

Furthermore, the individual variability in CRA can facilitate study of the neural circuits underlying the spectrum of learned to innate avoidance in the same behavioral context. The existence of fish with innate threat avoidance suggests the robot's chasing actions may activate sensory areas associated with visual looming and motor circuits associated with instinctive escape behaviors^{18,19}. This raises the further question of which neural mechanisms enable fish to rapidly recognize specific predators, and what factors determine how long these associations endure? Dark looming visual stimuli (like those associated with the rapid robot approach in the CRA) are largely encoded in the optic tectum and Arborization Field 5 (AF5), two retino-recipient visual processing areas of the zebrafish brain^{18,19}. However, in the work of Zocchi *et al.*⁵, color is the main characteristic that distinguishes between 'aggressive' robots and benign robots in the testing phase of the experiment, when fish selectively avoid the aggressive robot. In future studies using the CRA paradigm, it would be interesting to determine how color perception facilitates reactivation of specific threat memories to produce persistent avoidance. Object color is encoded in the retina²⁰, and transmitted to multiple visual areas (the optic tectum, AF5, and so on). But it is currently unclear if and how color information is transmitted to the forebrain circuits identified in this paper, and how color-associated threat memories may selectively co-opt the innate motor circuits associated with escape (Figure 1C). With the CRA assay introduced by Zocchi *et al.*⁵, opportunities are now available for studying the neural basis of individual variability in threat perception and learning, and the ethological significance of that variability.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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Visual simulation: Catching a glimpse of what's to come

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Are humans unique in using visual simulation to see beyond the 'here and now' in the mind's eye? A new study has now shown that monkeys can employ simulation to anticipate how physical events will unfold.

Our everyday environments are never exactly the same twice, and it is striking how adeptly we reason about brand new scenarios. Take the example in Figure 1A:

when the ball rolls down the ramp, will it knock the red block off the table? Although you've likely never seen this scenario before, you can make a



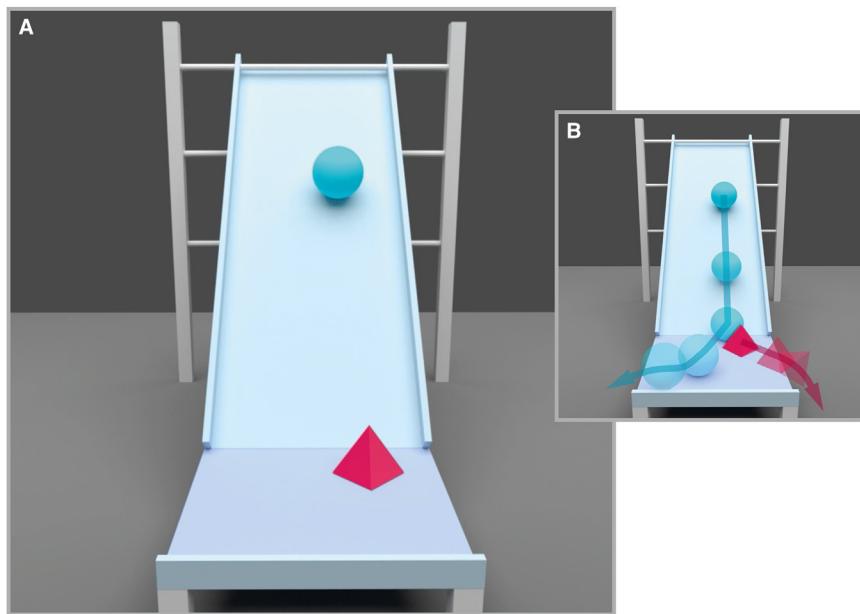


Figure 1. Visual simulation in a novel scenario.

(A) When the blue ball rolls down the ramp, will it knock the red pyramid off the platform? (B) To predict how the dynamics of the scene will unfold, we are able to mentally simulate the behaviors of the objects as they roll, collide, and slide.

well-reasoned judgment about what will happen as the scene unfolds. To do so, perhaps you ‘played forward’ the path of the ball in your mind’s eye, evaluating where it would strike the block, how the block would rotate, and how far the block would slide (Figure 1B). You may have even entertained alternative possibilities — perhaps the ball is a thin hollow shell and the block is solid concrete, leading to the ball glancing off the block and barely disturbing it. This ability to envision how the events of the world will unfold in the coming moments — supported by mental simulation^{1,2} — continually guides our decisions and actions in daily life^{3,4}. Are humans unique in our capacity to see beyond the immediate *here and now* of the sensory environment to anticipate what will happen next? A new study by Ahuja and colleagues⁵ reported in a recent issue of *Current Biology* shows that rhesus macaque monkeys can learn to use visual simulation to predict how the events of novel scenarios will play out, and they recruit homologous brain regions to humans in the process⁶. These findings point toward mental simulation being a broadly prevalent neural mechanism for understanding and predicting the vast

array of dynamic scenarios we encounter in daily life.

Ahuja *et al.*⁵ studied visual simulation in their monkeys using the ‘Planko’ task: on each trial, the monkey saw a ball positioned at the top of a board populated with randomly arranged planks. The monkey’s task was to determine which of two bins the ball would land in after traversing the planks on the way to the bottom. This task was adopted from their previous study on humans⁶, and was designed to encourage a visual simulation strategy. Still, a key challenge is that even in a situation such as this one that would seem to readily invite simulation, the visual system in the brain is keen to identify efficient workarounds. A downside to simulation is the time it takes — classic work has shown that the longer the ‘mental movie’ of objects moving and interacting, the longer it takes to mentally traverse the timeline of events leading to the outcome of interest^{7,8}. When possible, it is advantageous for the brain to learn a more direct mapping from the immediately available sensory cues to predictions about future states of the world.

In fact, sometimes it is entirely necessary to learn such shortcuts to act effectively. Take for example the challenge of hitting a fastball: a fastball

takes about 400 ms to arrive at the plate after it is released. Considering the minimum time required to execute a swing, a mental simulation of the ball’s trajectory would need to happen faster than the blink of an eye⁹. Instead, skilled batters have learned a direct mapping from a set of observed cues to experienced outcomes over the course of extensive training. Batters report using cues like the placement of the pitcher’s fingers on the ball and the spinning of the seams immediately after the ball’s release to predict where it will arrive without employing a simulation of the ball’s full path⁹. Most of us lack the training to hit a fastball, but we are highly trained on the particular tasks we perform in a consistent way on a regular basis (e.g., tying shoelaces). We become experts in mini-domains by way of extensive practice, often learning a pattern mapping from sensory cues to predicted outcomes that bypasses the need for simulation.

The monkeys studied by Ahuja *et al.*⁵ were highly trained on the Planko task by necessity. As a result of that training, did they come to solve the task via a set of shortcuts? This question is at the heart of the extensive analyses carried out in the study. The researchers tracked the monkeys’ eyes as they performed the task, providing a window to their underlying mental processes. When predicting the ball’s trajectory from a static image, the monkeys traced the anticipated path of the ball with their eyes, looking to the same parts of the scene as they did when viewing a movie of the dynamics unfolding. The researchers also trained a recurrent neural network model (in which simulation-like strategies have been shown to emerge¹⁰) to solve the Planko task. Monkeys’ eye traces closely aligned with the hidden layer activity maps from the trained model, showing that they looked to the same parts of the scenes that the model deemed salient. Finally, a functional brain imaging experiment conducted on one of the monkeys while it performed the same task yielded complementary findings: simulation of the ball’s trajectory evoked responses in visual motion-selective brain regions, and the patterns of response were highly correlated with those evoked when the monkey watched the scenes’ dynamics unfold. The findings demonstrate a tight connection between

visually simulating an object's path and actually seeing the object's dynamics unfold, at both the behavioral and the neural levels.

The monkeys' reliance on visual simulation to perform the Planko task owes, at least in part, to the heterogeneity of scenarios built into the task — monkeys saw a new configuration of planks on every trial. With conditions that are more constrained over the course of extended experience, studies of expertise show that people can transition from using a simulation-based strategy to leveraging more efficient (but scenario-specific) learned visual patterns. For example, Crespi *et al.*¹¹ studied novice and expert billiards players, tracking their eyes as they predicted the trajectory of a shot bouncing off the table's bumpers. They found that novice players traced the predicted path of the ball with their eyes much like the monkeys did in the Planko task, showing evidence of mental simulation. Expert players, however, jumped straight to specific visual landmarks that provided shortcuts for prediction. Simulation, then, is the brain's 'brute force' solution to predicting the behavior of the world under ever-changing conditions. It is time-consuming and has limited bandwidth, but it is general-purpose and allows us to make reasonable predictions even in scenarios we've had little or no experience with. Indeed, recent work has shown that the same general-purpose mental model of physics applies to a wide variety of prediction tasks with different scene contents and demands^{12,13}. In practice, mental simulations in everyday life might incorporate simplifications (e.g., only simulating the components of a scene deemed relevant) to be faster and more tractable¹⁴.

As highlighted by Ahuja *et al.*⁵, mental simulation is one of the most sophisticated feats of human cognition, yet we understand precious little about how simulation is carried out in the brain. The finding that monkeys use visual simulation to predict the behavior of the world opens the door to the study of the underlying neural mechanisms at a level of detail not possible in humans. At the same time, there is a broader implication of the findings for how we should think about the divide between human cognition and that of non-humans. One school of thought holds that non-human

animals do not have the capacity to mentally represent unobservable states¹⁵, with their mental world being limited to first-order reasoning about the immediately observable scene. If this is true, then all the benefits of mental simulation described above are the sole purview of human cognition. That would seem to be at odds with the surprisingly nuanced problem-solving displayed by animals in novel scenarios, such as thinking about alternative futures^{16,17} and making use of latent variables such as objects' masses for decision making¹⁸. The perennial counterargument to such examples is that the tasks involved could have been solved through some clever first order reasoning that deals only in the immediate observables. Ahuja *et al.*⁵, building on other recent work¹⁹, deftly outmaneuver this argument by peering more directly into the method monkeys use to solve the task. Even if monkeys could have foregone the need for mental simulation, they employed a simulation strategy nonetheless. The result is a compelling demonstration that monkeys mentally represent hypothetical future states of the world that have not yet come to pass — reasoning that undoubtedly goes beyond the immediately observable.

DECLARATION OF INTERESTS

The author declares no competing interests.

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