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Understanding Human Cognitive Uniqueness

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Abstract

Humanity has regarded itself as intellectually superior to other species for millennia, yet human cognitive uniqueness remains poorly understood. Here, we evaluate candidate traits plausibly underlying our distinctive cognition (including mental time travel, tool use, problem solving, social cognition, and communication) as well as domain generality, and we consider how human cognitive uniqueness may have evolved. We conclude that there are no traits present in humans and absent in other animals that in isolation explain our species' superior cognitive performance; rather, there are many cognitive domains in which humans possess unusually potent capabilities compared to those found in other species. Humans are flexible cognitive all-rounders, whose proficiency arises through interactions and reinforcement between cognitive domains at multiple scales.

Contents

A UNIQUELY UNIQUE SPECIES?

All biological species are unique, yet the qualities that differentiate our species from others may be of particular significance. Our population size and range are out of kilter with global patterns for vertebrates, we control vast flows of energy and matter, and our technology is far more complex than that of other animals. Yet claims of human uniqueness usually relate to the thesis that human minds are special. Our species' achievements, it is supposed, follow from our uniquely powerful cognition.

What exactly is the evidence for this superior cognition, and in which domains is it manifest? Is it our language, intelligence, or culture that makes us special? Historically, different theories sought to explain the evolution of human cognition by emphasizing particular traits. However, those leading theories are not mutually exclusive, nor are the abilities that they highlight encapsulated, raising the possibility that human cognitive uniqueness arises through some combination of abilities or their interaction. Here we draw on research across a variety of fields to try to pinpoint what, if anything, is special about human cognition.

Research over the last few decades has uncovered a great many similarities between the cognitive abilities of humans and other animals. Where once a gulf was perceived between rational humans and instinctual animals, research into animal cognition has established striking similarities. Impressive feats of animal cognition fill the pages of leading scientific journals. Specific animals can make and use tools, manipulate symbols, plan for the future, solve problems, understand intentions, and exhibit numerous aspects of cognition once regarded as uniquely human. To our knowledge, all scientific attempts to isolate human cognitive uniqueness have been exposed as inflated by subsequent research. Progress requires due caution.

Among the most influential research in this domain are experiments that directly compare the performance of animals (e.g., nonhuman primates, corvids) with humans at various stages of development, seeking either to pinpoint key differences or to reveal similarities. Of course, it is one thing to find differences in performance and quite another to isolate the cognitive mechanism responsible for them, as all tests draw upon many abilities. Differences in interpretation in part reflect this challenge, but they also expose the alternative agendas, research methodologies, and conceptual frameworks of the diverse fields (comparative psychology, developmental psychology, behavioral ecology, primatology, neuroscience, evolutionary biology) that contribute to this literature.

Here we attempt to overcome these challenges and provide an honest, rigorous, and pluralistic account of the science. We focus on five observable domains in which human cognitive uniqueness is seemingly in evidence (without suggesting that the cognition at work is specific to any one domain) and on domain-general cognition, and we explore how our unique cognition has evolved. In the final section, we summarize how human cognitive uniqueness can best be characterized and discuss complexities and methodological challenges. It would take a book-length treatment to do the topic justice, and we acknowledge that our review is inevitably incomplete in important respects.

THE DATA: EVALUATING THE CASE FOR HUMAN COGNITIVE UNIQUENESS

Despite the growing evidence of mental continuity between humans and other animals in the study of human cognition, some distinctive aspects of the cognitive abilities of humans have started to crystallize. Here we stress some key findings of this literature, recognizing that the topography of any distinctively human cognition remains only vaguely mapped.

Humans Remember the Past and Imagine the Future

Humans remember specific events from their past (episodic memory) and imagine future scenarios (episodic future thinking), sometimes drawing on their memories to simulate alternative courses of action. "Mental time travel" is the general term for this ability to project oneself in time (Suddendorf & Corballis 2007). Not all memory is episodic: People also remember facts divorced from the context in which they were learned (semantic memory) and sequences of actions, such as how to ride a bike (procedural memory). To some extent all memory systems earn their keep by helping to anticipate the future state of the world, but episodic memory is notoriously patchy and unreliable because its primary function is useful prediction rather than accurate recall (Clayton et al. 2003).

Neuroscientific evidence links past remembering with future planning. Patients with conditions that leave them unable to remember personal episodes from their past are typically also impaired in imagining the future (Addis & Schacter 2012, Hassabis et al. 2007, Klein et al. 2002; cf. Miloyan et al. 2019). Moreover, fMRI studies show that the same brain circuits (including the hippocampus) are activated when healthy participants are asked to remember past and imagine future episodes (Schacter et al. 2007, Hassabis & Maguire 2007). These data have stimulated interest in the so-called prospective brain, that is, the idea that "a crucial function of the brain is to use stored information to imagine, simulate and predict possible future events" (Schacter et al. 2007, p. 657). Simulation of future episodes seemingly requires a system that can flexibly recombine details from past events (Schacter & Addis 2007). Both episodic memory and future planning may rely on the ability to construct a scene in one's imagination (Mullally & Maguire 2014), and they engage brain regions that are similar to those involved in taking another individual's perspective (Buckner & Carroll 2007). Plausibly, the ability to imagine a scene or episode, both as an individual planning an action and as a group of individuals coordinating with each other, may have played an important part in human evolution, facilitating behavior such as hunting large game or cooperative foraging. Is it this capability that sets humans apart?

There is a long-standing debate about whether mental time travel is unique to humans (Cheke & Clayton 2010, Clayton 2017, Corballis 2013, Suddendorf & Corballis 2007, Tulving 2005). Research on primates, corvids, and rodents suggests that at least some aspects of episodic memory (e.g., remembering what, where, and when), as well as some level of future planning, are shared with some other animals (Clayton 2017, Clayton et al. 2003, Redshaw & Bulley 2018). For instance, Clayton & Dickinson (1998) conducted experimental studies of Western scrub-jays showing that these birds can remember what food they cached, where, and when—a capability that they label "episodic-like memory" (i.e., episodic memory stripped of the implication of subjective experience). A diverse range of animals have been shown to be capable of remembering what happened, where, and on which occasion, including species of rodents, corvids, and apes (Clayton 2017).

Animals can also use past experiences to take appropriate action for a future event (Tulving 2005). Raby et al. (2007) showed that Western scrub-jays planned for tomorrow's breakfast: The jays cached more food in a room that they knew from previous experience never contained food compared to an alternative room that historically contained food, averting the possible hunger they might experience the next day. Osvath & Osvath (2008) used a similar procedure to show that apes would choose a tool that could only be used at a future time to access a desired reward, even if this meant missing out on a less-desired reward in the present. Children pass similar tasks from ages 4–5 (Atance et al. 2014). The question of the evolutionary emergence of truly future-oriented thinking (i.e., not triggered by association with features of the present environment) remains unresolved. Nevertheless, the intriguing observation that place cells in the rat hippocampus both replay routes in a maze that the rat recently took and preplay alternative routes (Gupta et al. 2010) has led one author who historically emphasized human uniqueness to embrace continuity instead (Corballis 2013). There remains no way to know whether the animals' ability to plan for the future involves projecting themselves in time or mentally constructing scenes or events in imagination (Clayton 2017), but this constitutes absence of evidence rather than evidence of absence.

The selection of the best course of future action among alternatives is facilitated by metacognition, that is, the ability to reflect on one's own or others' thinking (e.g., whether a prediction might be wrong). Recently, Redshaw and Suddendorf have suggested that the interplay between meta-representation and episodic cognition might explain what makes human mental time travel unique (Redshaw 2014, Redshaw & Suddendorf 2016, Redshaw & Bulley 2018). They found that the ability to plan for multiple future possibilities (e.g., by extending both hands when a single reward could emerge from one of two exits) was present in human children from ages 3–4 but absent in nonhuman apes.

The hypothesis that humans are particularly adept at dealing with environmental uncertainty, as they are able to represent mentally multiple alternative versions of the future and prepare accordingly, has only limited empirical support and is subject to other interpretations (Ingvar 1979, Jing et al. 2017, Redshaw & Suddendorf 2016, Seed & Dickerson 2016). Nonetheless it is attractive for bringing nuance to the current debate. We humans seemingly excel in the flexibility with which we recombine details from past events (Schacter & Addis 2007), imbuing our imagined episodes with relationships, hopes, fears, and attributions. Language extends these possibilities, allowing us to share our forecasts and expectations with others and consider their thoughts, memories, and foresight (Suddendorf & Corballis 2007, Suddendorf 2013). Computational investigations reveal that knowledge sharing hugely increases the efficiency with which individuals search a large space of possibilities (Rendell et al. 2010), implying that the collective planning of a future strategy would lead to more reliable projection. Yet, effective sorting between alternatives is critically reliant on meta-representation. If mental time travel underpins human cognitive uniqueness, it is probably because, rather than being encapsulated, it can be enhanced by interaction with other mental abilities, such as language and metacognition.

Humans Devise Complex Tools and Technology

Human societies are heavily reliant on tools, and tool use has long been regarded as playing pivotal roles in both our evolution and our ecological success. Might an unusual aptitude for technology underlie our uniqueness?

Tool use is documented in less than 1% of animal genera, and a smaller percentage of animals manufacture tools (Visalberghi et al. 2017). This apparent rarity, however, follows from common definitions requiring that a tool be unattached to the substrate. Broader definitions (e.g., "using an object to alter the position or form of another object or individual"; see Call 2013, p. 4) allow animal constructions, such as spiders' webs and birds' nests, which are ostensibly no less complex than other tools (Hansell & Ruxton 2008), to be recognized as equivalent. From this wider perspective, tool use and construction behavior is common.

If humans are not unique for using tools, they may be exceptional in their flexible deployment of them (Vaesen 2012). Much animal tool use and artifact construction involves specialist or stereotyped behavior (e.g., digger wasps use stones to block their burrow's entrance) (Brockmann 1985). Such tool-use adaptations (Biro et al. 2013) can be contrasted with flexible or creative tool use (Call 2013, Hunt et al. 2013), which involves "the use of different tools possibly in different contexts to reach different types of goals" (Visalberghi et al. 2017, p. 674) as well as the innovative use of tools to adapt to new situations (Call 2013), which is often heavily influenced by learning. Flexible tool use, manifest in just a handful of species of birds (e.g., Galapagos woodpecker finches, New Caledonian crows) and primates (e.g., chimpanzees, capuchins), has been associated with intelligence (Call 2013, Visalberghi et al. 2017). Consistent with this, innovative tool use is strongly correlated with brain size in both birds and primates (Navarrete et al. 2016, Overington et al. 2009). Common chimpanzees, for instance, exhibit multiple cases of innovation in tool use (Reader & Laland 2001). They possess diverse tool kits (used in foraging, sociality, sex, health) comprising about 20 types of tool (McGrew 2010), many of which (e.g., brush tools) they process to enhance efficiency (Sanz et al. 2009), using up to five separate tools to achieve a goal (Boesch et al. 2009).

Experiments show that tool-using birds and primates reliably select the most suitable tool given a choice, indicating that they do recognize functionally relevant features of the tool, such as length, solidity, or weight (Ruiz & Santos 2013, Visalberghi et al. 2017). However, primates do poorly on tool-choice tasks in which the tool's causal properties are not perceptually obvious, often failing tasks that require consideration of causal forces such as gravity and support (Povinelli 2000, Ruiz & Santos 2013). Some researchers suggest that human cognitive uniqueness derives primarily from our prowess in physical or causal cognition (e.g., Povinelli 2000), but nonhuman causal understanding might have been underestimated by tests that overly tax other cognitive resources such as attention or working memory (Seed et al. 2012). Conversely, recent studies report that adult humans also have an impoverished understanding of the causal bases of even simple tools (Lawson 2006) and commonly invent causation myths about technology (Derex et al. 2019, Henrich 2016).

Nonetheless, human children are extremely competent tool users: They are able to deploy simple tools such as hooks and rakes from ages 1–2 (Brown 1990) and an impressive repertoire of tools, from pencils to iPads, by ages 4–5. Children also think about physical events in terms of their causal underpinnings from an early age (Gopnik et al. 2017). However, they do not acquire these skills in a vacuum: Two-year-olds rapidly learn to use tools by watching other individuals (McGuigan & Whiten 2009). When tasked with manufacturing a tool on their own, children do not seem to outperform other flexible tool-using species until they are aged 8–9—for example, bending a wire to make a hook tool (Beck et al. 2011), a task also solved by a crow (Weir et al.

2002). Distinctively human patterns of tool use may arise only at a point at which other distinctive features are in evidence, including social cognition and language (Spelke 2009).

Children's innovation might be constrained by the "double-edged sword of pedagogy" (Bonawitz et al. 2011). They are less likely to discover all functions of a new object when introduced to it by a seemingly knowledgeable adult who only demonstrates one function, perhaps assuming that the adult will not only be informative but also exhaustive when introducing a device. Although this can be limiting, the ability to make strong and rapid inferences about an object's function from a knowledgeable teacher is a powerful route to learning. The natural pedagogy hypothesis suggests that a tendency to teach, and to be receptive to ostensive signals, is an important contributor to human uniqueness, facilitating competence with causally opaque artefacts (Csibra 2010, Csibra & Gergely 2011).

Ruiz & Santos (2013) agree that human understanding of tools largely comes from watching other individuals and primarily involves learning what tools do (i.e., based on a teleological-intentional stance) rather than how they work (i.e., their physical affordances). Observational learning studies show that humans, but not chimpanzees, copy causally irrelevant actions such as tapping a box before raking out a reward (Horner & Whiten 2005), an observation labeled "overimitation" because of its seeming irrationality (Hoehl et al. 2019). Ruiz & Santos (2013) note that chimpanzees and capuchins live in a world where nearly all tools have perceptually obvious functional properties, rendering a focus on the physical properties of objects adaptive. In contrast, for hundreds of thousands of years, humans have utilized complex technology whose physical affordances are often hidden and mechanisms are causally opaque, circumstances that may favor blind copying and/or a focus on the tool user's intentions (Csibra & Gergely 2011, Laland 2017, Tomasello et al. 2005). It is not that primates are incapable of attending to intentional information: Chimpanzees and capuchins treat "unable" and "unwilling" experimenters who provision them differently, waiting patiently for the first and giving up on the second (Call et al. 2004, Phillips et al. 2009). Rather, humans and other animals seemingly differ in their weighting of teleological-intentional versus physical cues (Ruiz & Santos 2013). From an early age, children infer the existence of a pedagogical intention, which makes it rational to privilege information given by a teacher even when this conflicts with functional information (Buchsbaum et al. 2012).

Humans Are Exceptional Problem Solvers

The fact that our species has flourished in such a wide range of environments suggests that humans may be particular adept problem solvers, capable of "overcoming some obstacle to achieve a goal when the entire solution is neither in the species-typical repertoire nor socially learned" (Seed & Mayer 2017, p. 601). Ostensibly, problem solving (including tool use) is reliant on inferential and causal reasoning, exploration, innovation, intelligence, and executive functions (Povinelli 2000, Seed & Mayer 2017).

Inferential reasoning entails transformations of mental representations to make predictions, often combining spatiotemporally separate events (Völter & Call 2017). There is evidence for inferential reasoning in animals. For instance, having learned through training that food is hidden under one of two cups, and being shown that one is empty, many animals can infer that food is under the alternative cup (what is called disjunctive syllogism). Elaborations on this basic task rule out alternative explanations, for instance testing whether the animals can mentally represent the movement of hidden objects (called invisible displacement). When such procedures are deployed, compelling evidence of understanding invisible displacement remains only for great apes (Jaakkola 2014). Other forms of reasoning, including diagnostic inference (e.g., if a visual trail leads to a cup, the animal infers that food is hidden there) and transitive inference (e.g., reasoning that if animal A is dominant to animal B, and B is dominant to C, then A is dominant to C), have been investigated experimentally in animals, leading to claims that apes, corvids, and parrots have these capabilities (Völter & Call 2017). However, such tests typically (and understandably) rely on ecologically relevant designs tailored to the species, leading to the counterclaim that animals lack a generalized and logical capacity for reasoning and can only solve such tasks in an egocentric and context-specific manner (Penn et al. 2008, Povinelli 2000, Suddendorf 2013). A variety of taxa, including chimpanzees, monkeys, rats, and bees, have been shown to be capable of first-order relational processing, for instance discriminating between unfamiliar icons that are similar or different from each other. Chimpanzees exhibit second-order relational processing, which requires understanding how stimuli relate to one another and whether that relationship is the same as or different from the one observed among other pairs of stimuli (Wasserman et al. 2017), implying some capability for analogical reasoning.

Knowledge of the properties of objects, such as their solidity, continuity, weight, and rigidity, as well as of hidden forces (e.g., gravity), is important to problem solving (Seed & Mayer 2017). A useful illustration of the experimental approach to investigating these issues in animals is provided by the trap task (Visalberghi & Limongelli 1994). In the basic task, subjects must extract an item of food from a box or tube with a hole at the center, under which is a trap that captures whatever falls in. Pushing the food one way allows the subject to access it, while the other way results in it falling in the trap. Children, capuchins, apes, and corvids solve the basic task (Völter & Call 2017). However, to ascertain whether success reflects an understanding of causal relations a transfer task is required, which decouples the trap's perceptual properties from its functional role (e.g., putting the trap in a new position such that it either continues to be a blockage or serves as a supporting bridge). Most chimpanzees and corvids fail to treat the object flexibly based on the causal relationship between it and the reward (Seed et al. 2006, Tebbich et al. 2007), whereas preschoolers typically pass the transfer test (Seed & Call 2014). Seemingly, animals understand some functional or structural features of objects but are not able to reason about causality in a theory-like fashion (e.g., to diagnose invisible causes) (Penn et al. 2008, Seed & Mayer 2017, Völter & Call 2017).

Gopnik suggests that children undergo a uniquely protracted developmental period in which they are motivated to explore and explain the world in causal terms (Buchsbaum et al. 2012, Gopnik et al. 2017). Pretend play, counterfactual inferences (reasoning about alternatives to life events), and interventional reasoning (predicting the consequences of intervention) may all involve the same cognitive machinery: the ability to consider events that have not occurred. Consistent with this, experiments show that the pretend play and counterfactual reasoning capabilities of 3–4-year-old children are correlated (Buchsbaum et al. 2012). Many young primates engage in play, but clear experimental evidence that they build causal knowledge through it is only found in children.

The motivation to explore, including through object play, is nonetheless linked to problem solving in animals. Those primates and birds who are most adept at problem solving are also renowned for object play (Bateson & Martin 2013). Sophisticated problem solvers (e.g., parrots, corvids, chimpanzees, capuchins) devote considerable time and energy to manipulating objects, and they spontaneously combine objects with one another or with the substrate when they play (Seed & Mayer 2017, Visalberghi et al. 2017). A survey of parrots found the highest levels of combinatorial play in species (Goffins cockatoos and New Caledonian crows) that are adept at problem solving (Auersperg et al. 2015). Children are an extreme example, as they often seem to derive intrinsic pleasure from interactions with artefacts and experimental apparatuses (e.g., Dean et al. 2012) and can be characterized as "little scientists" (Gopnik & Meltzoff 1997). By ages

4–5, children use exploration strategically to disambiguate confounded evidence and infer causality (Schultz et al. 2007), and by age 7 they are more reliant on functional information than on reward (Loissel et al. 2018).

Griffin & Guez (2014) report a relationship between motor diversity and problem solving, with those animals that express a greater range of motor actions being more likely or faster to solve problems. The findings fit with recent thinking on a general class of exploratory mechanisms within biology (e.g., adaptive immunity) that operate by iteratively generating variation at random and selecting the best solutions (Gerhart & Kirschner 1997). Other comparative studies link problem-solving capabilities to exploratory tendencies (Amici et al. 2019, Kendal et al. 2005). The association between motor diversity and problem solving may reflect a more widespread use of exploration and selection in ontogeny to find effective solutions in changing, variable, and unpredictable contexts (see also Gopnik et al. 2015).

Such reasoning implies that humans may be effective problem solvers partly because we are unusually generative (Fuentes 2017). The inventing of new behavior (i.e., innovation) is widespread in animals (Amici et al. 2019, Reader et al. 2016), and innovativeness (i.e., the number of different types of innovation devised) in general (Lefebvre et al. 1997, Reader & Laland 2002) and technical innovation in particular (Navarrete et al. 2016, Overington et al. 2009) correlate strongly with brain size measures in both birds and primates. By extrapolation, humans are extreme in innovativeness and brain size. Innovativeness seems to develop slowly over childhood (Beck et al. 2011), which might reflect the fact that strategic and systematic (i.e., theory-driven) exploration in pursuit of a goal might require well-developed executive control (to escape perseveration on a previously successful solution) or simulation capabilities (to generate novelty).

In sum, there is evidence that apes, monkeys, and corvids possess sufficient knowledge of object properties to make inferences in a manner not easily explained through associative learning (Seed & Mayer 2017, Völter & Call 2017). However, there is little support for the suggestion that animals deploy the generalized, systematic, and logical capacity for reasoning that is manifest in humans' construction of theories (Gopnik & Meltzoff 1997) describing how hidden causes (e.g., forces) operate (Povinelli 2000) or in counterfactual and interventional reasoning (Buchsbaum et al. 2012).

Humans Exhibit Complex Social Cognition

Social relationships also appear central to our unique cognition. We seem predisposed to work together toward shared goals, pooling information and resources, and we excel in our cooperative tendencies (Henrich 2016, Richerson & Boyd 2005, Slocombe & Seed 2019, Tomasello 2009), which may reflect a motivation and ability to share intentions that is unique to humans (Tomasello 2009, Tomasello et al. 2005). Helping behavior emerges early in childhood and becomes increasingly complex and selective with age, mediated by a concern for others to which humans are physiologically sensitive (Slocombe & Seed 2019).

In experiments in which a clumped reward can only be accessed through collaboration, children work together and generally share the spoils (Warneken & Tomasello 2009). In contrast, chimpanzees struggle to cooperate outside of preferred social partnerships, largely because the sharing is difficult (Melis et al. 2006), although bonobos will share food (Hare & Kwetuenda 2010). Chimpanzees show limited regard for others' interests when cooperating: For example, in contrast to humans (e.g., Fehr et al. 2008), they do not make nor expect an equal distribution of rewards (Jensen et al. 2006, Silk et al. 2005). Unlike 5-year-old children, who work together until each secures rewards, apes will abandon a joint task as soon as they receive their own reward (Tomasello 2009).

Humans also possess distinctive information transmission mechanisms underlying their culture, notably language and teaching (Boyd & Richerson 1985, Henrich & McElreath 2003, Tennie et al. 2009). There is experimental evidence for motor (and vocal) imitation in several animals, including contextual imitation (e.g., pigeons) (Dorrance & Zentall 2002) and production imitation (e.g., chimpanzees) (Whiten 1998), but humans may imitate unusually faithfully, more frequently, and with higher fidelity (e.g., Dean et al. 2012, Herrmann et al. 2007, Horner & Whiten 2005). Significant here are studies demonstrating that humans but not chimpanzees frequently imitate causally irrelevant actions (Hoehl et al. 2019, Lyons et al. 2007). Bayesian observational causal learning (Buchsbaum et al. 2011) neatly makes sense of these differences, suggesting that, from age 3, humans have a prior expectation that the demonstrator will impart useful information. Species differences in the tendency to copy faithfully may reflect differences in the ability to integrate evidence from actions with information about another's intention to teach (Buchsbaum et al. 2011, Keupp et al. 2018), they may reflect other social motivations to copy (Legare & Nielsen 2015, Over & Carpenter 2013), or they may result from a combination of both.

Another distinction between the social learning of humans and of other animals is that only the former is heavily reliant on teaching. When teaching is characterized in functional terms (e.g., as behavior that functions to enhance learning in another individual), criteria can be devised to detect teaching in animals (Caro & Hauser 1992), and experimental studies provide evidence that some animals (e.g., ants, bees, meerkats) meet these criteria (Franks & Richardson 2006, Hoppitt et al. 2008, Thornton & McAuliffe 2006). Nonetheless, teaching appears to be rare in the animal kingdom, and some authors have suggested that there are human-unique adaptations to pedagogy, for both teachers and learners, including the tendency to produce and follow ostensive communication preceding information sharing (Csibra & Gergely 2011). Comparative evidence to test this idea is sparse, providing mixed evidence as to whether or not apes take ostension into account when interpreting human communication (Moore 2016).

Pedagogy in humans comprises subtle scaffolding and cueing, such as attention-grabbing verbalizations or directing pupil's gaze to relevant objects (Csibra & Gergely 2011). Humans cue infant learning with simple actions or calls that generate referential expectations, triggering a tendency to follow the gaze of adults (Csibra 2010, Gergely et al. 2007). Infants check the facial expressions of adults responding to unfamiliar objects and use this to guide their approach or avoidance (Walden & Ogan 1988). These cues, and the resulting gaze and joint attention, contribute to infants' learning about the properties of objects and the meanings of words (Csibra 2010, Gergely et al. 2007, Tomasello 1999).

From 12 months of age human infants inform others by pointing, including pointing to objects that benefit others but not themselves (Liszkowski et al. 2006). In contrast, other apes do not point to help others (Leavens et al. 2005) and seemingly do not understand when humans do (Tomasello 2009). Animals produce alarm calls, for instance after perceiving a predator, but (excepting rare cases of teaching) often these are emitted not to inform other individuals but rather to benefit the caller (e.g., by notifying a predator that it has been spotted) (Zuberbuhler et al. 1999). If other animals actively inform each other with useful information it is under restricted conditions (Hoppitt et al. 2008) and in marked contrast to the extensive informing, teaching, and telling present in human societies (Tehrani & Riede 2008, Tomasello 2009). Much human teaching is mediated by language, which is a cheap, accurate, and flexible means to teach (Fitch 2004, Laland 2017).

In sum, at least three features collectively underpin humanity's uniquely potent capacity for cultural learning: (*a*) an unusually accurate, and intention-oriented, capacity for imitation; (*b*) a generalized capacity for teaching (including through shared attention) and other subtle forms of information donation; and (*c*) a symbolic language, with its enhanced capability for accurate, low-cost, and flexible instruction and information exchange. Theoretical work has shown that high-fidelity information transmission is necessary for culture to become cumulative (Lewis & Laland 2012), leading to a ratcheting in complexity (Henrich & McElreath 2003, Tennie et al. 2009). These conclusions are supported by a comparative experiment reporting cumulative cultural learning in children but not in chimpanzees or capuchins, with variations in performance both within and between species strongly correlated with the incidence of imitation, teaching, and verbal instruction (Dean et al. 2012).

Also relevant here is the ability to represent the mental states of others (and oneself) such as knowledge, belief, desires, and intentions, known as theory of mind. This ability develops over the preschool years, with notable gains between 3 and 5 years of age in the ability to answer questions about the beliefs of others (i.e., to understand that others can have false beliefs) (Wellman et al. 2001). This advance may be explained by the ability to represent another's perspective (Perner 1991), the reinforcing effects of language (Pyers & Senghas 2009), or the executive control needed to hold in mind and shift between contrasting perspectives (Kloo et al. 2020). Chimpanzees can infer a human experimenter's intentions (e.g., by reacting differently when a person does something on purpose rather than by accident) (Call & Tomasello 1998, Call et al. 2004), but there remains no unambiguous evidence that nonhuman primates can pass a false-belief test (Call & Tomasello 2008; cf. Krupenye et al. 2016).

The unprecedented scale of human cooperation (no less manifest in warfare as in altruistic endeavor) is widely thought to reflect our reliance on socially learned and transmitted norms (Boyd & Richerson 1985, Henrich 2016, Tomasello 2009). Such norms and regulations are often nonintuitive, require linguistic specification, and are sufficiently complex that they must be taught (e.g., why citizens pay taxes, the rules of the road). Yet experimental studies show that young children acquire such norms readily (typically, from ages 3–5) and rapidly and spontaneously enforce them (Chudek & Henrich 2011, Tomasello 2009). It remains unclear whether human cooperative tendencies reflect evolved altruistic social preferences (Chudek & Henrich 2011, Tomasello 2009) or other systems of core knowledge (e.g., reasoning about objects and agents) that are integrated and scaffolded by language learning (Santos et al. 2002, Spelke 2009). Either way, humans show an unusual proficiency at working together to achieve joint goals, helping others through teaching (and expecting to be taught), and taking other's perspectives and intentions into account. Tomasello (2018) provides a developmental account of how these skills could be built from experience in engaging in joint attention with others from the first year of life, an activity that can make contrasting perspectives and knowledge manifest on a daily basis. These contrasts, which become especially salient during language learning (Tomasello 2018), highlight an important role for developmental feedback.

Humans Communicate Flexibly

Communication is perhaps the most obvious domain in which there appears to be a divide between humans and other animals. Whether language originated in vocalizations or manual gestures is much debated (Christiansen & Kirby 2003, Corballis 2017), but either way, the gap with nonhuman primate communication appears striking. Some primate vocalizations, known as functionally referential calls, may symbolize objects in the world. Famously, vervet monkeys possess three distinct calls thought to be labels for avian, mammalian, and snake predators (Seyfarth et al. 1980). Similar claims have been made for the social, food, and alarm calls of a range of primates, meerkats, prairie dogs, and chickens (Hauser et al. 2002, Wheeler & Fischer 2012). However, primate vocalizations largely consist of single, unrelated signals that are rarely put together to transmit more complex messages (cf. Casar et al. 2013). Moreover, whether monkey calls are truly referential remains contested (Wheeler & Fischer 2012, 2015): Acoustically distinctive calls may represent different emotional states rather than specific predators (Owren & Rendall 1997), with referentiality restricted to the receiver (Hauser et al. 2002).

There is also little evidence that nonhuman primates can learn new vocalizations or imitate sounds, and most species appear to have only limited ability to modify their natural vocalizations (Hauser et al. 2002, Pfenning et al. 2014), perhaps reflecting limited flexibility in vocal control (Wheeler & Fischer 2012; cf. Schel et al. 2013). In vervets, the emotional reactions of receivers to the structure of signals appear unlearned, with only the behavioral responses (e.g., climbing a tree versus hiding in bushes) being shaped by experience (Wheeler & Fischer 2012). These findings provide little evidence of unusual sophistication in nonhuman primate vocalization. Apes possess a rich repertoire of gestures (e.g., to initiate play or to be carried), which have learned elements (Hobaiter & Byrne 2011, Pika et al. 2005); however, although these gestures are intentional and communicative, they exhibit neither symbolism nor syntax (Corballis 2017, Pika et al. 2005).

Vocal learning is widespread in bats, cetaceans, elephants, pinnipeds, songbirds, and parrots, and birdsong has long been studied as a model for human speech acquisition (Bolhuis et al. 2010). Researchers note several parallels between birdsong and language, including vocal learning, auditory feedback, error correction, sensitive periods, babbling (subsong), shared brain circuitry (e.g., mirror neurons), shared genes (e.g., *FOXP2*), and syntax. Despite this structural complexity, avian (and cetacean) songs lack a representational quality and seemingly convey messages no more complex than other animal signals.

Animals might be capable of more complex communication than they exhibit in their natural environments when taught to use symbols (Gardner & Gardner 1969, Pepperberg 2017, Terrace 1979). In the 1960s a young chimpanzee called Washoe was taught American Sign Language and learned the meaning of over 300 signs. The investigation triggered a series of studies that continue to this day, in which an assortment of animal taxa (including apes, birds, and cetaceans) are taught signs or a symbolic lexicon. Through such experiments, apes, dolphins, and parrots have been shown to be capable of using signs intentionally to make their needs and wants clear, using signs in appropriate contexts, comprehending the meaning of a large repertoire of signs, teaching other animals signs, devising appropriate signed names for novel objects, answering questions using signs, acquiring and using a range of abstract concepts, and following simple noun-verb phrase instructions (Hauser et al. 2002; Herman et al. 1984; Pepperberg 1999, 2017). Such investigations demonstrate that animals can achieve a rudimentary capability for symbolic communication.

Yet these capabilities fall short of human language in important respects, including that they are typically relatively simple one- or two-symbol combinations, are tied to the present, and show little evidence for the comprehension of tense, syntax, or grammar as well as little recursion and limited meanings. For illustration, the longest recorded utterance of chimpanzee Nim Chimpsky was, "*Give orange me give eat orange me eat orange give me eat orange give me you*" (Terrace 1979). In contrast, 2-year-old children produce a variety of complex sentences, comprising verbs, nouns, prepositions, and determiners, in the correct grammatical relations and on a diverse range of topics; 3-year-olds can communicate about past and future and distant objects; and high-school graduates know up to 60,000 words (Hauser et al. 2002). The talking animals experiments strongly suggest that human language not only is the product of a uniquely scaffolded developmental experience but also reflects a distinctively human evolved cognition.

A key feature of human language, labeled unbounded merge, is that constituents can be recursively combined to create the infinite generativity of thought and language (Chomsky 1980). What makes this possible is recursion (Hauser et al. 2002), whereby the rules of grammar allow words or phrases to be organized iteratively, sequentially, and hierarchically, with embedded elements extending or nested within one another. More generally, sequence learning (i.e., the ability to encode and represent the order of discrete elements in a string) is a common feature of human cognition, manifest in tasks ranging from extracting meaning from a speech stream to learning to manufacture tools. Comparative studies reveal evidence that (like humans from 8 months of age; see Saffran et al. 1996) nonhuman primates readily learn fixed sequences and can extract frequently co-occurring elements from continuous streams by detecting statistical regularities (Conway & Christiansen 2001). However, they struggle to learn complex hierarchical structures to sequences, which is the very feature necessary for processing recursion (Conway & Christiansen 2001, Fitch & Hauser 2004, Fitch et al. 2005). Fitch & Hauser (2004) found that while tamarin monkeys recognize sequential regularities in acoustic strings, unlike humans, they were unable to process a simple phase structure in which elements at one portion of the string were related to elements some distance away. Seemingly, a focus on the immediate surface features of the stimuli prevents the tamarins from perceiving more abstract relations.

Many bird and whale songs do show some level of hierarchical organization (phrases and subphrases) (Bolhuis et al. 2010, Cholewiak et al. 2012), albeit with little evidence of the nesting of elements and long-distance hierarchical dependencies that characterize the phrase-structure grammar of language. Hierarchical structure is manifest in the complex sequences of manual actions that mountain gorillas learn to overcome the defenses of edible plants, but the number of embedded layers is modest (Byrne & Russon 1998). Analyses of the spontaneous behavior of humans and other apes reveal substantially higher levels of hierarchical complexity in the behavior of humans (Conway & Christiansen 2001). Evidence suggests that while simple forms of recursion are found in animals, humans are distinct in the ability to recognize and remember phrase-structure rules in learned sequences, which may be language specific or reflect a more general enhanced capability for statistical learning.

Other distinctive aspects of human cognition contribute to our capacity for language. Joint attention (e.g., orientating to the transmitter, following gaze) is important for successful communication, particularly during language learning (Tomasello 2011). The motivation and ability to inform others, to teach or tell useful information, and to comprehend that others seek to inform us are also vital (Csibra & Gergely 2011, Laland 2017), as is the recognition that others are intentional agents with their own beliefs and desires, which can be influenced and manipulated by our communication (Tomasello 2011). The ability to refer to matters that are not physically present, including communicating about past experiences, future possibilities, and imagined worlds, would seem to require mental time travel and mental simulation competence (Corballis 2017). Likewise, language is reliant on the ability to learn and process hierarchically organized temporal sequences, another domain in which humans show superior performance (Conway & Christiansen 2001). While the exploitation of these additional capabilities in language could signify that the mechanisms were all collectively shaped by natural selection as a uniquely human adaptation for communication (Pinker & Jackendoff 2005), it is at least equally plausible that additional unique elements are exaptations that evolved for other reasons and were co-opted for human language.

DOMAIN-GENERAL THINKING

The preceding section implies that exceptional aspects of human cognition arise through interactions between capabilities. Could a capacity for domain-general processing set us apart? In humans, levels of performance across a number of cognitive tasks are positively correlated, and factor analysis consistently reveals a single dominant factor, *g*, that explains a substantial proportion (>40%) of variation in task performance (Carroll 1993). This *g* factor is widely interpreted as a measure of general intelligence, defined as "the ability to reason, plan, solve problems, think abstractly, comprehend complex ideas, learn quickly and learn from experience" (Deary 2001,

p. 17). Neuroscientific evidence also implies that humans are domain-general thinkers. Few parts of the brain, or cognitive domains, are modular in an encapsulated way, with extensive evidence for top-down effects, cross-domain integration, cross-modal neural plasticity, and overlapping neural circuitry for functionally distinct tasks (Anderson 2010, Anderson & Finlay 2014, Buller & Hardcastle 2000). A meta-analysis of data from 1,469 fMRI studies established that, independent of scale, a typical brain region is activated by tasks in multiple (mean = 9) different domains (Anderson 2010). For illustration, Broca's area is strongly associated with language but is also involved in movement preparation, action sequencing, action recognition, and motor imitation. The widespread reuse of neural circuitry across different domains in the human brain is seemingly incompatible both with structural modularity and with encapsulated conceptions of functional modularity (Anderson 2010, Anderson & Finlay 2014).

In animals, by contrast, the tradition within behavioral and neuro-ecology over recent years has been to emphasize functional neural specializations in response to species-specific adaptive problems, such as the avian song nuclei or the enlarged hippocampi of food-storing birds (e.g., Healy & Krebs 1996, Shettleworth 2010). However, a simple dichotomy in which animal minds are construed as collections of domain-specific cognitive adaptations while humans possess domain-general intelligence is untenable (Burkart et al. 2017, Reader et al. 2011). In mice and rats, for instance, there is clear and robust evidence for strong correlations in performance (i.e., *g*) across multiple test batteries. In primates the data are less clear—almost certainly because, in contrast to the rodent work, such studies typically lack statistical power because of small sample size (Burkart et al. 2017)—with evidence consistent with *g* in several studies, including on rhesus monkeys, tamarins, and chimpanzees (see Burkart et al. 2017), but not all (see Herrmann et al. 2010 on chimpanzees). Broad comparative analyses have also been conducted across primate species, again revealing strong positive correlations in performance (called *G*, following Burkart et al. 2017), including across diverse laboratory tests of learning and cognition (Deaner et al. 2006), and spanning naturalistic measures of primate cognition (tool use, social learning, innovation, diet breadth, and deception) (Reader & Laland 2002, Reader et al. 2011). Animal measures of *g* and *G* have been validated in various ways, including correlation with brain size, working memory, and learning, and they are not easily explained away as artifacts (Burkart et al. 2017, Reader et al. 2011).

In mammals, allometric covariation of brain parts is extremely high (Finlay & Darlington 1995), leaving only a few percentage points of residual anatomical variance to map behavioral variation onto (Anderson & Finlay 2014). The aspects of cognition discussed above (e.g., tool use, social learning, social cognition, innovation) are not associated with species-specific nuclei or neural circuits but are rather distributed over large regions in a manner representative of broad taxa, such as primates, mammals, or vertebrates (Anderson & Finlay 2014, Striedter 2005). Nonetheless, the absence of much neuroimaging data in animals leaves *g* and *G* consistent with both domain generality and correlated domain specificity.

Is there evidence in animals for cognitive processes that operate across domains? In principle, variation in executive functions, such as working memory, inhibitory control, or attentional shifting, could account for a significant proportion of *g* and *G*. This is important because, in principle, noncognitive factors such as differences in visual acuity or manual dexterity could explain this variation, leaving domain-general processing uniquely human. Executive functions are strong candidates for the sources of variation underlying correlated performance on diverse cognitive tasks. They include high-level cognitive processes (aka System 2 thinking; see Kahneman 2011), which are manifest in the abilities to stop automatic responses, resist distraction, switch between tasks, hold items in working memory, plan, and multitask (Friedman & Miyake 2017). In humans, executive function tasks cluster around three latent variables (inhibitory control, working memory, and attention shifting), with positive correlations within and between them (Friedman & Miyake 2017).

There are few direct experimental comparisons of executive function in humans and other animals. Behavioral neuroscientists have established that the core characteristics of working memory, attentional shifting, and inhibition are present in other mammals such as rodents and monkeys and rely on overlapping, conserved brain areas, particularly the prefrontal cortex (Brown & Bowman 2002). However, these studies are focused on developing animal models of cognitive aging and dementia rather than on exploring differences among species. More recently, there have been studies that seek to compare executive functions across species. In a study that garnered substantial attention, a highly trained juvenile chimpanzee outperformed university students at a spatial working-memory task (Inoue & Matsuzawa 2007). However, in later experiments in which students were given equivalent training to the chimpanzee, the students did "substantially outperform" the chimpanzee (Cook & Wilson 2010). Humans also outperformed monkeys at a change-detection task (Elmore et al. 2011). However, wider reviews of the literature reveal similarities between humans and other animals in signatures of working memory such as duration of retention, ability to resist interference, and active rehearsal of information (e.g., Brady & Hampton 2018, Lind et al. 2015, Roberts & Santi 2017, Völter et al. 2018). Two large comparative studies have found that inhibitory control is correlated with absolute but not relative brain size in primates (MacLean et al. 2014, Stevens 2014) as well as with innovation, social learning, tool use, diet breadth, and intelligence (MacLean et al. 2014).

Interpreting the cognitive causes of these differences in performance is complicated, however, because the measures have not been validated as indexing variation in inhibitory control: For example, the two measures of inhibitory control used by MacLean et al. (2014) do not correlate (Völter et al. 2018). Executive functions are control systems that have evolved to deal with conditions that are novel or variable over the life span and that demand a flexible response. It stands to reason that performance will be highly plastic and dependent on experience and the nature of the stimuli employed. Measures need to make use of systematic variation and performance over a range of conditions to establish signature limits, test-retest reliability, and convergent as well as divergent validity.

Thus, comparative cognition studies have established that humans are not unique in possessing domain-general processing, and to date they provide little evidence that humans' capacity for domain-general thinking is vastly superior to that of other animals. Nonetheless, a uniquely potent human capacity for domain-general processing remains a possibility (Heyes 2018, Laland 2017). The well-documented and substantial anatomical, histological, genomic, transcriptomic, developmental, and physiological differences between human and chimpanzee brains, most of which have arisen in the hominin lineage (Somel et al. 2013, 2014), attest to the plausibility of general differences in human and animal cognition. Compared to chimpanzee brains, human brains have three times the volume and number of neurons, a higher proportion of neocortex (especially the prefrontal and temporal cortices), increased connections within the prefrontal cortex, increased dendritic arbor, increased glia-to-neuron ratio, prolonged development, higher activity of metabolic pathways, and other differences (Sherwood 2018, Somel et al. 2014), any of which might translate into enhanced cognition. The enlarged and better connected human prefrontal cortex, in particular, is widely thought to afford enhanced executive control (Striedter 2005), while the correlated expansion of the cerebellum is thought to play a role in sensory-motor control and action planning (Barton & Venditti 2014). Genetic studies have identified hundreds of human genes subject to recent positive selection that show major changes in expression in the brain, including the upregulation of genes expressed in energy production and neuronal signaling in the neocortex as well as extended plasticity in brain development (Somel et al. 2014, Uddin et al. 2004). Such profound and general changes plausibly influence the intelligence, learning, or cognition of humans in ways not yet captured by comparative cognition studies. There are hints of this in the exceptional performance of humans in learning language, long-distance hierarchical dependencies, and cultural knowledge (Christiansen & MacDonald 2009; Hauser et al. 2002; Tomasello 1999, 2008).

THE EVOLUTION OF HUMAN COGNITIVE UNIQUENESS

Dynamical feedbacks between mutually reinforcing aspects of cognition are equally characteristic of the evolution of our cognitive uniqueness. Given the emerging consensus that human success is critically reliant on our ability to share and build upon learned knowledge ("to stand on the shoulders of giants"), culture is a natural starting point for any analysis of the origins of human cognition (Henrich 2016, Heyes 2018, Kaplan et al. 2000, Laland 2017, Richerson & Boyd, 2005, Tomasello 1999, Whiten et al. 2017). Rationales for this reasoning include the dependence of human societies on learned know-how (e.g., concerning processing food or manufacturing tools), often accumulated over centuries (Henrich 2016, Kaplan et al. 2000, Richerson & Boyd 2005); the survival failures of lost European explorers deprived of such local cultural knowledge (Henrich 2016, Henrich & McElreath 2003); and the superior performance of social compared to asocial learning in solving complex problems (e.g., Whalen et al. 2015). If culture is what makes our species successful today, the evolution of complex culture may be tied to the emergence of sophisticated cognition (Henrich 2016, Laland 2017).

Social learning and innovation are key components of culture; they are widespread in animals and reach their zenith in the apes (Reader et al. 2016; Whiten et al. 2012, 2017). Like rate of innovation, incidence of social learning and tool use correlates with brain size measures in primates (Lefebvre et al. 2004, Navarrete et al. 2016, Reader & Laland 2002, Reader et al. 2011, Street et al. 2017). While such associations need not be causal, and many factors covary with brain size (Dunbar & Shultz 2017), the available evidence points to an important role for cultural processes as drivers of brain evolution and intelligence. Brains are energetically costly organs, and only through social learning and collaborative foraging can smart animals gather the calorie-dense, skill-intensive, and large-sized food resources necessary to grow and maintain a very large brain efficiently (Dunbar & Shultz 2017, Kaplan et al. 2000, Laland 2017, Street et al. 2017, Tomasello 2009), a point reinforced by more mechanistic models (González-Forero & Gardner 2018).

Diverse evolutionary analyses (e.g., Dunbar & Shultz 2017, Forss et al. 2016, González-Forero & Gardner 2018, Kaplan et al. 2000, Navarrete et al. 2016) report associations between cultural complexity, longevity and extended development, general intelligence, and brain size in primates. Taken together, these works tell a story in which complex cognition, large brains, and longer lives coevolved in hominins because our ancestors' intellectual (and particularly cultural) capabilities allowed them to exploit high-quality, but otherwise difficult-to-access, food resources (which provided the food nutrients to sustain brain growth), with increased longevity favored by natural selection because it allowed them more time to cash in on complex, and difficult-to-master, foraging skills (Kaplan et al. 2000, Laland 2017, Navarrete et al. 2016, Street et al. 2017). Enhanced capabilities for shared attention, greater social tolerance, and increased sensitivity to social information are also plausible targets of this selection, particularly if cooperation allowed for access to nutrient-rich food such as meat (Henrich 2016, Laland 2017, Tomasello 2009), as is a protected childhood in which effort and energy are dedicated to building causal models of the social and physical world (Gopnik et al. 2017).

Cultural intelligence is not the only important factor responsible for primate brain evolution, however, and the adaptive response to the pressure to share resources and information was shaped by earlier events. Beginning about 35 mya, a major grade shift occurred with the evolution of the anthropoids (monkeys and apes), who had larger brains, linked to a greater reliance on binocular color vision, and shifted their diet toward consumption of plant parts, particularly fruits and leaves (Clutton-Brock & Harvey 1980, DeCasien et al. 2017, Dunbar & Shultz 2017). Further encephalization occurred in the apes, and in particular in the hominins, who specialized in eating ripe fruits and in using complex techniques for extracting foods from protected substrates (Kaplan et al. 2000, van Schaik et al. 2003, Whiten et al. 1999). High levels of knowledge, skill, and coordination are required to exploit such high-quality dietary resources, which often involve tool use, extractive foraging, food processing, and coordinated hunting. Such knowledge and skills are typically acquired socially and take time to maximize return rates (Kaplan et al. 2000, Laland 2017, Street et al. 2017, Whiten et al. 2017). The coevolution of ecological, technical, and cultural intelligences would explain why flexible tool users tend to have broad omnivorous diets and exhibit both enhanced dexterity and a tendency for object manipulation (Visalberghi et al. 2017).

Central to this cluster of cultural drive or cultural intelligence explanations for human cognitive evolution (e.g., Herrmann et al. 2007, 2010; Hill et al. 2009; Laland 2017; Reader & Laland 2002; Whiten & Erdal 2012; Whiten & van Schaik 2007) is a dynamical interplay between genetic and cultural processes in primate, and particularly hominin, evolution. These explanations imply a positive feedback loop in which accurate and efficient social learning enhances the payoff of technical competences, including tool use, which can then benefit not just the individual innovator but also their relatives. Computational analyses of the evolution of learning (Rendell et al. 2010) provide a clear rationale for this cultural engine of selection, and neuroanatomical and molecular data support the inference that culture has driven hominin brain evolution (Laland 2017; Laland et al. 2010; Somel et al. 2013, 2014).

Human culture is distinctive for its accumulation of knowledge and complexification. Comparative work (Dean et al. 2012, Tomasello 1999), experimental archaeological studies (Morgan et al. 2015), and theoretical analyses (Fogarty et al. 2011, Lewis & Laland 2012) all suggest that cumulative culture requires high-fidelity transmission. While the origins of language remain unclear, a parsimonious suggestion is that language, too, arose through a cultural-drive mechanism (Laland 2017, Muthukrishna et al. 2018). The language system appears to be a part of the larger mirror neuron system (Molenberghs et al. 2012) and exhibits extensive overlap with neural circuitry deployed in stone tool manufacture (Stout & Chaminade 2012). Cognitive abilities that are manifest in language recursion may have originally evolved for food processing and tool manufacture (Greenfield 1991, Laland 2017, Stout & Chaminade 2012). Dediu & Levinson (2013) argue that sophisticated language probably goes back at least 500,000 years to the common ancestors of humans, Neanderthals and Denisovans. Given that languages have been found to acquire efficiencies in transmission (Kirby et al. 2008), and that sign languages have a strong iconic component (Corballis 2017), the arbitrariness characterizing contemporary languages plausibly arose through cultural evolution, with selection for efficiency and clarity leading to loss of iconicity (Corballis 2017).

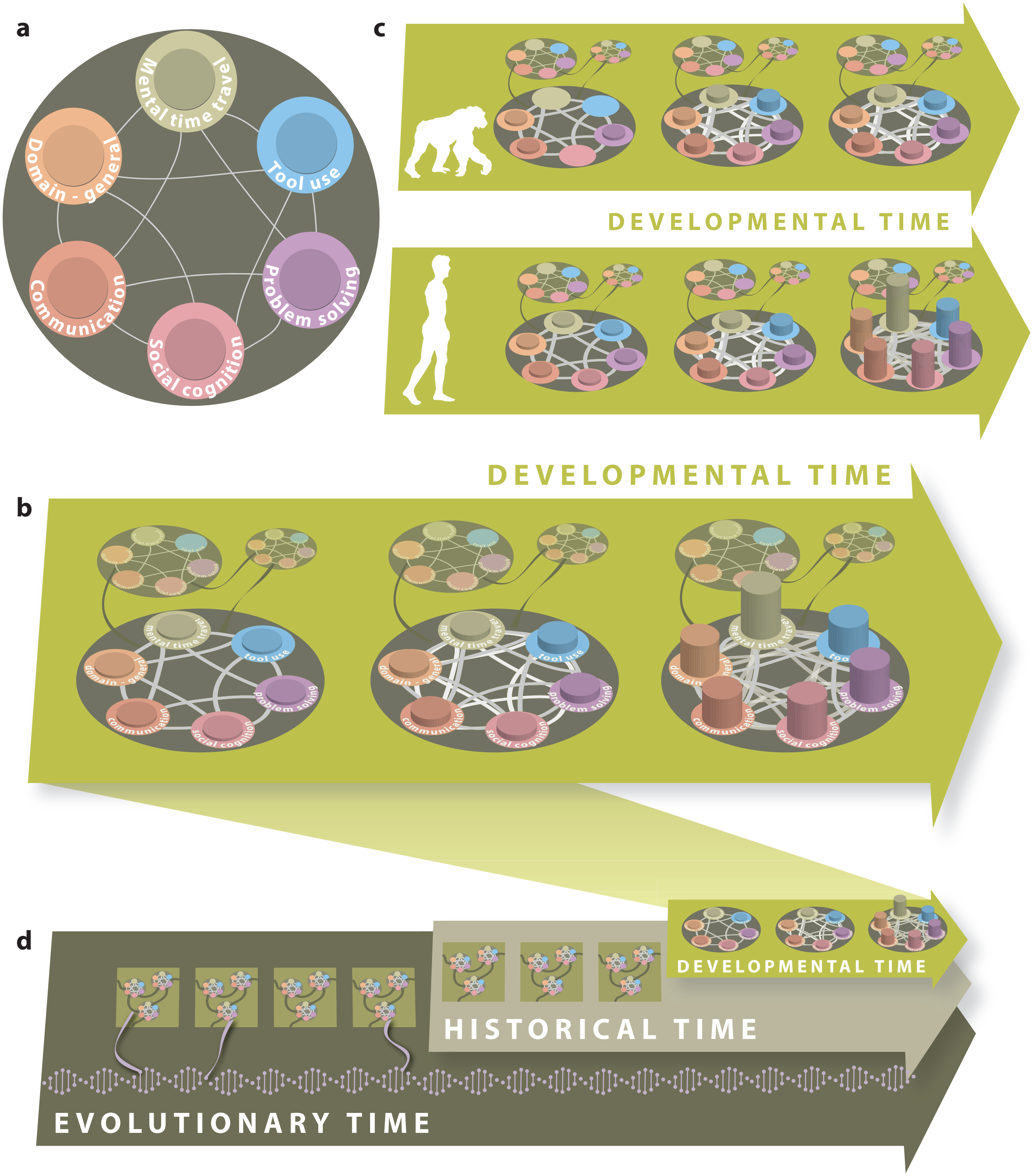
The origins of language are seemingly intimately linked to our ancestors working together, sharing attention and perception, understanding intention in coordinated collaborative foraging and other forms of joint action (Tomasello 2008, 2009), and sharing information through social learning and teaching (Csibra & Gergely 2011, Fitch 2004, Gergely & Csibra 2005, Gergely et al. 2007, Laland 2017). In turn, these capabilities supported other forms of cooperation, including mutualism, trade, reciprocity, and cultural group selection (Henrich 2016, Nowak & Highfield 2011, Pagel 2012). Language provided our ancestors with tools for thought as well as for communication, connecting symbols and meanings, stabilizing and interweaving concepts, integrating experiences, and supporting inductive reasoning and theory-based inference (Chomsky 1980). While the origin of human cognition is not explained by a single magic bullet, key innovations such as joint attention and language could have been game changers that integrated and greatly enhanced the performance of other elements of human cognition.

DISCUSSION

No candidate traits present in humans and absent in all other animals, if taken in isolation, explain our species' superior cognitive performance. Claims that humans uniquely possess some specific cognitive trait generally fail, as science reveals other species with the attribute. At higher levels of analysis, a case can be made that humans uniquely possess certain aspects of cognition (e.g., language), but when these are broken down into lower-level elements, the components are neither uniquely human nor unique to the trait. There are nonetheless many spheres in which humans possess unusually potent capabilities. We may not be the only innovators, tool makers, or general-process thinkers in the animal kingdom, nor are we alone in possessing culture and rich collaboration, but we do excel in all these regards. Other animals possess specialist competences that can rival our own, but no other species consistently outperforms humans across multiple cognitive domains.

The exceptionalism manifest in human cognition arises largely from interactions in development between abilities, with extensive knowledge flow across mutually reinforcing domains (**Figure 1**). For instance, distinctively human patterns of tool use appear only after the emergence of language, allowing infants to combine representations of objects and actions (Spelke 2009). Likewise, language increments with recognition that others are intentional agents. The studies reviewed here commonly identify a change associated with more meta-cognitive awareness or explicit theorizing around ages 4–5. Humans rerepresent their implicit knowledge explicitly, making it available to other domains (Karmiloff-Smith 1995). Children partly construct their cognition by seeking to understand their own thinking, which leads to representational flexibility, theory building, and mental simulation. This process of representational redescription is not available to, or is impoverished in, other species (Karmiloff-Smith 1995). At a neural level, it almost certainly hangs critically on the extended plasticity of human brain development, which allows for experience- and usage-based neural reorganization, interconnection, and pruning. Peak expression of synaptic genes in the prefrontal cortex occurs approximately five years after birth in humans, compared to several months after birth in chimpanzees (Somel et al. 2013, 2014).

Human cognitive uniqueness arises from feedbacks between abilities over three timescales: developmental (Karmiloff-Smith 1995), cultural evolutionary (Heyes 2018), and gene–culture coevolutionary (Laland 2017) (**Figure 1**). Our cognitive uniqueness is actually an evolving network of interacting traits that changed along our biological lineage, changed throughout history, and continue to change, with each increment in one trait dragging up performance in others. Humans would have appeared less cognitively distinct 50,000 years ago, and our ancestors would have appeared less exceptional prior to the extinction of other hominins. While extended developmental plasticity may leave human cognition unusually sensitive to early life experiences, our uniqueness is not solely a product of enriched development. The feedback between domains and representational redescription that augments a child's cognitive performance does not occur in isolation but in the context of a uniquely sophisticated, dynamically changing symbolic and cultural realm, mediated by active agents that are themselves developing cognitively and many of whom (parents, siblings, teachers) possess vested interests in the child's development. Heyes (2018, p. 20) argues compellingly that individual cognition is shaped by a cultural evolutionary process and offers reading as an exemplar of a "cognitive gadget" with its own distinctive neural circuitry that "has major, constructive effects on the neurocognitive system." Unquestionably, the flexibility of neural development allows functional efficiencies in neural architecture to arise in development (D'Souza &



(*Caption appears on following page*)

Figure 1 (*Figure appears on preceding page*)

(*a*) Human cognitive uniqueness arises through interactions (here, connecting lines) between several cognitive domains (nodes) in a network; (*b*) performance in each domain (here, stack height) is enhanced over developmental time through mutual reinforcement and representational redescription, scaffolded by interactions (connecting ribbons) with other individuals and (*c*) with species differences in performance collectively generated by predispositions, developmental experiences, and social interactions. (*d*) Interactions and feedbacks between domains occur over developmental, historical (i.e., cultural evolutionary), and evolutionary (i.e., gene–culture coevolutionary) timescales. Stack heights are for illustrative purposes only and do not attempt to quantify capabilities. Domains partly reflect extended cognition through objects, artefacts, and social interaction and do not signify commitment to a modular or brain-based view of cognition.

Karmiloff-Smith 2011). Reading may be a cognitive gadget but it develops by "reusing" (Anderson 2010) preexisting circuitry (e.g., for speech) and hence does not necessarily imply that our language capability, or cognition in general, is composed of gadgets. Our uniqueness is not solely a product of cultural evolution, although this is an important part of the story.

The fact that human-reared apes have been found to exhibit superior performance compared to their more naturalistically reared counterparts (based on the so-called enculturation hypothesis; see Tomasello & Call 1997) indicates that the cognition of nonhuman species can benefit from cultural immersion. This presents further challenges to pinpointing human uniqueness, since it implies that any level of chimpanzee cognition we may find provides only a fuzzy and unstable benchmark against which to gauge human cognition. Nonetheless, the clear cognitive differences between encultured chimpanzees and humans provide strong evidence, if it were needed, that human cognitive uniqueness builds upon fundamental biological disparities evolved over time.

Contrary to the tradition within biology that emphasizes mosaic brain evolution (e.g., Barton & Harvey 2000), cognitive neuroscience places greater stress on concerted brain evolution (Finlay & Darlington 1995, Finlay & Uchiyama 2014). Cognitive neuroscientists have distinguished between easy and difficult modes of brain evolution (Anderson & Finlay 2014, Finlay & Darlington 1995, Finlay & Uchiyama 2017), with the former constituting selection on the duration of neural development (which generates concerted evolution of the whole brain) and the latter requiring coordinated enlargement of independent functional components. Primate comparative phylogenetic analyses establish that behaviors thought to require complex cognition have coevolved with each other and with absolute brain size (Navarrete et al. 2016, Street et al. 2017), with faster evolution of cognitive abilities loading strongly on *G* (Fernandes et al. 2014). Neuroscientific data reinforce this picture (Anderson 2010, Anderson & Finlay 2014). For instance, stone-tool use is associated with distributed brain circuitry that shows extensive overlap with the circuitry involved in speech (Stout & Chaminade 2012) and event prediction (Fischer et al. 2016). Seemingly, at least in primates, the easiest way to evolve enhanced cognition is to grow the whole brain for longer while coopting existing circuitry for new functions, because the costs of excess neural tissue are ameliorated by the demand-based mechanisms of neural plasticity (which removes unnecessary connections) and because much complex cognition is distributed over brain structures that are large and develop late (Anderson 2010, Anderson & Finlay 2014, Finlay & Darlington 1995). This implies that attempts to identify cognitive adaptation as a departure in the relative size of neural structures from taxon-general regression lines may fail to detect important cognitive adaptations that arise through selection on whole-brain size or duration of neurogenesis.

One interesting finding from the neural reuse literature is that more recently evolved functions exploit a greater number of widely scattered brain areas than do evolutionarily older functions (Anderson 2010). Recent functions are more likely to encounter useful preexisting neural circuits that can be incorporated into the developing complex. Language and reasoning are recently evolved capabilities and exhibit scattered circuitry that integrates spatially separate regions of the brain (Anderson 2010, Anderson & Finlay 2014). Humans may be cognitively unique, in part, because extensive reuse of neural circuitry has generated greater neural integration. This would explain why humans can reason abstractly across domains whereas animals are often constrained to reason in more naturalistic contexts, why language can be deployed flexibly to enhance other aspects of cognition, and perhaps even why human language learning can be so rapid (as it is able to exploit a distributed neural network that links mutually reinforcing concepts, actions, sensory experiences, symbols, and phonological units).

Our review highlights challenges to identifying human cognitive uniqueness: Can researchers be sure that experimental tasks are fair to all species? Does an animal's performance reflect its abilities when tested in captivity? Is it legitimate to compare children to chimpanzees of all ages? As these issues are well rehearsed we do not dwell on them here, but rather we concentrate on two less discussed points. First, although researchers often find evidence for differences between humans and other animals in behavior, identifying the cognitive mechanism that underlies those differences is rarely straightforward. Performance differences may reflect the focal cognitive trait, but they could also be manifestations of more general cognitive differences (e.g., in working memory, inhibitory control, intelligence) or noncognitive differences (e.g., in visual acuity, manual dexterity, motivation). We encourage researchers to test these competing hypotheses. Second, as many aspects of human cognition appear to develop their exceptional quality through interaction with other abilities, progress in understanding human cognitive uniqueness will require a developmental perspective and methodologies designed to tap into between-domain interactions. Karmiloff-Smith's (1995) model of conceptual change and Tomasello's (2018) account of theory-of-mind development are promising, but testing these theories may require greater pluralism and collaboration than accomplished so far. Exploiting natural variation in, for example, social input in experimentation as well as cross-cultural comparisons and movements like ManyBabies (**https://manybabies.github.io**) and ManyPrimates (**https://manyprimates.github.io**) shows promise as a platform for the requisite work.

In sum, human cognitive uniqueness does not arise from traits other animals lack but rather from trait interactions and feedbacks, with culturally scaffolded developmental experiences building upon and reinforcing evolved biological differences. Predispositions that have evolved solely in humans, together with sensory experiences that are dependent on the developmental stage, kick-start cognitive development by focusing the infant's attention on relevant inputs (Carey 2009, Fausey et al. 2016, Karmiloff-Smith 1995, Spelke 2000); then, (possibly uniquely human) domain-general processes, exploiting (uniquely human) neural plasticity, build upon those capabilities in response to (uniquely human) culturally constructed and symbolically encoded environments (Carey 2009, Karmiloff-Smith 1995, Tomasello 2018) to support (uniquely human) representational redescription (Karmiloff-Smith 1995). This framing brings home how multifaceted human cognitive uniqueness is.

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