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Cognitive neuroscience: Mental replay in monkeys

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Cognition allows sensory experiences to inform later actions in flexible ways. A new study shows that, in a cognitively demanding task, monkeys store visual information in short-term memory and replay it when they need it to make a decision.

If I play the first few notes of your favorite old song, I bet you will recognize it quickly. If I then ask you about the chorus, you might require a few additional seconds to mentally finish the verse before you can recall it. Then, having accessed this part of your memory, you could report it to me in any of a variety of ways. You could hum the first few notes, tap out the rhythm, or sing a few of the lyrics. You could even push a blue button if the first word has an even number of syllables or a yellow button if that number is odd. A sensory stimulus, once recalled from memory, can guide a whole range of actions, as anybody who has ever been caught dancing to the song that is playing in their head can attest. How does the brain accomplish this?

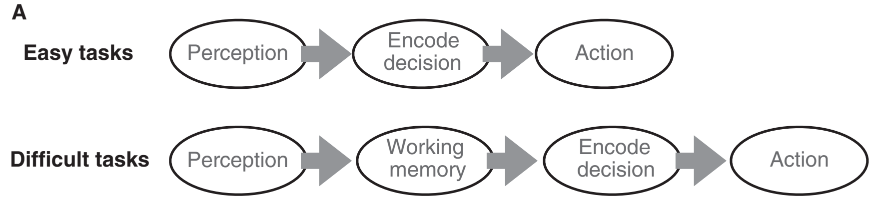
In this issue of *Current Biology*, Shushruth *et al.*[1] report a study in which Rhesus monkeys were trained to perform an abstract perceptual decision-making task that shares some features with the familiar experience described above. The monkeys were asked to remember a particular sensory experience: a field of dots moving either left or right, recently viewed. A short time after the motion stimulus vanished, following a brief delay imposed by the experimenters, the animals reported the direction of motion with a rapid eye movement (a saccade) to one of two targets. A key feature of the task paradigm is that the monkeys had to select a target on the basis of its color; for one monkey, blue meant rightward and yellow meant leftward, and for the other monkey the motion-color association was the opposite. After extensive training, each monkey learned its abstract rule and performed the task well.

How did the animals achieve this cognitive feat? Before playing monkey psychologist, a bit of introspection is in order: How would you go about solving this task? Well, for some initial insight, note that you could learn it in about two minutes, just from reading the above description and maybe performing a few practice trials. Perhaps you would adopt the following strategy: after viewing the motion stimulus and evaluating its direction, you might use a mental token, perhaps mentally rehearsing the words 'left motion' or 'right motion', or equivalently for this particular task, 'pick blue' or 'pick yellow', during the delay period that intervened between viewing the stimulus and performing your action. Once the choice targets appeared, just one or two additional cognitive steps would be required to select the correct one (Figure 1A, first row). A second option could be to conjure up a mental image of leftward or rightward motion, holding it in mind, and using it once the two targets appear to select the correct one (Figure 1A, second row). Of course, it is also possible that you might form some internal representation of the relevant information that is completely abstract, sharing essentially nothing with a sensation of motion, or of color, nor their lexical labels, nor a motor intention. And, of course, we must acknowledge that introspection might be a poor, or even misleading, guide to the actual underlying neural computations.

Which (if any) of these cognitive strategies are available to the monkeys? A first hint comes from the fact that it took months for the monkeys to learn to perform this task. Lacking language, monkeys may also have only a limited capacity for symbolic thought. This means that the human strategy of using cognitive 'tokens' (lexical or otherwise) might be unavailable to them. As Shushruth *et al.*[1] show, visual mental imagery appears to be the strategy the monkeys use to solve the task. What is more surprising, at least to a human introspector, is how they appear to use that visual imagery: available evidence suggests that, once the choice targets appeared, the animals replayed their memory of the visual stimulus, accumulating evidence from it as it replayed, which then enabled them to select the correct target. Perhaps most surprisingly, the entire process of sensory recall and decision making appears to begin only after the two choice targets appear. This certainly seems like a bizarre strategy, and given how unexpected this is, it makes sense to weigh the evidence for this interpretation carefully.

The first piece of evidence that the animals have adopted this 'wait, then

A



B

	Monkeys	Humans
Easy task	Conventional sensory-discrimination task	Abstract decision-making task
Difficult task	Abstract decision-making task	Remembering a route

Current Biology

Figure 1. Monkeys and humans may adopt similar cognitive strategies, according to what is easy or difficult for each species.
(A) Both species may solve easy decision-making tasks by rapidly forming a decision based on sensory information. Tasks more difficult for each species might be solved by storing the sensory information in memory, to allow for flexibility in its use later on. (B) Even though we would find the abstract decision-making task of Shushruth and colleagues[1] easy enough to perform, it might engage cognitive processes in monkeys akin to those that humans would use when performing more complex sequential memory tasks, such as retracing an unfamiliar route.

replay' strategy comes from their reaction times. When the targets appeared, one monkey waited an unusually long time to make a saccade. Had she already decided she was going to choose, say, blue, her saccade should have occurred within about 200 milliseconds of target appearance. Instead, it took about four times longer. The reason for this delay is hinted at by its relationship to the strength of the motion stimulus. When the strength of the evidence in the motion stimulus was strong (that is, when it was easy to decide if the motion was right or left), then her reaction time was briefer. The animal's measured reaction times are exactly what we would expect if the monkey deferred consideration of the motion evidence until the targets appeared.

Further evidence for replay triggered by the appearance of the targets comes from neural recordings in parietal area LIP. This area has been implicated in the intention to act, the selection of a target for action, the accumulation of sensory evidence to inform the selection of an action, and attending to the behaviorally-relevant features of a visual scene. In short, LIP is a natural place to look for a putative memory-replay signal. The first noteworthy finding in the Shushruth *et al.*[1] study regarding LIP neurons is that they were more-or-less quiescent while the motion stimulus was on the screen. If the monkey were accumulating sensory evidence during the motion-viewing epoch, one might expect to see a buildup of neural activity in area LIP, consistent with many previous studies. However, by this task design, the process of evidence-accumulation appears to be put on hold. Once the saccade targets appeared, LIP neuronal activity increased gradually and at a rate that was determined by the strength of the remembered motion stimulus: If the monkey was remembering a challenging, weak motion stimulus, activity ramped-up slowly, and if the monkey was remembering an easy, strong motion stimulus, activity ramped-up quickly. This surprising result has all the fingerprints of a replay of the visual stimulus from memory, which suggests that the same process of evidence accumulation that was earlier reported[2] during the motion-viewing period now takes place only once the targets appear, being fed in to LIP from memory.

It is natural to wonder next where in the brain the memory is stored, and of course, how it is stored. Shushruth and colleagues propose that the visual information may be held in iconic memory[3], compressed at either the time of storage or retrieval. Other possibilities abound, but just as importantly, many are now ruled out. In particular, any theory that posits that information about motion strength (rather than just its direction) is discarded prior to target appearance can be rejected. This includes the idea that the monkey encodes the direction of motion with a single bit per trial (e.g. 0 = leftward and 1 = rightward), or by using direction-selective or color-selective neural populations to encode their decision about the stimulus. Whatever "gist" the monkeys are extracting, it probably hews closely to the original sensory experience, and includes motion strength information, which seems like it is not the way we would perform this task.

This study is a culmination of a rich legacy of neurophysiological investigations into decision-making, for which Shadlen, the senior author of the new study, is among the pioneers. Other researchers, including the authors of this dispatch, have devised experimental paradigms that dissociate the perceptual and motor aspects of this task, albeit none as completely or as elegantly as does the current study. Our prior work[4], along with other earlier studies using similar behavioral tasks[5], came to the exact opposite conclusion of the current study. All of us concluded that an abstract perceptual decision was remembered in the form of a spatial location. We termed this mechanism a “spatial mnemonic”. Now, Shushruth and colleagues show that the spatial mnemonic strategy is not one that all monkeys tumble to on their own. In ours and other studies, the animals had first been trained to associate the direction of visual motion with the direction of response, even if only briefly or for only a few directions. Shushruth and colleagues patiently and persistently trained their two animals without any intermediate steps that provided cognitive aids. When the training proceeds in this manner, the spatial mnemonic strategy apparently does not develop.

Given how surprising the monkey’s strategy for solving this task appears to be, one might ponder if, as researchers push toward the limits of monkey cognition, we might be starting to run into some fundamental differences in how humans and other primates solve cognitive tasks. However, we submit that there may be tasks that humans would solve in precisely the same way (Figure 1). Consider what happens if you find yourself lost in an unfamiliar city. Lexical shorthands are probably insufficient to guide you back to your hotel. Instead, you will probably play back information acquired during your errant journey. Familiar experiences like mentally retracing a route or conjuring a song from memory show that when a sensory stimulus is sufficiently complex, and indirectly related to behavior, we must recall fragments of the original sensory experience when that information is needed, just like Shushruth’s monkeys did. This means that before we conclude the monkeys solve tasks like these in a manner unlike how humans might, we should note that the human mind is a special case of a primate mind, with expanded cognitive capacities. Thus, by studying the primate brain, we may derive our best opportunity to gain insights into the neural basis of human cognition for quite some time to come.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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