

*Review*

# Modularity, comparative cognition and human uniqueness

Sara J. Shettleworth\*

*Department of Psychology, University of Toronto, Toronto, Ontario, Canada M5S 3G3*

Darwin's claim 'that the difference in mind between man and the higher animals . . . is certainly one of degree and not of kind' is at the core of the comparative study of cognition. Recent research provides unprecedented support for Darwin's claim as well as new reasons to question it, stimulating new theories of human cognitive uniqueness. This article compares and evaluates approaches to such theories. Some prominent theories propose sweeping domain-general characterizations of the difference in cognitive capabilities and/or mechanisms between adult humans and other animals. Dual-process theories for some cognitive domains propose that adult human cognition shares simple basic processes with that of other animals while additionally including slower-developing and more explicit uniquely human processes. These theories are consistent with a modular account of cognition and the 'core knowledge' account of children's cognitive development. A complementary proposal is that human infants have unique social and/or cognitive adaptations for uniquely human learning. A view of human cognitive architecture as a mosaic of unique and species-general modular and domain-general processes together with a focus on uniquely human developmental mechanisms is consistent with modern evolutionary-developmental biology and suggests new questions for comparative research.

**Keywords:** cognitive evolution; human uniqueness; modularity; dual process theories

## 1. INTRODUCTION

In the past 30 years or so, research on comparative cognition has provided unprecedented support for Darwin's [1, p. 105] claim that 'the difference in mind between man and the higher animals . . . is certainly one of degree and not of kind'. At the same time, however, experiments on processes such as planning, physical understanding and theory of mind in non-human animals (henceforth *animals*) have provided new reasons to question this claim, so many that on one view [2] it is 'Darwin's mistake'. For example, although many animals are exquisitely sensitive to past and present behaviour of social companions, their responses need not demand theory of mind [3–5]. Such 'killjoy' [6] interpretations of animals' human-like behaviour, together with increasing amounts of relevant data, have stimulated a virtual epidemic of new theories of human cognitive uniqueness. The most prominent are domain-general, sweeping characterizations of the differences between humans and other species. Meanwhile, human cognitive psychology is seeing the development of domain-specific dual-process theories with a common theme: adult humans' cognition shares simple basic processes with that of other animals while additionally including one or more unique, slower-developing, usually slower-acting and more explicit, consciously accessible, processes.

In this article, I discuss contemporary approaches to human cognitive uniqueness, starting with domain-general theories and then, after a digression on cognitive modularity, looking at domain-specific theories. I conclude with theories that go beyond characterizing the differences between adult humans and animals to ask what species-specific process(es) underlie the development of uniquely human aspects of cognition. Besides being most consistent with evolutionary-developmental biology more generally, this approach suggests new questions for comparative research.

A few foundational issues are brushed under the carpet here. First, consideration of Darwin's claim assumes that researchers can agree in any given case on what counts as a 'kind' versus a mere 'degree' of cognitive difference. But evidence for human cognitive uniqueness ranges from clear-cut to deeply contentious. The continuing evolution of relevant data and theory for humans may make agreement difficult. Moreover, reports of unexpectedly human-like performance in another animal often stimulate sceptics to suggest explanations based on 'simpler' mechanisms than those believed to be used by humans [7]. For instance, monkeys and apes may perform actions that benefit conspecifics, not because they reason about the effects of their actions on others but because of the reinforcement histories of those actions [7].

A second issue is what species are compared. Strictly speaking, any claim that humans are cognitively unique is impossible to sustain because it presupposes comparison with *all* other extant species. It also presupposes species comparisons that are

\*shettle@psych.utoronto.ca

One contribution of 14 to a Discussion Meeting Issue 'Animal minds: from computation to evolution'.

thorough and methodologically sound, e.g. 'fair' to all species involved [8], well controlled for contextual variables [9], and with multiple tests pointing to the same conclusion. Most provocative new findings do not rise to this standard right away. The traditional approach in comparative psychology, taking a broad sample of species from honeybees to monkeys, largely supported Darwin, by providing evidence for common processes of memory and association formation across the animal kingdom [7,10]. Contemporary discussions are often based on increasingly rich and detailed comparisons between humans and other primates, particularly great apes [11]. However, some birds may share human cognitive abilities that the common ancestor of birds and mammals lacked, apparent cases of convergent evolution [12]. All these approaches are important for understanding the evolution and function of cognition, but the bottom line is that theories of human uniqueness are inevitably provisional. In any case, although writers tend to focus on their pet version of 'the small difference that made a big difference', most recognize that the multitudinous behavioural and cognitive differences between humans and other species cannot necessarily be boiled down to a single description or process.

Notwithstanding such caveats, it is important to consider what kind of account of human cognitive uniqueness we want. Which approach is most consistent with the position of comparative cognition at the intersection of other biological and behavioural sciences? Which is most likely to provide new insights into the nature, evolution and function of species differences in cognition? Which best accommodates the fact that the glass is both half empty and half full, that is, that we are both like and unlike other species cognitively, as in other ways.

## 2. DOMAIN-GENERAL THEORIES

Any complete account of human cognitive uniqueness—or indeed of cognitive differences among any species—must include at least two basic levels of explanation, what Penn *et al.* [2] term the functional and the representational levels. The functional level is the characterization of what humans can do that other species cannot. An example is Premack's [13] claim that accomplishments such as teaching, planning and transitive inference in animals differ from their human counterparts in being domain-specific, whereas human intelligence represents an interweaving [14] of abilities that in animals are restricted to a single goal or behaviour system, if they are shown at all. For example, meerkats teach their young only food-handling skills, and that by mechanisms quite different from those such as theory of mind involved in human teaching [15]. And so far, the most convincing evidence of planning in another species [16] is restricted to food-caching.

But a functional characterization of human cognitive uniqueness requires explanation in terms of an underlying process, what Penn *et al.* [2] term the representational level. It might be better termed the level of cognitive mechanism or algorithm because the unique cognitive process(es) postulated to explain

human cognitive performance need not be essentially representational. Ultimately, of course, a complete theory does not end here. Mechanisms can at the same time be genetic and/or neural, and the most comprehensive discussions include speculation about how and why special human cognitive abilities may have evolved. This article evaluates functional- and representational-level theories, keeping in mind their consistency with other aspects of comparative biology.

One of the most ambitious in depth and scope is Penn *et al.*'s [2] analysis of recent comparative research on both social and physical cognition, which concludes that humans are uniquely capable of reasoning about higher-order relationships. Animals learn about events, categorize and act almost entirely in terms of first-order or perceptual relationships, whereas we commonly conceptualize the world and reason in terms of abstractions from first-order relationships. This characterization captures and extends to other domains what Povinelli and co-workers, e.g. [17], have long discussed as the absence of evidence in animals for an understanding of the world in terms of unseen physical or social forces such as gravity or belief. Following Karmiloff-Smith [18], Penn *et al.* [2] termed the process underlying it as *relational reinterpretation*. Like domain-specific theories, the relational reinterpretation theory recognizes that we share many basic processes with other animals. Relational reinterpretation is in effect a human-specific 'supermodule' [2], a higher-level process shared across domains.

Not all approaches to human cognitive uniqueness are so clear on the distinction between the proposed generalization over the data to be explained and the psychological process that explains it. Somewhere between descriptive generalization and process is Corballis's [19] proposal that human thought and action are recursive to a degree that other species' are not. For Corballis [19], the key characteristics of human cognitive uniqueness are mental time travel, theory of mind and—of course—language. Each of these implicitly or explicitly involves recursion, the embedding of one entity within another of the same kind, and each has—so far—proved beyond the grasp of any other animal. For instance, in planning (mental time travel into the future) memories of the past are embedded in thoughts about the future. Theory of mind can involve high levels of recursion, as in 'I suspect that you know that he wants me to believe him'. According to Corballis, although language is used to express such thoughts, their recursive nature is independent of language and likely preceded its evolution. Like 'interweaving' [14], recursion can be taken as an all-embracing characterization of uniquely human cognitive accomplishments or a process-level explanation of them. Also as with 'interweaving', it is unclear how recursion can account for all the uniquely human aspects of thought identified by Penn *et al.* [2].

Contrasting with these theories are proposals that a 'difference in degree' in a well-studied cognitive process makes human cognition 'different in kind' from that of other primates, just as an extreme difference in leg length makes snakes 'different in kind' from other reptiles. Corballis [19] acknowledges that some animals may have some small degree of recursive ability, and Penn *et al.* [2] recognize that animals use some

syntactically structured first-order representations. However, the proposal that humans simply have superior working memory is the account of human uniqueness most obviously based on a quantitative difference in an ability already well studied in both humans and animals. This proposal comes in part from students of human cultural evolution as an account of the appearance of tools and artefacts that seem to demand the ability to hold more things in mind than any animal can: a stone and a woman's body and the plan to use a tool to craft the one into a representation of the other [20].

Although it may seem plausible that increased working memory capacity played a role in human cultural evolution, relevant comparative data from present-day species are ambiguous, illustrating the methodological challenges confronting claims of 'differences in degree'. For instance, chimpanzees' visual short-term memory capacity at one time appeared to exceed that of university students, but students can do as well as the apes when they have as much training [21]. A related claim, linked to findings in cognitive neuroscience, is that humans surpass all other species in executive control. This is supported by comparative studies of primates in discrimination reversal learning [22] and 'patience' or ability to wait for a large delayed reward [23]. It is not clear, however, how either superior working memory or executive control alone could account for the full range of proposed (e.g. by [2]) discontinuities in performance between humans and other animals. And the foregoing survey hardly exhausts the domain-general functional or process-level accounts of human cognitive uniqueness. For instance, a classic explanation for human cognitive uniqueness is that humans are the only species with (human) language, which might be said to underpin every level of recursive thought, relational reinterpretation and interweaving of domain-specific knowledge.

All the proposals just surveyed focus on cognitive differences between adult humans and adults of other species. However, any species comparison that neglects differences among young animals and developmental trajectories is both incomplete and inconsistent with contemporary evolutionary-developmental biology. It is also inconsistent with increasing recognition in comparative cognitive psychology that species comparisons in cognition, as with any other character right down to genes, can be expected to reveal both elements that are shared and elements that are unique in each one. Cognitive development and shared characters are highlighted in a growing number of domain-specific theories that address in a unified way performance of human adults, infants and young children as well as commonalities between young children and animals. We turn to these before concluding with proposals that unique domain-general processes in cognitive development underlie the unique cognitive capacities of human adults. But first a digression on cognitive modularity.

### 3. MODULARITY IN COGNITION AND DEVELOPMENT

*Modularity* is the property of being made up of somewhat self-contained and independently functioning

parts. In any complex system—including biological systems from genomes to bodies—a hierarchical modular structure allows a part to break down or be modified without the whole ceasing to function [24]. Evolvability may be possible only in modular systems, in which parts of the organism can change while other, well-adapted, parts remain relatively unchanged. Modularity is therefore a key principle of evolutionary developmental biology ('evo devo'), which has produced vast amounts of evidence for it [25,26]. For instance, conspicuous differences in beak size and shape among Darwin's finches reflect activity of a common gene involved in avian beak growth [27]. Similarly in comparative cognition, species that encounter extraordinary demands for spatial memory in retrieving stored food or defending large territories may evolve exceptional spatial memories and hippocampi, while remaining otherwise cognitively and behaviourally similar to their close relatives [28].

But although modularity is an accepted principle in biology, it is deeply controversial in the cognitive sciences, where it retains the connotations given it by Fodor [29] over a quarter century ago. Fodorian modules are domain-specific, peripheral, perceptual (as opposed to central decision-making) mechanisms, innate, fast-acting (like a reflex), unconscious, obligatory (i.e. acting regardless of circumstances) and *encapsulated* (i.e. impervious to information outside their particular domain, as olfaction is impervious to auditory information). They are also generally assumed to be neurally specific, i.e. localizable within the brain. Even Fodor himself did not always require cognitive modules to have all these properties [30]. Barrett & Kurzban [31] have convincingly argued that the key property of cognitive modularity is functional specificity: distinct domains of information require distinct processes to operate on them, rules of operation in Sherry & Schacter's [32] terms. Whether such functional modules have other Fodorian properties is an empirical question (see also [30]).

As a field that straddles the cognitive sciences and evolutionary biology, comparative cognition can lead the way towards an integration of biological conceptions of modularity into cognitive psychology like that proposed by Ploeger & Galis [26] in their discussion of the relevance of key ideas in evo devo for cognitive science. And indeed there is no better evidence for functional modularity in cognition than that from non-human animals [33]. Distinct operations on computationally distinct kinds of inputs are demanded by spatial, temporal and numerical cognition, recognition of animacy or social relationships and so on. Even associative learning is not a general process of information acquisition but a specialization for tracking contingencies, or temporally predictive relationships, among events [34]. But the output of different modules must ultimately be integrated in some way to determine action [35]. Outputs are integrated in memory too, as in episodic-like memory for the what, where and when of events [36]. A strictly modular view seems to preclude processes like associative learning, attention or working memory that cut across domains, although it does not preclude separate modules having some properties in common. It also seems to have no place for general intelligence, for

which there is increasing evidence in non-human species ([37,38], but see [39]). Again, in developmental biology, integration of modular processes is unproblematical, and the sometimes dynamic balance between modularity and integration is of interest in itself [25,26].

The way in which issues surrounding modularity play out in comparative cognition is well illustrated by analysis of the 'geometric module' for spatial orientation. The paradigmatic Fodorian modular process is a visual illusion, encapsulated because even knowing one is seeing an illusion does not prevent it. This property inspired Cheng [40] to attribute disoriented rats' reliance on the shape of an enclosure and disregard of more informative coloured walls and objects marking a goal to a geometric module. Young children and individuals of other species show the same domination by geometry, but all overcome it with experience [41]. For humans, language plays a role here [42]. These findings suggest to some [43] that rather than being modular, processing of geometry is 'adaptively combined' with other spatial information. But if the essence of modularity is specificity of processing rules to content (i.e. information domain), some degree of modularity is not incompatible with the use of multiple information sources.

In any case, effective navigation depends on more dissociable, informationally distinct, mechanisms than those involved in processing the geometry of enclosures and local cues within them [34]. The general learning mechanisms discussed by Heyes [7] ensure that a beacon at the location of a goal becomes associated with that goal and acquires value in itself. The valued beacon is now approached from wherever it can be detected, but the representation of the beacon has no inherently spatial content, unlike that of landmark, i.e. objects displaced from goals but in reliable spatial relationships to them. The goals are then localized via remembered and presently perceived direction and distance information, in implicit vector addition. In the classic 'water maze' test for rodents [44], the difference between these two computationally distinct kinds of learned representation is captured by testing with the dry platform visible (beacon learning) versus invisible (landmark, or inherently spatial, learning). The hippocampus is more important for the latter, an example of neural as well as formal modularity.

An additional basic spatial memory process in vertebrates and invertebrates alike is path integration (or dead reckoning), the ability to keep track of one's direction and distance from a starting point despite twists and turns along the way. Even in a novel environment devoid of landmarks, this short-term memory process analogous to vector addition permits an immediate straight return to the start (usually a nest or burrow) after a single outward journey. Path integration interacts with other spatial learning systems in interesting ways [34]. For example, only if path integration is disrupted by repeatedly rotating the subject (producing 'disorientation') is reliance on geometry revealed. Thus although space might be considered an information domain, *domain* is evidently a fractal concept, including at least path integration and separate (computationally and experimentally dissociable) mechanisms for localizing oneself and/or goals relative to geometry, beacons and

landmarks. Neurobiological analysis reveals yet other processes [45]. Understanding how these interact during learning and performance, at both behavioural and neural levels, is an ongoing project [34,42,45].

Research on the geometric module makes another important point. Although comparative research since Darwin has been testing for human abilities in animals, research going the other way—testing human children and adults for commonalities with other animals—has an equally important contribution to make to theories of human cognitive uniqueness (see also [42]). Exclusive control by the geometry of an enclosure despite the availability of more informative cues seems irrational, something people would never show, but in fact under the right conditions not only human toddlers but also adults behave exactly like rats [42]. In another example, discussed further below, approximate numerosity discrimination is a shared modular process with the same signature properties in human adults, monkeys and rats [34,46], but procedures that preclude verbal counting are necessary for uncovering it. Similarly in the study of tool use, a skill long thought uniquely human (though not by Darwin, see [1, p. 51], new observations of tool use by wild primates and birds have inspired laboratory tests of the human-like physical understanding assumed to underlie it. Again animals appear to act irrationally, here defying the predictions of folk psychology by failing to avoid traps when using a tool to obtain a reward [47]. But the everyday intuitions of folk psychology are not an infallible predictor of human tool-related behaviour either. For example, human adults choose a tool that merely contacts a reward rather than connecting with it [48], and without specific experiences, children below the ages of 7 or 8 are poor at innovating simple hook tools [49]. Such findings highlight the need to test folk psychological assumptions by giving comparable tests to humans and animals before drawing conclusions about 'differences in kind'.

#### 4. DOMAIN-SPECIFIC THEORIES

##### (a) *Dual processes and their interactions*

Whether or not they subscribe to a modular view of cognitive architecture, most researchers focus on just one or another of Darwin's [1] 'mental powers': memory, language, tool use, imitation and so on. Recent years have seen the development of a number of domain-specific theories encompassing performance not only of human adults but also of young children and other animals. Those sketched here have a common theme: very young children perform much like other species, whereas adults show in addition some uniquely human process(es) or capabilities. Several are embraced by the 'core cognition' approach to cognitive development [42,50–52] discussed in §5a.

If young children respond in ways shared with other animals and only gradually develop uniquely human forms of cognition, what happens to the simple shared processes? We have already seen suggestions that rather than disappearing or being transformed into something uniquely human, they remain intact, to be revealed in appropriate conditions. The situation for adults is thus as depicted in 'dual process' accounts

of reasoning [53] or memory [54], with two coexisting processes: a basic, quick, unconscious or implicit process which is evolutionarily ancient, present relatively early in life, and shared with other species, and a later-developing, slower, more explicit, uniquely human process. These processes may compete with or complement each other. For example, the 'heuristics and biases' approach to decision-making [55] suggests that mechanisms supporting optimal behaviour for ancestral environments underlie apparently irrational choices in contemporary environments. In common with many other species, humans appear to devalue delayed rewards and to be unduly influenced by relative rather than absolute values of outcomes [56]. Such biases can override any ability to compute the outcome with objectively greater value.

In other cases, as with the geometric module, only when adults are prevented from using the appropriate uniquely human mechanism is the developmentally prior, species-general, one revealed. An example involves the non-verbal transitive inference problems in which animals learn to choose the 'better' in each of a linked set of four or more pairs of items. Human subjects who are required to learn pairs of non-sense items (Japanese characters) while unaware that the items form an ordered set perform like other animals in tests with novel pairs ([57], see also [58]). Implicit transitive inference, the product of associative learning, is evidently available when explicit reasoning is not.

#### (b) *Tool use*

Many animals are now known to use tools [49,59], but their behaviour generally reflects little or no understanding of physical principles [60]. Most evidence for this conclusion comes from laboratory studies in which primates and tool-using birds are tested for their ability to transfer successful tool use to conceptually related but perceptually altered tasks. For example, rooks and chimpanzees learned which end of a stick tool to pull or push to avoid losing a reward down a 'trap' in each of two differently designed transparent tubes. When features of the two training tubes were combined so that only understanding how the traps worked would lead to success, the majority of animals chose randomly [59]. Such findings support a recent theoretical account of human tool use, according to which it involves two processes: technical reasoning (or physical causal understanding) and instrumentally learned skills built on perception of the affordances of objects together with trial and error learning [61]. As other reviewers [59,60] also conclude, the latter is shared with other animals, whereas the former is unique to humans. By analogy to the proposal about theory of mind to be discussed next [62], it may be that when people use familiar tools in familiar ways, only the latter, species-general, process is engaged, whereas reasoning about how a tool works is used mainly to explain or predict.

#### (c) *Social cognition and theory of mind*

Many aspects of social cognition also reflect one or more developmentally early, cognitively simple, phylogenetically ancient cognitive systems coexisting with a

later-developing, more demanding, uniquely human system [63]. Stimulated by Premack & Woodruff's [64] provocative article 'Does the chimpanzee have a theory of mind?', research in this area originally focused on theory of mind in chimpanzees, but it now embraces many other species and aspects of social cognition [34]. Theory of mind is the understanding that other creatures have minds: perceptions, beliefs, desires and the like. In humans, it contributes to many social interactions—communicating, cooperating, teaching and so on. With animals, most relevant research has focused on interactions over food, either cooperative (e.g. seeking information from a knowledgeable human) or competitive (e.g. hiding food from a rival).

Many animals behave as if sensitive to others' knowledge in some tests of this kind, but it is generally agreed [3,4,65] that none pass a test of the theoretically critical ability to understand that another individual holds a false belief, a test passed by children by the age of about four. Like younger children, animals pass simpler tests, but whether this is actually evidence for theory of mind is hotly debated [4]. For example, heading for food of which a competitor is ignorant requires only sensitivity to and memory for where the competitor was looking when food was hidden [5]. On one view [3], no evidence yet available compels the conclusion that animals do anything other than sophisticated 'behaviour reading'. They may generalize over behavioural cues to respond appropriately in novel situations, but they do not understand the causes of others' behaviour in mentalistic terms. Consistent with this view, on one current proposal about human theory of mind [62], adults have both the fast 'behaviour reading' system available to animals, and slowly developing, more explicit and cognitively demanding, 'mind reading'. The former is primarily responsible for online responses in most social interactions. Support for this theory includes evidence that in human adults concurrent cognitive demands interfere with explicit theory of mind judgements, whereas responses to simple behavioural cues to another's perspective are difficult to inhibit [62]. This dual process theory is supported by a functional argument: rapid, cognitively undemanding, responses to others' behaviour are essential to leave cognitive resources available for other aspects of ongoing cooperative or competitive tasks.

The situations just sketched do not capture all the cognitively interesting processes engaged by social interactions. A contemporary theme in human social psychology is the importance of quick unconscious processes such as automatic evaluation of others [66], but the extent to which these represent homologies with other species generally remains to be analysed. Comparisons with apes suggest that some, including responses to unfairness and other forms of prosocial behaviour, may be unique to humans, and their evolution may have been the key to the evolution of human culture [67].

#### (d) *Numerical cognition*

Comparative and developmental research on numerical cognition presents the same picture as that on theory of mind. Human infants and other animals have two basic systems of numerical cognition [46]. The small number or object tracking system precisely

encodes quantities up to three or four. All numerosities within this signature range are discriminated equally well. In contrast, the approximate large number system discriminates among sets of any numerosity as described by Weber's law: ratios matter, not absolute differences. Sometime during childhood, children in a numerate culture begin to learn about integers, arithmetical operations and eventually perhaps higher mathematics. Learning about integers, the counting numbers that precisely label any numerosity, suggests that the appreciation of number characteristic of the small number system is somehow extended to all numbers. (Authors who recognize only the approximate system give a different account, see [51].) But the developmentally and evolutionarily prior systems remain intact, as evidenced when numerate adults are given tests that preclude verbal counting [46]. And in tests of the two core systems, numerate controls perform identically to people whose language lacks words for precise quantities greater than three or four [68].

#### (e) *Space, language and other things*

The structure of adult human spatial cognition has much in common with that of numerical cognition. Basic phylogenetically widespread processes including path integration and responses to landmarks, beacons and the geometry of enclosing structures coexist with a uniquely human ability to use maps and spatial language [42,69]. In comparative work, this analysis replaces a traditional focus on the anthropomorphic question, 'Do animals have cognitive maps?' [70]. It is a good example of how the yes–no questions traditionally pervading research on animal cognition ('Do animals count?' 'Do animals talk?') are better answered by breaking the ability in question into elements and asking which are shared among which species and why. Hauser *et al.*'s [71] comparative approach to language is an excellent example. On their view, basic conceptual and communicative abilities contributing to language are shared with other species, but the ability to create and understand recursive structures is uniquely human.

Although such an approach is applicable to other comparative questions about cognition, it has not always been developed. Dependence of key data on verbal reports can create a virtually insurmountable barrier to deciding how much of a process is uniquely human. This is the case with the contention [72] that humans are uniquely able to 'mentally time travel' to their personal past and future. But here too a retreat from 'do they or don't they' questions may be useful [73] and, as with tool use [4,49], studying how young children perform in non-verbal tasks like those given animals may be illuminating [74]. The best default assumption in comparisons of humans with other species is almost certainly that we will find differences not solely in kind or in degree but combinations of uniquely human and shared elements. The framework suggested by dual process theorizing to be outlined in the next section promises a powerful account of findings from some cognitive domains, but it is not necessarily applicable to others, such as language.

### 5. DEVELOPMENT AND HUMAN UNIQUENESS: MODULARITY PLUS DOMAIN-GENERALITY

A fundamental observation in biology is that species differences are less pronounced among young animals than among adults. Any species comparison is therefore incomplete without comparison of developmental trajectories and an account of the species-specific mechanism(s) involved. Domain-specific theories sketched in the preceding section suggest that this is as true of cognition as of other characters. This section highlights two such accounts of human cognitive development: the core cognition approach [42,50,52,75] and the 'shared intentionality' theory of human versus ape social-cognitive motivation [76]. Each assumes a shared modular architecture for human and animal cognition while proposing a uniquely human domain-general developmental mechanism. Because one deals primarily with mechanisms for cognitive change and the other primarily with socio-cognitive motivations, they are largely complementary. Together, they provide the best current hypothesis for how we are both similar to and different from other animals cognitively.

#### (a) *Core knowledge and conceptual change*

A core knowledge system is a set of processes for acquiring and operating on domain-specific information in characteristic ways that is present very early in life (innate) [42,52], one of the cognitive processes that human infants share with animals. Core mathematics, for instance, includes the ability to recognize approximate numerosities and (implicitly) take their ratios. Although what counts as a core system varies [42,51,52,75], they generally include the precise small number and approximate large number systems, and processing spatial geometry and animacy (or agency). But if infants start out with the same core knowledge systems as other species, they must also have mechanisms for learning and conceptual change that make the development of specifically human understanding possible.

On the account developed by Carey [51,75], conceptual change during development results from 'Quinian bootstrapping', by analogy with scientific discovery. 'Bootstrapping' implies that a child 'pulls herself up by her own bootstraps', using concepts and core knowledge she already has to grasp a concept she does not yet have. For instance, Carey claims that appreciation of integers as quantities each of which is one more than the one before, on to infinity, requires a cognitive leap during which children realize (if only implicitly) that when any set has one more added to it, the numerosity is always the next number in the already-memorized list of counting words. Chimpanzees never grasp this: each new association of symbol with set size takes as long to learn as the one before [77]. In addition to human-specific cognitive developmental capacities indicated by findings like this one, language and culture make essential contributions: the discrepancy between what the child understands and what others around her express is what instigates 'bootstrapping'. However, even if a person eventually understands higher mathematics, the original core systems remain intact. Not all who agree about 'core systems' agree on

bootstrapping as a key developmental mechanism [51]. Bayesian statistical learning is another candidate [78] as is representational redescription as originally proposed by Karmiloff-Smith [18]. Basic domain-general mechanisms such as working memory, associative learning and language also play a role [42,52]. All operate in the context of human culture, likely to some extent via the uniquely human brand of social interactions proposed by the complementary domain-general developmental theory.

### (b) *Shared intentionality and ape–human differences*

According to Tomasello *et al.* [76], the psychological key to human uniqueness is motivational as much as cognitive, a capacity for *shared intentionality*. As shown by extensive experimental comparisons of young children and apes, only children participate with others in ‘cooperative communicative’ interactions, jointly attending to and acting on things. The motivation and ability to share intentions and goals is a uniquely human form of cooperation that ‘scaffolds up’ the acquisition of language, cognitive skills in the physical domain and other ingredients of culture. This proposal is supported by results of comparisons between 2.5-year-old children and apes in which children performed similarly to apes on spatial and numerical cognition and simple tool use, but outperformed the apes on social tasks [11]; (however, the appropriateness of these comparisons can be questioned, as in [8]). A separate social factor was needed in a factor analysis to account for the performance of children but not of chimpanzees [79]. There was no evidence for a general intelligence factor (*g*), underlining the implication that the ape–human difference is in one particular module or aspect of intelligence. However, shared intentionality plays a role in all cultural learning, making this proposal modular and domain-general at the same time. It is consistent not only with increasing data on differences between apes and young children on cognitive tasks, but also with the idea that unique forms of human cooperation evolved along with and made possible human society and culture.

## 6. THE FUTURE OF HUMAN UNIQUENESS

The view that human cognition includes basic modular and domain-general processes shared with other animals, as well as social and cognitive developmental mechanisms that make adult cognition unique, places comparative cognition squarely in the framework of evolutionary developmental biology. A model of this framework in action is a recent demonstration that two basic patterns of electromyograph (EMG) activity shown during reflexive stepping in human infants are the same as those shown during walking in adult rats, cats, monkeys and even quail [80]. In toddlers, these two modular primitives (the authors’ terms) are supplemented by two others, also shared with the other four species, whereas human adults show some unique patterns (for an example from cognitive neuroscience compare [81]). But the value of comparing developmental trajectories across species transcends

comparisons involving humans. An example is the suggestion that bonobos differ from chimpanzees in being neotenized, i.e. retaining more juvenile characteristics into adulthood [82].

This picture of human cognitive architecture is already suggesting new questions and new approaches for comparative research. For instance, as children develop uniquely human cognitive skills such as map-reading and full-blown theory of mind, the simple shared processes they started out with are not transformed into adult understanding but coexist with it, resulting in a situation like that depicted in dual process theories of reasoning [53], or theories of automatic versus effortful or conscious processing in memory [54] or social behaviour [63]. As we have seen, the interactions of these two kinds of processes seem to vary across domains, from supportive to competitive, raising the question of whether some general theory of such interactions is possible.

The ongoing integration of research on human adults and children with that on other animals at both behavioural and neural levels has other implications. For instance, in the past 20 years or so, a lot of attention has been given to experiments testing other animals in the same way as humans, in studies on memory, planning, imitation, understanding tools and so on [6]. The equally important enterprise of testing human adults and children in ways designed for other animals is beginning to get more attention [49,74,83,84]. As we approach the 150th anniversary of Darwin’s [1] pronouncement, researchers may be learning not to try so hard to prove he was right by looking for the human-like in animals and adopting a more even-handed approach, giving equal importance to what species share with one another and what is unique to each one.

This article develops ideas in [85], ch. 5. Thanks to Derek Penn, Kristin Andrews and an anonymous reviewer for comments on the manuscript.

## REFERENCES

- 1 Darwin, C. 1871 *The descent of man and selection in relation to sex*. London, UK: John Murray.
- 2 Penn, D. C., Holyoak, K. J. & Povinelli, D. J. 2008 Darwin’s mistake: explaining the discontinuity between human and nonhuman minds. *Behav. Brain. Sci.* **31**, 109–178. (doi:10.1017/S0140525X08003543)
- 3 Penn, D. C. & Povinelli, D. J. 2007 On the lack of evidence that non-human animals possess anything remotely resembling a ‘theory of mind’. *Phil. Trans. R. Soc. B* **362**, 731–744. (doi:10.1098/rstb.2006.2023)
- 4 Seed, A. M., Seddon, E., Greene, B. & Call, J. 2012 Chimpanzee ‘folk physics’: bringing failures into focus. *Phil. Trans. R. Soc. B* **367**, 2743–2752. (doi:10.1098/rstb.2012.0222)
- 5 van der Vaart, E., Verbrugge, R. & Hemelrijk, C. 2012 Corvid re-caching without ‘theory of mind’. *PLoS ONE* **7**, e32904. (doi:10.1371/journal.pone.0032904)
- 6 Shettleworth, S. J. 2010 Clever animals and killjoy explanations in comparative psychology. *Trends Cogn. Sci.* **14**, 477–481. (doi:10.1016/j.tics.2010.07.002)
- 7 Heyes, C. 2012 Simple minds: a qualified defence of associative learning. *Phil. Trans. R. Soc. B* **367**, 2695–2703. (doi:10.1098/rstb.2012.0217)

- 8 Boesch, C. 2007 What makes us human (*Homo sapiens*)? The challenge of cognitive cross-species comparison. *J. Comp. Psychol.* **121**, 227–240. (doi:10.1037/0735-7036.121.3.227)
- 9 Macphail, E. M. 1987 The comparative psychology of intelligence. *Behav. Brain Sci.* **10**, 645–695. (doi:10.1017/S0140525X00054984)
- 10 Papini, M. R. 2008 *Comparative psychology*, 2nd edn. New York, NY: Psychology Press.
- 11 Herrmann, E., Call, J., Hernández-Lloreda, M. V., Hare, B. & Tomasello, M. 2007 Humans have evolved specialized skills of social cognition: the cultural intelligence hypothesis. *Science* **317**, 1360–1366. (doi:10.1126/science.1146282)
- 12 Emery, N. J. & Clayton, N. S. 2004 The mentality of crows: convergent evolution of intelligence in corvids and apes. *Science* **306**, 1903–1907. (doi:10.1126/science.1098410)
- 13 Premack, D. 2007 Human and animal cognition: continuity and discontinuity. *Proc. Natl Acad. Sci. USA* **104**, 13 861–13 867. (doi:10.1073/pnas.0706147104)
- 14 Premack, D. 2010 Why humans are unique: three theories. *Perspect. Psychol. Sci.* **5**, 22–32. (doi:10.1177/1745691609356782)
- 15 Thornton, A. & Raihani, N. J. 2008 The evolution of teaching. *Anim. Behav.* **75**, 1823–1826. (doi:10.1016/j.anbehav.2007.12.014)
- 16 Cheke, L. G. & Clayton, N. S. 2011 Eurasian jays (*Garrulus glaudarius*) overcome their current desires to anticipate future needs and plan for them appropriately. *Biol. Lett.* **8**, 171–175. (doi:10.1098/rsbl.2011.0909)
- 17 Vonk, J. & Povinelli, D. J. 2006 Similarity and difference in the conceptual systems of primates: the unobservability hypothesis. In *Comparative cognition* (eds E. A. Wasserman & T. R. Zentall), pp. 363–387. New York, NY: Oxford University Press.
- 18 Karmiloff-Smith, A. 1992 *Beyond modularity: a developmental perspective on cognitive science*. Cambridge, MA: MIT Press.
- 19 Corballis, M. C. 2011 *The recursive mind*. Princeton, NJ: Princeton University Press.
- 20 Read, D. W. 2008 Working memory: a cognitive limit to non-human primate recursive thinking prior to hominid evolution. *Evol. Psychol.* **6**, 676–714.
- 21 Cook, P. & Wilson, M. 2010 Do young chimpanzees have extraordinary working memory? *Psychon. Bull. Rev.* **17**, 599–600. (doi:10.3758/PBR.17.4.599)
- 22 Rumbaugh, D. M., Savage-Rumbaugh, E. S. & Washburn, D. A. 1996 Toward a new outlook on primate learning and behavior: complex learning and emergent processes in comparative perspective. *Jpn. Psychol. Res.* **38**, 113–125. (doi:10.1111/j.1468-5884.1996.tb00016.x)
- 23 MacLean, E. L. *et al.* 2012 How does cognition evolve?: phylogenetic comparative psychology. *Anim. Cogn.* **15**, 223–238. (doi:10.1007/s10071-011-0448-8)
- 24 Simon, H. A. 1962 The architecture of complexity. *Proc. Am. Philos. Soc.* **106**, 467–482.
- 25 West-Eberhard, M. J. 2003 *Developmental plasticity and evolution*. New York, NY: Oxford University Press.
- 26 Ploeger, A. & Galis, F. 2011 Evo devo and cognitive science. *WIREs Cognitive Science* **2**, 429–440. (doi:10.1002/wcs.137)
- 27 Grant, P. R. & Grant, B. R. 2008 *How and why species multiply*. Princeton, NJ: Princeton University Press.
- 28 Sherry, D. F. 2006 Neuroecology. *Annu. Rev. Psychol.* **57**, 167–197. (doi:10.1146/annurev.psych.56.091103.070324)
- 29 Fodor, J. A. 1983 *The modularity of mind*. Cambridge, MA: MIT Press.
- 30 Coltheart, M. 1999 Modularity and cognition. *Trends Cogn. Sci.* **3**, 115–120. (doi:10.1016/S1364-6613(99)01289-9)
- 31 Barrett, H. C. & Kurzban, R. 2006 Modularity in cognition: framing the debate. *Psychol. Rev.* **113**, 628–647. (doi:10.1037/0033-295X.113.3.628)
- 32 Sherry, D. F. & Schacter, D. L. 1987 The evolution of multiple memory systems. *Psychol. Rev.* **94**, 439–454. (doi:10.1037/0033-295X.94.4.439)
- 33 Carruthers, P. 2006 *The architecture of the mind: massive modularity and the flexibility of thought*. Oxford, UK: Oxford University Press.
- 34 Shettleworth, S. J. 2010 *Cognition, evolution, and behavior*, 2nd edn. New York, NY: Oxford University Press.
- 35 Shanahan, M. 2012 The brain's connective core and its role in animal cognition. *Phil. Trans. R. Soc. B* **367**, 2704–2714. (doi:10.1098/rstb.2012.0128)
- 36 Clayton, N. S., Griffiths, D. P., Emery, N. J. & Dickinson, A. 2001 Elements of episodic-like memory in animals. *Phil. Trans. R. Soc. Lond B* **356**, 1483–1491. (doi:10.1098/rstb.2001.0947)
- 37 Matzel, L. D. & Kolata, S. 2010 Selective attention, working memory, and animal intelligence. *Neurosci. Biobehav. Rev.* **34**, 23–30. (doi:10.1016/j.neubiorev.2009.07.002)
- 38 Reader, S. M., Hager, Y. & Laland, K. N. 2011 The evolution of primate general and cultural intelligence. *Phil. Trans. R. Soc. B* **366**, 1017–1027. (doi:10.1098/rstb.2010.0342)
- 39 Herrmann, E. & Call, J. 2012 Are there geniuses among the apes? *Phil. Trans. R. Soc. B* **367**, 2753–2761. (doi:10.1098/rstb.2012.0191)
- 40 Cheng, K. 1986 A purely geometric module in the rat's spatial representation. *Cognition* **23**, 149–178. (doi:10.1016/0010-0277(86)90041-7)
- 41 Cheng, K. & Newcombe, N. S. 2005 Is there a geometric module for spatial orientation? Squaring theory and evidence. *Psychon. Bull. Rev.* **12**, 1–23. (doi:10.3758/BF03196346)
- 42 Spelke, E. S. & Lee, S. A. 2012 Core systems of geometry in animal minds. *Phil. Trans. R. Soc. B* **367**, 2784–2793. (doi:10.1098/rstb.2012.0210)
- 43 Twyman, A. D. & Newcombe, N. S. 2010 Five reasons to doubt the existence of a geometric module. *Cogn. Sci.* **34**, 1315–1356. (doi:10.1111/j.1551-6709.2009.01081.x)
- 44 Morris, R. G. M. 1981 Spatial localization does not require the presence of local cues. *Learn. Motiv.* **12**, 239–260. (doi:10.1016/0023-9690(81)90020-5)
- 45 Jeffery, K. J. 2010 Theoretical accounts of spatial learning: a neurobiological view (commentary on Pearce, 2009). *Q. J. Exp. Psychol.* **63**, 1683–1699. (doi:10.1080/17470210903540771)
- 46 Feigenson, L., Dehaene, S. & Spelke, E. 2004 Core systems of number. *Trends Cogn. Sci.* **8**, 307–314. (doi:10.1016/j.tics.2004.05.002)
- 47 Povinelli, D. J. 2000 *Folk physics for apes*. New York, NY: Oxford University Press.
- 48 Silva, F. J., Silva, K. M., Cover, K. M., Leslie, A. L. & Rubalcaba, M. A. 2008 Humans' folk physics is sensitive to physical connection and contact between a tool and reward. *Behav. Processes* **77**, 327–333. (doi:10.1016/j.beproc.2007.08.001)
- 49 Beck, S. R., Apperly, I. A., Chappell, J., Guthrie, C. & Cutting, N. 2011 Making tools isn't child's play. *Cognition* **119**, 301–306. (doi:10.1016/j.cognition.2011.01.003)
- 50 Spelke, E. S. & Kinzler, K. D. 2007 Core knowledge. *Dev. Sci.* **10**, 89–96. (doi:10.1111/j.1467-7687.2007.00569.x)
- 51 Carey, S. 2011 Precipice of the origin of concepts. *Behav. Brain Sci.* **34**, 113–167. (doi:10.1017/S0140525X10000919)
- 52 Gelman, R. 2009 Learning in core and noncore domains. In *Cognitive biology*. (eds L. Tommasi, M. A. Peterson & L. Nadel), pp. 247–260. Cambridge, MA: MIT Press.



- 53 Evans, J. S. B. T. 2003 In two minds: dual-process accounts of reasoning. *Trends Cogn. Sci.* **7**, 454–459. (doi:10.1016/j.tics.2003.08.012)
- 54 Hasher, L. & Zacks, R. T. 1984 Automatic processing of fundamental information. *Am. Psychol.* **39**, 1372–1388. (doi:10.1037/0003-066X.39.12.1372)
- 55 Todd, P. M. & Gigerenzer, G. 2007 Mechanisms of ecological rationality: heuristics and environments that make us smart. In *The Oxford handbook of evolutionary psychology* (eds R. I. M. Dunbar & L. Barrett), pp. 197–210. Oxford, UK: Oxford University Press.
- 56 Santos, L. R. & Hughes, K. D. 2009 Economic cognition in animals and humans: the search for core mechanisms. *Curr. Opin. Neurobiol.* **19**, 63–66. (doi:10.1016/j.conb.2009.05.005)
- 57 Frank, M. J., Rudy, J. W., Levy, W. B. & O'Reilly, R. C. 2005 When logic fails: implicit transitive inference in humans. *Mem. Cognit.* **33**, 742–750. (doi:10.3758/BF03195340)
- 58 Lazareva, O. F. & Wasserman, E. A. 2010 Nonverbal transitive inference: effects of task and awareness on human performance. *Behav. Processes* **83**, 99–112. (doi:10.1016/j.beproc.2009.11.002)
- 59 Seed, A. & Byrne, R. 2010 Animal tool-use. *Curr. Biol.* **20**, R1032–R1039. (doi:10.1016/j.cub.2010.09.042)
- 60 Penn, D. C. & Povinelli, D. J. 2007 Causal cognition in human and nonhuman animals: a comparative, critical review. *Annu. Rev. Psychol.* **58**, 97–118. (doi:10.1146/annurev.psych.58.110405.085555)
- 61 Osiurak, F., Jarry, C. & LeGall, D. 2010 Grasping the affordances, understanding the reasoning: toward a dialectical theory of human tool use. *Psychol. Rev.* **117**, 517–540. (doi:10.1037/a0019004)
- 62 Apperly, I. A. & Butterfill, S. A. 2009 Do humans have two systems to track beliefs and belief-like states? *Psychol. Rev.* **116**, 953–970. (doi:10.1037/a0016923)
- 63 Adolphs, R. 2009 The social brain: neural basis of social knowledge. *Annu. Rev. Psychol.* **60**, 693–716. (doi:10.1146/annurev.psych.60.110707.163514)
- 64 Premack, D. & Woodruff, G. 1978 Does the chimpanzee have a theory of mind? *Behav. Brain Sci.* **4**, 515–526. (doi:10.1017/S0140525X00076512)
- 65 Call, J. & Tomasello, M. 2008 Does the chimpanzee have a theory of mind? 30 years later. *Trends Cogn. Sci.* **12**, 187–192. (doi:10.1016/j.tics.2008.02.010)
- 66 Baumeister, R. F. & Masicampo, E. J. 2010 Conscious thought is for facilitating social and cultural interactions: how mental simulations serve the animal-culture interface. *Psychol. Rev.* **117**, 945–971. (doi:10.1037/a0019393)
- 67 Silk, J. B. & House, B. R. 2012 The phylogeny and ontogeny of prosocial behavior. In *Oxford handbook of comparative evolutionary psychology* (eds J. Vonk & T. Shackelford), pp. 381–398. New York, NY: Oxford University Press.
- 68 Pica, P., Lemer, C., Izard, V. & Dehaene, S. 2004 Exact and approximate arithmetic in an Amazonian indigene group. *Science* **306**, 499–503. (doi:10.1126/science.1102085)
- 69 Landau, B. & Lakusta, L. 2009 Spatial representation across species: geometry, language, and maps. *Curr. Opin. Neurobiol.* **19**, 12–19. (doi:10.1016/j.conb.2009.02.001)
- 70 Wang, R. F. & Spelke, E. S. 2002 Human spatial representation: insights from animals. *Trends Cogn. Sci.* **6**, 376–382. (doi:10.1016/S1364-6613(02)01961-7)
- 71 Hauser, M. D., Chomsky, N. & Fitch, W. T. 2002 The faculty of language: what is it, who has it, and how did it evolve? *Science* **298**, 1569–1579. (doi:10.1126/science.298.5598.1569)
- 72 Suddendorf, T. & Corballis, M. C. 1997 Mental time travel and the evolution of the human mind. *Genet. Soc. Gen. Psychol. Monogr.* **123**, 133–167.
- 73 Raby, C. R. & Clayton, N. S. 2009 Prospective cognition in animals. *Behav. Processes* **80**, 314–324. (doi:10.1016/j.beproc.2008.12.005)
- 74 Russell, J., Alexis, D. & Clayton, N. 2010 Episodic future thinking in 3- to 5-year-old children: the ability to think what will be needed from a different point of view. *Cognition* **114**, 56–71. (doi:10.1016/j.cognition.2009.08.013)
- 75 Carey, S. 2009 *The origin of concepts*. New York, NY: Oxford University Press.
- 76 Tomasello, M., Carpenter, M., Call, J., Behne, T. & Moll, H. 2005 Understanding and sharing intentions: the origins of cultural cognition. *Behav. Brain Sci.* **28**, 675–735. (doi:10.1017/S0140525X05000129)
- 77 Matsuzawa, T. 2009 Symbolic representation of number in chimpanzees. *Curr. Opin. Neurobiol.* **19**, 92–98. (doi:10.1016/j.conb.2009.04.007)
- 78 Spelke, E. S. & Kinzler, K. D. 2009 Innateness, learning, and rationality. *Child Dev. Perspect.* **3**, 96–98. (doi:10.1111/j.1750-8606.2009.00085.x)
- 79 Herrmann, E., Hernandez-Lloreda, M. V., Call, J., Hare, B. & Tomasello, M. 2010 The structure of individual differences in the cognitive abilities of children and chimpanzees. *Psychol. Sci.* **21**, 102–110. (doi:10.1177/0956797609356511)
- 80 Dominici, N. *et al.* 2011 Locomotor primitives in newborn babies and their development. *Science* **334**, 997–999. (doi:10.1126/science.1210617)
- 81 Hyde, D. C. & Spelke, E. S. 2011 Neural signatures of number processing in human infants: evidence for two core systems underlying numerical cognition. *Dev. Sci.* **14**, 360–371.
- 82 Wobber, V., Wrangham, R. & Hare, B. 2010 Application of the heterochrony framework to the study of behavior. *Communicative Integr. Biol.* **3**, 337–339. (doi:10.4161/cib.3.4.11762)
- 83 Brosnan, S. F., Parrish, A., Beran, M. J., Flemming, T., Heimbauer, L., Talbot, C. F., Lambeth, S. P., Schapiro, S. J. & Wilson, B. J. 2011 Responses to the assurance game in monkeys, apes, and humans using equivalent procedures. *Proc. Natl Acad. Sci. USA* **108**, 3442–3447. (doi:10.1073/pnas.1016269108)
- 84 Silva, F. J. & Silva, K. M. 2008 How do adult humans compare with New Caledonian crows in tool selectivity? *Learn. Behav.* **38**, 87–95. (doi:10.3758/LB.38.1.87)
- 85 Shettleworth, S. J. 2012 *Fundamentals of comparative cognition*. New York, NY: Oxford University Press.