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# The Architecture of Intelligence: Converging Evidence From Studies of Humans and Animals

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## Abstract

A person's performance across multiple cognitive tests tends to covary. This ubiquitous observation suggests that various cognitive domains are regulated in common, and this covariance underlies the interpretation of many quantitative tests of "intelligence." We find that, as in humans, differences in intelligence exist across genetically heterogeneous mice. Specifically, we have observed a covariance in the performance of mice across diverse tests of learning, reasoning, and attention. As in humans, the processing efficacy of working memory is both correlated with animals' general cognitive abilities and may in some instances serve to regulate behaviors indicative of intelligence. Beyond its axiomatic significance in demonstrating the evolutionary conservation of a cognitive trait, studies of mice may provide unique opportunities to assess the molecular (e.g., brain-specific RNA expression; transgenics) and neuroanatomic substrates for intelligence. One such approach is briefly described here. Using this approach, we have determined that the signaling efficacy of the dopamine D1 receptor in the prefrontal cortex is one potential link between performance on both working-memory tasks and tests of intelligence. In combination, studies of both humans and nonhuman animals provide converging lines of evidence that might evade either approach in isolation.

## Keywords

general intelligence, learning, attention, working memory, short-term memory, prefrontal cortex, dopamine

Intelligence varies across individuals. Although we struggle with the definition of intelligence (Jensen, 1989), its impact on academic, career, and social success is empirically established (Gottfredson, 1998) and immediately apparent to even the most casual observer. Differences in intelligence are not merely a social construct (as some would suggest) but instead reflect the complex interaction between innate and experienced influences. The elucidation of this multidimensional trait will require the integration of diverse methods, including those provided by genetics, neuroscience, cognitive science, and comparative psychology. Here we will describe a view of variations in intelligence that emerges from complementary studies of both human and nonhuman animals.

## Intelligence: Definition and Measurement

Standard methods for assessing intelligence in humans (e.g., the Raven's Matrix, the Wechsler Adult Intelligence

Scale) are in wide use and need not be described here. To estimate intelligence among animals, one must consider the constituents of this cognitive trait. A committee of the American Psychological Association (Neisser et al., 1996) stated that "Individuals differ from one another in their ability to understand complex ideas, to adapt effectively to the environment, to learn from experience, [and] to engage in various forms of reasoning . . ." (p. 81). Although vague, such a definition is the foundation from which we have attempted to assess intelligence in genetically heterogeneous mice.

To begin, genetically diverse mice were tested on batteries of five to nine learning tasks, each of which made unique sensory, motor, and motivational demands on the animals (Matzel et al., 2003; Matzel et al., 2006). This test

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battery was analogous to the design of “classic” human intelligence tests, wherein various tasks impinged on different information processing skills. The tasks were rudimentary in nature (e.g., associative fear conditioning, passive avoidance, path integration, odor discrimination, and spatial navigation) such that all animals could attain comparable levels of performance, but did so with different efficiencies. Animals that performed efficiently in one task tended to do so in other tasks in the battery. A positive correlation of each animal’s rate of acquisition across all tasks was observed, and factor analysis indicated that 32% to 48% of the variance across tasks was attributable to a single factor, which we described as “general learning ability.” Others described this trait as qualitatively analogous to what is described in humans as “intelligence” (Blinkhorn, 2003), and in a comprehensive test of 241 mice, Kolata, Light, and Matzel (2008) reported a hierarchical structure of the general cognitive abilities of mice (where a general factor influenced domain-specific factors, including spatial abilities). Indeed, such a hierarchy is a hallmark of human intelligence test performance.

Although learning abilities and intelligence are highly related (Jensen, 1989), no definition of intelligence would begin and end with a statement about the ability to learn. Instead, most definitions make reference to the capacity to “think rationally” and “engage in reasoning” (Manktelow, 1999), and most human intelligence test batteries include components specifically intended to assess these abilities. This premise led us to ask whether animals’ general learning abilities were correlated with their capacity for reasoning.

To assess reasoning in mice, a test based on the concept of “fast mapping” was developed. Fast mapping (Carey & Bartlett, 1978) is believed to play a critical role in the extraordinarily rapid and seemingly effortless acquisition of information during early human development, and it explains (in part) the prodigious rate at which children gain vocabulary. For example, when faced with a group of familiar items described by familiar words, a child will quickly conclude that an unfamiliar word designates a novel item within the set. This logical inference is often asserted to be a hallmark of reasoning.

To assess fast mapping in mice, animals were first taught to associate pairs of objects. Upon choosing the correct paired associate, the animal could retrieve a food reward. After learning a number of such pairs, the animals were shown a novel object, and were allowed to choose among a field of several objects, all of which except one had acquired prior meaning. Under these conditions, the principle of fast mapping suggests that a rational animal should conclude that because the sample object was novel, the food reward should be located under the unfamiliar object in the field. Performance on

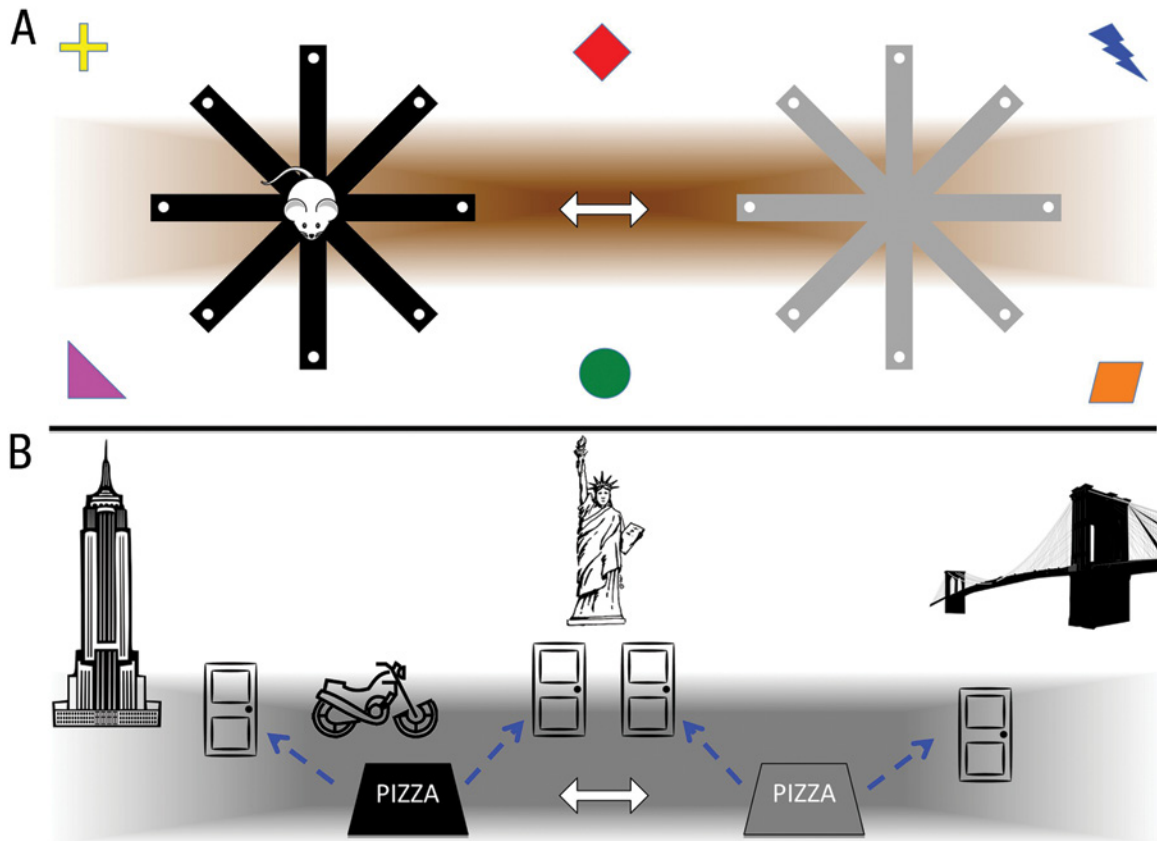
this reasoning task was strongly correlated with animals’ aggregate performance in the learning battery; that is, better learners tended to make fewer (or no) fast-mapping errors, indicating that this rudimentary form of reasoning was indeed related to other cognitive abilities (C. Wass et al., 2012).

## The Relationship of Working Memory to General Intelligence

Owing to its ubiquitous role in “higher cognitive functions,” working memory is viewed by many as a potential source of variance underlying intelligence (e.g., Engle, Tuholski, Laughlin, & Conway, 1999; Kyllonen & Christal, 1990; Matzel & Kolata, 2010). However, Daneman and Carpenter (1980) reported that simple memory span (i.e., list retention) was only weakly predictive of performance on tests of intelligence, whereas complex span (the ability to retain and recall the last words in a series of related sentences) was strongly correlated. Although both simple and complex span each engage working-memory storage, only complex span taxes the processing components of working memory (i.e., the capacity to maintain/update information while simultaneously manipulating that information to complete a directed task). Numerous studies have supported this contention (e.g., Ackerman, 2005; Colom, Rebollo, Palacios, Jaun-Espinosa, & Kyllonen, 2004; Conway & Engle, 1996; Engle et al., 1999; Sub, Oberauer, Wittman, Wilhelm, & Schulze, 2002).

On the basis of these considerations, we began to assess the relationship of complex working memory to the general learning performance of mice. Animals were trained to perform in two separate and distinct (e.g., differing in color) eight-choice radial-arm mazes and were subsequently required to alternate choices in the two mazes (i.e., choices in one maze alternated with choices in the second maze) (Fig. 1). Because the spatial cues used to guide the animals’ choices were common to both mazes (the mazes were located in a single room), this manipulation taxed aggregate working memory; that is, information from one maze had to be retained and updated while performing in a second, related maze. In this task, the number of errors (i.e., returns to empty arms) committed by animals was inversely related to their aggregate performance across a battery of learning tasks (Kolata et al., 2005), leading us to conclude that the efficacy of complex working memory was indeed related to the mouse’s general intelligence.

As implied earlier, working memory is not a singular process but instead encompasses both the storage of information and the processing of information (Baddeley, 2003; Jarrod & Towse, 2008). Kolata et al.’s (2005) data did not allow us to discern the relative relationships of



**Fig. 1.** Radial arm mazes (grey and black) were used to assess working memory in mice (A). Animals were trained independently in each of two mazes. The end of each of the arms on the mazes was baited with a desirable food. After training, the animal will navigate the mazes in an efficient manner; that is, it will collect all of the food without re-entering empty arms (which would constitute an error). This performance is guided by spatial cues that surround the mazes. After performance in each maze had stabilized, animals undergo a procedure where on occasional trials, they alternate choices between the mazes. This “alternating maze” (complex working memory) version of the task requires that the animals maintain a list of locations (those that still hold food) while performing a second, related, memory task that is guided by a common set of spatial cues. Unlike the simple version of this task, the alternating version taxes several aspects of working memory, including demands on attention. Under these conditions, animals begin to make errors. Individual differences in the efficacy of working memory. In some experiments, animals undergo extensive training in the alternating maze task. This training promotes an improvement in the execution of this task and results in an improvement in animals’ performance across batteries of unrelated learning and attentional tasks. Illustrated is an analogous task commonly engaged in by humans outside of the laboratory (B). A person is simultaneously making pizza deliveries for two restaurants (a common practice in cities such as Manhattan). Starting at Black’s Restaurant, he is given a list of nearby locations to which he must make deliveries throughout his shift. After any given delivery, he shuttles to Grey’s Restaurant, where they provide him with another list of locations scheduled for delivery, and the process repeats many times during this man’s shift. A novice at this task may use a written list and a map of the surrounding streets to guide his deliveries. However, an experienced delivery man may forego the written list and may use landmark cues to guide his deliveries. However, the cues are common to the deliveries that are scheduled for each restaurant! Whereas a novice might easily become confused, the expert delivery person (or one with a high capacity for working memory and attention) will perform quite efficiently and will earn big tips.

these components to general intelligence. To resolve this issue, we assessed the performance of mice on distinct components of the working-memory system (Kolata, Matzel, & Light, 2007). First, mice were required to maintain the memory of up to six visual symbols associated with food rewards. We found that this measure of simple span (i.e., storage) was only moderately correlated with

the animals’ aggregate performance in the learning battery. To measure processing aspects of working memory independent of simple storage, we found inspiration in a well-established and “process pure” test of attention: the Stroop Color-Word Interference Test (Stroop, 1935). This test requires human subjects to name the color used to print the name of another color (e.g., the word *blue*

might be printed with red letters). This incongruence impairs both the accuracy and speed of responses, and performance on the Stroop Test is strongly predictive of general intelligence (Huang, Mo, & Li, 2012). In a Stroop-like test for mice, animals were trained on a three-choice visual discrimination and a three-choice olfactory discrimination (in two highly distinct contexts). Then, both the odor and visual cues were simultaneously presented in the context that cued the visual discrimination; that is, the odors served as task-relevant distractors. Unlike simple short-term memory, performance on this attentional test was strongly correlated with each animal's aggregate performance in the learning battery, suggesting that attentional control is critical to the relationship between working memory and general intelligence.

Recent reports suggest that training on tasks that tax working memory can have at least transient beneficial effects on a person's performance on tests of intelligence (Buschkuhl & Jaeggi, 2010; Jaeggi, Buschkuhl, Jonides, & Perrig, 2008; Jaeggi, Buschkuhl, Jonides, & Shah, 2011; Tang & Posner, 2009). Despite these successes, the reliance of the imposed training procedures on working memory has been questioned (Redick et al., 2012; Shipstead, Redick, & Engle, 2012), and the reported impact on measures of intelligence have been quite small or, in some cases, altogether absent (Redick et al., 2012; Weng-Tink & Thompson, 2012). In these respects, work with animals may be beneficial. It is noteworthy that laboratory animals are a "captive audience." Whereas humans regularly use working memory in their day-to-day lives (thus minimizing the impact of laboratory manipulations), laboratory animals lead sterile lives (less dependent on working memory) and can be exposed to intense levels of training. To assess the causal relationship between working memory and general learning abilities in mice, we (Light et al., 2010; Matzel et al., 2011) provided mice with working-memory "exercise" by training them (over a period of weeks) in the dual-maze task described in the last paragraph. This training promoted an improvement in working memory, attention, and aggregate performance across a six-task learning battery. These effects were not merely a consequence of a storage exercise, because animals that spent comparable time performing in a single eight-arm radial maze, or radial arm mazes that did not share overlapping spatial cues, did not exhibit the same improvements.

Although working-memory training promoted aggregate learning abilities, performance was improved only on a subset of the learning tasks. However, working-memory training did promote an improvement in attentional performance across four independent experiments. Thus it is more likely that, as opposed to directly affecting intelligence, working-memory training promoted attention, which could transfer (depending on test conditions) to some of the learning tests. This conclusion is

consistent with some of the criticisms of the working-memory training literature offered by Redick et al. (2012) and Shipstead et al. (2012).

## Animals Provide Unique Converging Evidence

Imaging studies of humans demonstrate that working-memory tasks activate memory systems in both domain-specific (i.e., task-dependent) areas as well as "executive-attentional" networks located in the prefrontal cortex (Cohen et al., 1997; Gazzaley, Cooney, McEvoy, Knight, & D'Esposito, 2005; Rowe, Toni, Josephs, Frackowiak, & Passingham, 2000). Thus it has been concluded that the prefrontal cortex is principally involved in the processing aspects of working memory and thus may be critically involved in the instantiation of general intelligence (Jung & Haier, 2007).

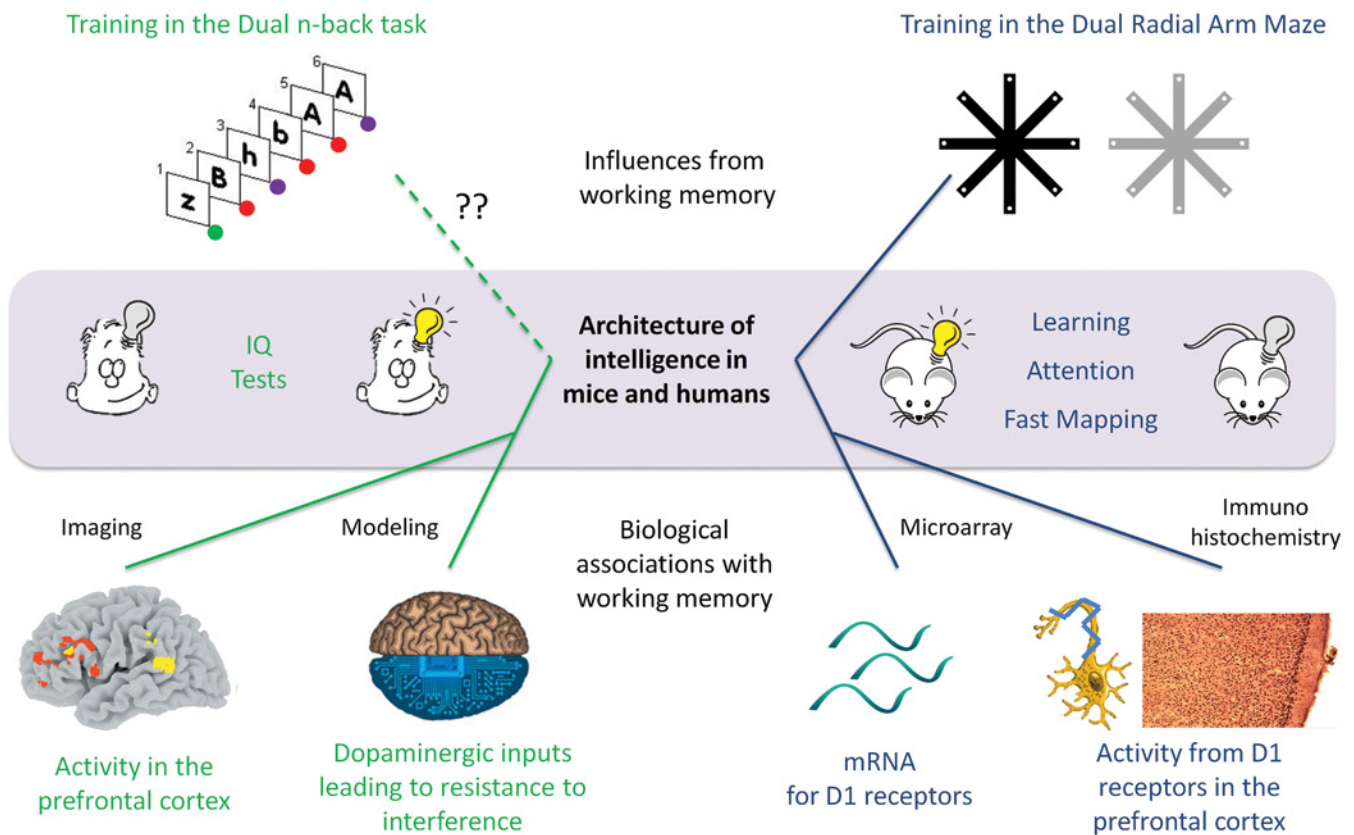
On a molecular level, the relationship between working memory and intelligence has largely eluded researchers using human subjects. Although we have appreciated for decades that a high proportion of individual variations in intelligence emerges from genetic influences, specific genetic determinants are unknown (Deary, Johnson, & Houlihan, 2009) and false-positive identifications have been exceedingly common (Chabris et al., 2012). These difficulties are due in part to limitations on work with humans. For instance, human studies are largely confined to the assessment of differences in DNA sequence (because the sequence in a neuron is homologous with that obtained from blood, skin, or saliva, the latter of which are available to the human researcher). In contrast, with animals, we can easily induce transgenes and study the structure of brain-specific DNA (the epigenetic inheritance) by measuring DNA expression (e.g., messenger RNA from brain tissue) and methylation. In addition, the greater control afforded by the use of animal subjects, both on phenotype (e.g., behavioral assessment) and genotype (e.g., intercross of inbred strains), allows a better resolution to detect genetic interactions (epistasis) in the DNA sequence. Hence, studies with animals might reveal epigenetic and epistatic effects to account for the "missing heritability" of intelligence.

As an example of one facet of this approach, Kolata et al. (2010) characterized the general intelligence of 60 outbred mice, and quantified the expression of approximately 25,000 genes in specific brain areas. Across several replications, Kolata et al. reported that the expression of one cluster of three dopaminergic genes (*Drd1a*, *Darpp-32*, and *Rgs9*) related to D1 signaling in the prefrontal cortex was correlated with animals' general cognitive performance. On the basis of this observation, we then assessed D1 signaling in prefrontal networks of animals classified for their general intelligence (C. D. Wass et al., in press). A significant correlation between

D1-induced activity and general intelligence was observed in the medial prefrontal cortex (and a somewhat weaker correlation in the dorsolateral prefrontal cortex). Furthermore, working-memory training induced an increase in the sensitivity of the same class of D1 receptors that was associated with differences in innate general intelligence. Thus with assessment tools that are not available to researchers working with human subjects, we have been able to establish across levels of analysis that D1 signaling in the prefrontal cortex plays a specific role in the regulation of intelligence. This is not to suggest that D1 signaling is the lone determinant of variations in intelligence. For instance, our gene

microarray analysis indicated that as few as 10 genes were relevant, but depending on one's proclivity for Type 1 error, hundreds or even thousands of genes could be similarly "identified."

Does converging evidence support a conclusion regarding the relationship of D1 signaling to intelligence? Durstewitz, Seamans, and Sejnowski (2000) modeled the persistent activity of prefrontal cortex neurons during the execution of a working-memory task and observed that dopaminergic inputs to this network stabilized the memory traces and protected them from imposed interference. Likewise, Jung and Haier (2007) and Gray, Chabris, and Braver (2003) have reported that regions associated with



**Fig. 2.** The architecture of intelligence, with a focus on the relationship with working memory and the utility of animals in providing converging lines of evidence. Differences between low-intelligence (white light bulb) and high-intelligence (yellow light bulb) can be assessed in humans through IQ tests (e.g., the fourth edition of the Wechsler Adult Intelligence Scale), and in mice through batteries of learning tasks that have high correlation with reasoning tasks (e.g., fast mapping) and attentional tasks (e.g., the mouse Stroop test). The roles of working memory in humans (green text) and mice (blue text) are separated by biological associations and causal influences. In biological associations, from left to right: *imaging* represents studies in humans in which working-memory performance and performance on IQ tests commonly activate the prefrontal cortex (Cohen et al., 1997; Gazzaley, Cooney, McEvoy, Knight, & D'Esposito, 2005; Rowe, Toni, Josephs, Frackowiak, & Passingham, 2000); *modeling* represents computer models suggesting that dopaminergic inputs in the prefrontal cortex protect activity ("stored information") from interference during working-memory tasks (Durstewitz et al., 2000); *microarray* shows that high-intelligence mice have increased expression in the prefrontal cortex of the gene *Drd1a* that codes for dopamine D1 receptors (Kolata et al., 2010); *immunohistochemistry* shows that high-intelligence mice have increased neuronal activity in the prefrontal cortex induced by D1 agonists (C. D. Wass et al., in press). The top panels represent influences from working memory, which include controversial studies of working-memory training in humans (represented with a dashed line; Buschkuhl & Jaeggi, 2010; Jaeggi, Buschkuhl, Jonides, & Perrig, 2008; Jaeggi, Buschkuhl, Jonides, & Shah, 2011; Tang & Posner, 2009), as well as evidence from mice indicating that working-memory training promotes attention, which in some instances positively affects learning performance (Light et al., 2010; Matzel et al., 2011).

the processing of working memory are engaged by many of the same tasks used to estimate intelligence. In combination, modeling, human correlational studies, and correlational and experimental work with animals converge on a role for dopamine signaling in the prefrontal cortex in working memory and, in turn, the regulation of general intelligence.

## Summary

Learning, attention, and reasoning are coregulated in genetically heterogeneous mice. Thus, as in humans, mice exhibit variations in a cognitive trait analogous to “intelligence.” In addition, as in humans, the expression of intelligence in mice is to some extent dependent on the processing efficacy of working memory and attentional control.

Although genetic and neuroanatomic work with laboratory animals is in an early stage, animals provide a source of converging evidence that may ultimately elucidate complex cognitive traits (and their neuroanatomic/neurophysiological/genetic substrates) such as intelligence. Figure 2 summarizes a model of the architecture of intelligence that has benefited from work on both humans and animals. Although this model is tentative (and incomplete, at best), it illustrates the levels of analysis and informative interactions that can be attained through a combination of human and animal research (Sauce & Matzel, 2013).

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The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

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