Review

Development of mental transformation abilities

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Mental representation and transformation of spatial information is often examined with mental rotation (MR) tasks, which require deciding whether a rotated image is the same as or the mirror version of an upright image. Recent research with infants shows early discrimination of objects from mirror-image versions. However, even at the age of 4 years, many children perform at near chance level on more standard measures. Similar age discrepancies can be observed in other domains, including perspective taking, theory of mind, and intuitive physics. These paradoxical results raise the questions of how performance relates to competence and how to conceptualize developmental change. There may be a common underlying mechanism: the development of the ability to imagine things and mentally transform them in a prospective fashion.

Introduction

One of the most impressive skills of the human species is the ability to represent and mentally transform the shapes of objects. People can generate mental images of 2D shapes or 3D objects and can transform them in various ways (e.g., rotating, bending, or folding them) [1]. Such flexible representations are vital for making predictions regarding the positions of moving objects; for example, to avoid collisions when crossing a street. They also allow anticipation of the effects of actions when manipulating objects or using tools. Furthermore, the ability to perform mental spatial transformations predicts number and mathematics skills [2,3]. Thus, determining the origins and development of mental transformations is a central and topical problem in cognitive science, with translational implications for intervention. However, research on this issue has led to paradoxical findings, with infants showing remarkable abilities but young children failing on seemingly similar tasks. In this review we put these contrasting results in context with similar findings in other domains and suggest an underlying mechanism.

Age discrepancies in mental transformation

Much of the previous research on mental transformation has focused on a specific kind of spatial transformation termed mental rotation (MR), which refers to imagining a rotational movement of an object (or array of objects) in 2D or 3D space. In a classic MR task [4], participants must decide whether a rotated image is the same as a comparison image or its mirror image. In developmental research, this paradigm has been adapted for use with children and even infants, with oddly contrasting results.

Studies with preschoolers and young children

Although Marmor [5,6] found that 4–5-year-olds were able to perform MR, there has been controversy about her conclusions [7]. A follow-up study employing the same procedure with different stimuli failed to replicate Marmor's results [8]. Other studies showed that, at 4–5 years, many children performed at chance level and only few showed signs of MR [9–11]. Even efforts to simplify the tasks by using a touch screen or presenting simple and engaging stimuli have failed to demonstrate MR in 3-year-olds, let alone younger children [12,13]. Some other tasks that have been used with toddlers and young children can be solved by using feature strategies and may not require MR (Box 1).

Infant studies

In sharp contrast to research with preschoolers, recent research has shown that infants can discriminate mirror images despite differences in orientation [14–21]. For example, in two such studies [14,15], infants saw an asymmetrical object being moved straight down behind an occluder. When the occluder was lowered, it revealed either the same object (possible event) or its mirror image (impossible event) in one of five different orientations (Figure 1). Infants had been shown beforehand that the backside of the object looked different, so the mirror image was impossible. Six-month-olds looked longer at the impossible than at the possible outcomes, suggesting that they discriminated mirror images. Other studies using similar violation-of-expectation paradigms showed that infants looked longer at incongruent than at congruent outcome orientations of objects undergoing a hidden rotation [22–24].

These findings suggest that infants possess fairly sophisticated abilities, yet much older children struggle with MR tasks. Thus, it is unclear whether infant and preschool tasks measure the same ability, how performance on these tasks relates to competence, and how to conceptualize mechanisms of developmental change. Adding to the heterogeneous picture, sex differences in MR seem to be

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Box 1. Distinctive stimulus features

Some researchers have used manipulation tasks to study MR in toddlers between 2 and 5 years of age [3,63,64]. The goal of these tasks was to rotate an object manually into the same orientation as a reference object, to its upright (canonical) position, or so that it would fit through an aperture. The assumption has been that toddlers mentally rotate the object first to form an (efficient) action plan. However, it can be argued that toddlers do not need MR to succeed in these tasks. Instead they may infer in which direction an object needs to be turned based on object features, such as the orientation of the longest axis or the position of its top (head) or base. For instance, if we showed a child a figurine lying on a table and asked the child to stand it up, the child may identify the figurine's feet and then simply put it 'on its feet'. The child does not necessarily need to mentally rotate the figurine beforehand, because a simple strategy to 'bring the feet to the lowest possible position' would lead to success.

When children are presented with alternatives that can be distinguished based on features (cf. [2,65–68]), we cannot draw firm conclusions about MR unless we can exclude such feature strategies, for instance by using mirror images, as suggested by Shepard and Metzler in their original study [4].

robust in adults but have only rarely been found before 9 years of age (Box 2). However, there are various potential reasons for the observed performance differences, because paradigms used with infants differ from those used with children in several ways.

Task differences

Presentation of motion or multiple views

In MR paradigms used with adults [4] and children [5,6,9,25–27], stimuli are typically static images in single orientations. By contrast, infant often see objects in actual physical rotation before the test [16,17,20,21,23,24] or in multiple static orientations [18,19]. This may allow infants to extrapolate motion or to interpolate between familiar views [28]. Indeed, research has demonstrated that infants

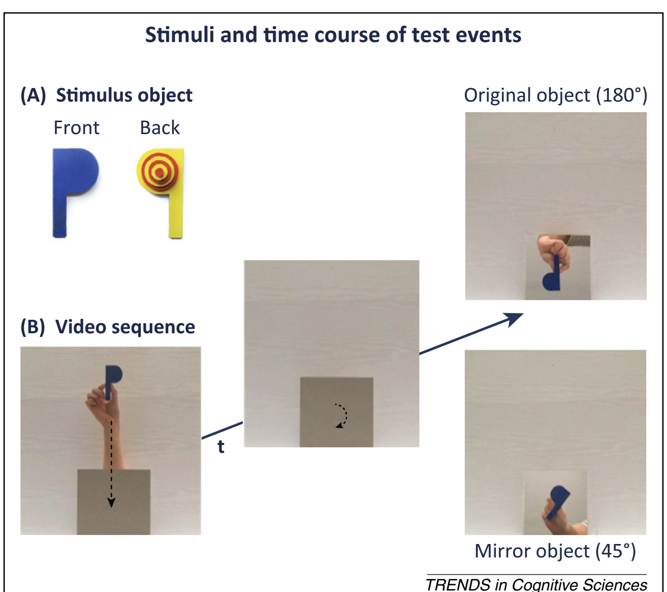

Figure 1. **(A)** Front and back views of the stimulus object and **(B)** sequence of test events used by Möhring and Frick, with examples of possible (top) and impossible (bottom) outcomes (t, timeline; broken lines, movement trajectory of stimulus object). Adapted, with permission, from [14,15].

Box 2. Sex differences

Research on adults' MR has generally yielded a male advantage [69,70]; however, the underlying reasons for the difference are unclear, as is the age when the difference is first evident. Although some studies suggested that the sex difference is largely due to different speed/accuracy trade-offs, with females responding more slowly but more accurately than males [71], a meta-analysis with participants between 8 and 29 years of age showed that sex differences are smaller and yet not eliminated by unspeeded conditions [72]. Some researchers have proposed biological reasons for the male advantage, based on findings that exposure to heightened levels of prenatal androgens due to congenital adrenal hyperplasia [73] or the presence of a male twin [74] was associated with higher MR performance in females.

In line with biological explanations, some MR studies [16–19] showed a male advantage in infants as young as 3–10 months. However, a majority of studies with infants did not show sex differences [14,15,20–24]. Moreover, several studies with preschool through primary school children did not report any systematic advantages (e.g., [5,6,9,13,25–27,75,76]) or they even found higher error rates in boys [11]. Interestingly, a meta-analysis found an increase in effect size as a function of chronological age [70] and more recent research suggests that gender differences emerge around 9 years of age [77,78]. These findings raise the question of what factors may promote sex differences around that age.

One such factor may lie in males experiencing more activities that involve spatial thinking compared with females (such as playing video games [79–81]). Another factor is suggested by studies [82,83] showing that instruction-induced expectations about gender differences can affect performance. Neuroimaging results [84] indicate that negative stereotypes promote less efficient neural strategies and increase emotional load, whereas positive stereotypes are associated with heightened activation in visual processing areas and working memory processes. Surprisingly, such negative correlations between spatial anxiety and MR performance can be found in girls as young as 5–8 years [67]. The question of how biological, psychological, or social factors interact to influence sex differences in MR is currently unsettled [85].

are better at recognizing objects that are presented in motion compared with static views [29].

However, showing motion or multiple views can now be excluded as the sole explanation for early success, in light of recent evidence suggesting that 6-month-olds are able to discriminate an object from its tilted mirror version, even after being familiarized to the upright object only [14,15]. Nevertheless, presenting an object in motion or multiple views may lower task difficulty, causing infants as young as 3–4 months to succeed [16,18,23,24].

Presentation of outcome

Another task difference lies in the fact that infants typically are confronted with congruent and incongruent outcomes of rotational events, whereas children have to predict the outcome [30]. Thus, infants' reasoning may be limited to recognizing incongruities retrospectively and they may simply react to violations of basic principles such as object solidity and continuity. By contrast, children's tasks require prospective spatial transformations that may be more cognitively demanding because they involve mentally simulating a rotational event and inhibiting current sensory input [31].

Differences in measurement

Tasks in infancy research use dependent variables such as looking time, eye movement, event-related potentials

(ERPs), and heart rate. Such variables may tap different cognitive competencies than dependent variables that require explicit judgment, conscious choice, or decision making. Moreover, older children generally must perform a motor response that may increase cognitive load, leading to a cognition/action trade-off [32]. Indeed, discrepancies between reports of amazing abilities in infants and profound lacks in older children are not confined to MR but are also found in other cognitive domains.

Age discrepancies in other domains

Perspective taking

Perspective taking refers to the ability to adopt someone else's spatial perspective. It is logically akin to MR, as it involves mentally rotating oneself into another vantage point. However, despite this similarity, perspective taking and MR are dissociated in various behavioral and neural ways [33–35]. Developmental research has shown that perspective taking emerges at around 4 or 5 years but improves considerably through the age of 8 years [36]. Although preschoolers perform better on tasks in which responses are not influenced by conflicting frames of reference [37], they still make many egocentric errors.

In contrast, infants as young as 14 months succeeded in perspective-taking tasks that measured looking times [38,39]. For example, when asked to help an experimenter find an object, 24-month-olds inferred whether an object was visible or hidden from the experimenter's point of view and helped in obtaining the occluded object [38].

Theory of mind

The development of metacognitive knowledge, or theory of mind [40], is often assessed by a false-belief task [41]. For example, suppose a character (Maxi) aims to retrieve chocolate that has been relocated in his absence. Asked where Maxi will look for the chocolate, all 3–4-year-olds and almost half of 4–6-year-olds say that Maxi will look in the new place (where the children know the chocolate is) rather than in the original place (where Maxi falsely believes the chocolate is). Such results suggest that it is not until 4–6 years of age that the ability to represent another person's epistemic state emerges.

By contrast, infant studies have suggested an early ability to attribute complex mental states and false beliefs to others [40,42]. For example, a study that followed the logic of the Maxi study [43] showed that 15-month-olds looked reliably longer if an experimenter searched for a toy in a place where it was relocated to in her absence, as compared to when she searched where she had previously observed the toy being hidden.

Intuitive physics

Another domain where age discrepancies have been found concerns children's understanding of the physical world [30]. A large body of research revealed that young infants show a stunning sophistication in their understanding of basic physical principles [44]. Spelke and colleagues [45] showed that infants as young as 2½ months have a sense of solidity and continuity and respond with prolonged looking if a solid object passes through or jumps over an obstacle. However, contrasting findings suggested a surprising lack of such knowledge in 2- and 3-year-olds (e.g., [46–48]).

To investigate these age discrepancies within a single study, Hood, Cole-Davies, and Dias [49] tested preschoolers on an observation task as well as a search task. Children watched a ball rolling behind a screen that partly occluded a solid barrier. Whereas the children's looking times suggested that they detected violations of solidity (i.e., the ball seemingly passed through the barrier), this sensitivity was not associated with successful search behavior.

Conceptualizing development

How can these paradoxical age discrepancies be explained? One possible interpretation is to assume a U-shaped developmental trajectory (Figure 2A), in which infants possess an early ability that is temporarily lost and reacquired later.

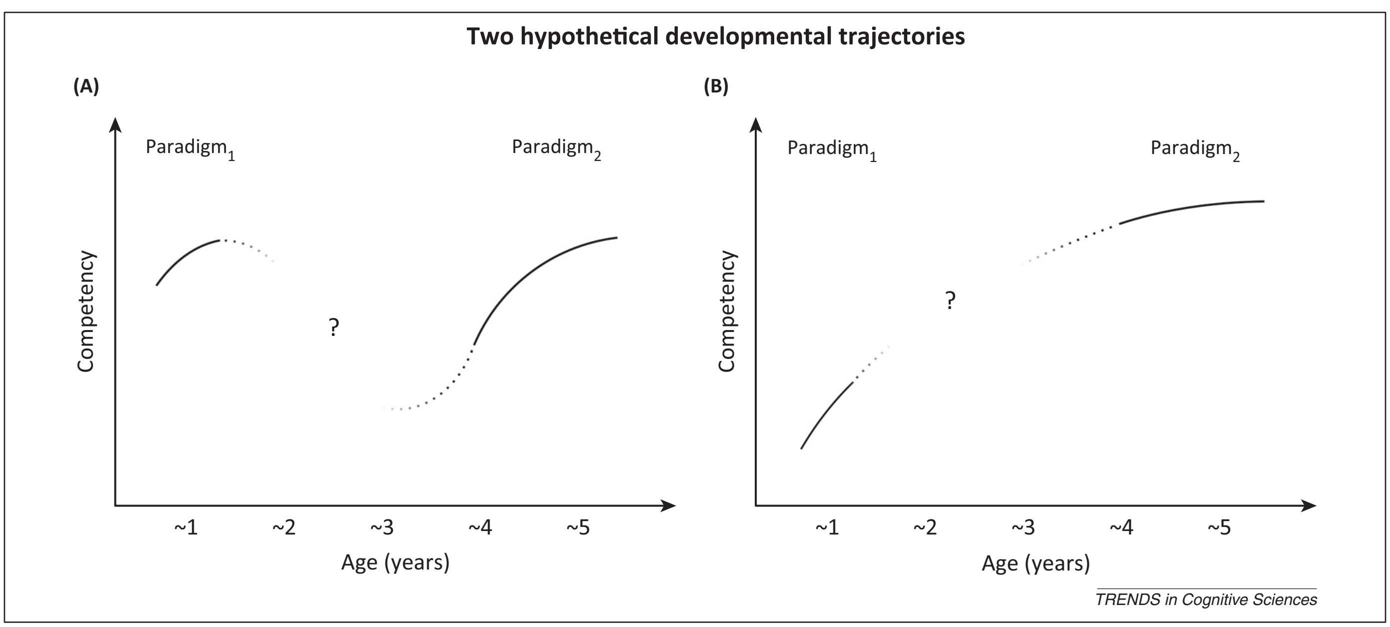

Figure 2. Schematic illustrations of hypothetical developmental trajectories, assuming a U-shaped **(A)** or a more linear **(B)** developmental progression of competency, measured by infant paradigms (Paradigm$_1$) and paradigms used with preschoolers and children (Paradigm$_2$).

However, as discussed above regarding MR, infant paradigms ($Paradigm_1$) and paradigms used with older children ($Paradigm_2$) differ in many ways. Hence, we should also consider an alternative trajectory (Figure 2B) with two possible versions. In one scenario, $Paradigm_1$ and $Paradigm_2$ measure entirely different abilities. In a more parsimonious scenario, $Paradigm_1$ and $Paradigm_2$ tap the same ability on different levels of sophistication. In the case of MR, further research is needed to distinguish between these two scenarios; in particular, finding a method for indexing the time infants take to rotate a stimulus mentally (in analogy to adults' response times) would advance our understanding.

In the domain of intuitive physics, Hespos and Baillargeon [50] found that developmental patters observed in looking-time paradigms also hold for reaching tasks, supporting the view that looking-time and reaching tasks tap the same physical knowledge, rendering a U-shaped development unlikely. The notion that different tasks may tap the same knowledge at different levels of abstraction is also supported by the fact that adults who show misconceptions about physical laws in their explicit judgments are nevertheless able to perform mental simulations and behave in accordance with the same laws (e.g., [51–53]).

Regarding theory of mind, Perner and Roessler [40] assume that early sensitivity is shown in implicit 'online tasks', in which engagement with ongoing events reflects expectations, whereas traditional tasks require explicit judgment and an intentional switch of perspectives. For perspective taking, there is general agreement that the ability can be measured at different levels of sophistication [36]. Infant tasks typically measure Level-1 perspective taking, which requires an understanding of what another person sees – an inference that can be made by tracing the line of sight. Older children fail on Level-2 tasks, requiring a more sophisticated understanding of how a person sees the environment. Thus, in line with the assumed trajectory in Figure 2B, children's tasks assess perspective taking at a higher level, which presumably requires mentally assuming someone's viewpoint while ignoring one's actual perceptual input.

Common mechanism?

Taken together, contrasting results of seemingly sophisticated competencies in infancy and surprisingly low performance in preschoolers can be found in several cognitive domains. Some of these domains appear closely related, such as perspective taking and theory of mind; others do not seem to have much in common, such as knowing how a ball rolls and reasoning about another person's beliefs. Furthermore, it is remarkable that similar age dissociations are found not only in areas such as intuitive physics and theory of mind, which have conceptual content, but also for spatial transformations that are generally considered to be analog and perception-like in nature [54]. However, the findings of similar dissociations across cognitive domains may be informative, indicating a common underlying mechanism. In particular, the fundamental ability to transform mental representations may be instrumental in understanding other people's perspectives, mental states, and physical events [9,55].

A great deal of research has provided evidence for mental simulation as a strategy to solve mechanical and dynamic physical problems (e.g., [52]). Such mental simulations may tap tacit or implicit knowledge about physical constraints such as object constancy, solidity, or inertia that may be present early in life. Schwartz and Black [56] argued that people may fall back on imagistic mental models in situations where they do not have adequate explicit knowledge. However, although implicit knowledge may be activated during mental simulation, it may not be consciously accessible or open to reflection. Wilson [57] assumes that these simulations piggyback on mental structures that originally evolved for perception or action and can now be run 'offline', dissociated from physical inputs and outputs (cf. [58] for ideas on conceptualizing such decoupling). This notion is in line with findings that MR ability is closely linked to motor activity and motor development (Box 3).

Mental simulation has also been used to explain the mechanisms underlying theory of mind. Whereas theory theorists posit that children acquire a conceptual understanding of the mind, simulation theorists claim that we

Box 3. Motor effects

Research on embodied cognition suggests that motor processes are involved in MR. Studies with adults have shown that motor areas of the brain are recruited during MR, with specific activation of the supplementary motor area (see [35,86] for a meta-analysis and review). This area is associated with motor control and simulation, suggesting that participants may perform covert motor simulation during MR. Such motor simulation strategies can be induced through training, as manual rotation or rotation of hand stimuli led to increased activity in motor areas in subsequent object-rotation tasks [87,88]. Behavioral studies demonstrated that even training in seemingly unrelated activities such as juggling [89] or wrestling [90] can improve MR performance. Moreover, studies using double-task paradigms showed that hand movements that are compatible or incompatible with the direction of MR [91–93], or even just the planning of such movement [94], can have differential effects on the MR of objects, suggesting that manual and mental rotations share common processes.

Similarly, developmental studies have shown effects of simultaneous hand movements or postures on children's MR [26,95] or mental simulations of physical events [96]. Interestingly, these studies have suggested that the effects of action on cognition decrease over development. Other studies have shown that 10-year-olds' MR was facilitated by training to rotate objects manually by means of a joystick [97]. There is also correlational evidence for an association between MR and the development of motor abilities, specifically the development of motor control in 5–6-year-olds [75].

Research with infants has demonstrated that motor development, especially locomotor ability, is associated with MR performance [14,20,21]. Increased experience with self-initiated movement may enable infants to think about spatial relations between objects in more allocentric terms. In addition to correlational data, there is experimental evidence that infant's MR is facilitated by active motor experience [15,22], but such active exploration becomes less crucial as infants grow older. Active hands-on exploration may be especially beneficial for young infants because such interactions may lead to a more stable mental representation of the object [98], which in turn may be more resistant to decay during MR. Overall, developmental findings suggest that motor processes play a functional role in the development of MR abilities and that MR performance becomes increasingly dissociated from overt motor activity, perhaps due to an increasing ability to perform covert motor simulations.

can infer what another person thinks, knows, or plans by mentally simulating their situations [59]. According to simulation theory, we form predictions about our own or other's actions by engaging in a kind of 'pretend play' while suppressing behavioral output.

Developmental progress in the understanding of other people's minds may therefore be due to increasing imaginative skills, allowing children to simulate more complex situations [9]. Others [60] have postulated that self-projection may be a common mechanism underlying theory of mind, prospection, episodic memory, and navigation, with all of these cognitive abilities relying on autobiographical information. Here we go a step further, proposing that the ability to flexibly change mental representations may be even more fundamental, also allowing the anticipation of nonbiological motion and physical events.

Concluding remarks

Developmental research has shown apparently sophisticated abilities in infants across multiple domains, whereas older children struggle with seemingly similar tasks. Recent infant studies in the domain of MR have demonstrated similar patterns of paradoxical age discrepancies, providing new support for the claim that mental simulation may be key to successful performance in many cognitive domains. Whereas content, modality, and simulated perceptual inputs may vary across domains, the ability to flexibly transform mental representations regardless of the sensed, known, or believed actuality may be a common mechanism of fundamental importance for a host of cognitive abilities and their development (Box 4).

In line with a simulation account, Perner and Roessler [40] note that early sensitivity is observed only in spontaneous and immediate responses, suggesting that implicit knowledge is available only briefly after stimulus presentation. Thus, mental simulations may initially be too short-lived and weak to guide complex verbal or action responses. Along with developing mental transformation abilities, they may become stronger, more resistant to decay, and hence more behaviorally relevant. Furthermore, in accordance with the notion of graded representations [61], different tasks may be more or less likely to evoke mental simulations and therefore require different representational strength. Developmental progression in mental transformation ability, possibly along with growing executive functions [31,62] that allow for ignoring perceptual input and inhibiting motor output, may enable more complex and more sustained simulations of alternative scenarios, raising the abilities in these cognitive domains to a higher level.

Box 4. Outstanding questions and future directions

- If mental transformation ability is a common mechanism that is fundamental to successful performance in all of the domains discussed, do these cognitive activities rely on similar brain processes and share a common neural substrate? We know from neuroimaging studies that, although some brain regions appear to be selectively activated by tasks requiring object versus perspective transformations, a much larger number of brain regions are commonly activated during both of these tasks [35]. Whereas much of the previous research has aimed at distinguishing these processes, future research could focus on commonalities and investigate whether an area of neural overlap can be identified (see [60] for a discussion of neural overlap between theory of mind, perspective taking, and prospective thinking). Furthermore, correlational studies should address whether good mental transformation skills are associated with better performance in the other domains and training studies should test whether practicing mental transformation skills would lead to improved simulations of physical events or other people's mental states.
- From a developmental perspective, it would be informative to investigate whether mental simulation and the abilities in the above-mentioned cognitive domains are related to the development of executive functions; specifically, inhibitory control, which is presumably necessary for inhibiting current perceptual input and motor output while simulating alternative realities.

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