additionally showed that while moral reasoning skills generally improve through the
416 lifespan they start to reduce in old adulthood (Armon & Dawson 1997). Moran et al. (2013) proposed
417 that ageing differences in moral judgment are related to theory of mind impairments but also discussed
418 the possibility that they may also be related to a more general cognitive decline (Moran 2013). Future
419 studies that take a model-based approach to capture theory of mind could be crucial here. They contain
420 parameters such as the beta parameter that can capture noisiness in decision-making and inattention
421 (Lockwood & Klein-Flügge 2021; Zhang et al. 2019). By using a computational framework, differences
422 in theory of mind ability and general decision-making ability could be separated.

423

424 **Moral learning and deciding for others**

425

426 In addition to learning about moral character, sometimes we simply make decisions that have an impact
427 on another person and therefore have moral responsibility. Examples include when we learn to help
428 and avoid harming others, or when we learn and decide to punish other people. These decisions are
429 governed by normative principles to help and not harm. Such social decisions can often have more
430 wide-reaching moral implications for society. For example, a commons dilemma where my decision to
fly to Ibiza for a winter break directly benefits myself but can negatively impact others and future

431 generations. In addition, in order to be prosocial, we need to understand others' preferences to know to
432 help them, an ability likely to be influenced by theory of mind. So how do we learn and decide when we
433 must do so on behalf of another person?

434

435 *Learning and deciding for others in infancy and childhood*

436

437 Studies on learning and deciding for others in infancy are somewhat limited, given the challenges of
438 measuring learning and decision-making in this age group, and that it is a developmental stage with a
439 strong self focus as described above. However, capacity for associative and reinforcement learning (**RL**
440 **Sidebar**) in non-moral settings does emerge early in life. Ten-week-old infants increase the rate at
441 which they kick their feet toward a brightly coloured wooden mobile compared to a mobile that does not
442 provide reinforcement (Rovee & Rovee 1969). Six-month-old infants can learn to look more often at a
443 coloured shape if it leads to a video cartoon (reward) than if it leads to nothing (Tummeltshammer et al.
444 2014). This early propensity for associative learning is clearly foundational in moral development.

445

446 Whilst some researchers have suggested that learning and deciding to help others is highly prevalent
447 in our early years (Beier et al. 2014; Hamlin 2013) others have challenged whether observations of
448 toddlers helping behaviours are evidence of altruism and cooperation, or simply reflect an interest in
449 what others are doing and infants wanting to participate in adult activities (reviewed in (Carpendale et
450 al. 2015)). In one of the first studies to report that toddlers learn and decide for others, (Rheingold 1982)
451 reported that toddlers would help with household chores and would do so unprompted, suggesting that
452 deciding for others occurs early in development. 18 months may decide to help others even if it is
453 effortful, and by age 20 months they will stop playing with toys to help an experimenter (Warneken &
454 Tomasello 2009). These researchers interpreted such behaviour as reflecting evolved altruistic
455 tendencies.

456

457 In general, older children ages 3 to 6 decide to help both adults and peers in need, and this interpretation
458 has received less controversy (Paulus 2020). By age 8 aspects of theory of mind and model-based
459 reasoning have developed (**Figure 2**) as evidenced by the observation that children will reduce their
460 own resources to make sure rewards are shared equally with a partner (Lee & Setoh 2023). It is
461 important to note that in economic games developmental changes could reflect a reduced valuation of
462 rewards for oneself, rather than a higher prosocial preference to benefit others as the cost is financial.
463 The valuation of reward is crucial to understand across all life stages including older adulthood where
464 older adults have accumulated more wealth, which we will return to later.

465

466 Another way in which we learn and decide for others is when we engage in third party punishment
467 (TPP). A typical TPP paradigm involves three parties: a perpetrator, a victim, and a third party who
468 observes an interaction between the first two. The perpetrator is given the opportunity to harm the victim
469 — often through the allocation of resources — in a way that violates a social norm or rule. The third
470 party observes this interaction and is then given the chance to punish the perpetrator, or help the victim,
471 usually at some cost to themselves (Fehr & Fischbacher 2004a). Empirical evidence supports that TPP
472 is central to constructing morality. Young children expect third-party punishment to occur to perpetrators
473 that harm ingroup members (Decety & Cowell 2018). Later, an understanding that harmful actions cause
474 suffering emerges, followed by the integration of rules dependent on social contexts and cultures
475 (Decety & Cowell 2018). These processes may be underpinned by the maturation of frontal lobes such
476 as the vmPFC where age-related increases in activity in response to viewing scenarios depicting
477 intentional vs. accidental harm occur from age 4-37 (Decety et al. 2012).

478

479 *Learning and deciding for others in adolescence*

480

481 Taking an early lifespan perspective, Piaget (Piaget 2013) proposed that development of distributive
482 justice, fair resource distribution, goes through distinct developmental phases; 1) young children view

483 fairness egocentrically, with a focus on self-interest, 2) around 7-8 years they see justice as obedience
484 to unchangeable rules, 3) when they approach adolescence they recognize rules as social constructs
485 open to interpretation, and 4) older adolescents appreciate that true equity may require different
486 treatment for different people to address individual needs and circumstances. However, more recent
487 studies, found that young children aged 3 to 8 years already distinguished among various situational
488 and personal factors, such as merit (Baumard et al. 2012; Kanngiesser & Warneken 2012), and need
489 (Li et al. 2014; Paulus 2016). Although young children begin to distinguish various factors that influence
490 fair distribution, studies also report that more complex coordination processes emerge in adolescence
491 (Almås et al. 2010; Kienbaum & Wilkening 2009).

492
493 As in infancy, one behavioural measure to gauge responses to the fairness of distributions is TPP. A
494 developmental study of TPP by Gummerum and Chu (2014) showed that children and adolescents
495 consistently punished players who proposed unfair offers in a DG/UG, however both age groups
496 focused mainly on outcomes rather than intentions. However, in a second study (Gummerum et al.
497 2020) showed that adolescents' punishment became more proportional to the inequality inflicted by the
498 perpetrator with age. In a similar set of studies, participants observe the exclusion of an individual in
499 the virtual ball-tossing game (Cyberball), and can punish the perpetrator or help the victim by dividing
500 money between themselves, the perpetrators, and the victim. One study demonstrated a gradual age-
501 related increase in money given to the victim from age 9 to 22 and a gradual decrease in money
502 allocated to the excluders from age 9 to 16 (Will et al. 2013). Importantly, this study also showed that
503 perspective-taking predicted both compensation of the victim and punishment of the excluders. In a
504 developmental fMRI study, it was found that observing exclusion activated regions linked with in
505 mentalizing (i.e., mPFC), particularly among highly empathic adolescents. Additionally, adolescents
506 who displayed more activity in these regions during observed exclusion subsequently showed more
507 prosocial behaviour towards victims. In line with these findings, Tousignant et al ((Tousignant et al.
508 2018)) showed that adolescents who were more empathic and prosocial had more activation in the TPJ
509 and mPFC. Taken together, these studies suggest that deciding about others also increasingly involves
510 the integration of more complex situational factors as well as theory of mind.

511
512 The TPP studies show that adolescents are not passive bystanders but are willing to take moral
513 responsibility and situational factors into account. However, to be able to support others in more
514 dynamic situations it may be necessary to put in more effort and to learn how to best do this or learn
515 about their preferences. The prosocial learning task captures how we learn to help others (Lockwood
516 et al. 2016). A recent study with adolescents examined performance differences in a prosocial and self-
517 benefitting learning task where outcomes were for self or others. It was found that performance in the
518 learning task improved with age. Moreover, age-related improvement in performance was larger when
519 learning for others than when learning for self. Computational modeling showed that improved
520 performance was associated with lower learning rates in older adolescents, which indicates that they
521 take a longer history of choices into account. At the neural level, increased performance was paralleled
522 by an age-related increase in vmPFC activity when learning to reward others (encoding a prosocial PE)
523 (Westhoff et al. 2021). Activity in vmPFC was also correlated with measures of perspective taking,
524 suggesting that this processes further supports learning how to help others. In line with these results
525 Kwak and others found that children/adolescents, compared to adults, were more sensitive to rewards
526 directed to a charity than to self (Kwak & Huettel 2016), suggesting that these results extend to society
527 at large.

528
529 *Learning and deciding for others in adulthood*

530
531 In adulthood, studies have also used similar paradigms to those used in adolescence to examine how
532 we learn about outcomes for others. Prosocial learning based on moral concerns such as learning to
533 avoid electric shocks for another person (Lockwood et al. 2020b) or when learning to choose between
534 options paired with probabilistic monetary rewards for oneself and shocks for a confederate has been

535 studied (Fornari et al. 2023). When learning to avoid harm to others versus self, a stronger relative
536 balance was observed toward model-free over model-based learning. The caudate nucleus
537 distinguished PE for avoiding harm to others versus self (Lockwood et al. 2020b). Ventral striatum
538 encoded PE of pain avoidance for self and others and the subgenual anterior cingulate cortex (sgACC),
539 a region known to be implicated in moral agency (Zahn et al. 2020), was engaged when deciding to
540 stay vs. switch after no pain for others vs self. The sgACC is also engaged in prosocial PE (i.e gaining
541 rewards for others) (Lockwood et al. 2016, 2018) and in receiving unexpected positive feedback from
542 others (Will et al. 2017).

543
544 More complex decisions for others come in the form of TPP which has been investigated by combining
545 the UG with fMRI. Participants, as observers, may pay to punish unfair allocations of endowments by
546 one of two others. fMRI meta-analyses of social punishment have reported common (dlPFC and
547 bilateral AI) and specific brain regions (AI) for second- and third-party punishments (TPJ) (Bellucci et
548 al. 2020; Feng et al. 2015). Moreover, inequity aversion has been proposed to be a key motive driving
549 TPP (Blake et al. 2015; Fehr & Fischbacher 2004b; Raihani & McAuliffe 2012), with payoff difference
550 between proposer and receiver defining the extent of inequity (Zhong et al. 2016). Some brain regions
551 representing TPP are similar to those representing inequity aversion, including the ACC and AI (Zhong
552 et al. 2016). Engagement of these regions is positively associated with the detection of distributional
553 inequity, while dlPFC activity is associated with the assessment of intentionality to the norm violator.

554
555 One important limitation of these TPP studies is that they have ignored the possible social ties between
556 the third-party and the dictator, simply assuming that they were strangers. A recent study showed that
557 third-party punished norm violators more severely as social distance between them increased, and
558 disentangled key computations contributing to TPP, such as inequity aversion, social distance between
559 participant and norm violator and integration of the cost to punish with these signals (Tang et al. 2023).
560 The inequity aversion and social distance brain signals and the cost to punish were integrated in a value
561 signal of sanctions that modulated activity in the vmPFC. This study reveals the neurocomputational
562 underpinnings of TPP and how social distance modulates the enforcement of moral norms in humans.

563
564 Pushing further the importance of social relationships between a wrongdoer and the recipient of an
565 immoral action, it has been shown that immoral behaviours vary depending on who receives specific
566 benefits (Earp et al. 2021; Qu et al. 2020). To identify the neurocomputational mechanisms underlying
567 such moral flexibility, adults were presented with offers requiring a tradeoff between a moral cost and a
568 benefit for either oneself or a charity (Qu et al. 2020). Participants were more willing to obtain ill-gotten
569 profits for themselves than for a charity, driven by a devaluation of the moral cost when deciding for
570 their own interests. Subjective valuation of the immoral offer recruited the vmPFC regardless of
571 beneficiaries. Individual differences in moral preference modulated choice-specific signals in the dlPFC
572 according to who benefited from the decisions. These findings provide insights for understanding the
573 neurobiological basis of moral flexibility.

574
575 Together, these neuroimaging studies in adults indicate that moral concerns may act in concert with
576 inequity aversion and the willingness to punish norm violators, even when one is not directly involved
577 as a victim of the norm violation.

578
579 *Learning and deciding for others in ageing*

580
581 Although human aging is often associated with declines in cognitive and behavioural processes
582 including memory, learning and motor abilities, how moral decision-making differs as we get older is
583 less well studied. Intriguingly, recent research suggests that people believe that morality declines in
584 older-age (Mastroianni & Gilbert 2023), but in fact, several studies suggest that moral learning and
585 decision-making for others may be preserved or even enhanced in older age (Cutler et al. 2021a,b;
586 Hubbard et al. 2016; Kettner & Waichman 2016; Mayr & Freund 2020). One challenge with

587 understanding moral learning and decision-making in this age group is that most of the literature has
588 used economic games. Such games may be unable to distinguish whether lifespan differences reflect
589 differences in valuing rewards or distinctly moral and prosocial behaviours (See Future Issues).

590
591 Older adults (age 60–80) have been shown to have preserved prosocial learning, despite a decline in
592 learning that benefits only themselves (Cutler et al. 2021b). This prosocial learning for others in older
593 adults also varies with subclinical psychopathic traits including empathy and guilt such that those older
594 adults highest in psychopathic traits learn slowest to help the other person. In this study reinforcement
595 learning was model-free and it would be interesting for future studies to examine whether such prosocial
596 learning is preserved in a model-based context, where older adults have been suggested to have
597 greater learning challenges (Eppinger & Bruckner 2015a; Hämmerer et al. 2019).

598
599 When examining basic economic games such as the dictator game studies have suggested an
600 increased preference to be generous towards others with advancing age (Engel 2011) a result
601 replicated around the world (Cutler et al. 2021a). However, the bias to help people perceived as in one's
602 in-group rather than out-group also inflates (from age 18-99) (Cutler et al. 2021a). This in-group bias is
603 robust even in very young children (Over et al. 2018). It would be interesting for future studies to
604 compare in-group bias across the whole lifespan to examine non-linear impacts on learning and
605 deciding for others. Intriguingly, studies of differences in TPP in older compared to younger adults are
606 not available, to the best of our knowledge, an important avenue for future research.

607

Moral influence and contagion

608

609 Finally, moral learning and decision-making can also be under the influence of other people including
610 peers, strangers, or society. Several studies have suggested that humans are susceptible to such moral
611 influence and the extent to which they are may differ from infancy to old age. In a historical period of
612 huge social information available online, it is essential to understand how such susceptibility differs
613 across the lifespan, and whether certain life stages are associated with specific vulnerabilities to moral
614 influence by others.

615

Moral influence and contagion in infancy and childhood

616

617
618 Evaluating whether infants and children are morally influenced by others is challenging experimentally.
619 However, theoretically, early models of development highlight how observational social learning occurs
620 the context of aggression (Bandura 1965). Others have emphasised associative learning between
621 actions and outcomes is a key mechanism for developing moral architecture (Heyes 2012).

622

623 Observational learning is a fundamental ability apparent from the first years of life (Foti et al. 2018;
624 Herold & Akhtar 2008; Matheson et al. 2013). If adults show their intention prior to demonstration, 16-
625 months-old infants can learn tool use by observation (Fagard et al. 2016). But are they influenced by
626 learning about moral behaviours? One study suggested 5-7 year olds who observed someone sharing
627 were more likely to share themselves. Ma et al (2018) found that children aged 5 were more honest
628 after observing a classmate benefit from being honest (Ma et al. 2018). Together these results suggest
629 that the basic mechanisms of action-outcome pairing and moral influence emerge from infancy to
630 childhood. In later years these abilities become more sophisticated.

631

Moral influence and contagion in adolescence

632

633
634 Adolescence is a period of strong changes in socially motivated behavior and it may therefore not be a
635 surprise that adolescents tend to respond more strongly to information from others, specifically their
636 peers, compared to other age groups (Albert et al. 2013; Blakemore & Mills 2014; Molleman et al. 2019,
637 2022; Silva et al. 2016). Whether this increased peer influence is negative or positive appears to be

638 context-dependent. Social influence among adolescents is often associated with increased risk taking
639 and negative outcomes (e.g. anti-social behavior and substance abuse (Chein et al. 2011; Ciranka &
640 van den Bos 2019; Dishion & Tipsord 2011; Reyna & Farley 2006). Indeed, in many experimental
641 settings risky behavior of peers can lead to increased risky behavior (Chein et al. 2011; Gardner &
642 Steinberg 2005; Smith et al. 2014), but several studies also showed that observing risk-averse peers
643 or risk-averse advice had at least the same amount of impact on reducing risky-behavior (Bingham et
644 al. 2016). Similarly, observing prosocial behavior of peer can also both in- and decrease prosocial
645 behavior of adolescents (Sullivan et al. 2022; van Hoorn et al. 2016).

646
647 Recently, the effects of peers in different domains have been studied, which suggested that there is 1)
648 a single factor underlying the developmental changes in social information use in adolescence, and 2)
649 a significant reduction in sensitivity to social information during this period. Pinho et al., have shown
650 that adolescents are influenced by observing strong disapproval of risk-taking or strong approval of
651 prosocial behaviour (Pinho et al. 2021) and this may be linked to TPJ. For example, variability in TPJ
652 response in adolescents has been related to their own charitable giving (Tashjian et al. 2018). Thus,
653 information about norms and or observations of single individuals can change adolescents' attitudes
654 and behaviours. Researchers have also developed paradigms where participants receive positive (i.e.,
655 acceptance) or negative (i.e., rejection) feedback from peers (Achterberg et al. 2018; Guyer et al. 2012;
656 van Hoorn et al. 2016). In one imaging study adolescents gave more, at their own expense, when they
657 were being observed, and even more when they received feedback (Van Hoorn et al. 2016). Importantly,
658 peer presence was associated with activation in the mPFC, TPJ, precuneus, and STS, and adolescents'
659 TPJ activity was associated with their level of generosity.

660
661 In sum, this pattern of results is consistent with a shift from model-free to more model-based
662 reinforcement learning (**Figure 2**) which is associated with increased engagement of brain regions such
663 as the TPJ.

664 665 *Moral influence and contagion in adulthood*

666
667 In adults, social influence has been proposed as an important mechanism to explain why people follow
668 others' choices (Lee & Chung 2022; Toelch & Dolan 2015; Yu et al. 2021). In a moral context, both the
669 size of a jury judging a crime scenario and the confidence that each jury member has in their own moral
670 judgment determine how much a given individual adapts to the judgment of the jury (social influence)
671 (Park et al. 2017). At the time of judgment adaptation following influence from others, individuals trade
672 off the credibility inferred from their own confidence levels against the credibility of social information.
673 The dACC represents belief updates during moral judgments when conforming to other jurors, while
674 the lateral frontopolar cortex monitors the changes in credibility assigned to social information. These
675 results provide a neurocomputational understanding of social influence on moral choices.

676
677 Social influences can also affect how we consider our moral choices in the eyes of others. Indeed, we
678 tend to behave in a more egoistic manner under guaranteed anonymity and more pro-socially when
679 observed by others (Izuma 2012). The influence of being observed by others has been investigated
680 when making both moral and amoral choices (Obeso et al. 2018; Qu et al. 2020). Two types of choices
681 were considered: whether to earn money by contributing to a 'bad cause' and whether to sacrifice
682 money to contribute to a 'good cause'. Adults were more likely to choose the prosocial option when they
683 had to make a public donation. Regardless of the type of dilemma, the ACC, AI and the rTPJ were more
684 engaged in public than in private settings. Moreover, distinct valuation systems were engaged to solve
685 these dilemmas: AI and IPFC when weighing monetary benefits and moral costs, and ventral putamen
686 when weighing monetary costs against compliance with one's moral values.

687
688 When observing dishonest individuals, adults, like infants, might progressively become more and more
689 dishonest (Dimant 2019; Gino et al. 2009). Thus, learning about others' behaviour can dynamically

690 change one's own preferences or bias one's own valuation process (Lee & Chung 2022; Yu et al. 2018).
691 The dlPFC may integrate social factors such as moral norms as well as moral preferences into the
692 decision process during moral choices (Buckholtz 2015; Carlson & Crockett 2018; Crockett et al. 2017).
693 One study in adults showed that the extent to which participants engage in self-serving dishonesty
694 increases with repetition and this effect is associated with a reduced amygdala sensitivity to the history
695 of dishonest behavior (Garrett et al. 2016). Together, these studies suggest social influence continues
696 to be a strong driver of following moral norms in adulthood.

697 *Moral influence and contagion in ageing*

698
699
700 Like adolescents, older adults show an increased or preserved processing of rewards in social contexts,
701 and this pattern is even present across species (Almeling et al. 2016; Foulkes & Blakemore 2016;
702 Samanez-Larkin & Knutson 2015). Processing rewarding outcomes is a fundamental mechanism that
703 is the first stage of moral influence and contagion, and as already discussed, is apparent in childhood.
704 Recent evidence suggests in non-moral contexts that older adults might be more affected by social
705 conformity of economic preferences (Su et al. 2024) particularly when these preferences are impulsive
706 compared to patient. Experience sampling work suggests that for daily desires, self-control increases
707 from young to older adulthood and social influence decreases (Castrellon et al. 2023).

708
709 These differences in susceptibility to social and moral influence may again reflect differing reliance on
710 theory of mind and model-based strategies (**Figure 2**). It is possible that resisting moral pressure
711 depends on theory of mind to reveal the intention of others which could be learnt by observation. Several
712 studies have suggested that theory of mind ability, as measured by tasks where participants infer others'
713 mental states by viewing faces, cartoons, or stories - is typically impaired in older adults (Kemp et al.
714 2012), **Figure 2**). Importantly, such impairments are at least partly independent of general cognitive
715 decline (Kemp et al. 2012). One study reported age-related improvements in theory of mind in a
716 vignettes task (Happé et al. 1998), yet a later meta-analysis supported older adults performing more
717 poorly than younger adults across all theory of mind measures (Henry et al. 2013). Future studies
718 incorporating the need to engage in mentalising during actual social interactions, and in a value-based
719 framework (e.g. (Hampton et al. 2008; Hill et al. 2017) are needed to precisely measure index theory of
720 mind ability in older adults. In terms of neural correlates, several studies have suggested that
721 connectivity between frontal and parietal areas, often suggested to support theory of mind (Koster-Hale
722 & Saxe 2013; Lockwood et al. 2020a; Wittmann et al. 2018), changes in older adulthood (Setton et al.
723 2022). Such changes may underpin these cognitive and affective differences.

724 725 **Summary**

726
727 We reviewed four key concepts that may be fundamental for understanding moral learning and decision-
728 making across the lifespan (**Figure 1**). These were learning and experiencing moral emotions, learning
729 and deciding about moral character, learning and deciding for others, and moral influence and
730 contagion. These concepts show key similarities and differences across the lifespan from infancy to
731 older age. In the earliest years, a sense of self-other distinction is foundational for the development of
732 many key abilities. Sensitivity to the intention vs. the outcome of decisions is also crucial for moral
733 judgement and learning and deciding for others which differs with age, interestingly being the most
734 similar in our earliest and oldest years. Third-party punishment may develop early in life, yet we still
735 know little about how these processes may differ during senescence. Across all ages, basic shifts in
736 the influence of theory of mind and the balance between model-free and model-based reasoning appear
737 important to support aspects of morality (**Figure 2**). As well as these general conclusions, future
738 challenges and opportunities remain.

739 740 741 **Future issues**

742

743 **Domain-general and domain-specific moral learning and decision-making**

744

745 It remains unclear whether the learning processes involved in moral cognition engage distinct
746 algorithms and different neural implementations from non-moral learning (Hopp et al. 2023; Lockwood
747 et al. 2020a; Qu et al. 2022). Some advocate social learning can be explained by domain-general
748 learning processes at the algorithmic level (Heyes 2012, 2018; Heyes & Pearce 2015; Lind et al. 2019),
749 while others argue that it requires metacognitive knowledge about whom to learn from (Heyes 2016;
750 Kendal et al. 2018). At the implementational level, there are arguments for common or distinct neural
751 processes involved in social and moral vs. non-social learning (Lockwood et al. 2020a; Vogel &
752 Lockwood 2024). The paradigms used are crucial here. Many older adults have accumulated more
753 wealth than younger adults, and therefore economic games that have a purely financial cost may hide
754 developmental differences. Instead, it is possible to use other costs to oneself, such as time and effort,
755 or calibrate reward values across ages. For example, in younger children, a choice can be given
756 between a financial reward and an object of equal value.

757

758 **The importance of longitudinal studies**

759

760 Most studies reported in this review present cross-sectional data, and often compare one or two age
761 groups that represent a small slice of the whole lifespan. This lack of longitudinal studies may not
762 account for shifts in social norms and thus cohort effects (Baltes 2009). Longitudinal studies would
763 require the consistent use of the same task for participants of all ages. Thus far, versions of economic
764 games have been useful given their simplicity and game like nature. New advances in designing
765 paradigms based on theories in ecology could also be beneficial given that these probe cognitive
766 processes that the brain evolved to solve (Gabay & Apps 2021; Scholl & Klein-Flügge 2018).
767 Computational modeling using a consistent formalization of learning and decision-making processes
768 can further harmonize the results of moral behavior in different age groups and can provide deeper
769 insights in the developmental processes that lead to changes in behavior with age (van den Bos et al.
770 2018). In developmental computational neuroscience, researchers have mainly focused on the
771 developmental changes in certain parameters. However, it is also possible that it is not only the
772 parameters of a model that changes with age, but rather there is a shift in strategies, or moral heuristics
773 (Gigerenzer 2008; Lindström et al. 2018; Sunstein 2003), thus different models that describe the
774 behaviour best for different age groups (van den Bos et al. 2018). Finally, it is important that if variables
775 of computational models are being used to compare age groups these are robust and reliable (Schaaf
776 et al. 2023; Waltmann et al. 2022), here hierarchical Bayesian modeling can help, specifically if there
777 are only a few data points per individual to model.

778

779 **Atypical moral development across the lifespan**

780

781 When examining lifespan differences in moral learning and decision-making most of the research has
782 focussed on typical rather than atypical development, since studies of atypical development often
783 compare groups of individuals rather than differences across age. However, important insights can be
784 gained by understanding the trajectories of atypical development (Hu et al. 2021). For example, conduct
785 disorder, which may be considered the archetypal moral disorder is associated with behaviours which
786 violate the rights of others and an absence of certain moral emotions such as empathy and guilt (Blair
787 2013; Fairchild et al. 2019; Frick & Kemp 2021; Pauli & Lockwood 2023). In addition, in a study with the
788 mini-UG adolescent delinquents showed they cared less about the intentions behind unfair offers, and
789 this behaviour was associated with reduced activation in the TPJ (van den Bos et al. 2014). Importantly
790 conduct problems often onset either in childhood or adolescence and there is little evidence that it
791 occurs later in life. Indeed, cross-sectional studies have shown that psychopathic traits are lower in
792 older compared to younger adults (Cutler et al. 2021b). Studies that follow atypical development
793 longitudinally are crucial as well as more carefully documenting the typical trajectories over longer time

794 scales to understand the mechanisms behind possible reduced levels of psychopathy and antisocial
795 behaviour in later life.

796

797 **Artificial Intelligence and lifespan development**

798

799 One interesting implication of the recent development of computational models of moral choices across
800 the lifespan is to consider how future artificial agents (e.g. automatic cars, robots, bots.) will be able to
801 flexibly adapt to moral behavior of people from different ages (from children to older adults) (Bonneton
802 et al. 2024; Köbis et al. 2022). For example, recent computational models of theory of mind in children
803 indicate that the same computational model of theory of mind cannot be applied to children between 3-
804 8 and above 8 years old (Nong et al. 2023; Philippe et al. 2022). It may therefore become necessary to
805 equip artificial agents not only with algorithms mimicking computations used for moral choices from the
806 adult human brain (Philippe et al. 2022), but also with algorithms accounting for computations
807 accounting for moral choices of young children or older adults.

808

809 **[Sidebar] Reinforcement Learning**

810

811 Reinforcement Learning (RL) describes how an agent learns to make optimal decisions in an
812 environment. Q -Learning is a Model-Free RL (MF-RL) algorithm that seeks to find the best action (a)
813 given the current state (s) (Watkins & Dayan 1992). During learning the Q -value, a "quality" score for a
814 state-action combination, is updated by comparing the experienced outcome (r) with the expected
815 outcome ($Q(s,a)$). The extent to which the Q -value is updated is regulated by the learning rate (α):

816

$$817 Q_{t+1}(s,a) \leftarrow Q_t(s,a) + \alpha[r_t - Q_t(s,a)]$$

818

819 Model-Based RL (MB-RL) involves the agent creating a model of its environment and using this model
820 to plan actions by simulating future steps (Dayan & Berridge 2014). This allows the agent to anticipate
821 the consequences of actions without needing to try them all. However, building a model takes up more
822 cognitive resources than MF-RL. Developmental studies have shown asymmetries in learning rates for
823 outcomes that are better or worse than expected (Van den Bos et al. 2012), and a shift from MF-RL
824 towards more MB-RL in adulthood (Decker et al. 2016), with a later reversal to MF-RL in ageing
825 (Eppinger & Bruckner 2015b). RL models can also explain how a history of pairing social phenomena
826 with positive or negative outcomes influences complex moral behaviours (Christopoulos et al. 2017;
827 FeldmanHall & Dunsmoor 2019).

828

829

830 **Definitions**

831

832 **In group bias** is the tendency to favour those who are perceived as belonging to one's own group over
833 other groups.

834

835 **Inequity aversion** concerns decisions that minimize inequity in outcomes, as the difference between
836 one's own material self-interest and others' payoffs.

837

838 **Vicarious rewards**: Rewards received by others.

839

840 **Empathy** is the capacity to understand and vicariously experience the affect of other people.

841

842 **Theory of mind** also known as mentalising is the ability to attribute mental states such as beliefs,
843 desires, and intentions to other individuals.

844

845 **Intention** a mental state in which the agent commits themselves to a course of action.
846
847 **Third-party punishment** is when individuals punish transgressors or norm violators who have not
848 harmed them directly.
849
850 **Guilt** occurs when the violation of social norms induces harm or suffering to other individuals, typically
851 in a relationship or among members of the same group.
852
853 **Shame** is a 'self-focused negative emotion' experienced when a person believes that she transgresses
854 certain rules. Shame is related to how we perceive ourselves.
855
856 **Envy** refers to a comparison between someone's negative situation and another individual's positive
857 situation.
858

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