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Darwin's mistake: Explaining the discontinuity between human and nonhuman minds

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Abstract: Over the last quarter century, the dominant tendency in comparative cognitive psychology has been to emphasize the similarities between human and nonhuman minds and to downplay the differences as "one of degree and not of kind" (Darwin 1871). In the present target article, we argue that Darwin was mistaken: the profound biological continuity between human and nonhuman animals masks an equally profound discontinuity between human and nonhuman minds. To wit, there is a significant discontinuity in the degree to which human and nonhuman animals are able to approximate the higher-order, systematic, relational capabilities of a physical symbol system (PSS) (Newell 1980). We show that this symbolic-relational discontinuity pervades nearly every domain of cognition and runs much deeper than even the spectacular scaffolding provided by language or culture alone can explain. We propose a representational-level specification as to where human and nonhuman animals' abilities to approximate a PSS are similar and where they differ. We conclude by suggesting that recent symbolic-connectionist models of cognition shed new light on the mechanisms that underlie the gap between human and nonhuman minds.

Keywords: analogy; animal cognition; causal learning; connectionism; Darwin; discontinuity; evolution; human mind; language; language of thought; physical symbol system; reasoning; same-different; theory of mind

1. Introduction

Human animals – and no other – build fires and wheels, diagnose each other's illnesses, communicate using symbols, navigate with maps, risk their lives for ideals, collaborate with each other, explain the world in terms of hypothetical causes, punish strangers for breaking rules, imagine impossible scenarios, and teach each other how to do all of the above. At first blush, it might appear obvious that human minds are qualitatively different from those of every other animal on the planet. Ever since Darwin, however, the dominant tendency in comparative cognitive psychology has been to emphasize the continuity between human and nonhuman minds and to downplay the differences as "one of degree and not of kind" (Darwin 1871). Particularly in the last quarter century, many prominent comparative researchers have claimed that the traditional hallmarks of human cognition – for example, complex tool use, grammatically structured language, causal-logical reasoning, mental state attribution, metacognition, analogical inferences, mental time travel, culture, and so on – are not nearly as unique as we once thought (see, e.g., Bekoff et al. 2002; Call 2006; Clayton et al. 2003; de Waal & Tyack 2003; Matsuzawa 2001; Pepperberg 2002; Rendell & Whitehead 2001; Savage-Rumbaugh et al. 1998; Smith et al. 2003; Tomasello et al. 2003a). Pepperberg (2005, p. 469) aptly sums up the comparative consensus as follows: "for over 35 years, researchers have been demonstrating through tests both in the field and in the laboratory that the capacities of nonhuman animals to solve complex problems form a continuum with those of humans."

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Of course, many scholars continue to claim that there is something qualitatively different about at least some human faculties, particularly those associated with language and a representational theory of mind (see, e.g., Bermudez 2003; Carruthers 2002; Donald 2001; Mithen 1996; Premack 2007; Suddendorf & Corballis 2007a). Nearly everyone agrees that there is something uniquely human about our ability to represent and reason about our own and others' mental states (e.g., Tomasello et al. 2005). And most linguists and psycho-linguists argue that there is a fundamental discontinuity between human and nonhuman forms of communication (e.g., Chomsky 1980; Jackendoff 2002; Pinker 1994). But the trend among comparative researchers is to construe the uniquely human aspect of these faculties in increasingly narrow terms. Hauser et al. (2002a), for example, continue to claim that grammatically structured languages are unique to the human species, but suggest that the only component of the human language faculty that is, in fact, uniquely human is the computational mechanism of recursion. The rest of our "conceptual-intentional" system, they argue, differs from that of nonhuman animals only in "quantity rather than kind" (Hauser et al. 2002a, p. 1573). Similarly, Tomasello and Rakoczy (2003, p. 121) argue that the ability to participate in cultural activities with shared goals and intentions is uniquely human, but claim that the cognitive skills of a human child born on a desert island and somehow magically kept alive by itself until adulthood "would not differ very much – perhaps a little, but not very much" from the cognitive skills of other great apes (see also Tomasello et al. 2003a; Tomasello et al. 2005).

Notwithstanding the broad comparative consensus arrayed against us, the hypothesis we will be proposing in the present paper is that Darwin was mistaken: The profound biological continuity between human and nonhuman animals masks an equally profound functional discontinuity between the human and nonhuman mind.[1] Indeed, we will argue that the functional discontinuity between human and nonhuman minds pervades nearly every domain of cognition – from reasoning about spatial relations to deceiving conspecifics – and runs much deeper than even the spectacular scaffolding provided by language or culture alone can explain.

At the same time, we know from Darwin's more well-grounded principles that there are no unbridgeable gaps in evolution. Therefore, one of the most important challenges confronting cognitive scientists of all stripes, in our view, is to explain how the manifest functional discontinuity between extant human and nonhuman minds could have evolved in a biologically plausible manner.

The first – and probably most important – step in answering this question is to clearly identify the similarities and the dissimilarities between human and nonhuman cognition from a purely functional point of view. We therefore spend the bulk of the paper reexamining the evidence for "human-like" cognitive abilities among nonhuman animals at a functional level, before speculating as to how these processes might be implemented. We cover a wide variety of domains, species, and experimental protocols – ranging from spatial relations and mental state reasoning in the lab to dominance relations and transitive inferences in the wild. Across all these disparate cases, a consistent pattern emerges: Although there is a profound similarity between human and nonhuman animals' abilities to learn about and act on the perceptual relations between events, properties, and objects in the world, only humans appear capable of reinterpreting the higher-order relation between these perceptual relations in a structurally systematic and inferentially productive fashion. In particular, only humans form general categories based on structural rather than perceptual criteria, find analogies between perceptually disparate relations, draw inferences based on the hierarchical or logical relation between relations, cognize the abstract functional role played by constituents in a relation as distinct from the constituents' perceptual characteristics, or postulate relations involving unobservable causes such as mental states and hypothetical physical forces. There is not simply a consistent absence of evidence for any of these higher-order relational operations in nonhuman animals; there is compelling evidence of an absence.

In the last part of the article, we argue for the representational-level implications of our analysis. Povinelli and colleagues have previously proposed that humans alone are able to "reinterpret" the world in terms of unobservable, hypothetical entities such as mental states and causal

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forces and that our ability to do so relies on a unique representational system that has been grafted onto the cognitive architecture we inherited from our nonhuman ancestors (Povinelli 2000; 2004; Povinelli & Giambrone 2001; Povinelli & Preuss 1995; Povinelli & Vonk 2003; 2004; Vonk & Povinelli 2006). Independently, Holyoak, Hummel, and colleagues have argued that the ability to reason about higher-order relations in a structurally systematic and inferentially productive fashion is a defining feature of the human mind and requires the distinctive representational capabilities of a "biological symbol system" (Holyoak & Hummel 2000; 2001; Hummel & Holyoak 1997; 2001; 2003; Kroger et al. 2004; Robin & Holyoak 1995). Herein we combine, revise, and substantially expand on the hypotheses proposed by these two research groups.

We argue that most of the salient functional discontinuities between human and nonhuman minds – including our species' unique linguistic, mentalistic, cultural, logical, and causal reasoning abilities – result in part from the difference in degree to which human and nonhuman cognitive architectures are able to approximate the higher-order, systematic, relational capabilities of a physical symbol system (Newell 1980; Newell & Simon 1976). Although human and nonhuman animals share many similar cognitive mechanisms, our *relational reinterpretation hypothesis* (RR) is that only human animals possess the representational processes necessary for systematically reinterpreting first-order perceptual relations in terms of higher-order, role-governed relational structures akin to those found in a *physical symbol system* (PSS). We conclude by suggesting that recent advances in symbolic-connectionist models of cognition provide one possible explanation for how our species' unique ability to approximate the higher-order relational capabilities of a physical symbol system might have been grafted onto the *proto-symbolic* cognitive architecture we inherited from our nonhuman ancestors in a biologically plausible manner.

2. Similarity

2.1. Perceptual versus relational similarity

We begin our review of the similarities and differences between human and nonhuman cognition with what William James (1890/1950) called "the very keel and backbone of our thinking": *sameness*. The ability to evaluate the perceptual similarity between stimuli is clearly the sine qua non of biological cognition, subserving nearly every cognitive process from stimulus generalization and Pavlovian conditioning to object recognition, categorization, and inductive reasoning. Humans, however, are not limited to evaluating the similarity between objects based on perceptual regularities alone. Humans not only recognize when two physical stimuli are perceptually similar, they can also recognize that two ideas, two mental states, two grammatical constructions, or two causal-logical relations are similar as well. Even preschool-age children understand that the relation between a bird and its nest is similar to the relation between a dog and its doghouse despite the fact that there is little "surface" or "object" similarity between the relations' constituents (Goswami & Brown 1989; 1990). Indeed, as numerous researchers have shown, the propensity to evaluate the similarity between states of affairs based on the causal-logical and structural characteristics of the underlying relations rather than on their shared perceptual features appears quite early and spontaneously in all normal humans – as early as 2–5 years of age, depending on the domain and complexity of the task (Gentner 1977; Goswami 2001; Halford 1993; Holyoak et al. 1984; Namy & Gentner 2002; Rattermann & Gentner 1998a; Richland et al. 2006).

In short, there appear to be at least two kinds of similarity judgments at work in human thought: judgments of perceptual similarity based on the relation between observed features of stimuli; and judgments of non-perceptual relational similarity based on logical, functional, and/or structural similarities between relations and systematic correspondences between the abstract roles that elements play in those relations (Gentner 1983; Gick & Holyoak 1980; 1983; Goswami 2001; Markman & Gentner 2000). The question we are interested in here is whether or not there is any evidence for non-perceptual relational similarity judgments in nonhuman animals as well.

2.2. Same-different relations

Among comparative researchers, the most widely replicated test of relational concept learning over the last quarter century has been the simultaneous same-different (S/D) task, in which the subject is trained to respond one way if two simultaneously presented stimuli are the *same* and to respond a different way if the two stimuli are *different*. In the purportedly more challenging relational match-to-sample (RMTS) task, the subject must select the choice display in which the perceptual similarity among elements in the display is the same as the perceptual similarity among elements in the sample stimulus. For example, presented with a pair of identical objects, AA, as a sample stimulus, the subject should select BB rather than CD; presented with a pair of dissimilar objects, EF, as the sample stimulus, the subject should select GH rather than JJ (see Thompson & Oden 2000 for a seminal discussion).

Although Premack (1983a; 1983b) initially reported that only language-trained chimpanzees passed S/D and RMTS tasks, success on two-item S/D tasks has since been demonstrated in parrots (Pepperberg 1987), dolphins (Herman et al. 1993b; Mercado et al. 2000), baboons (Bovet & Vauclair 2001), and pigeons (Blaisdell & Cook 2005; Katz & Wright 2006), among others. Thompson et al. (1997) showed that language-naive chimpanzees with some exposure to token-based symbol systems are able to pass a two-item RMTS task (cf. Premack 1988). Vonk (2003) has reported that three orangutans and one gorilla were able to pass a complex two-item RMTS task without any explicit symbol or language training at all. Fagot et al. (2001) have shown that language-naïve baboons can pass an RMTS task involving arrays of elements (see discussion below); and Cook and Wasserman (in press) have reported successful results on an array-based RMTS task with pigeons. So passing S/D and RMTS tasks does not appear to be limited to language-trained apes or even primates.

Regardless of which nonhuman species are capable of passing S/D and RMTS tasks, the more critical and largely overlooked point is this: Both of these experimental protocols lack the power, even in principle, of demonstrating that a subject cognizes *sameness* and *difference* as abstract, relational concepts which are (1) independent of any particular source of stimulus control, and (2) available to serve in a variety of further higher-order inferences in a systematic fashion. A functional decomposition of the S/D and RMTS protocols reveals that the minimum cognitive capabilities necessary to pass these tests are much more modest.

The fundamental problem is that the *same-different* relation at stake in the classic S/D task can be reduced to a continuous, analog estimate of the degree of perceptual variability between the elements in each display. Halford et al. (1998a) refer to this type of cognitive trick as "conceptual chunking." *Chunking* reduces the complexity of processing a relation at the cost of losing the original structure and components of the relation itself, but suffices when the task does not require the structure of the relation itself to be taken into account. A cognizer could pass a classic S/D task by calculating an analog estimate of the variability between items in the sample display and then employ a simple conditional discrimination to select the appropriate behavioral response to this chunked result. Hence, success on an S/D task may imply that a subject can generalize a rule-like discrimination beyond any particular feature in the training stimuli; but it cannot be taken as evidence that the subject has understood *sameness* and *difference* as structured relations that are mutually exclusive or that can be freely generalized beyond the modality-specific rule the subject used in a particular learning context.

The same deflationary functional analysis applies, mutatis mutandis, to the RMTS task. The apparent relational complexity of the RMTS task can be significantly reduced by segmenting the task into separate chunked operations that are evaluated sequentially. First, the subject can evaluate the variability within the first-order relations by chunking them into analog variables. Second, the subject can employ a straightforward conditional discrimination to select the appropriate choice display: for example, < if the variability of the sample display is *low*, select the choice display with a *low* variability > . Although this may qualify as a "higher-order" operation, it does not qualify as a higher-order relational operation since the constituent structures of the first-order relations are no longer relevant or available to the higher-order process (see again, Halford et al. 1998a). At best, the RMTS task demonstrates that nonhuman animals can select the choice display that has the same degree of between-item variability as the sample display. But the task says nothing about nonhuman animals' ability to evaluate the non-perceptual relational similarity between those relations.

The preceding functional decomposition of the S/D and RMTS tasks is not merely a hypothetical possibility. There is now good experimental evidence that chunking and segmentation are precisely the tactics that nonhuman animals employ when they succeed at S/D and RMTS tasks. Wasserman and colleagues, for example, have shown that both pigeons and baboons have much less difficulty passing S/D tasks when there are 16 items in each set than when there are only 2 items in each set (Wasserman et al. 2001; Young & Wasserman 1997). Wasserman et al. showed that a simple measure of item variability, based on Shannon and Weaver's (1949) measure of informational *entropy*, nicely captures the functional pattern of nonhuman subjects' discriminations across a variety of experimental conditions (reviewed in Wasserman et al. 2004). Nonhuman animals' performance on S/D tasks differs markedly from the categorical, logical distinction that humans make between *sameness* and *difference*. Human subjects' responses to S/D tasks are also influenced by the degree of variability in the stimuli (Castro et al. 2007; Young & Wasserman 2001); but most human subjects exhibit a categorical distinction between displays with no item variability (i.e., *same*) and those with any item variability at all (i.e., *different*).

An analogous discontinuity between human and nonhuman judgments of similarity has also been documented on RMTS tasks. Fagot et al. (2001) presented two adult baboons and two adult human subjects with an RMTS task using arrays of 16 visual icons that were either all alike or all different. Both baboon and human subjects learned to pass the RMTS test and successfully generalized to novel sets of stimuli. When the authors reduced the number of items in the sample set from 16 to 2 icons, the difference between the two species, however, was notable. The impact on the human subjects' responses was insignificant. The baboons' performance, however, fell to chance on *different* trials, whereas their performance on *same* trials remained unchanged. This markedly asymmetric effect is exactly what one would expect if the baboons were discriminating between second-order *same* and *different* relations by comparing the amount of variability (e.g., entropy) in the two displays. That is, *same* trials with 2 icons continue to yield zero entropy, but *different* trials now yield a small entropy value that is more difficult to discriminate from zero.

Entropy is certainly not the only factor modulating nonhuman subjects' judgments of sameness and difference. Stimulus oddity as well as spatial organization and degree of similarity also play an important role (see Cook & Wasserman 2006 for an important review). Vonk (2003) has shown that language-naive apes can judge variability along specific perceptual dimensions (e.g., color rather than size or shape). And Bovet and Vauclair (2001) have shown that baboons can pass a "conceptual" S/D task in which pairs of objects are to be treated as *same* if they share a similar learning history or biological significance (e.g., objects-I-have-eaten vs. objects-I-have-not-eaten). These results demonstrate that nonhuman animals – and not just language-trained chimpanzees – are capable of learning novel, sophisticated, rule-governed discriminations that generalize beyond any specific perceptual cue. But in all of the results reported to date, the relevant discriminations are bound to a particular source of stimulus control (e.g., entropy, oddity, edibility). There is no evidence that nonhuman animals understand what "sameness" in one task has in common with "sameness" in another. For example, after passing a "perceptual" S/D task and having been trained to categorize objects as either "food" or "not food," the baboons in Bovet and Vauclair's (2001) study nevertheless required an average of 14,576 additional trials on the "conceptual" S/D task before their responses were correct 80% of the time on trials involving novel pairs of objects.

The available evidence therefore suggests that the formative discontinuity in same-different reasoning lies not between monkeys and apes, as Thompson and Oden (2000) proposed, but between nonhumans and humans. Chimpanzees and other nonhuman apes can pass RMTS tasks with only 2 items in the sample display (e.g., Thompson et al. 1997; Vonk 2003). Baboons can pass RMTS tasks with as few as 3–4 items in each sample (Fagot et al. 2001); and pigeons can pass RMTS tasks with 16 items in each sample (Cook & Wasserman, in press). The difference between the performance of language-naive pigeons and language-trained chimps on these tasks often comes down to a question of the number of items in each set and the number of trials necessary to reach criterion. As Katz and colleagues point out (see Katz & Wright 2006; Katz et al. 2002), this strongly suggests that there is a difference in degree between various nonhuman species' sensitivity to similarity discriminations (influenced by training regimen), not a difference in kind between their conceptual abilities to predicate same-different relations.

The performance of human subjects, on the other hand, contrasts sharply with the performance of all other animal species. Humans manifest an abrupt, categorical distinction between displays in which there is no variability and displays in which there is any variability at all (Cook & Wasserman 2006; Wasserman et al. 2004). More importantly, contra Castro et al. (2007), we believe that human subjects possess a qualitatively distinct system for reinterpreting *sameness* and *difference* in a logical and abstract fashion that generalizes beyond any particular source of stimulus control. In short, even with respect to the most basic and ubiquitous of all cognitive phenomena – judgments of similarity – there is already a distinctive seam between human and nonhuman minds.

2.3. Analogical relations

Premack (1983a, p. 357) suggested that the RMTS task is an implicit form of analogy and claimed that "animals that can make same/different judgments should be able to do analogies." Indeed, it is still widely accepted that the ability to pass an RMTS task is the "cognitive primitive" for analogical reasoning (see, e.g., Thompson & Oden 2000, p. 378). We disagree. While recognizing perceptual similarities is certainly a necessary condition for making analogical inferences (inter alia), there is a qualitative difference between the kind of cognitive processes necessary to pass an S/D or RMTS task and the kind of cognitive processes necessary to reason in an analogical fashion. The relations at issue in S/D and RMTS tasks are based solely on the perceptual features of the constituents; and the constituents play undifferentiated and symmetrical roles in those relations (e.g., two objects are symmetrically either the same or different).

Most true analogies, on the other hand, are based on relations in which the constituents play asymmetrical, causal-logical roles (e.g., the role that *John* plays in forming the relation, *John loves Mary*, is not equivalent to the role that *Mary* plays, perhaps to John's dismay). Furthermore, genuine analogical inferences are made by finding systematic structural similarities between perceptually disparate relations, allowing the cognizer to draw novel inferences about the target domain independently from the perceptual similarity between the relations' constituents (Gentner 1983; Gentner & Markman 1997; Holyoak & Thagard 1995). Accordingly, analogical relations sensu stricto cannot be reduced via chunking and segmentation, but require the cognizer to evaluate the abstract, higher-order relations at stake in a structurally systematic and inferentially productive fashion.

Analogical reasoning is a fundamental and ubiquitous aspect of human thought. It is at the core of creative problem solving, scientific heuristics, causal reasoning, and poetic metaphor (Gentner 2003; Gentner et al. 2001; Holyoak & Thagard 1995; 1997; Lien & Cheng 2000). And it is also central to the more prosaic ways that typical human children learn about the world and each other (Goswami 1992; 2001; Halford 1993; Holyoak et al. 1984). To date, however, the only evidence that any nonhuman animal is capable of analogical reasoning sensu stricto comes from the unreplicated feats of a single chimpanzee, Sarah, reported more than 25 years ago by Gillan et al. (1981). Sarah reportedly constructed and completed two distinct kinds of analogies. The first was based on judging whether or not two geometric relationships were the same or different (e.g., large blue triangle is to small blue triangle as large yellow crescent is to small yellow crescent). The second was based on judging the similarity between two "functional" relationships (e.g., padlock is to key as tin can is to can opener). Gillan et al. (1981) reported that Sarah was successful on both tests.

Savage-Rumbaugh was the first to point out that Sarah's performance on the geometric version of the original tests could have been the result of a simple, feature-matching heuristic (cited by Oden et al. 2001). In response, Oden et al. (2001) followed up Gillan et al.'s original experiment on geometric analogies with a series of more carefully constructed tests designed to flesh out Sarah's actual cognitive strategy. These new experiments used geometric forms that varied along one or more featural dimensions (e.g., size, color, shape, and/or fill). After extensive testing, Oden et al. showed that Sarah was actually tracking the number of within-pair featural differences rather than the kind of relation between pairs of figures. For example, whereas a human would see a color plus a shape change as differing from a size plus a fill change, Sarah saw these two transformations as equivalent because they both entailed two featural changes.

Oden et al. (2001) argued that this strategy still demonstrates Sarah's ability to reason about the "relation between relations." But there is a profound difference between the feature-based heuristic Sarah apparently adopted and the role-based structural operations that are the basis of analogical inference sensu stricto. To be sure, keeping track of the number of within-pair featural changes certainly requires quite sophisticated representational processes. But the fact that Sarah apparently ignored the structure of the relation between pairs of figures suggests that she represented any featural change as an undifferentiated chunk for the purposes of this task. Therefore, her strategy on this task appears to be computationally equivalent to the kind of chunking and segmentation strategies other nonhuman primates use to solve RMTS tasks. According to Oden et al.'s (2001) own analysis, Sarah failed to demonstrate a systematic sensitivity to the higher-order structural relation between relations. It is this systematic sensitivity to higher-order structural relations which is, as Gentner (1983) has long argued, the hallmark of analogical reasoning in humans.

Therefore, the claim that nonhuman animals are capable of analogical inferences rests solely on Sarah's performance in the test of functional analogies reported by Gillan et al. (1981). There are many reasons to be skeptical of these results as well. For one, Sarah's performance on these analogies has never been replicated either by Sarah herself or by any other nonhuman subject. Second, of the two experiments (3A and 3B) devoted to functional analogies, the authors themselves admit that the first, 3A, is open to an alternative feature-based account. Furthermore, the second experiment, 3B, did not require Sarah to complete or construct analogies. It merely required her to respond to the relation between two pairs of objects with one of two plastic tokens that her experimenters interpreted as meaning *same* and *different*. Sarah's extensive prior exposure to the objects used in this experiment, however, makes it very difficult to judge how she learned to cognize the relation between these objects (e.g., how exactly did Sarah understand that the relation between "torn cloth" and "needle and thread" is the same as the relation between "marked, torn paper" and "tape"?). Indeed, the authors themselves admit that Sarah's "unique experimental history" may have contributed to her success on these tasks (Gillan et al. 1981, p. 11).

In short, what is sorely needed is a more extensive series of tests, like those carried out by Oden et al. (2001), to systematically tease apart the salient parameters in Sarah's cognitive strategy. Until then, Sarah's remarkable and unreplicated success on experiment 3B as reported by Gillan et al. (1981) constitutes thin support for claiming that nonhuman animals are capable of analogical reasoning.

3. Rules

One of the hallmarks of human cognition is our ability to freely generalize abstract relational operations to novel cases beyond the scope in which the relation was originally learned (see Marcus 2001 for a lucid exposition). It is widely recognized, for example, that the ability to freely generalize relational operations over role-based variables is a necessary condition for using human languages (Gomez & Gerken 2000). Furthermore, experiments in artificial grammar learning (AGL) have shown that human subjects' ability to learn and generalize abstract relations over role-based abstractions is not limited to natural languages (e.g., Altmann et al. 1995; Gomez 1997; Marcus et al. 1999; Reber 1967). Although it is quite controversial how the human cognitive architecture performs these rule-like feats (see, e.g., Marcus 1999; McClelland & Plaut 1999; Seidenberg & Elman 1999), the fact that human subjects manifest these rule-like generalizations is "undisputed" (Perruchet & Pacton 2006). The question we want to focus on here is whether or not this undisputable behavioral "fact" also holds for nonhuman animals.

To date, the strongest positive evidence that nonhuman animals are able to generalize novel rules in a systematic fashion comes from an experiment with tamarin monkeys (Hauser et al. 2002b), which replicated an AGL experiment that Marcus et al. (1999) had previously performed on 7-month-old children. In this *"ga ti ga"* protocol, subjects were habituated to sequences of nonsense syllables in one of two patterns (e.g., AAB vs. ABB). Following habituation, the subjects were presented with test sequences drawn from an entirely novel set of syllables. Some of the test sequences followed the grammatical pattern presented during habituation and some did not. Hauser et al. (2002b) showed that tamarin monkeys, like human children, were more likely to dishabituate to the novel, "ungrammatical" pattern.

In our view, the claim that this experiment provides evidence for "rule learning" in a nonhuman species is not entirely unfounded; but it needs to be carefully qualified, as the kind of rules that tamarin monkeys learned in this experiment is qualitatively different from the kind of rules that is characteristic of human language and thought. Many early AGL experiments failed to distinguish between tasks that required subjects to learn perceptually bound relations from tasks that required subjects to learn non-perceptual structural relations over role-based variables (for a critical review, see Redington & Chater 1996). Tunney and Altmann (1999), for example, point out that there are at least two forms of sequential dependencies that might be learned in an AGL experiment: "repeating" dependencies in which the occurrence of an element in one position determines the occurrence of the *same* element in a subsequent position, and "nonrepeating" dependencies in which the occurrence of an element in one position determines the occurrence of a *different* element in a subsequent position. Repeating elements share a higher-order perceptual regularity (i.e., perceptual similarity), whereas purely structural dependencies between non-repeating elements do not. Therefore, sensitivity to sequential dependencies between repeating elements does not necessarily imply sensitivity to sequential dependencies between nonrepeating elements. Indeed, Tunney and Altmann (2001) demonstrate that adult human subjects appear to have distinct and dissociable mechanisms for learning each kind of dependency. At best, Hauser et al.'s (2002b) results demonstrate that tamarin monkeys possess the ability to learn repeating, perceptually based dependencies.

Similarly, Gomez and Gerken (2000) distinguish between "pattern-based" and "category-based" rules. In the former case, the rule is abstracted from the sequence of perceptual relations between elements in a given array of training stimuli; in the latter case, the rule is based on the structural relation between abstract functional roles. The AAB and ABB patterns learned by tamarin monkeys in Hauser et al.'s (2002b) study are an example of the former, pattern-based type of rule; the noun-verb-noun pattern learned by human language users is an example of the latter, role-based type of rule. Both kinds of operations may qualify as "rule-like" in the sense that they generalize a given relation beyond the feature set on which it was originally trained. But it is role-based (i.e., "algebraic") rules, as Marcus (2001) points out, that are the hallmarks of human thought and language. To date, there is no evidence for this kind of rule learning in any nonhuman animal.

4. Higher-order spatial relations

All normal adult humans are capable of using allocentric representations of spatial relations and of reasoning about the higher-order relation between spatial relations at different scales. The ubiquity of maps, diagrams, graphs, gestures, and artificial spatial representations of all sorts in human culture speaks for itself. Indeed, by the age of 3, all normal humans are able to reason about the higher-order relation between small-scale artificial spatial models and large-scale spatial relations in the real world (see Gattis 2005 for a review). DeLoache (2004) has argued that this ability represents a crucial step in children's progress towards becoming "symbol minded." The question at hand is whether there is any evidence that nonhuman animals can reason about the higher-order relation between spatial relations in a similar fashion.

The best evidence to date for higher-order spatial reasoning in a nonhuman animal comes from the work of Kuhlmeier and colleagues (Kuhlmeier & Boysen 2001; 2002; Kuhlmeier et al. 1999). Kuhlmeier et al. (1999) first instructed seven captive chimpanzees to associate the miniature and the full-sized versions of four distinct objects by drawing their attention to the association "verbally and gesturally" (p. 397). After this initial training, the chimpanzees watched as the experimenter hid a miniature can of soda behind a miniature version of one of the four objects within a 1:7 scale model of a full-sized room or outdoor enclosure. Then the chimpanzees were given the opportunity to find the real can of soda in the adjacent full-sized space. When the chimpanzees were tested on a version of the task in which they were rewarded only if they retrieved the can of soda on the first search attempt (Kuhlmeier & Boysen 2001), six out of the seven subjects performed above chance.

These results demonstrate that chimpanzees are able to learn to associate two objects (the real object and its miniature) that are highly similar perceptually and to locate a reward based on this association. But this is a far cry from being able to reason about the higher-order relation between a scale model and its real-world referent. Indeed, Kuhlmeier et al. (1999, p. 397) reported that one chimpanzee was able to locate the food rewards simply upon being shown the miniature version of the hiding place without referring to the scale model at all. In short, this first protocol did not require the chimpanzees to reason about the higher-order spatial relation between the scale model and full-sized room. A simple, learned association between two arbitrary cues sufficed.

In a follow-up experiment designed to eliminate purely associative cues, Kuhlmeier and Boysen (2002) varied the congruency of the color, shape, or position of the miniatures relative to the full-sized version of the hiding site. As a group, the chimpanzees were successful when positional cues were absent. However, when all the hiding sites were visually identical and the correct one had to be found based on its relative location within the scale model alone, only two of the seven chimpanzees performed above chance.

It is clear from these results that reasoning in terms of relative spatial locations alone is significantly more difficult for chimpanzees than is reasoning in terms of object-based cues alone. But it must be noted that even the successful performance of two out of the seven subjects does not demonstrate higher-order relational abilities, since the four locations in which the hiding sites were placed remained constant across all of these experiments (Kuhlmeier, personal communication). Hence, it is impossible to know whether the two successful chimpanzees were reasoning on the basis of a general, systematic understanding of the analogy between spatial locations in the scale model and spatial locations in the outdoor enclosure, or whether, more modestly, they had simply learned over the course of their long experimental history with this particular protocol to associate a particular location in the scale model with a particular location in the enclosure.

It remains to be seen whether chimpanzees, or any other nonhuman animal, could succeed in this protocol if the hiding sites were randomly relocated on each trial. In the meantime, there is a conspicuous absence of evidence that any nonhuman animal can reason about scale models, maps, or higher-order spatial relations in a human-like fashion.

5. Transitive inference

Ever since Piaget (1928; 1955), the ability to make systematic inferences about unobserved transitive relations has been taken as a litmus test of logical-relational reasoning (but see Wright 2001). For example, told that "Bill is taller than Charles" and "Abe is taller than Bill," human children can infer that "Abe is taller than Charles" without being given any information about the absolute heights of Abe, Bill, or Charles (Halford 1984). Over the last quarter century, comparative researchers have persistently claimed that nonhuman animals are capable of making transitive inferences in a purely logical-relational fashion, as well. Upon closer examination of the evidence, however, it becomes apparent that the kinds of transitive inferences that are made by nonhuman animals do not require a systematic, domain-general logical-relational competence, but rather, can be made using much more prosaic, domain-specific, and egocentric information-processing mechanisms.

5.1. Transitive choices in the lab

For many decades now, the classic comparative test of transitive inference has been a nonverbal five-item task developed by Bryant and Trabasso (1971) in which subjects are incrementally trained on pairs of stimuli (i.e., A + B-, B+C-, C+D-, D+E-) and then tested on non-adjacent untrained pairs. The discriminative relation between the stimuli used in most of these studies is not, in fact, transitive; it is the subjects' choices that become transitive as a result of the pattern of differential reinforcement: that is, repeated reinforcement of the choice of A over B and of B over C eventually leads to the subject preferring A over C. As Halford et al. (1998b) pointed out, a subject's preferences can become transitive through incremental reinforcement without there being a transitive relation between the underlying task elements themselves, and therefore without requiring the subject to understand anything about transitivity as a logical property. Indeed, many researchers have shown that successfully selecting B over D in the traditional five-item incremental protocol can be achieved using purely associative operations (De Lillo et al. 2001; Wynne 1995).

To be sure, reinforcement history cannot be the whole story, as Lazareva et al. (2004) have recently demonstrated. Lazareva et al. (2004) trained eight hooded crows in a clever variation on Bryant and Trabasso's five-item protocol. Five colored cards were used to represent the elements in the series, A through E. The color on one side of the card served as the choice stimulus, and a circle of the same color on the underside of the card served as the post-choice feedback stimulus. The crows were asked to choose one of two simultaneously presented cards. Importantly, the colored circles on the underside of the cards were displayed to the crows only after they had selected one of the two choice stimuli. The crows were divided into two experimental groups. In the *ordered-feedback* group, the diameter of the circles associated with the choice stimuli became progressively smaller from A to E. In the *constant-feedback* group, the diameter of the feedback circles did not change. After initial training, Lazareva et al. (2004) overexposed both groups of crows to D+E- pairings. Under traditional associative models, massive overexposure to D+E- pairings should lead to preferentially selecting D over B. Nevertheless, the crows in the ordered-feedback group selected B over D in the BD pairings, whereas the crows in the constant-feedback group either chose at random or preferred D over B.

Lazareva et al.'s (2004) results show that reinforcement history alone cannot account for the emergence of choice transitivity among nonhuman animals. Moreover, we agree with Lazareva et al. (2004) that these results are consistent with some kind of "spatial representation" hypothesis (Gillan 1981). But what is not often noted by comparative researchers is that evidence for an integrated representation of an ordered series is not in and of itself evidence for transitive reasoning or relational integration in a logical-deductive sense. There is more to making logically underpinned transitive inferences than constructing an ordered representation of one's choices.

As Lazareva et al. (2004) themselves point out, in order to claim evidence for logically underpinned transitive inferences, one must show that the organism can, in fact, distinguish between transitive and non-transitive relations and that it makes its choices on the basis of this logical relation independently of other non-logical factors such as reinforcement history and training regime (see also Halford et al. 1998a; Wright 2001). The results reported by Lazareva et al. (2004) do not provide evidence for either of these criteria.

In a follow-up experiment, Lazareva and Wasserman (2006) showed that pigeons select B over D stimuli in the same protocol employed by Lazareva et al. (2004) even when the size of the post-choice cues is constant– which demonstrates that the transitive perceptual relation between the post-choice cues is not, in fact, computationally necessary for successfully passing this particular protocol. It is unclear why crows – but not pigeons – were unable to pass the test in the constant-feedback condition. There are many possible explanations. For example, Lazareva et al. (2004) did not rule out the possibility that it was simply the variability between post-choice cues that encouraged the crows' successful responses rather than their transitivity per se. In any case, in order to warrant the claim that the crows were reasoning on the basis of the logical relation between post-choice stimuli independently of other non-logical factors, it would be necessary to show that the crows could systematically generalize to novel stimuli on a first trial basis: For example, trained to associate a novel choice stimulus, X, with a colored circle of a given diameter, could the crows correctly choose between X and any stimulus from the set, A through E, on a first-trial basis in a systematic manner? To date, there is no evidence that crows, or any other nonhuman animal, could pass such a test.

5.2. Transitive inferences in the wild

Many researchers have argued that animals' full transitive reasoning capabilities are most likely to manifest themselves in inferences involving social relations (e.g., Bond et al. 2003; Grosenick et al. 2007; Kamil 2004; Paz et al. 2004). Much of the early fieldwork focused on nonhuman primates (see Tomasello & Call 1997 for a review). The strongest evidence to date for transitive social inferences in a nonhuman animal comes not from primates, however, but from birds (see review by Kamil 2004) and fish (see Grosenick et al. 2007). Paz et al. (2004), for example, showed that male pinyon jays can anticipate their own subordinance relation to a stranger after having witnessed the stranger win a series of confrontations with a familiar but dominant conspecific. Similarly, Grosenick et al. (2007) allowed territorial *A. burtoni* male fish to observe pairwise fights between five rivals (i.e., AB, BC, CD, DE), with the outcomes implying a dominance ordering of $A > B > C > D > E$. When subsequently given a choice between B and D, observers preferred to spend more time adjacent to D rather than B.

Results such as these demonstrate that the ability to keep track of the dominance relations between tertiary dyads is not limited to nonhuman primates or even to mammals (cf. Tomasello & Call 1997). Furthermore, fish and birds, in addition to nonhuman primates, can apparently use this information to make rational (i.e., ecologically adaptive) choices about how to respond to potential rivals (see also Bergman et al. 2003; Bond et al. 2003; Hogue et al. 1996; Silk 1999). The accumulated evidence therefore rules out a traditional associative explanation and strongly supports a more complex, information-processing account of how nonhuman animals keep track of and respond to dominance relations among conspecifics.

But none of the available comparative evidence suggests that nonhuman animals are able to process transitive inferences in a systematic or logical fashion, even in the social domain. The experiments reported by Paz et al. (2004) and Grosenick et al. (2007) provide evidence for only one particular kind of transitive inference: an inference from watching a series of agonistic interactions between conspecifics to an egocentric prediction about how to respond to a potentially dominant rival. Neither experiment provides any evidence that these subjects would also be able to systematically predict the relation between unobserved third-party dyads or could use their own interactions with a conspecific to predict that conspecific's relation to other rivals – let alone answer the kind of omni-directional queries of which humans are manifestly capable: For example, what individuals are dominant to B? What is the relation between C and A? Is A dominant to C to a greater or lesser extent than B is dominant to C? (Goodwin & Johnson-Laird 2005; Halford et al. 1998a).

In short, whereas at least some nonhuman animals clearly are able to make transitive inferences about their own relation to potential rivals to a degree that rules out purely associative learning mechanisms, the comparative evidence accumulated to date is nevertheless consistent with the hypothesis that nonhuman animals' understanding of transitive relations is punctate, egocentric, non-logical, and context-specific.

6. Hierarchical relations

Being able to process recursive operations over hierarchical relations is unarguably a key prerequisite for using a human language (Hauser et al. 2002a). And most normal human children are capable of reasoning about hierarchical class relations in a systematic and combinatorial fashion by the age of five (Andrews & Halford 2002; cf. Inhelder & Piaget 1964). Given the ubiquity and importance of hierarchical relations in human thought, the lack of any similar ability in nonhuman animals would therefore constitute a marked discontinuity between human and nonhuman minds.

6.1. Seriated cups and hierarchical reasoning

A number of comparative researchers have reinterpreted the behavior of nonhuman animals in hierarchical terms (e.g., Byrne & Russon 1998; Greenfield 1991; Matsuzawa 1996). In each of these cases, however, there is no evidence that the nonhuman animals themselves cognized the task in hierarchical terms or employed hierarchically structured mental representations to do so. The most widely cited case of hierarchical reasoning among nonhuman animals, for example, has come from experiments involving seriated cups. It has been claimed that "subassembly" (i.e., combining two or more cups as a subunit with one or more other cups) requires the subject to represent these nested relations in a combinatorial and "reversible" fashion (Greenfield 1991; Westergaard & Suomi 1994). Indeed, Greenfield (1991) argued that children's ability to nest cups develops in parallel with their ability to employ hierarchical phonological and grammatical constructions, and therefore, that the ability of nonhuman primates to seriate cups is the precursor to comprehending hierarchical grammars (see Matsuzawa 1996 for claims of a similar "isomorphism" between tool and symbol use).

But is it actually necessary to cognize hierarchically structured relations in order to assemble nested cups? To date, Johnson-Pynn, Fragaszy, and colleagues have provided the most convincing evidence that a nonhuman animal can use subassembly to assemble seriated cups (Fragaszy et al. 2002; Johnson-Pynn & Fragaszy 2001; Johnson-Pynn et al. 1999). Yet, Johnson-Pynn and Fragaszy themselves dispute the claim that this behavior requires hierarchical relational operations of the kind suggested by Greenfield (1991).

Fragaszy et al. (2002), for example, presented seriated cups to adult capuchin monkeys, chimpanzees, and 11-, 16-, and 21-month-old children. Children of all three ages created five-cup sets less consistently than the nonhuman subjects did, and they were rarely able to place a sixth cup into a seriated set. Bizarrely, at least for a purely relational interpretation of the results, monkeys were more successful than either apes or human children on the more challenging six-cup trials, yet were also the most inefficient (in terms of number of moves) of the three populations.

Fragaszy et al.'s (2002) explanation for these anomalous results is quite sensible (see also Fragaszy & Cummins-Sebree 2005): They hypothesize that the seriation task does not, in fact, require the subject to reason about combinatorial, hierarchical relations per se, but depends more simply on situated, embodied sensory-motor skills that are experientially, rather than conceptually, driven. Apes and monkeys do better than children because they are more physically adept than 11- to 21-month-old children are – not because they have a more sophisticated representation of the combinatorial and hierarchical relations involved. Although subassembly may be a more physically "complex" strategy than other methods of seriation, it does not necessarily require the subject to cognize the spatial-physical relations involved as hierarchical; and therefore there is no reason to claim an isomorphism between the embodied manipulation of nested cups and the cognitive manipulation of symbolic-relational representations (cf. Greenfield 1991; Matsuzawa 1996).

6.2. Hierarchical relations in the wild

The strongest evidence to date in support of the claim that nonhuman animals can reason about hierarchically structured relations in the social domain comes from Bergman et al.'s (2003) study of free-ranging baboons. Bergman et al. designed an elegant playback experiment in which female baboons heard a sequence of recorded calls mimicking a fight between two other females. Mock agonistic confrontations were created by playing the "threat-grunt" of one individual followed by the subordinate screams of another. On separate days, the same subject heard one of three different call sequences: (1) an anomalous sequence mimicking a rank reversal between members of the same matrilineal family (i.e., sisters, mothers, daughters, or nieces); (2) an anomalous sequence mimicking a between-family rank reversal (i.e., between members of two different matrilineal families in which one of the families is dominant to the other); or (3) a control sequence replicating an existing dominant-subordinate relationship (i.e., no rank reversal) using between-family or within-family dyads. As predicted, there was a significant difference in the focal subjects' responses to the three different kinds of call sequences. Subjects looked longest at between-family rank reversals. There was no significant difference between within-family reversals and no-reversal control sequences. According to Bergman et al., the reason the baboons responded more strongly to between-family rank reversals than within-family sequences is because the baboons recognized that the former imply a superordinate reorganization of matrilineal subgroups. Bergman et al. (2003, p. 1236) conclude: "Our results suggest that baboons organize their companions into a hierarchical, rule-governed structure based simultaneously on kinship and rank" (see also Seyfarth et al. 2005).

In our view, the evidence reported by Bergman et al. (2003) does not support this conclusion. Even if baboons do make a categorical distinction between kin and non-kin dyads based on interaction history, familiarity, spatial proximity, phenotypic cues, or some other observable regularity (see Silk 2002a for a review of the possibilities), this does not necessarily mean that they represent the entire matrilineal social structure as an integrated relational schema in which non-kin relations are logically superordinate to between-kin relations. As Bergman et al. (2003) themselves point out, between-family rank reversals are much more disruptive to baboon social life than within-family rank reversals. Therefore, Bergman et al.'s (2003) results are consistent with the hypothesis that female baboons have learned that rank reversals among non-kin are more salient (i.e., associated with greater social turmoil and personal risk) than are within-kin rank reversals occurring in someone else's family (notably, Bergman et al. did not test rank reversals within the focal subject's own family). While baboons clearly recognize particular conspecifics' vocalizations and represent dominance and kin relations in a combinatorial manner, there is nothing in Bergman et al.'s data that remotely suggests a higher-order, hierarchical relation among these representations.

Once again, there is not simply an absence of evidence; there is evidence of an absence. Bergman et al. (2003) note that the subjects' responses to apparent rank reversals were unrelated to the rank distance separating the two signalers: that is, subjects paid as much attention to mock rank reversals involving closely ranked opponents as those involving more distantly ranked opponents. Bergman et al. use this fact to rebut the hypothesis that the baboons were responding more strongly to between-family rank reversals simply because the individuals involved had more disparate ranks. However, the data cut both ways: If the baboons did cognize the relation between female conspecifics as an integrated matrilineal dominance hierarchy, *ceteris paribus*, they should have been more surprised at a rank reversal between a very low ranking and a very high ranking individual than by a rank reversal between two individuals of adjacent ranks. Ironically, Bergman et al.'s results provide some of the strongest evidence to date that female baboons do not, in fact, cognize the structure of their conspecifics' matrilineal social relationships in a systematic or hierarchical fashion.

7. Causal relations

There is ample evidence that traditional associationist models are inadequate to account for nonhuman causal cognition; but the available comparative evidence also suggests that there is a critical and qualitative difference between the ways that human and nonhuman animals reason about causal relations (see Penn & Povinelli 2007a for a more extensive review and discussion). Humans explicitly reason in terms of unobservable and/or hidden causes (Hagmayer & Waldmann 2004; Kushnir et al. 2005; Saxe et al. 2005), distinguish between "genuine" and "spurious" causes (Lien & Cheng 2000), reason diagnostically from effects to their possible causes (Waldmann & Holyoak 1992), and plan their own interventions in a quasi-experimental fashion to elucidate ambiguous causal relations (Hagmayer et al. 2007). Numerous researchers have argued that normal humans – not just scientists or philosophers – form "intuitive theories" or "mental models" about the unobservable principles and causal forces that shape relations in a specific domain (e.g., Carey 1985; Gopnik & Meltzoff 1997; Keil 1989; Murphy & Medin 1985). These tacit systems of higher-order relations at various levels of generality modulate how human subjects judge and discover novel relations within those domains by a process akin to analogical inference (Goldvarg & Johnson-Laird 2001; Lee & Holyoak 2007; Lien & Cheng 2000; Tenenbaum et al. 2007). In short, the ability to reason about higher-order, analogical relations in a systematic and productive fashion appears to be an integral aspect of human causal cognition.

In stark contrast to the human case, there is no compelling evidence that nonhuman animals form tacit theories about the unobservable causal mechanisms at work in the world, seek out explanations for anomalous causal relations, reason diagnostically about unobserved causes, or distinguish between genuine and spurious causal relations on the basis of their prior knowledge of abstract causal mechanisms.[2] Indeed, there is consistent evidence of an absence across a variety of protocols (see, e.g., Penn & Povinelli 2007a; Povinelli 2000; Povinelli & Dunphy-Lelii 2001; Visalberghi & Tomasello 1998).

A variety of nonhuman animal species – and certainly not primates alone (Emery & Clayton 2004b) – are able to construct and use tools in a flexible and adaptive fashion. But a series of seminal experiments, initiated by Visalberghi and colleagues (see Visalberghi & Limongelli 1996 for a review), provides a particularly compelling example of how nonhuman animals' remarkable use of tools nevertheless belies a fundamental discontinuity with our human understanding of causal relations.

Visalberghi and Limongelli (1994) tested capuchin monkeys' ability to retrieve a piece of food placed inside a transparent tube using a straight stick. In the middle of the tube, there was a highly visible hole with a small transparent cup attached. If the subject pushed the food over the hole, the food fell into the cup and was inaccessible ("trap-down" condition). Visalberghi and Limongelli (1994) tested four capuchin monkeys to see whether they would understand that they needed to push the food out the end of the tube away from the hole. After about 90 trials, only one out of the four capuchin monkeys learned to push the food away from the hole, and even this one learned the correct behavior through trial and error. Worse, once the experimenters rotated the tube so that the trap hole was now facing up and causally irrelevant ("trap-up" condition), the one successful capuchin still persisted in treating the hole as if it needed to be avoided – making it obvious that even this subject misunderstood the causal relation between the trap hole and the retrieval of the reward.

Povinelli (2000) and colleagues subsequently replicated Visalberghi's trap-tube protocol with seven chimpanzees. Povinelli performed the experiments once when the chimpanzees were juveniles (5 to 6 years old) and again when they were young adults (10 years old). Three out of the seven chimps learned to solve the trap-down version of the task as adults, with one chimp, Megan, learning to solve the task within 100 trials. However, none of the chimps showed any evidence of distinguishing between the trap-up and trap-down versions of the task. By way of comparison, it should be noted that children as young as 3 years of age successfully solve the trap-tube task after only a few trials (see Limongelli et al. 1995).

Recently, Mulcahy and Call (2006b) tested ten great apes on a version of the trap-tube task that allowed subjects to choose whether to pull or push the reward through the tube. Three out of the ten subjects learned to avoid the trap when pulling rather than pushing. However, the majority of subjects still failed the task. Indeed, even the three successful subjects took an average of 44 trials to achieve above-chance performance, and then continued to fail Visalberghi and Limongelli's (1994) push-only version of the task. Therefore, these latest results seem to confirm two earlier hypotheses: (1) nonhuman apes are more adept at pulling than pushing in tool-use tasks such as these (see, e.g., Povinelli 2000, Ch. 5); and (2) nonhuman primates' causal knowledge is tightly coupled to specific task parameters and bodily movements: in particular, they do not appear to grasp the abstract, *analogical* similarity between perceptually disparate but functionally equivalent tasks (Penn & Povinelli 2007a; Povinelli 2000; Visalberghi & Tomasello 1998).

Nonhuman primates are not the only animals that seem to be incapable of cognizing the general causal principles at issue in the trap-tube task. Seed et al. (2006) recently presented eight rooks with a clever modification to Visalberghi's trap-tube task in which each tube contained two traps, one which was functional and one which was not. Seven out of eight rooks rapidly learned to pull the food away from the functional trap and successfully transferred this solution to a novel but perceptually similar version of the task. Nevertheless, when presented with transfer tasks in which the visual cues that were associated with success in the initial tasks were absent or confounded, only one of the seven subjects passed. In a follow-up experiment (Tebbich et al. 2007), none of the rooks passed the transfer tasks.

Seed et al.'s (2006) results add to the growing evidence that corvids are quite adept at using stick-like tools (see, e.g., Weir & Kacelnik 2007). But as Seed et al. (2006) point out, these results also suggest that rooks share a common cognitive limitation with nonhuman primates: they do not understand "unobservable causal properties" such as gravity and support; nor do they reason about the higher-order relation between causal relations in an analogical or theory-like fashion. Instead, rooks, like other nonhuman animals, appear to solve tool-use problems based on evolved, domain-specific expectations about what perceptual features are likely to be most salient in a given context and a general ability to reason about the causal relation between observable contingencies in a flexible, goal-directed but task-specific fashion (see also Penn & Povinelli 2007a).

8. Theory of mind

Nonhuman animals certainly manifest many sophisticated social-cognitive abilities. But having a *theory of mind* (ToM) sensu Premack and Woodruff (1978) means something more specific than being a socially savvy animal: it means being able to impute unobservable, contentful mental states to other agents and then to reason in a theory-like fashion about the causal relation between these unobservable mental states and the agents' subsequent behavior (see Penn & Povinelli 2007b for a more extensive discussion of this point). Of course, theory-like inferences are not the only way in which a cognizer might reason about other agents' mental states (see Carruthers & Smith 1996 for a review of the possibilities). Mentalistic simulation, for example, provides an alternative and popular explanation. However, all but the most radical simulation-oriented theories do not deny that humans represent causal relations involving other agents' unobservable mental states. They simply propose an alternative, analogical mechanism for how humans do so.

Whiten (1996; 2000) has proposed another, influential hypothesis about how nonhuman apes (and young children) might represent the mental states of their conspecifics without relying on theory-like metarepresentations. Whiten proposed that nonhuman apes use "intervening variables" to stand in for generalizations about the causal role played by a given mental state in a set of disparate behavioral patterns. For example, a chimpanzee that encodes the observable patterns "X saw Y put food in bin A," "X hid food in bin A," and "X sees Y glancing at bin A" as members of the same abstract equivalence class could be said, on Whiten's account, to recognize that "X *knows* food is in bin A" and, therefore, be capable of "explicit mindreading" (Whiten 1996).

Notice that Whiten's example of "explicit mindreading" is a textbook example of analogical reasoning: Whiten's hypothetical chimpanzee must infer a systematic higher-order relation among disparate behavioral patterns that have nothing in common other than a shared but unobservable causal mechanism: that is, what X "knows." If this is an "intervening variable," it is an intervening variable that requires reasoning about the higher-order, role-governed relational similarity between perceptually disparate causal relations in order to be produced.

We believe Whiten is right in this sense: If a nonhuman animal were capable of inferring that these disparate behavioral patterns were actually instances of the same superordinate causal relation, then the animal would surely have demonstrated that it possessed a ToM and the ability to reason analogically, as well. There is, however, no such evidence on offer. Indeed, until recently, there has been a fragile consensus that nonhuman animals lack anything even remotely resembling a ToM (Cheney & Seyfarth 1998; Heyes 1998; Tomasello & Call 1997; Visalberghi & Tomasello 1998).

A few years ago, however, Hare et al. (2000; 2001) reported "breakthrough" evidence that chimpanzees do, in fact, reason about certain psychological states in their conspecifics (see, particularly, Tomasello et al. 2003a; 2003b). And since then, there have been a flurry of similar claims on behalf of corvids and monkeys based on similar protocols (Bugnyar & Heinrich 2005; 2006; Dally et al. 2006; Emery & Clayton 2001; in press; Flombaum & Santos 2005; Santos et al. 2006). Because Povinelli and colleagues have provided detailed critiques of Hare et al.'s (2000; 2001) protocol and results elsewhere (see Penn & Povinelli 2007b; Povinelli 2004; Povinelli & Vonk 2003; 2004), here we will focus on the best available evidence for a ToM system among non-primates. As will become apparent, our original critique of Hare et al.'s (2000; 2001) protocol applies, mutatis mutandis, to the new claims being made on behalf of corvids, as well.

The best evidence for a ToM system in a non-primate comes from the work of Emery, Clayton and colleagues (Emery & Clayton 2001; 2004b; in press). Dally et al. (2006), for example, had scrub-jays cache food items under one of four conditions: (1) in the presence of a dominant conspecific, (2) in the presence of a subordinate, (3) in the presence of the storer's preferred partner, or (4) in private. The storers were allowed to cache the food in two trays, one nearer and one farther away from the observer, and then they were allowed to recover their caches in private three hours later. Dally et al. (2006) showed that birds that had stored food in the presence of a dominant or subordinate competitor tended to re-cache food predominantly from the near tray, and that the proportion of food that was re-cached was greatest for birds that had stored food in the presence of a dominant competitor. In a follow-up experiment, scrub-jays were given the chance to cache successively in two trays, each in view of a different observer. After three hours, storers were allowed to recover their caches. Dally et al. (2006) reported that significantly more food caches were re-cached when a previous observer was present than when the storers retrieved their caches in private or in view of a control bird that had not witnessed the original caching. Furthermore, if a previous observer was present, storers tended to re-cache from the tray that the previous observer had actually observed.

Results such as these leave no doubt that corvids are remarkably intelligent creatures, able to keep track of the social context of specific past events, as well as the what, when, and where information associated with those events (Clayton et al. 2001). But nothing in the results reported to date suggests that corvids actually reason about their conspecifics' mental states – or even understand that their conspecifics have mental states at all – as distinct from their conspecifics' past and occurrent behaviors and the subjects' own knowledge of past and current states of affairs (Penn & Povinelli 2007b; Povinelli et al. 2000; Povinelli & Vonk 2003; 2004).[3]

In the case of Dally et al.'s (2006) experiment, for example, it suffices for the subjects to keep track of which competitor was present during which caching event and to formulate strategies on the basis of observable features of the task alone: for example, < *Re-cache food if a competitor has oriented towards it in the past* >, < *Try to cache food in sites that are farther away from potential competitors* >, < *Attempt to pilfer food if the competitor that cached it is not present* >, and so on. Since none of the protocols required the subjects to reason in terms of the specific contents of the competitor's epistemic mental states, the additional inference that the subjects acted the way they did because they understood that < *The competitor knows where the food is located* > does no additional cognitive or explanatory work. This additional mentalistic claim merely satisfies our all-too-human need to posit an explicit, conscious, propositional reason for the birds' behaviors. But it is obvious that animals – including humans – do not necessarily need to "know" why they are acting the way they are acting in order for a behavior to be flexible, effective, and (biologically) rational (see lucid discussions by Heyes & Papineau 2006; Kacelnik 2006).

Indeed, many of the same researchers who claim evidence for ToM abilities in corvids explicitly acknowledge that an explanation based on responding to observed cues alone would be sufficient to account for the existing data. Dally et al. (2006, p. 1665), for example, point out that scrub-jays' ability to keep track of which competitors have observed which cache sites "need not require a human-like 'theory of mind' in terms of unobservable mental states, but [. . .] may result from behavioral predispositions in combination with specific learning algorithms or from reasoning about future risk." Similarly, Bugnyar and Heinrich (2006, p. 374) acknowledge that a representation of "states in the physical world" and "responses to subtle behavioral cues given by the competitor" would be sufficient to explain the available evidence concerning the manipulative behaviors of ravens – as well, we would add, as all the other comparative evidence claiming to show ToM-like abilities in nonhuman animals to date (for examples of the kind of protocols that could, in principle, provide evidence for a ToM system in a nonhuman animal, see Penn & Povinelli 2007b).

9. Explaining the discontinuity

Up to this point in the article, we have focused solely on showing that there is, in fact, a pervasive functional discontinuity between human and nonhuman minds, and that this discontinuity is located specifically in the way that human and nonhuman animals reason about relations. Now we turn to the daunting question of how to account for this pervasive discontinuity. Let us first consider the three most influential hypotheses that have been proposed in recent years.

9.1. The massive modularity hypothesis

A "modular" explanation for the evolution of human cognition is popular among many evolutionary-minded theorists (e.g., Barkow et al. 1992). Certainly, many central cognitive processes – including almost all of the cognitive mechanisms we share with nonhuman animals – are at least moderately modular once the notion of modularity has been defined in a purely functional sense (see Barrett 2006). But the modular story alone does not provide a satisfying explanation for the disparity between human and nonhuman minds.

As we have seen in our review of the comparative evidence, the pattern of similarities and differences between human and nonhuman relational reasoning is remarkably consistent across every domain of cognition, from same-different reasoning and spatial relations to tool use and ToM. Therefore, it seems highly implausible that the disparities in each domain are the result of independent, module-specific adaptations. It seems much more likely (not to mention, parsimonious) that a common set of specializations – perhaps in some more general "supermodule" – is responsible for augmenting the relational capabilities of all of the cognitive modules we inherited from our nonhuman ancestors. Unfortunately, the two most popular supermodules that have been proposed to date – ToM and language – do not do a good job of accounting for the comparative evidence.

9.2. The ToM hypothesis

A number of comparative researchers believe that the discontinuity between human and nonhuman minds can be traced back to some limitation in nonhuman animals' social-cognitive abilities (e.g., Cheney & Seyfarth 1998; Terrace 2005a; Tomasello et al. 2005). Although we certainly agree that nonhuman animals do not appear to possess anything remotely resembling a ToM, the hypothesis that some aspect of our ToM alone is responsible for the disparity between human and nonhuman cognition seems difficult to sustain. For example, it is very hard to see how a discontinuity in social-cognitive abilities alone could explain the profound differences between human and nonhuman animals' abilities to reason about causal relations in the physical world or nonhuman animals' inability to reason about higher-order spatial relations. Even Tomasello and his colleagues have admitted that trying to explain all the differences between human and nonhuman cognition in terms of a difference in ToM skills is "highly speculative" at best (Tomasello & Call 1997, p. 418). Indeed, in a different context, Tomasello has himself argued (e.g., Tomasello 2000) that human language learners rely on cognitive capacities – such as analogical reasoning and abstract rule learning – that are independent from ToM and absent in nonhuman animals. So while our ability to participate in collaborative activities and to take each others' mental states into account may be a distinctive feature of the human lineage, it is clearly not the only or even the most basic one.

9.3. The language-only hypothesis

The oldest and still most popular explanation for the wide-ranging disparity between human and nonhuman animals' cognitive abilities is language (for recent examples of this venerable argument, see Bermudez 2003; Carruthers 2002; Clark 2006). Dennett (1996, p. 17) described the extreme version of this hypothesis in characteristically pithy terms: "Perhaps the kind of mind you get when you add language to it is so different from the kind of mind you can have without language that calling them both minds is a mistake."

To be sure, language clearly plays an enormous and crucial role in subserving the differences between human and nonhuman cognition. But we believe that language alone is not sufficient to account for the discontinuity between human and nonhuman minds. In order to make our case, we need to distinguish between three distinct versions of the *language-only hypothesis*: (1) that verbalized (or imaged) natural language sentences are responsible for the disparity between human and nonhuman cognition; (2) that some aspect of our internal "language faculty" is responsible for the disparity; and (3) that the communicative and/or cognitive function of language served as the prime mover in the evolution of the uniquely human features of the human mind.

9.3.1. Are natural language sentences what makes the human mind human? Natural language tokens clearly play an enormous role in "extending" and even in "rewiring" the human mind (Bermudez 2005; Clark 2006; Dennett 1996). Gentner and colleagues, for example, have shown that relational labels play an instrumental role in facilitating young human learners' sensitivity to relational similarities and potential analogies (Gentner & Rattermann 1991; Loewenstein & Gentner 2005). Our ability to reason about large quantities of countable objects in a generative and systematic fashion seems to require the acquisition of numeric symbols and a linguistic counting system (Bloom & Wynn 1997). Numerous studies have shown that subjects with language impairment exhibit a variety of cognitive deficits (e.g., Baldo et al. 2005) and that deaf children from hearing families (i.e., "late signers") show persistent deficits in ToM tasks (see Siegal et al. 2001 for a review). Furthermore, there is good evidence that a child's ability to pass certain kinds of ToM tests is intricately tied to the acquisition of specific sentential structures (de Villiers 2000). Normal human cognition clearly depends on normal linguistic capabilities.

But although natural language clearly subserves and catalyzes normal human cognition, there is compelling evidence that the human mind is distinctively human even in the absence of normal natural language sentences (see Bloom 2000; Garfield et al. 2001; Siegal et al. 2001). Varley and Siegal (2000), for example, studied the higher-order reasoning abilities of an agrammatic aphasic man who was incapable of producing or comprehending sentences and whose vocabulary was essentially limited to perceptual nouns. In particular, he had lost all his vocabulary for mentalistic entities such as "beliefs" and "wants." Yet this patient continued to take care of the family finances and passed a battery of causal reasoning and ToM tests (see also Varley et al. 2001; 2005). Although late-signing deaf children's cognitive abilities may not be "normal," they nevertheless manifest grammatical, logical, and causal reasoning abilities far beyond those of any nonhuman subject (Peterson & Siegal 2000). And the many remarkable cases of congenitally deaf children spontaneously "inventing" gestural languages with hierarchical and compositional structure provide further confirmation that the human mind is indomitably human even in the absence of normal linguistic enculturation (see, e.g., Goldin-Meadow 2003; Sandler et al. 2005; Senghas et al. 2004).

Of course, the process of learning a language may "rewire" the human brain in ways that make certain kinds of cognition possible that would not be possible otherwise, even if the subject subsequently loses the ability to use language later in life. But this ontogenetic version of the "rewiring hypothesis" (Bermudez 2005) begs the question of what allows language to so profoundly rewire the *human* mind, but no other.

Over the last 35 years, comparative researchers have invested considerable effort in teaching nonhuman animals of a variety of taxa to use and/or comprehend language-like symbol systems. Many of these animals have experienced protracted periods of enculturation that rival those of modern (coddled) human children. The stars of these animal language projects have indeed been able to approximate certain superficial aspects of human language, including the ability to associate arbitrary sounds, tokens, and gestures with external objects, properties, and actions and a rudimentary sensitivity to the order in which these "symbols" appear when interpreting novel "sentences" (Herman et al. 1984; Pepperberg 2002; Savage-Rumbaugh & Lewin 1994; Schusterman & Krieger 1986). But even after decades of exhaustive training, no nonhuman animal has demonstrated a clear mastery of abstract grammatical categories, closed-class items, hierarchical syntactic structures, or any of the other defining features of a human language (cf. Kako 1999). Furthermore, there is still no evidence that symbol-trained animals are any more adept than symbol-naive ones at reasoning about unobservable causal forces, mental states, analogical inferences, or any of the other tasks that require the ability to cognize higher-order relations in a systematic, structural fashion (cf. Thompson & Oden 2000).

If the history of animal language research demonstrates nothing else, it demonstrates that you cannot create a human mind simply by taking a nonhuman one and teaching it to use language-like symbols. There must be substantive differences between human and nonhuman minds that allow the former, but not any of the latter, to master grammatically structured languages to begin with (cf. Clark 2001).

9.3.2. Is some aspect of the human language faculty the key? A more plausible variation on the language-only hypothesis is that some aspect of our internal faculty for language is responsible for our unique cognitive abilities. In a recent and influential version of this proposal, Hauser et al. (2002a) distinguish between the *faculty of language in the narrow sense* (FLN) and the *faculty of language in the broad sense* (FLB). They define FLN as including only the computational mechanisms specific to "narrow syntax" and to mapping syntactic representations into the systems of phonology and semantics. FLB, on the other hand, encompasses all the aspects of our sensory and cognitive systems that go into the production and comprehension of language, including the sensory-motor systems responsible for perceiving and producing the perceptual patterns of language, and the conceptual-intentional systems responsible both for representing the semantic/conceptual meaning of linguistic expressions and for reasoning about their implications. According to Hauser et al. (2002a), "most, if not all, of FLB is based on mechanisms shared with nonhuman animals" (p. 1573). On the narrowest and most ambitious version of their hypothesis (i.e., "Hypothesis 3," p. 1573), the only aspect of human cognition that is qualitatively unique to our species is specific to FLN, and in particular, to the computational mechanisms responsible for recursion.

We believe the available comparative evidence firmly rules out the narrowest and most ambitious version of Hauser et al.'s (2002a) hypothesis. While the computational mechanisms responsible for recursion – at least the kind of recursion characteristic of human languages – certainly appear to be unique to the human mind, there are many other aspects of human languages that are also uniquely human but not included in Hauser et al.'s (2002a) construal of FLN (see Pinker & Jackendoff 2005). More generally, over the course of this article, we have argued that there are many aspects of the human conceptual-intentional system that are unique to human subjects but are not specifically linguistic, ranging from our ability to reason about hierarchical social relations to our ability to theorize about unobservable causal mechanisms and mental states. Some of these cognitive capabilities also seem to require recursive operations over hierarchically structured representations (see our discussion regarding "the proper treatment of symbols in a nonhuman cognitive architecture" in section 10 of this article), suggesting that recursion is not specific to FLN. Indeed, Hauser et al. (2002a) themselves suggest that recursion evolved first in some noncommunicative domain. So, even according to their own hypothesis, the discontinuity between human and nonhuman minds presumably began before the evolution of the language faculty narrowly construed – although their hypothesis leaves unanswered what exactly changed in the human conceptual-intentional system to allow for the advent of recursive operations over hierarchically structured representations.

Carruthers (2002; 2005a) has proposed a much broader – and, we believe, more plausible – role for the language faculty in subserving human cognition. Carruthers argues that the distinctively human capacity for non–domain-specific, cross-modular thinking implicates representations in what Chomsky (1995) calls "logical form" (LF).[4] The LF hypothesis has much to recommend it. We do not doubt, for example, that there are many human cognitive abilities that rely on linguaform representations, including, but certainly not limited to, our ability to reinterpret our own thoughts in a propositional and domain-general fashion. What we dispute, however, is the implication that, aside from our language faculty, human and nonhuman minds are fundamentally the same.

Our review of the comparative evidence has highlighted a number of domains in which human subjects are able to reason in a fashion that seems beyond the grasp of any nonhuman animal. In order to support the claim that LF representations alone are responsible for the discontinuity between human and nonhuman cognition, one would have to argue that all of these uniquely human abilities – from our ability to reason about higher-order causal relations to our ability to impute unobservable mental states – are causally dependent on LF representations. But this seems inconsistent with the available evidence. Carruthers (2002) himself argues that the full-fledged, uniquely human ToM system that comes online at about four years of age is essentially "language-independent" in its mature form (p. 672). Hence, ToM provides at least one example of a cognitive module that is distinctively human but that is not entirely dependent on occurrent LF representations. Causal and logical reasoning provide two further examples. The disparities we highlighted between human and nonhuman causal cognition often occur in highly domain-specific, embodied tasks – for example, pushing a food reward out of a tube – which would seem to definitively rule out Carruthers's hypothesis that the discontinuity between human and nonhuman cognition is limited to non–domain-specific, cross-modular kinds of thinking. Furthermore, many prominent theories of logical and relational reasoning postulate that human subjects employ quasi-imagistic "mental models" (e.g., Goodwin & Johnson-Laird 2005). Carruthers (2002, p. 658) acknowledges the indispensable role these models play in human cognition; but there is good evidence that the mental models employed by human beings are non-sentential in structure and yet qualitatively different from those employed by nonhuman animals.

Finally, while LF representations may very well be necessary to reason about certain kinds of higher-order relations, particularly those involving linguistically mediated representations (Bermudez 2003; 2005), there is little reason to believe that LF representations are necessary in order to reason about any sort of higher-order relations at all. Indeed, the available evidence suggests otherwise. We noted above that humans without any appreciable grammatical or linguistic ability are nevertheless often able to reason quasi-normally about higher-order causal relations and mental states (e.g., Siegal et al. 2001). Conversely, subjects who suffer from frontal forms of frontotemporal dementia show selective impairment in the ability to integrate higher-order visuospatial relations (Waltz et al. 1999) and to pass ToM tests (Gregory et al. 2002) even when their linguistic abilities are still largely normal (see also Blair et al. 2007). This double dissociation suggests that the ability to reason about higher-order relations is not entirely encapsulated within our language faculty narrowly construed (i.e., FLN).

9.3.3. Did the adaptive functions of language drive the evolution of the human mind? The third – and, we believe, most plausible – version of the language-only hypothesis is that the communicative and/or cognitive functions of language played an instrumental role in the evolution of the human brain. Learning a language seems to require the ability to cognize higher-order abstract relations in a systematic, generative, and structural fashion. And it seems indisputable – at least to us – that the language faculty, broadly construed, is the product of extensive evolutionary tinkering (Pinker & Bloom 1990; Pinker & Jackendoff 2005). So it is possible that our ability to reason about higher-order relations evolved first in order to accommodate the requirements of language, and then was co-opted, exported, and/or duplicated for other purposes in nonlinguistic domains.

But there are good reasons, we would argue, to favor a more complex, coevolutionary relationship between human thought and human language (see also Bloom 1994; 2000; Bloom & Keil 2001). While the advantages of symbolic communication are enormous, the adaptive advantages of being able to reason in a relational fashion have a certain primacy over the communicative function of language. It is quite difficult to imagine how communicating in hierarchically structured sentences would be of any use without the ability to entertain hierarchically structured thoughts. But it is quite easy to imagine how the ability to reason about higher-order relations – particularly causal and mentalistic relations – might be highly adaptive without the ability to communicate those thoughts to anyone else. If one is a tool-using bipedal ape in a rapidly-changing environment surrounded by ambitious and conniving conspecifics, the evolutionary advantages of reasoning about higher-order relations go far beyond the ability to communicate hierarchical thoughts to those conspecifics.

Over the course of this target article, we have argued that our ability to reason about higher-order relations subserves a wide variety of distinctively human capabilities. It seems possible that the adaptive advantages of one or more of these capabilities might have played a critical role in pushing the human brain in a relational direction either in conjunction with, or even prior to, the evolution of the language faculty narrowly construed. Our coevolutionary story does not make language an exaptation (cf. Hauser et al. 2002a); nor does it make our prelinguistic relational capabilities a "pre-adaptation" for language (cf. Christiansen & Kirby 2003); nor does it deny the enormous evolutionary importance that language has had in "rewiring" the human mind (cf. Bermudez 2005). We are simply hypothesizing that the communicative function of language may have been just one among a number of factors that pushed the cognitive architecture of our species in a relational direction.

In any case, regardless of which factors most strongly contributed to the unique evolution of the human brain, language alone is no longer directly and entirely responsible for the functional discontinuity between extant human and nonhuman minds.

10. On the proper treatment of symbols in a nonhuman cognitive architecture

The crux of the matter, then, is to identify the specific changes to the hominoid cognitive architecture that enabled *Homo sapiens sapiens* to reason about higher-order relations in a structurally systematic and inferentially productive fashion, and ultimately resulted in the evolution of our unique linguistic, mentalistic, logical, and causal reasoning abilities. Behavioral evidence from extant animal species alone cannot tell us what changed in the neural architecture of the human brain since the split from our nonhuman ancestors. But when that evidence is combined with recent advances in computational models of biological cognition, it becomes possible to sketch a fairly detailed representational-level specification of the kind of changes we should be looking for.

10.1. The PSS hypothesis

The classical school of thought in cognitive psychology has insisted for more than three decades that both human and nonhuman minds are the product of a physical symbol system (Fodor 1975; 1997; Fodor & McLaughlin 1990; Fodor & Pylyshyn 1988; Newell 1980; 1990; Newell & Simon 1976; Pinker & Prince 1988). According to the now familiar tenets of the physical symbol system (PSS) hypothesis, mental representations are composed of discrete, symbolic tokens, which can be combined into complex representations by forming syntactically structured relations of various types. Cognitive processes, according to the classical view, are rule-governed algorithms that operate over the formal structure of these mental representations in a truth-preserving fashion. The classic defense of the PSS hypothesis is that it provides a computational account for several of the most spectacular aspects of human thought, including our abilities to generalize rule-like relations over abstract categorical variables, to reason in an inferentially coherent fashion, and to use the artificial symbols of a natural language in a systematic, recursive, and generative manner (Fodor & Pylyshyn 1988; Marcus 2001; Newell 1980; Pinker & Prince 1988).

The PSS hypothesis is certainly not the "only game in town" (Fodor 1975). Indeed, the PSS hypothesis has been roundly criticized for a variety of reasons, ranging from its biological implausibility to its inability to deal with the graded semantic flexibility of many cognitive processes (e.g., Barsalou 1999; Clark 1997; Rumelhart & McClelland 1986; van Gelder 1998). However, even among those who see the PSS hypothesis as fundamentally misguided, most would agree that human subjects are often able to approximate the systematic, higher-order, relational capabilities putatively associated with a PSS, at least in their linguistically mediated behavior. Smolensky (1999) calls this the "Symbolic Approximation" hypothesis: that is, the hypothesis that some – though certainly not all – aspects of human mental representations admit of abstract, higher-level descriptions that are closely approximated by the kinds of discrete, abstract structures posited by symbolic, linguistic theory.

In our view, the Symbolic Approximation hypothesis defines an essential and irreducible benchmark for any viable model of human cognition, far beyond the confines of linguistically mediated processes and symbolic, linguistic theory (Holyoak & Hummel 2000; 2001; Hummel & Holyoak 2003; 2005). Although the classical version of the PSS hypothesis appears dead as a model of biological cognition in general, there are compelling reasons to believe that something closely approximating the functionality of a PSS is necessary in order to subserve the systematic, higher-order relational inferences of which human subjects are manifestly capable (Gentner 2003; Goodwin & Johnson-Laird 2005; Halford et al. 1998a; Holyoak & Thagard 1995). Indeed, all of the most successful neurally inspired computational models of relational reasoning employ – or at least try to approximate the capabilities of – a PSS (e.g., Eliasmith & Thagard 2001; Hummel & Holyoak 2003; Plate 2000; Wilson et al. 2001). In our view, the operational question for researchers interested in modeling the human mind should no longer be whether the human mind implements a PSS, but rather how the higher-order relational capabilities of a PSS can be combined with the associative and generalization capabilities of a nonclassical system in a neurally plausible cognitive architecture (for similar views but alternative answers to this question, see Eliasmith & Thagard 2001; Marcus 2001; Plate 2000; Pollack 1990; Shastri & Ajjanagadde 1993; Smolensky 1990; 1999; Wilson et al. 2001).

The situation with respect to nonhuman minds, however, is quite different. In the following subsections, we evaluate the degree to which nonhuman minds approximate the defining features of a PSS. As will become quickly apparent, the comparative evidence does not support the all-or-nothing position taken by the orthodox version of the PSS hypothesis (e.g., Fodor & Pylyshyn 1988). Unlike the PSS hypothesis, however, the Symbolic Approximation hypothesis invites the possibility that different cognitive organisms may approximate different features of a PSS to varying degrees or even, pace Fodor and Pylyshyn (1988), in a punctate and content-specific manner. And, in fact, this is exactly what the comparative evidence suggests is the case.

10.2. Symbols

The PPS hypothesis is often construed as the claim that mental representations are *symbolic*. The problem with this construal is that there is little consensus among cognitive researchers on what it means for a representation to be "symbolic" (see discussion by Marcus 2001). Therefore, to sidestep the nettlesome issue of what counts as a "symbol" sensu stricto, we will start with a generic definition of a "mental representation" sensu largo and then ask which, if any, of the additional symbolic abilities postulated by the PSS hypothesis are found in the cognitive behavior of nonhuman animals.

Markman and Dietrich (2000) propose a sensible, minimalist definition of a mental representation as any internal information-carrying state that mediates a cognitive system's furtherance of its goals. We will not pretend that this definition puts to rest the entire – or even a small part – of the controversy surrounding what counts as a mental representation. But we nevertheless propose to stipulate without further argument that nonhuman animals employ "representations" in this minimalist sense, as even the most bare-boned associationist theory of animal learning agrees on the causal relevance of information-carrying mediating states, as well as the explanatory need for these states within comparative research.

The additional claim that nonhuman mental representations carry information about particular states of affairs and that these same representations can subsequently be used off-line in a productive fashion is slightly more controversial, but it should not be. It seems unarguable that nonhuman animals are capable of forming internal representations about discrete states of affairs that endure beyond the sensory-motor inputs giving rise to them. Honey-bees may not be capable of constructing full-fledged cognitive maps, but they are manifestly capable of keeping track of information associated with multiple landmarks they have encountered in the past and then using these representations of absent states of affairs in order to find their way home (e.g., Menzel et al. 2005). Scrub-jays may not have a theory of mind; but they are manifestly capable of remembering the "what," "when," and "where" information associated with tens of thousands of independent cache sites, and they can keep track of "who saw what when" for the purposes of protecting those sites from potential pilferers (Emery 2004; Emery & Clayton 2004b). Bermudez (2003), following Strawson (1959), calls these "particular-involving" representations; and we feel that it is indisputable that nonhuman animals represent the world in particular-involving ways.

Moreover, nonhuman animals apparently have the ability to update representations associated with a particular state of affairs – for example, where and when one particular piece of food was cached – without catastrophically affecting representations associated with other similar states of affairs – for example, where all the other pieces of food were cached. And they are able to update these representations in response to a single exposure (see, e.g., Clayton et al. 2003). For reasons cogently set forth by Blackmon et al. (2004), this means that the nonhuman animals are *atomistic learners* and that at least some of their internal representations are *functionally discrete*.

10.3. Compositionality

Perhaps the single most contentious claim of the PSS hypothesis is that mental representations are *compositional* – that is, complex mental representations are formed by combining discrete representational states into more complex structures such that different combinations of simpler representations can be used to represent different states of affairs in a combinatorial fashion. Few dispute the fact that human thought can approximate the functional effects of compositionality (cf. Prinz & Clark 2004). The purported compositionality of nonhuman animals' mental representations, on the other hand, has been the object of innumerable, hard-fought battles, particularly between the "associationist" and "symbolic" theoretical camps that have dominated comparative debate for many decades. In our view, the comparative evidence accumulated over the past quarter-century comes down firmly in favor of neither of these venerable theoretical alternatives. Instead, the available comparative evidence suggests that compositionality is a ubiquitous feature of animal cognition, albeit not necessarily the kind of compositionality posited by the PSS hypothesis or "symbolic" accounts of nonhuman cognition.

The PSS hypothesis argues not only that mental representations are compositional but also that they are compositional in a specific fashion: Complex compositional representations in a PSS are formed by *concatenation*, thereby retaining the identity of the original constituents, rather than by some other conjunctive mechanism that sacrifices the integrity of the original constituents (see discussions by Aydede 1997; Horgan & Tienson 1996; van Gelder 1990). Van Gelder (1990) has suggested that any cognitive system should be considered "functionally compositional" if it possesses generally reliable and effective mechanisms for (1) producing a complex representation given its constituents, and (2) decomposing a complex representation back into those constituents – regardless of whether these complex representations are formed by concatenation or by some other means.

As we see it, the comparative evidence leaves no doubt that the nonhuman mind employs enduring, functionally discrete, particular-involving mental representations that are at least functionally compositional in van Gelder's agnostic sense. As Horgan and Tienson (1996) point out, the complexity of social relationships among nonhuman animals would be literally unthinkable without the ability to represent novel dyadic relations by combining discrete representations associated with each individual in a combinatorial fashion. More generally, the well-documented ability of nonhuman animals to keep track of means-ends contingencies and predicate-argument relationships in a combinatorial fashion implies that they possess some generally reliable and productive mechanism for encoding the relation between particular constituents. Such a mechanism is necessary in order to ensure that when multiple relations predicate the same property, the fact that it is the same property in each case is somehow manifest in the structural similarity between the representations. Horgan and Tienson (1996) argue that this is all it should take in order for a representational system to qualify as "syntactically structured"; and therefore one must conclude, they argue, that nonhuman animals employ syntactically structured mental representations, albeit not necessarily in the concatenative sense posited by the PSS hypothesis.

We agree. And this conclusion rules out most traditional associative and distributed connectionist models as plausible accounts of the nonhuman mind (see again Marcus 2001). However, any number of researchers have proposed nonclassical connectionist architectures that are functionally discrete, particular-involving, and syntactically structured without being concatenatively compositional in the sense postulated by the PSS hypothesis (e.g., Plate 1991; Pollack 1990; Smolensky 1990; van Gelder 1990; Wilson et al. 2001). Many of these proposals can account for the kind of compositionality manifested by nonhuman animals. Therefore, none of the comparative evidence available to date warrants the widespread assumption among comparative cognitive researchers (e.g., Gallistel 2006) that nonhuman animals necessarily form compositional representations in the concatenative fashion proposed by the PSS hypothesis.

Indeed, as we will see below, nonhuman animals do not even come close to approximating any of the other, more distinctive, higher-order features of a PSS. Therefore, at least in biological organisms, the various representational capabilities putatively associated with a PSS are not a package deal as a matter of nomological necessity (see Hadley 1997).

10.4. Types and tokens

The distinction between types (e.g., kinds, classes, roles, variables) and tokens (e.g., individuals, instances, fillers, values) is one of the essential characteristics of a genuine PSS. A PSS maintains explicit information about the syntactic type identity of each structural relation it employs and the type identity of its allowable constituents as distinct from the constituents involved in any particular relational instance. For example, in a PSS, the abstract characteristics of the *loves* relation is explicitly represented and invariant to whether *John loves Mary* or *Mary loves John*.

The ability to reason about the relation between types and tokens pervades many aspects of human thought. Role-governed rules appear to be a formative feature of all human languages; and the universal ability of humans to learn novel role-governed rules is evident not only in their mastery of natural human languages but also in their ability to extract the abstract rules of artificial grammars in AGL experiments. "Role-governed categories" (Markman & Stilwell 2001) also play a central role in human concept formation far beyond the abstract grammatical structures of language. A human subject is perfectly capable of reasoning about a role-based category such as "lovers" or "mothers" or "tools" without there being any set of perceptual features that all lovers, mothers, or tools have in common. Moreover, the ubiquitous human capacity to find analogical correspondences between perceptually disparate relations appears to require an ability to find systematic correspondences between the roles defined for those relations as distinct from the perceptual similarity between the fillers of these roles (Gentner 1983; Gentner & Markman 1997; Markman & Gentner 1993; 2000). Therefore, analogical inferences – one of the hallmarks of the human mind and a prominent feature of abstract causal reasoning and ToM – seem to require the ability to distinguish between roles and their fillers and to dynamically "bind" one with the other without corrupting the independence of either. Notably, the ability to maintain role-filler independence while dynamically binding roles and fillers to particular relations seems to require the kind of concatenative compositionality posited by the PSS hypothesis (for more extensive discussions of this point, see Doumas

& Hummel 2005; Holyoak & Hummel 2000; Hummel & Holyoak 2003; Hummel et al. 2004).

Whereas an explicit and concatenative relation between types and tokens appears to be necessary to explain human subjects' higher-order relational capabilities, there is no need or evidence for this distinction in nonhuman cognitive behaviors. Nonhuman animals appear to reason on the basis of "feature-based categories" alone (Markman & Stilwell 2001) – that is, they appear to represent categories such as "mothers," "tools," or "kin" based on particular sets of features shared by members of the category (e.g., gender, perceptual affordances, affiliative behavior) rather than on the abstract role that members play in a given relational schema. Moreover, there is no evidence, as we argued above, that nonhuman animals are able to process analogical relations or role-governed rules in a human-like fashion. Thus, one of the fundamental features of a PSS, the explicit distinction between types and tokens, appears to be absent from the cognitive behavior of nonhuman animals.

10.5. Structural relations

Classical theories posit that there are a wide range of distinct structural relations between content-bearing representations, of which "constituency" is the most prominent example (Fodor & Pylyshyn 1988). One of the defining features of a PSS is that it allows cognitive processes to operate over the formal structure of a relation in a truth-preserving fashion independently of the relation's particular constituents. Among other things, this permits the PSS hypothesis to explain how recursive operations over hierarchically structured representations can be both inferentially coherent and computationally feasible.

We have argued earlier that nonhuman mental representations are functionally compositional and syntactically structured. Therefore, the nonhuman cognitive architecture must be capable of operating over a range of structural relations between content-bearing representations as well. The comparative evidence suggests, however, that nonhuman animals are unable to reason about the higher-order structural relation between these relations in a human-like fashion and are unable to perform those kinds of operations – such as recursion and deductive inference – which apply to the formal structure of a relation independently from the semantic or perceptual features of its constituents. Many theorists, for example, have suggested that humans form a "causal model" of the network of causal relations within a given domain and then use this causal network to make novel inferences and plan their interventions in a quasi-experimental fashion (Gopnik et al. 2004; Hagmayer et al. 2007; Waldmann & Holyoak 1992). Nonhuman animals also appear to be implicitly sensitive to the differences between certain basic causal structures (see Blaisdell et al. 2006). Unlike humans, however, nonhuman animals appear to be incapable of explicitly reasoning about these causal networks in a diagnostic manner, of recognizing the structural similarities between perceptually disparate causal relations, of generalizing their prior knowledge about causal structures to novel contexts, or of reasoning about the structure of causal relations independently of their particular perceptual features (see our discussion in Penn & Povinelli 2007a).

In our review of the comparative evidence for hierarchical representations and transitive inferences, we found that nonhuman animals reason solely in terms of first-order perceptual relations (e.g., rates of affiliation, reinforcement history, and outcomes of dyadic agonistic encounters), rather than in terms of the logical, role-governed, and/or structural aspects of the relations themselves. Although metrics such as "early association," "familiarity," and "age similarity" may provide heuristic proxies for the kinship relation between two conspecifics, these metrics reduce a role-based, structured relation to an analog chunk and forgo the ability to reason about the higher-order relation between these relations independently of their particular perceptual characteristics. There is no evidence, for example, that nonhuman animals understand the higher-order relation between the *grandmother-of* and *mother-of* relation, or the analogical similarity between the *father-of* and *mother-of* relation. Similarly, the performance of nonhuman animals on RMTS tasks suggests that nonhuman animals are chunking these relations into analog measures of variability, rather than reasoning about the structural relation between relations per se. And we came to similar conclusions with respect to nonhuman animals' performance on tests of transitive reasoning.

In short, the comparative evidence suggests that nonhuman mental representations are implicitly structured, but that nonhuman animals are incapable of representing these structural relations explicitly (i.e., of explicitly tokening the relation qua relation) and therefore are incapable of reasoning about the higher-order structural relation between relations in a recursive, systematic, or productive fashion.

10.6. Systematicity

Fodor and Pylyshyn (1988) famously argued that all cognitive organisms capable of understanding *aRb* must also understand *bRa*, where *a* and *b* are referential entities and *R* is some relation. An oft-cited example is that any organism that can understand *John loves Mary* will necessarily understand *Mary loves John* or any other systematic variant thereof. Fodor and Pylyshyn (1988) called this feature of thought *systematicity*. They argued that (1) systematicity is a unique effect of a PSS; (2) it is universally observed in all cognitive organisms; and therefore (3) all cognitive organisms must employ a PSS. As Fodor and Pylyshyn (1988, p. 28) put it, "that infraverbal cognition is pretty generally systematic seems, in short, to be about as secure as any empirical premise in this area can be."

Many critics have pointed out that Fodor and Pylyshyn's formulation of systematicity was not particularly well-defined or operationally tractable (e.g., Doumas & Hummel 2005; Hadley 1994; Niklasson & van Gelder 1994). Moreover, it turns out to be relatively easy for clever connectionist models to replicate many of the examples of systematicity cited by Fodor and Pylyshyn without resorting to classically structured representations (e.g., Chalmers 1990; Niklasson & van Gelder 1994; Plate 1991; Smolensky 1990).

The argument from systematicity fares even worse from a comparative point of view. Nonhuman cognition is certainly systematic and productive to some degree, but it does not appear to be systematic in the way or for the reasons postulated by the PSS hypothesis. Certainly, any animal capable of thinking the thought *dominates*(A, B) is likely to be able to think the thought *dominates*(B, A) for any arbitrary pair of conspecifics of the appropriate age and gender. And this kind of systematicity is often cited by advocates of the classical school of thought to support extending the PSS hypothesis to nonhuman animals (e.g., Carruthers 2004; Fodor & Pylyshyn 1988). But there is a fundamental difference between the kind of systematicity manifested by nonhuman animals and the kind of systematicity posited by the PSS hypothesis.

The kind of systematicity manifested by nonhuman animals is limited to perceptually based relations in which the values that each argument can take on in the relation are constrained only by observable features of the constituents in question (e.g., the gender and age of the conspecific). Feature-based systematicity such as this does not require the cognizer to posit relational roles distinct from the relations' constituents, nor to cognize the fact that certain relations logically imply certain other relations. Not coincidentally, this is also the kind of systematicity that happens to be easily implemented by many nonclassical connectionist models (e.g., Niklasson & van Gelder 1994). But as Fodor and colleagues have repeatedly argued (e.g., Fodor 1997; Fodor & McLaughlin 1990), the kind of systematicity posited by the PSS hypothesis is not statistical or accidental or a by-product of domain-specific adaptations; rather, it arises as a matter of nomological necessity from the fact that a PSS defines relations structurally. Classical systematicity entails cognizing the fact that certain relations necessarily imply other relations independently of any particular domain or learning context: for example, for all R, the relations R(a,b) and R(b,c) necessarily imply the relation R(a,c) provided that R is a transitive relation.

There is no evidence for this kind of classical, inferential, role-governed, domain-independent systematicity among nonhuman animals.

11. The relational reinterpretation hypothesis

Here's the pickle. On the one hand, despite its many flaws, the PSS hypothesis lays out a package of representational capabilities that appear to be well – though imperfectly – approximated by normal human minds. On the other hand, whereas nonhuman minds approximate some of these same capabilities to some degree, they do so to a significantly lesser degree than human minds do, and in some cases, not at all.

The comparative evidence therefore poses a serious challenge to the classical version of the PSS hypothesis. All of the strongest empirical arguments for the PSS hypothesis rest on representational capabilities that appear to be largely absent from nonhuman species – for example, inferential systematicity, types and tokens, concatenative compositionality, and explicitly hierarchical relations. In short, the evidence for a classical PSS among infraverbal organisms is a lot less "secure" than Fodor and Pylyshyn (1988) assumed.

The comparative evidence poses an equally serious challenge for many prominent nonclassical theories of cognition. The most extreme critics of the classical school have argued that one can do without the notion of "representation" and "computation" altogether (e.g., Brooks 1991; van Gelder 1995; 1998). But the comparative evidence definitively rules out any nonrepresentational, purely embodied, or traditional associative account of animal cognition; and it strongly suggests that nonhuman minds, like human ones, are highly structured, information-processing devices in a way that stomachs and Watt governors are not (cf. Clark 2001). Indeed, nonhuman minds approximate certain features of a PSS that are extremely problematic for the kind of traditional distributed connectionist systems that have been the principal antagonist to the PSS hypothesis for more than a quarter century (Elman 1996; Hinton et al. 1986; Rumelhart & McClelland 1986). Whatever kind of architecture the nonhuman mind employs, it is certainly not based solely on traditional distributed connectionist networks or associative learning.

The comparative evidence therefore leads us to propose a hybrid alternative to the orthodox debate between classical and nonclassical theories of cognition: what we call the *relational reinterpretation* (RR) *hypothesis.* Povinelli's "reinterpretation hypothesis" previously suggested that humans alone are able to "reinterpret" the world in terms of unobservable causal forces and mental states (e.g., Povinelli 2000; Povinelli et al. 2000). According to our relational reinterpretation hypothesis, the discontinuity between human and nonhuman minds extends much farther: to any cognitive capability that requires reinterpreting perceptual relations in terms of higher-order, structural, role-governed relations.

According to the RR hypothesis, animals of many taxa employ functionally compositional, particular-involving, syntactically structured mental representations about observable features, entities, and relations in the world around them. Furthermore, they form abstract representations about statistical regularities they perceive in the behavior of certain classes of physical objects (e.g., observable causal relations) and other animate agents (e.g., affiliative interactions) and are capable of using these representations off-line to make decisions in a flexible, reliable, and ecologically rational (i.e., adaptive) fashion. Human animals alone, however, possess the additional capability of reinterpreting these perceptually grounded representations in terms of higher-order, role-governed, inferentially systematic, explicitly structural relations – or, to be more precise, of approximating these higher-order features of a PSS, subject to the evolved, content-specific biases and processing capacity limitations of the human brain. *Ex hypothesi*, the discontinuity between the cognitive abilities of human and nonhuman animals – including our unique linguistic, logical, mentalistic, cultural and causal reasoning abilities – largely results from the substantial difference in degree to which human and nonhuman minds are able to approximate the relational capabilities of a PSS.

Our RR hypothesis bears more than a nominal resemblance to Karmiloff-Smith's (1992) "representational redescription" hypothesis and to the growing family of "dual-process" accounts of reasoning (Evans 2003). The case for two broad "systems" of reasoning within the human mind is already well-founded on the basis of the evidence from human cognitive behavior alone. Our review of the comparative evidence suggests that a dual-process account is well-founded from a comparative perspective as well. And our version of the RR hypothesis is indebted to Karmiloff-Smith's (1992) earlier and perspicacious argument that what makes human cognition unique lies in the manner that we "reinterpret" the lower-order representations we share with other animals (Povinelli et al. 2000). Unlike most dual-process account theorists, however, we do not believe that the nonhuman mind (a.k.a. "System 1") is limited to automatic, associative processes. Indeed, we believe that nonhuman animals are capable of many kinds of "representational redescriptions" – just not the structurally systematic, role-governed relational redescriptions that are the hallmark of the human mind.

Importantly, we are not claiming that our higher-order relational capabilities are the sole and sufficient condition for explaining all of our species' unique cognitive abilities. The uniquely human biological specializations associated with language (see Pinker & Jackendoff 2005), ToM (see Saxe 2006), and complex causal reasoning (see Johnson-Frey 2004) – to take only the most obvious candidates – are clearly much more multifarious than a domain-general capacity for higher-order relational reasoning alone. Our claim, rather, is that the ability to reason about higher-order structural relations in a systematic and productive fashion is a necessary – but not sufficient – condition for the normal development and full realization of these other capabilities in human subjects. Our further claim is that it is highly unlikely that the human ability to reason about higher-order relations evolved de novo and independently with each distinctively human cognitive capability. Rather, it seems much more likely that higher-order relational reasoning belongs to a single "supermodule" which is duplicated, reused, shared, or called upon by the functional "modules" associated with each of these other distinctively human cognitive capabilities (see Barrett 2006 for an important discussion of the many possible relationships between architectural, developmental, and functional modularity).

Nor should our RR hypothesis be reduced to the claim that human minds employ a classical "language of thought" (LoT) and nonhuman minds do not. We have argued, both here and elsewhere, that it is highly unlikely that human subjects are pure LoT processors in the sense imagined by the classical PSS hypothesis (see Doumas & Hummel 2005; Holyoak & Hummel 2000; Hummel & Holyoak 2003; 2005). Furthermore, given our analysis of the comparative evidence, the representational systems employed by nonhuman animals arguably merit being construed as a kind of nonclassical *proto*-LoT, analogous to the protolanguages that some researchers suggest preceded the evolution of human language (e.g., Bickerton 1995). Indeed, it seems likely to us that different species, as well as different "modules" within the cognitive architecture of a given species, approximate different features of a PSS to varying degrees. The evolutionary result, in our opinion, is that "every species gets the syntax it deserves" (Bloom 2000, p. 517), rather than a dichotomous distinction between those with a LoT and those without.

To be sure, we believe there is at least as great a discontinuity between our human LoT and the proto-LoTs of nonhuman animals as there is between the protolanguages of early humans and the languages employed by modern *Homo sapiens*. Accordingly, our RR hypothesis is more accurately portrayed as the claim that a distinctively human, modular system for approximating a LoT – that is, one that subserves higher-order, role-governed relational representations in a systematic and domain-general fashion – has evolved on top of and reinterprets the output of the *proto-symbolic* systems we still share with other animals.

Some readers may take the last few paragraphs as a retreat from our initial claim that Darwin was mistaken. Our disagreement with Darwin is, indeed, hedged. Contrary to Darwin's "mental continuity" hypothesis, we have argued that there is a functional discontinuity between human and nonhuman minds – specifically, that only human animals are able to reason about higher-order relations in a structurally systematic and inferentially productive fashion. But, at the same time, we have acknowledged from the outset that this cognitive gap must have evolved largely through incremental, Darwinian processes. The question that naturally arises, then, is this: What representational-level and physical-level innovations explain how this functional discontinuity between human and nonhuman minds arose in an evolutionarily plausible manner?

11.1. LISA: Relational reasoning in a biological symbol system

We do not by any means have a complete answer to this formidable question; but we can at least point to work that suggests one possible step towards an answer. Hummel and Holyoak (1997; 2003; 2005) have proposed a hybrid symbolic-connectionist model of relational reasoning – LISA (*Learning and Inference with Schemas and Analogies*) – which we view as one promising (though partial) approach to implementing our RR hypothesis in a computationally feasible and neurally plausible fashion (see also Holyoak & Hummel 2000; 2001; Morrison et al. 2004). LISA combines the syntactic strengths of a PSS with the semantic flexibility and generalization capabilities of a distributed connectionist system by using temporal synchrony to approximate the dynamic role-filler binding capabilities of a PSS within a connectionist architecture. Notably, LISA implements the distinctive higher-order relational capabilities of a PSS via an additional representational system that has been grafted onto a simpler system of conjunctive representations used for long-term storage. This simpler system provides conjunctive representations that are functionally, but not concatenatively, compositional and therefore is arguably sufficient to approximate the representational capabilities of nonhuman animals but insufficient to approximate the higher-order relational capabilities of humans.

LISA provides an existence proof that the higher-order relational capabilities of a PSS can, in fact, be grafted onto a neurally plausible, distributed connectionist architecture. At the same time, LISA shows that it is quite hard to approximate the higher-order relational capabilities of a PSS within a neural network – particularly to achieve both role-filler independence and dynamic role-filler binding. In other words, LISA suggests that approximating the higher-order, role-governed features of a PSS is not likely to be an ability that evolved by accident or as a by-product of increased brain size, greater neural plasticity, or larger processing capacity alone. There must be other substantive differences between human and nonhuman primate brains waiting to be discovered (Preuss 2004).

If LISA is broadly correct, the substantive difference between human and nonhuman brains will be found in the prefrontal cortices, and specifically in synchronized activity among prefrontal neural populations that support working memory, as well as among neural populations in the frontal and posterior cortical areas (see Lu et al. 2006; Morrison et al. 2004; Robin & Holyoak 1995; Waltz et al. 1999; 2004). Of course, we are not suggesting that temporal synchrony among prefrontal neural populations is the only possible neural-level explanation for the functional differences between human and nonhuman relational cognition, nor that it provides a full explanation (see, e.g., Jung & Haier 2007). We are simply suggesting that computational models of biological cognition such as LISA provide an important tool for comparative researchers wishing to formulate biologically plausible, representational-level hypotheses concerning the similarities and differences between human and nonhuman minds.

11.2. Moving forward

Admittedly, our RR hypothesis has a number of substantial holes. With respect to the empirical evidence, we have not directly addressed a number of important cognitive domains. In some cases – for example, numeracy, cooperation, and mental time travel – others have already proposed analyses of the functional discontinuity between human and nonhuman animals' capabilities that are largely consistent with the hypothesis defended in the present article (see, e.g., Dehaene 1997; McElreath et al. 2003; Suddendorf & Corballis 2007a). In other cases – for example, empathy and metacognition – the discontinuity between human and nonhuman minds continues to be challenged (cf. Preston & de Waal 2002; Smith et al. 2003). We believe our analysis and hypothesis can (and should) be extended to these latter domains as well. Indeed, we believe that our RR hypothesis offers a powerful framework for explaining what all these disparate cases – from cooperation and mental time travel to numeracy and metacognition – have in common. But we acknowledge that we have not had the space to extend our analysis to these other domains herein.

With respect to our representational-level claims, we have not specified how our proposed symbolic-relational supermodule combines inputs from such a motley collection of perceptual and conceptual modules in a computationally feasible fashion. Fodor (2000) has argued that this problem is unsolvable, and therefore that the human mind cannot, in the end, be entirely computational. We do not have a complete solution to Fodor's challenge; but, like many others, we do not believe it is in principle unsolvable (Barrett 2005; Carruthers 2005b; Pinker 2005). Hybrid symbolic-connectionist architectures such as LISA provide one possible solution that Fodor has not considered.

The most glaring weakness in our hypothesis is that we have no complete, biologically plausible model of nonhuman cognition to propose. Many who have adopted some form of the Symbolic Approximation hypothesis have taken on the ambitious goal of trying to determine how the unique symbolic capabilities of the human mind might be implemented in a neurally plausible architecture (e.g., Holyoak 1991; Hummel & Holyoak 2003; Marcus 2001; Plate 1991; Pollack 1990; Shastri & Ajjanagadde 1993; Smolensky 1990; 1999; Wilson et al. 2001). Although we applaud the efforts of these researchers and believe that they are already shedding new light on our species' unique relational capacities, relatively little effort has been invested in modeling the relational abilities of other cognitively sophisticated animals. In our view, the entire field of cognitive science – not just our particular hypothesis – would benefit if more effort were focused on constructing biologically plausible, behaviorally accurate, computationally feasible models of the cognitive abilities of honeybees, corvids, and chimpanzees, in addition to the cognitive abilities of enculturated, language-wielding humans.[5]

Fortunately, the fate of our RR hypothesis does not ride on the success or failure of any particular computational proposal. Our most important claim in this target article is simply that whatever "good trick" (Dennett 1996) was responsible for the advent of human beings' ability to reinterpret the world in a symbolic-relational fashion, it evolved in only one lineage – ours. Nonhuman animals didn't (and still don't) get it.

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NOTES

1. Let us be clear: All similarities and differences in biology are ultimately a matter of degree. Any apparent discontinuities between living species belie the underlying continuity of the evolutionary process and largely result from the fact that many, and often all, of the intermediate steps are no longer extant. In the present article, our claim that there is a "discontinuity" between human and nonhuman cognition is based on our claim that there is a significant gap between the functional capabilities of the human mind and those of all other extant species on the planet. Our point, to cut to the chase, is that the functional discontinuity between human and nonhuman minds is at least as great as the much more widely acknowledged discontinuity between human and nonhuman forms of communication. But we do not doubt that both evolved through standard evolutionary mechanisms.

2. It is important to distinguish between causes that are in principle unobservable (such as gravity and mental states) and causes that are temporarily absent or hidden in a particular context. We do not doubt that nonhuman animals can learn about the latter (e.g., Blaisdell et al. 2006; Call 2004; Wasserman & Castro 2005). What we doubt is that nonhuman animals can learn or reason about the former.

3. Importantly, we are *not* claiming (cf. Emery & Clayton, in press; Tomasello et al. 2003b) that corvids – or other nonhuman animals – are limited to reasoning about concrete, occurrent cues in the immediate environment. To the contrary, we believe it is obvious that nonhuman animals are perfectly capable of keeping track of past events, as well as forming general abstractions about observed behavioral regularities, and that they can use these multifarious representations in a flexible and adaptive fashion (see again Penn & Povinelli 2007b; Povinelli & Vonk 2004). Our claim is simply that nonhuman animals' representations do not extend to higher-order relations involving mental states.

4. It is important to note that LF representations are not the same thing as a "language of thought" (LoT). LF representations, Carruthers (2002) explains, contain lexical items drawn from the specific natural language spoken by the cognizer, whereas a LoT is purportedly independent of any particular natural language.

5. Let us add, the hypothesis we have proposed herein provides yet another argument for the necessity of keeping viable populations of these nonhuman species available for comparative cognitive research (Preuss 2006).

Open Peer Commentary

Out of their heads: Turning relational reinterpretation inside out

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Abstract: Although Penn et al's incisive critique of comparative cognition is welcomed, their heavily computational and representational account of cognition commits them to a purely internalist view of cognitive processes. This perhaps blinds them to a distributed alternative that raises the possibility that the human cognitive revolution occurred outside the head, and not in it.

Penn et al's reassessment of claims for the human-like nature of nonhuman cognition is both timely and welcome, and I agree wholly with its sentiments. On the one hand, a rejection of the anthropocentric (and often anthropomorphic) emphasis of current comparative research strategies serves to increase our recognition of, and receptiveness to, the potential diversity of psychological mechanisms that exist across the animal kingdom, and it draws us away from the evolutionarily impoverished view that other species' cognition will merely represent some or other variant of our own. On the other hand, and despite their rejection of "classical" physical symbol system (PSS) models, Penn et al. continue to rely heavily on a computational model of cognition that places all the interesting work to be done solely inside the organism's head. This diminishes Penn et al.'s otherwise laudable attempt to get things back on a more appropriate evolutionary footing while, at the same time, it leaves no room for the truly novel aspects of human cognition that seem likely to account for the differences that exist between us and other species. Specifically, Penn et al.'s rejection of "non-representational, purely embodied" processes as having anything much to tell us about nonhuman cognition, and their conclusion that the comparative data "strongly suggests that nonhuman minds are . . . highly structured, information-processing devices in a way that stomachs and Watt governors are not" (sect. 11, para. 3) seems premature, not least because the comparative literature reviewed in their article is framed and interpreted within a computational metaphor that regards internal representational structure and information processing as axiomatic; such data must inevitably support this conclusion, but do not rule out other possible mechanisms. By being in thrall to a representational theory of mind based on the computer metaphor, Penn et al. are obliged to draw a representational line in the sand that animals are unable to cross in order to account satisfactorily for the differences between ourselves and other animals. The suggestion here is that, if Penn et al. step back from this computational model and survey the problem more broadly, they may recognize the appeal of an embodied, embedded approach, where the ability of humans to outstrip other species may be a consequence of how we exploit the elaborate structures we construct in the world, rather than the exploitation of more elaborate structures inside our heads.

First and foremost, we need to recognize that all cognition is, by definition, "purely embodied," for how can it be otherwise? Indeed, even the use of the term "embodied cognition" is rather misleading, for it suggests that there is an alternative – a disembodied cognition – that does not, in fact, exist (with the exception of a computer interface, perhaps). The fact of the matter is that all animals possess bodies, and all animals did so before they possessed anything remotely recognizable as a brain: this is the substance of Brooks's (1991; 1999) criticism of classical approaches. As he correctly points out, most of evolutionary history has been spent perfecting the perception and action mechanisms that enable survival in a dynamic world. It is these mechanisms, rather than "high-level" forms of cognition, like planning, logical inference, and formal reasoning, that are most informative to an evolutionary cognitive science because they constrain the forms that these high-level processes can take. Linked to this is the idea that, unless we take perception-action mechanisms seriously, exploring both their scope and limits, the "cognitive processes" that we see may be illusory, reflecting only our own frame of reference and not that of the animal itself (Brooks 1991; 1999; Pfeifer & Bongard 2007). The realization that an organism's understanding of the world will be shaped by, and grounded in, the means by which it perceives and acts in the world, is at least as old as von Uexküll's (1934/1957) expression of the *Umwelt*, and it seems both necessary and vital to the comparative project. Equally, van Gelder's (1995) analogy of the Watt governor is as much about broadening the definition of a "cognitive system" to include the body and environment, as well as the brain – and the dynamic coupling that exists between these elements – as it is about contesting the notion of cognition as symbolic computation. Of course, cognitive systems are not literally like Watt governors, but neither are they literally like computers. Unlike these other analogies, however, the brain-as-computer has been taken both very literally and very seriously, and it underpins the particular view of cognition that current comparative studies, and Penn et al., endorse, where an animal's brain is placed at a remove from its body and the world in which it lives. This, in turn, implies that brain processing is completely insulated from the world, raising all the difficulties of the "symbol grounding" problem.

Giving the body and the environment their due as integral parts of biological cognitive systems has a further corollary, in that we should not expect evolved organisms to store or process information in costly ways, when they can use the structure of the environment, and their ability to act in it, to bear some of that cognitive load (Clark 1989; 1997). The Klipsch horns built by mole crickets to give their mating calls a boost and the watery vortices that blue fin tuna create and exploit to increase muscular propulsion while swimming are both superb examples of how organisms exploit the structure of the environment in adaptive fashion (Clark 1997). Why should cognitive systems be any different? If we think of cognitive systems as distributed across brain, body, and world (Clark 1997), it gives rise to a theory of cognition that is both fully grounded, as an evolutionary account requires, and able to account for the functional differences between ourselves and other animals in terms of the degree to which our minds are extended beyond the strictures of "skin and skull." As Clark (1989) has also suggested, this insight raises the prospect that many classic, symbolic van Neumann architectures may have mistakenly modeled "in-the-head" computation "on computation that, in humans, consists of both an in-the-head component and (to begin with) an in-the-world component" (p. 135). Our current ability, for example, to solve logical syllogisms by constructing Venn diagrams in our heads may only be possible because, initially, we were able to construct or observe such diagrams in a concrete, external physical form (Clark 1989, p. 133). From a purely internal perspective, then, the cognitive processes of humans and other animals may well be quite similar. The difference, paradoxically, may lie in our ability to create and exploit external structures in ways that allow us to augment, enhance, and support these rather mundane internal processes.

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The reinterpretation hypothesis: Explanation or redescription?

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Abstract: Penn et al. propose the *relational reinterpretation hypothesis* as an explanation of the profound discontinuities that they identify between human and nonhuman cognition. This hypothesis is not a genuine replacement for the explanations that they reject, however, because as it stands, it simply redescribes the phenomena it is trying to explain.

The target article provides a welcome corrective to many of the over-hasty conclusions that have been drawn about the cognitive abilities of nonlinguistic creatures. Penn et al. provide detailed critical analyses of many of the experiments routinely cited as evidence of cognitive commonalities between human and nonhuman animals. As the authors point out, many of these experiments warrant a far more parsimonious interpretation than they generally receive. The case that they make for a profound discontinuity between the human mind and the nonhuman mind is powerful indeed (although I imagine that other commentators will have much to say about the details of their arguments).

Nonetheless, the authors are categorical in rejecting the thesis that nonhumans are purely associative, stimulus-response machines. They claim (surely correctly) that nonhuman animals are capable of representing particular objects in ways that allow those objects to be re-identified and that involve sensitivity to some of the relations in which those objects can stand. From this it follows, they claim (again, surely correctly) that the cognitive abilities of nonlinguistic creatures must be compositional and systematic in some substantive sense. They propose that the representational systems of nonlinguistic creatures are *functionally compositional* and *featurally systematic*. These systems are functionally compositional in that they can represent structured entities in such a way that there are effective and reliable processes both for building representations from their constituents and for decomposing representations into their constituents. Representations can be functionally compositional without being concatenatively compositional – that is, without being literally built up in a way that reflects the structure of what they represent. Nonhuman representations are featurally systematic in that they permit a limited form of recombination: "The kind of systematicity manifested by nonhuman animals is limited to perceptually based relations in which the values that each argument can take on in the relation are constrained only by observable features of the constituents in question" (sect. 10.6, para. 4). This is much weaker than the much discussed classical notion of systematicity discussed by authors such as Fodor and Pylyshyn (1988).

Suppose that this is all true as a description of the differences between human and nonhuman cognition. It raises two obvious questions:

1. What is the relation between functional compositionality and featural systematicity?

2. What explains the fact that animal representational systems cannot be concatenatively compositional and classically systematic?

The relational reinterpretation hypothesis is intended as a first step in answering both these questions. Penn et al. write, "The discontinuity between human and nonhuman minds extends much farther: to any cognitive capability that requires reinterpreting perceptual relations in terms of higher-order, structural, role-governed relations" (sect. 11, para. 4). The basic idea is that nonhuman animals are capable of identifying and reasoning about certain classes of objects, properties, and relations – namely, those that can be identified through perceptible similarities and perceptible statistical regularities. What characterizes human cognition is the ability to represent higher-order, structural relations that, for example, permit objects to be classified in terms of their abstract roles and functions.

As far as the first question is concerned, the relation between functional compositionality and featural systematicity is that both are required for sensitivity to perceptual relations. And, with regard to the second question, concatenative compositionality and classical systematicity are ruled out for nonlinguistic creatures because they involve relational reinterpretation. The first answer has some plausibility. Sensitivity to perceptual relations requires the ability to track objects and to have minimally structured representations. The second answer, however, is less persuasive. The problem is that the relational reinterpretation hypothesis seems to only redescribe the phenomena it is trying to explain. It is hard to see what the difference is among the following:

(a) Being able to represent higher-order relations, abstract roles, and functions (the capacity for relational reinterpretation)

(b) Having representations that have components corresponding to higher-order relations, abstract roles, and functions (concatenative compositionality)

(c) Having representations that permit constituents to be recombined in ways constrained only by the abstract roles and functions of those constituents (classical systematicity)

If there is any difference at all between (a), on the one hand, and (b) and (c), on the other, it is simply that (b) and (c) are special cases of (a). This does not really help us to see *why* (b) and (c) are uniquely human cognitive achievements.

What would be needed to turn a redescription into an explanation is an account of why exactly (a) is unavailable to nonhuman animals. The authors do not have much to say about this. The LISA (Learning and Inference with Schemas and Analogies) model of relational reasoning that they propose at the end is a model of the mechanisms that enable (a), but again the model appears to recapitulate the basic description rather than do much explanatory work. As the authors describe it, LISA "implements the distinctive higher-order relational capabilities of a PSS [physical symbol system] via an additional representational system that has been grafted onto a simpler system . . . [providing] conjunctive representations that are functionally, but not concatenatively, compositional" (sect. 11.1, para. 1). Of course, this is interesting and important. But it fails to address the fundamental questions of why the representational systems of nonhuman animals must be of the "simpler" type and what it is about humans that allows them to have the "additional" system grafted onto the "simpler system."

One obvious way of answering these questions is to highlight the distinctiveness of human linguistic abilities – either by way of the "rewiring hypothesis" proposed by Dennett (1996), Mithen (1996), and Bermúdez (2003; 2005) or by Carruthers's appeal to the role of representations in logical form in domain-general, abstract thinking (Carruthers 2002). Penn et al. reject these proposals. Whatever their ultimate merits, however, these proposals quite plainly offer explanatory hypotheses. If Penn et al. are to offer a genuine alternative, they need to make clear just how their account is an explanation of the uniqueness of human cognition, rather than simply a description of that uniqueness.

Darwin's last word: How words changed cognition

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Abstract: Although Penn et al. make a good case for the existence of deep cognitive discontinuity between humans and animals, they fail to explain how such a discontinuity could have evolved. It is proposed that until the advent of words, no species had mental representations over which higher-order relations could be computed.

Kudos to Penn et al. for admitting what, if it were not politically incorrect (somewhere between Holocaust denial and rejection of global warming), would be obvious to all: the massive cognitive discontinuity between humans and all other animals. Since "kudos" has apparently become a count noun, how many kudos? I would say, two-and-a-half out of a possible four; that is averaging four for their analysis of the problem and one for their solution.

Penn et al. make clear that there are two quite separate human–nonhuman discontinuities: communicative and cognitive. What are the odds, in a single, otherwise unremarkable lineage of terrestrial apes, against two such dramatic discontinuities evolving independently? Yet Penn et al. dismiss three variants of the notion that language was what enhanced human cognition.

This is not their mistake, however. They are right to reject all three variants for the reasons stated. Their mistake lies in assuming that these proposals have exhausted the ways in which language might have influenced cognition, and in not looking more closely at what language did to the brain – the "rewiring" they admit it caused. Instead, they propose a solution – "relational reinterpretation," supported by the computational model LISA (Learning and Inference with Schemas and Analogies) – which explains distinctively human cognition in the same way Molière's "dormitive property" explains the narcotic effect of opium.

What does "relational reinterpretation" do, beyond renaming the phenomena it seeks to account for? The term may form a convenient summation of what the mind has somehow to do to achieve the results Penn et al. describe, and LISA may represent one possible way of achieving them. But the real issue is, how and when and why did "relational reinterpretation" evolve? To what selective pressures did it respond? And why didn't those pressures affect other, closely related species?

Penn et al. have no answers, because they share with most linguists and cognitive scientists a reluctance to grapple with what is known about human evolution. The many gaps and ambiguities in that record license extreme caution in handling it, but not, surely, ignoring it altogether. What the record spells out unambiguously are the radical differences in lifestyles, foraging patterns, nutrition, and relations with other species that separated human ancestors from ancestors of modern apes. Whether seeking origins for language or human cognition, it is surely among these differences – and their behavioral consequences – that we must start. Otherwise, we cannot explain why we are not just one out of several "intelligent" species on this planet.

Parsimony and evolutionary principles both suggest that one major discontinuity begat the other; here is how this could have happened.

The capacity to perceive and exploit higher-order relations between mental representations depends crucially on having the right kind of mental representations to begin with, a kind that can be manipulated, concatenated, hierarchically structured, linked at different levels of abstraction, and used to build structured chains of thought. Are nonhuman representations of this kind? If they are not, Penn et al.'s problem disappears: Other animals lack the cognitive powers of humans simply because they have no units over which higher-order mechanisms could operate. The question then becomes how we acquired the right kind of representations.

Suppose all nonhuman representations are distributed. This means, to take a concrete example, that although an animal might have representations corresponding to "what a leopard looks like" (numerous variants), "what a leopard sounds like" (ditto), "how a leopard moves," "what a leopard smells like," and so on, there is simply no place in the brain where these all come together to yield a single, comprehensive "leopard." Instead, each representation would be stored in its appropriate brain area (auditory, visual, etc.) and be directly linked to parts of the motor system so that the firing of any (sufficient subset) of these representations would activate the appropriate leopard-reaction program. If Penn et al. have any evidence – experimental or ethological – inconsistent with this proposal, I hope they include it in their Response to Commentary.

What would an animal need, beyond this? It would still enable categorization of presented stimuli, even ones as exotic as fish to pigeons (Herrnstein 1985); pigeons, having stored visual features of fish, would simply peck whenever a sufficient subset occurred, without requiring any generalized concept of fish. The only limitation would be that the animal would not be able to think about leopards, or fish, in their absence. (It is perhaps not coincidental that virtually all animal communication relates to the here-and-now.)

The role of motor-sensory feedback in the evolution of mind

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Abstract: Seemingly small changes in brain organization can have revolutionary consequences for function. An example is evolution's application of the primate action-planning mechanism to the management of communicative sequences. When feedback from utterances reaches the brain again through a mechanism that evolved to monitor action sequences, it makes another pass through the brain, amplifying the human power of thinking.

Both Darwin and Penn et al. are correct. There are enormous differences between human and animal minds, but enormous differences can arise from seemingly subtle changes in mental function. An example is the use of motor-sensory feedback to elaborate human thinking, based on plans that can circulate through the human brain repeatedly.

For the last century, the stimulus–response link has dominated psychology, connecting environment and behavior. The job of psychology was to explain what happened between stimulus and response, and not much else. In behaviorism this orientation was obvious, but modern cognitive psychology retains a similar orientation. The cognitive psychologist's theories allow additional boxes, representing internal processes, interposed between stimulus and response, but the diagrams always have a stimulus at one end and a response at the other. The approach of "new connectionism" is similar at a neural level of modeling, with hidden units allowed.

This psychology is incomplete in that the motivation for activating a particular block-diagram model remains unspecified. That is, we may understand how visual information from an object is processed, but the theory does not address why the subject was looking at the object in the first place. The act of looking was motivated by a plan, an internally held image of an intended achievement (Miller et al. 1960). The plan is defined more broadly here than in its everyday sense, to mean a scheme that can control a sequence of actions to achieve a goal. Because plans motivate behavior, they become the keys to understanding control of behavior (Shallice 1978).

The power of plans is that they allow an organism to escape the contingencies of its immediate surroundings, to be controlled instead by its own needs in the longer term. A simple animal responds to its environment and to its internal states without need for plans. The fly does not make a decision to feed: When food is at hand in the environment and internal receptors are in the right states, feeding simply happens. More complex organisms can store many plans simultaneously, executing one while holding others in abeyance. Humans typically have hundreds of plans, from small, immediate ones, such as hammering a nail, to large ones, such as earning a college degree. Large-scale plans contain a hierarchy of smaller-scale plans. As a plan is executed, a single goal or idea is unpacked into a series of actions. Plans can also be interpreted in terms of motivation; modern conceptions of motivation include the pathway from motivating influences such as instinctive needs or selective attention, through plans, to action (Heckhausen 1991). The plan becomes the path from motivation to action.

Organizing behavior by plans requires neurological machinery to support the planning function and its ancillary needs. There must be neurological devices to (1) make plans, (2) store them, (3) execute them, and (4) monitor them (Bridgeman 1986; 1988). In order to control behavior, the currently active plan must have access to memory and attention. It must link these functions with perception to guide action according to a combination of the internally held plan and the external realities of the perceptual world. The plan-executing module takes a parallel, simultaneous idea and converts it into a sequence of serial behaviors or subplans. The mechanism exists in all primates, perhaps in all mammals. Chimpanzees can plan a behavioral sequence of several steps, such as piling boxes to reach a banana suspended overhead (Koehler 1925/1959). Even dogs can solve detour problems requiring them to move away from a reward in order to reach it eventually.

During human evolution this plan-executing module became more complex and loomed ever more important in mental life. At one point, I suggest, it began to be pressed into service for organizing communication as well as action. A single idea is unpacked into a series of words, and those in turn into phonemes, in the same way that any other plan is elaborated. In both the execution of actions on the world and the execution of communications, an ordered sequence of internally organized acts replaces the environmentally released behaviors of simpler animals (Bridgeman 1992).

Analogously, speech understanding uses another existing module. It normally monitors the progress of plans, taking a sequence of events and packing them into an idea. Language could evolve quickly, on an evolutionary time scale, because it was made mostly out of old parts. The sequencing and comprehension mechanisms were already developed for the execution and monitoring of actions, respectively. Only the articulatory apparatus and perhaps a specialized grammatical ordering system (Bickerton 1984) had to be added.

Do planning and language share the same mechanism, or did a new planning mechanism evolve to specialize in language? Evolution of new functions often begins by doubling of genes, resulting in two copies of a morphological feature. Many cereal grains, for example, developed in this way. One of the copies is then free to evolve into something else. The open and flexible property of the planning mechanism, however, allows language to be added to its functions with little or no change. The mechanism already had the capacity to handle many plans simultaneously, to organize each one, to prioritize them, and to handle plans for different kinds of actions.

Once an utterance occurs, it is perceived like any other event. Perception of nonlinguistic utterances puts us in touch with emotions, whereas perception of our own language puts us in contact with our ideas. An animal is limited to awareness of its actions and emotional states through this mechanism, but for humans the same mechanism allows the conclusions of a thought process to be articulated by mechanisms that evolved for communication. Those conclusions re-enter the brain by mechanisms that evolved for understanding the communications of others, and the thought can make another cycle through the brain. The critical event is the planning, not the perception, because in human brains the sensory-to-motor feedback can be internalized. With this change, not in the mechanism of motor-sensory feedback, but rather, in its content, humans can think, whereas other animals are limited to whatever ideas pop into their heads.

The sun always rises: Scientists also need semantics

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Abstract: Penn et al. do not demonstrate Darwin made a mistake, because they largely ignore the semantics underlying the meanings of "degree" and "kind." An analysis based on the work of Mortimer Adler shows such terminology conflates at least three different meanings of "kind," only one of which challenges Darwin – and one which the authors almost certainly would reject.

> *We must also admit that there is a much wider interval in mental power between one of the lowest fishes, as a lamprey or lancelet, and one of the higher apes, than between an ape and man; yet this immense interval is filled with numberless gradations.*
>
> — Charles Darwin (1871, p. 35)

> *The distance between man and ape is greater than the distance between ape and ameba.*
>
> — William Gaylin (1990, p. 8)

Penn et al. provocatively critique some evidence for human-like mental processes in nonhuman animals. They also claim that Darwin was wrong in asserting that the difference between the minds of humans and nonhumans is "one of degree and not of kind." They insist that "the profound biological continuity between human and nonhuman animals masks an equally profound functional discontinuity between the human and nonhuman mind" (sect. 1, para. 3). There are many problems here. The mind is separated from biology, function is confused with underlying mechanisms, and there is a stereotypical human mind and a single type of nonhuman mind. Does the bonobo "mind" not differ from all non-bonobo minds in both degree and kind? What do "degree" and "kind" really mean anyway?

The complete sentence containing the phrase Penn et al. use to support their claim comes at the end of the summary of Chapters 2 (mental powers) and 3 (moral sense) in Darwin's *The*

Descent of Man (1871). Darwin begins by acknowledging "that the difference between the minds of the lowest man and that of the highest animal is immense" (Darwin 1871, p. 104). He follows with a hypothetical interview with an ape, in which the latter admits his limitations in terms of being able to make tools, communicate about ideas other than about stimuli and motivations, engage in metaphysical speculation, solve mathematical problems, reflect on God, or extend moral concern to all living creatures. Then Darwin adds, "Nevertheless, the difference in mind between man and the higher animals, great as it is, is certainly one of degree and not of kind" (Darwin 1871, p. 105).

Research over the last 40 years has shown that Darwin actually underestimated the mentality of apes, for example, in tool making, numerosity, and communication. Why question Darwin now when his case is stronger than ever? In evaluating the disparaging view of reptile behavior at the dawn of the romantic dinosaur renaissance, I wrote,

> How sad this is, and also how reminiscent of philosophers, theologians, psychologists, and humanists who, while intellectually accepting evolution are forever betraying their emotional insecurity by erecting ill-defined qualitative barriers between *Homo sapiens* and other primates. Whether these barriers are called language, tool using, tool making, reflection, soul, symbolism, or factor X, the motivation and consequences are similar. (Burghardt 1977, p. 178)

Does this plaint apply to the motivations of the target article's authors? I do not know, but I fear that the consequences are indeed similar.

Until 40 years ago, Darwin's continuity claim was ignored by philosophers and humanists. Mortimer Adler was prescient in anticipating, in light of Darwin's claims, the challenge to human distinctiveness presented by the emerging evidence for unexpected levels of cognitive achievements by animals. He provided a rigorous, relevant, but unfortunately forgotten, analysis (Adler 1968).

Adler laid out four alternatives for explaining differences. First, a difference may be one of degree. Species X has more of alpha than does species Y, and an infinite number of Zs with varying degrees of alpha connect X and Y. This is the default continuity position assumed by Penn et al. Second, there are "apparent differences in kind" that are really continuities. Species X has trait non-alpha, whereas Species Y has a high level of alpha. Adler notes that the non-alpha trait is really alpha at such a low level that it appears to create a qualitative difference, but absent intermediaries could fill the gap. Third, there are "superficial differences in kind." Suppose a threshold is reached in some beta that leads to the discontinuity in alpha resulting in species X being qualitatively different from species Y. For example, water and ice constitute real differences in kind. One is a liquid, the other a solid – a distinction in alpha/non-alpha with great functional importance. Here continuous variation in temperature (and hence molecular activity), the beta, leads to the qualitative difference in alpha. Similarly, Adler points out, one can postulate that when a certain threshold in neural or motor processing is reached, qualitative mental differences appear. This, I believe is the position of Penn et al., whereas the continuity claimants are more likely to opt for type 2. So the debate may be between those who claim that seemingly qualitative differences are just apparent versus those who claim they are real but nonetheless superficial.

The fourth alternative Adler posits, "radical difference in kind," is due to completely new, not even emergent, properties. Adler discusses living versus nonliving. Most scientists view this as a real, but superficial, difference in which organic processes fall below the threshold to maintain life, whereas vitalists positing something special and nonmaterial in living organisms, such as the soul or vital principle, view this as a profound and radical difference in kind.

Similarly to the vitalists, Adler concludes that humans and nonhumans differ radically and not superficially. What makes humans radically different in kind are language and thought. The difference must be "*psychologically explained by* the operation in man and in man *alone* of an *unobserved* factor" or simply the power of conceptual thought (Adler 1968, p. 142, emphasis in the original). Adler, although admitting he may be wrong, could not conceive how animals could possibly have acquired through natural processes the psychological abilities that underlie mental differences in kind between human and nonhuman. He even anticipates Penn et al. by claiming that "perceptual abstractions are the *only psychological* constructs needed to explain the *learned* behavior of animals" (pp. 154–55, Adler's emphasis).

Adler opted for a nonmaterial factor underlying differences between human and nonhuman mentality because he feared the consequences to morality and religion if the wall of separation was not maintained. In this he has a modern compatriot in the psychiatrist Will Gaylin, cofounder and former President of the Hastings Center. The opening quotation from Gaylin shows the depths to which such thinking can descend. Creationists and intelligent design advocates will find a wedge here. Penn et al. are acting similar to those who call for "missing links" and then raise the bar whenever they are found.

Did Darwin make a mistake? I do not think so. Any mistakes lie elsewhere.

Imaginative scrub-jays, causal rooks, and a liberal application of Occam's aftershave

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Abstract: We address the claim that nonhuman animals do not represent unobservable states, based on studies of physical cognition by rooks and social cognition by scrub-jays. In both cases, the most parsimonious explanation for the results is counter to the reinterpretation hypothesis. We suggest that imagination and prospection can be investigated in animals and included in models of cognitive architecture.

In a classic *Monty Python* sketch, scientists are embroiled in the age-old question of whether penguins are more intelligent than humans. Not surprisingly, the penguins failed human IQ tests. The penguins were then given cognitive tests in a naturalistic zoo enclosure, to which they gave no meaningful responses. Non-English-speaking Swedes in the same enclosure responded in a similar vein to the penguins. But how will we ever be able to ascertain whether species differences in cognition are *real* when the methodology used is automatically biased towards humans?

The cognitive differences between human and nonhuman animal minds suggested by Penn et al. are without exception impossible to quantify because of the reliance on language in experiments of human cognition. We are not aware of any cognitive tests given to adult humans that have been designed and implemented in *exactly* the same way as those given to animals. Boesch (2007) addressed this issue with regard to comparisons between humans and other apes. For example, humans are given instructions in their appropriate language, and their performance is determined by their language competency; in tests of social cognition, humans are used as stimuli and caregivers are present when testing human infants. We desperately need more studies on the cognitive capacities of humans applying the same conditions as used for animals before we can begin to qualify impossible statements such as "evidence of absence."

As with their previous critiques of the comparative literature, Penn et al. have been very selective in their choice of experiments to evaluate. The crux of their argument is that there is no evidence that any nonhuman animal represents unobservable states or relations of relations, so the choice of studies becomes important. Although we are glad that work on corvids is now being discussed, we would like to address a number of misinterpretations, absences, and misrepresentations of our work in the target article. We focus on two studies; the two trap-tube task in rooks (Seed et al. 2006) and experience projection by scrub-jays (Emery & Clayton 2001).

First, Penn et al. were quick to dismiss the results of the two trap-tube task without going into the essential details. Rooks do not use tools, and how could their performance on a tool-using task be due to "domain-specific expectations"? Seven rooks rapidly learned one of two configurations of the two trap-tube task, with a functional and a nonfunctional trap and transferred immediately to another, novel configuration. The two previously rewarded versions of the nonfunctional traps (i.e., no bottom so food falls through and the bottom raised so food passes over the trap) were then pitted against one another, so that either choice could lead to reward. However, a manipulation of the whole apparatus was performed which transformed one nonfunctional trap into a functional trap. Either the ends of the tube were blocked with rubber bungs so that the food would be trapped at one end or the whole apparatus was lowered so that food would fall into a now functional trap. At issue is the performance of one rook, Guillem, who instantly understood the problem, performing without errors on one version of the task and 90% correctly on the other.

We would like to discuss a second study investigating the ability of scrub-jays to re-cache food which they had previously cached in front of a conspecific, but only when they had previous experience of stealing another bird's caches; which we have suggested is an example of experience projection (Clayton et al. 2007; Emery 2004; Emery & Clayton 2004a). To selectively re-cache, we suggest that the birds will have had to retrieve a recent memory of whether they had been observed caching (as they do not re-cache if they had cached in private), which would be integrated with "knowledge" of what to do to avoid future pilferage, derived from their egocentric experience of pilferage. Penn and Povinelli (2007b) provided an alternative explanation, suggesting that the jays were behaving like monkeys who had been attacked and who subsequently redirected aggression to a third-party related to their attacker. We do not agree. In the monkey case, the victim receives aggression and then shortly afterwards attacks another, thereby reacting to an immediate past when in the same emotional state. By contrast, one group of scrub-jays sees another bird caching and then pilfers those caches, whereas a second group observes caching, but has no opportunity to steal those caches. Then months later, those same scrub-jays are given the opportunity to cache either when observed or when alone and then, three hours later, to recover those caches. Only the birds with pilfering experience re-hid their caches in new sites. We propose that re-caching functions to prevent future theft, and thus the most parsimonious explanation for why only those birds with pilfering experience do this is because they project this experience onto another bird and predict their future behaviour based on their "knowledge" of pilfering. Note that the scrub-jays cannot be basing their decisions on their emotional state, either three hours previously (as both groups should be in the same emotional state) or months previously.

Imagination and prospection are useful concepts to approach the problem of thought in nonverbal creatures. Indeed, it is impossible to think about the future (by its nature unobservable) without forming a "picture in the mind's eye." As recent studies in scrub-jays and apes have suggested (Correia et al. 2007; Mulcahy & Call 2006a; Raby et al. 2007), nonhuman animals may think about alternative futures outside the realm of perception. We believe that these complex processes should not be neglected in the type of cognitive architectures discussed by Penn et al.; indeed, we have argued that planning, imagination, and prospection can be included in such models (Emery & Clayton, in press). Imagination and planning have recently been included in a neurally inspired cognitive architecture derived from global workspace theory (Shanahan 2006; Shanahan & Baars 2005) based on the mammalian brain which could be applied to other animals.

Comparative intelligence and intelligent comparisons

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Abstract: Sound comparative psychology and modern evolutionary and developmental biology emphasize powerful effects of developmental conditions on the expression of genetic endowment. Both demand that evolutionary theorists recognize these effects. Sound comparative psychology also demands experimental procedures that prevent experimenters from shaping the responses of human and nonhuman beings to conform to theoretical expectations.

Darwin accounted for marvelous variety in living forms without invoking arbitrary supernatural forces. It is an approach to biology that leads to experimental questions. Experiment, in turn, leads to discovery, and Darwinism prevails throughout biology because it has been a springboard for so many discoveries. Nevertheless, where determinism of blood and bone soon swept the field, determinism of thought and feeling remains embattled to this day. Wallace's alternative to Darwin remains well entrenched:

> The Darwinian theory, even when carried out to its extreme logical conclusion, not only does not oppose, but lends a decided support to, a belief in the spiritual nature of man. It shows us how man's body may have been developed from that of a lower form under the law of natural selection; but it also teaches us that we possess intellectual and moral faculties which could not have been so developed, but must have had another origin; and for this origin we can only find an adequate cause in the unseen universe of Spirit. (Wallace 1889, p. 478)

Darwin's continuity has inspired discoveries based on fresh lines of investigation in field and in laboratory (Boesch 1991; Goodall 1986; Harlow 1949; Koehler 1925/1959; Russon & Galdikas 1993; Watanabe 1994, to name only a few). Wallace's noncontinuity has inspired nondiscovery after nondiscovery based on nonexperiments designed to reveal nonhuman failure without revealing anything fresh about the nature of intelligence. Many nondiscoveries of noncontinuity depend on experimental methods that pioneers of comparative psychology discredited roughly one hundred years ago.

Pygmalion in the laboratory. Karl Marbe, for example, studied Basso, a chimpanzee in the Frankfurt zoo, that solved arithmetic problems (Marbe 1917). Asked in German "How much is six plus four?" Basso selected a card bearing the number "10" as in Figure 1. Basso usually chose the correct card. Marbe observed Richard Burkardt, zoo keeper and trainer who drilled Basso on simple problems as one might drill a small school child.

Figure 1 (Gardner). Array for testing chimpanzee Basso (Marbe 1917). Note that virtually all child versus chimpanzee comparisons cited by Penn et al. allow tester to cue testee in this way.

Burkardt doubted that Basso knew arithmetic. Asked what he believed Basso was doing, Burkardt said, "She reads my mind." Marbe tested this hypothesis by asking the trainer to give Basso a series of arithmetic problems and think wrong answers. The result was decisive. Basso repeatedly gave the answer that Burkardt was thinking, regardless of the correct answer in arithmetic. She succeeded at mind reading where she failed at arithmetic.

Had Marbe stopped here, some current theorists might cite Basso as a pioneer demonstration of a chimpanzee with a theory of mind. Instead, Marbe administered further tests showing that Basso selected the card that Burkardt looked at. The trainer himself was unaware that he was gazing at particular cards and was sure that he never gave any hints whatsoever. Earlier, Pfungst (1911/1965) showed that Hans, a German horse, solved arithmetic problems and spelled out German words by following the gaze of human interlocutors who were also unaware that they were hinting. The horse also failed tests when his trainer thought he should fail. That is, the experimenter hints innocently shaped results to conform to experimenter expectations, as a sculptor shapes a lump of clay. After these pioneering studies, experimental procedures to control for inadvertent hints became standard in comparative psychology (B. Gardner & Gardner 1989, Fig. 4.1; Harlow 1949, Fig. 1; Warden & Warner 1928).

Oddly, a wave of recent claims of evidence for noncontinuity fail to use any controls for experimenter hints. This failure of method is apparent in virtually all of the experimental evidence that Penn et al. cite. Herrmann et al. (2007) is a very recent example. Fortunately, an online video published by *Science* clearly shows that experimenters were in full view of the children and chimpanzees they tested. Differences in experimenter expectations or rapport between experimenter and subject easily account for all results.

Interested readers can verify the persistence of this experimental error in evidence of noncontinuity cited throughout Penn et al.'s target article.

Intelligent nature and nurtured intelligence. Additionally, nonexperiments compare caged chimpanzees – lucky if they have a rubber tire to play with or a rope to swing from – with human children from suburban homes. Most modern psychologists would expect caged human children to lose rather than develop cognitive ability. Indeed, the longer chimpanzees live in cages, the lower they score on cognitive tasks (Povinelli et al. 1993; Tomasello et al. 1987).

Credible comparisons depend on comparable conditions. In sign language studies of cross-fostered chimpanzees (R. Gardner & Gardner 1989), homelike conditions simulated the rearing environment of human children. Chimpanzees acquired signs in spontaneous conversational interactions with their human foster families the way human children acquire their native languages. Conversations were embedded in the casual interactions of daily life (e.g., Bodamer & Gardner 2002; Chalcraft & Gardner, 2005; B. Gardner & Gardner 1998; R. Gardner & Gardner 1989; Jensvold & Gardner 2000; Shaw 2001; Van Cantfort et al. 1989). They are comparable to dialogues in similar research with human children because cross-fostered chimpanzees and human children carry on conversations under similar conditions.

Patterns of development were comparable to human patterns. Vocabulary, sentence constituents, utterances, phrases, and inflection, all grew robustly throughout five years of cross-fostering. Growth was patterned growth, and patterns were consistent across chimpanzees. Comparable measurements paralleled in detail characteristic patterns reported for human infants (Bodamer & Gardner 2002; B. Gardner & Gardner 1998; Jensvold & Gardner 2000; Van Cantfort et al. 1989). Development was slower than human development without reaching an asymptote.

Mind-numbing drill. Penn et al. discuss the tube-trap problem invented by Visalberghi and Limongelli (1994) as a demonstration of cognitive discontinuity. In fact, Visalberghi and Limongelli subjected their monkeys to highly repetitive drill, a traditional procedure for inducing stereotyped habits that interfere with human as well as nonhuman problem solving. R. Gardner and Gardner (1998, pp. 270–87) discuss decades of evidence for the universally mind-numbing effect of drill on human and nonhuman problem solving found in experiment after experiment for at least a century. Luchins and Luchins (1994) reviews nearly fifty years of closely parallel negative effects of repetitive drill on human problem solving.

Relational language supports relational cognition in humans and apes

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Abstract: We agree with Penn et al. that our human cognitive superiority derives from our exceptional relational ability. We far exceed other species in our ability to grasp analogies and to combine relations into higher-order structures (Gentner 2003). However, we argue here that possession of an elaborated symbol system – such as human language – is necessary to make our relational capacity operational.

Penn et al. make a far-ranging and convincing case that the ability to store and process higher-order relations is a defining feature of human cognition. We agree that our extraordinary relational ability is a central reason "why we're so smart" (Gentner 2003). But unlike Penn et al., we also accord central importance to language and other symbol systems.

In our view, human cognitive powers stem both from inborn relational capacity and from possession of a symbol system capable of expressing relational ideas. These two capacities form a positive feedback cycle. Analogical processes are integral to language learning (Casenhiser & Goldberg 2005; Gentner & Namy 2006; Tomasello 2000), and relational language fosters relational ability. We support this latter contention with four points.

1. *Relational language fosters the development of relational cognition.* Loewenstein and Gentner (2005) found that preschool children were better able to carry out a challenging spatial analogy when spatial relational terms (such as *top middle bottom*) were used to describe three-tiered arrays. We suggest that the relational terms induced a delineated representation of the spatial structure, which facilitated finding relational correspondences between the two arrays (see also Gentner & Rattermann 1991). Further, these representations endured beyond the session: Children retained this insight when retested days later, without further use of the spatial terms. Spelke and colleagues have also demonstrated effects of relational language on children's performance. For example, preschool children who know the terms *left* and *right* outperform their peers in relocating a hidden object placed relative to a landmark (Hermer-Vasquez et al. 2001).

2. *Children who lack conventional language are disadvantaged in some relational tasks.* One example is homesigners – congenitally deaf children of hearing parents who, deprived of a conventional language, invent their own "homesign" symbol systems (Goldin-Meadow 2003). Using the three-tiered arrays described above, we investigated homesigners in Turkey and found that (1) these children appeared not to have invented consistent terms for spatial relations, and (2) they performed substantially worse on the spatial mapping task than did hearing Turkish-speaking children (matched for performance on a simpler spatial task) (Gentner et al. 2007). Likewise, deficits in numerical ability have been found in Nicaraguan homesigners, whose invented language lacks a systematic counting system (Spaepen et al. 2007). Numerical deficits are also reported for the Pirahã people, who possess a *"one, two, many"* number system (Gordon 2004).

3. *Possessing relational symbols facilitates relational reasoning among nonhuman animals.* Research by Thompson et al. (1997) (discussed in Penn et al.'s article, but with an opposite conclusion) provides evidence for this claim. Five chimpanzees were given a relational-match-to-sample (RMTS) task, a notoriously difficult task for nonhuman animals (see Fig. 1):

XX

AA BC

Figure 1 (Gentner & Christie). The relational match-to-sample task.

Four of the chimps had previously had symbolic training – either same/different training or numerical training – and one had not. Only the four symbolically trained chimpanzees succeeded in the RMTS task – a crucial point that is not noted in Penn et al.'s discussion. Instead, Penn et al. link this RMTS task with array-matching tasks that are passed by naive animals (Wassermann et al. 2001). But two large arrays of identical elements (e.g., oooooooo and kkkkkkkk) can be seen as more alike than either is to an array of all-different elements (e.g., vlfxrtdei) on the basis of similar texture (cf. Goldmeier 1972), rather than via relational processing. In contrast, the two-item case does not afford a textural solution. It requires matching the SAME (X,X) relation to the SAME (A,A) relation (instead of to the DIFF (B,C) relation). This kind of relational reasoning is facilitated by relational symbols in chimpanzees just as in humans.

4. *The gap between humans and other apes develops gradually through the influence of language and culture.* Human children do not begin with adult-like relational insight. Rather, children show a relational shift from attention to objects to attention to relations (Gentner 1988; Halford 1987). For example, in the RMTS task with the same triads as described earlier, 3-year-olds respond randomly; they do not spontaneously notice relational similarity. Importantly, however, children show far greater relational responding if known labels (*double*) or even novel labels are used during the task (Christie & Gentner 2007).

Dramatic evidence for the developmental influence of language and culture on relational representation comes from research by Haun et al. (2006). They compared humans from different language communities with the other great apes (chimpanzees, bonobos, gorillas, and orangutans) on a locational encoding task. All four ape species used an allocentric (external) frame of reference. Interestingly, German 4-year-olds showed the same pattern. But older humans diverged in a language-specific way. Dutch 8-year-olds and adults used an egocentric frame of reference, consistent with the dominant spatial frame used in Dutch (and German). In contrast, Namibian 8-year-olds and adults, whose language (Haiǁom) uses a geocentric frame of reference, encoded locations allocentrically (specifically, geocentrically). These findings suggest a gradual developmental divergence of humans from great apes; and they further suggest that language is instrumental in this divergence.

Further points. Penn et al. cite the fact that deaf children of hearing parents invent their own homesign systems (Goldin-Meadow 2003) as evidence that external language is not needed. But as discussed earlier, homesign systems fall short precisely where our position would predict: in the invention and systematization of relational terms. Penn et al. also cite aphasics who retain relational cognition despite losing the ability to speak. This is problematic for accounts that hinge on the online use of internal speech. But in our account, the great benefit of relational language is that it fosters the *learning* of relational concepts, which then serve as cognitive representations.

Darwin was not so wrong. We agree with Penn et al. that relational ability is central to the human cognitive advantage. But the possession of language and other symbol systems is equally important. Without linguistic input to suggest relational concepts and combinatorial structures to use in conjoining them, a human child must invent her own verbs and prepositions, not to mention the vast array of relational nouns used in logic (*contradiction, converse*), science (*momentum, limit, contagion*) and everyday life (*gift, deadline*). Thus, whereas Penn et al. argue for a vast discontinuity between humans and nonhuman animals, we see a graded difference that becomes large through human learning and enculturation. Humans are born with the potential for relational thought, but language and culture are required to fully realize this potential.

The missing link: Dynamic, modifiable representations in working memory

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Abstract: We propose that the missing link from nonhuman to human cognition lies with our ability to form, modify, and re-form dynamic bindings between internal representations of world-states. This capacity goes beyond dynamic feature binding in perception and involves a new conception of working memory. We propose two tests for structured knowledge that might alleviate the impasse in empirical research in nonhuman animal cognition.

We agree with Penn et al. that the ability to recognise structural correspondences between relational representations accounts for many distinctive properties of higher cognition. We propose to take this argument further by defining both a conceptual and a methodological link between animal and human cognition. The conceptual link is to treat relational processing (Halford et al. 1998a) as dynamic bindings of chunks to a coordinate system in working memory (Oberauer et al. 2007). Such a coordinate system consists of slots and relations between them, and includes relational schemas (Halford & Busby 2007). Dynamic bindings are defined structurally, the governing factor being structural correspondence, which gives the flexibility that characterises higher cognition. It enables bindings to be modified, and it permits representations to be combined, giving the property of compositionality that is essential to higher cognition. It also permits premise integration, the core process of reasoning. Dynamic bindings involve the prefrontal cortex as well, which is late evolving and late developing (Wood & Grafman 2003), and is characterised by the sort of sustained activations needed to maintain a representation of task structure across different task instances. Working memory is at the core of higher cognitive processes, being the best single predictor of reasoning performance, accounting for more than 60% of the variance (Kane et al. 2004). We propose that dynamic binding to a coordinate system in working memory is a prerequisite for relational representations and therefore well worth studying in humans and nonhuman animals.

Humans' dynamic binding ability can be tested by briefly presenting words in separate slots, such as frames on a computer screen, then testing for recognition of the frame to which a word belonged (Oberauer 2005). This ability underlies the capacity for relational processing because the explicit representation of relational information requires binding to slots (the relation "larger than" comprises sets of ordered pairs in which the larger and smaller elements are bound to specific slots). We need a test for mapping to coordinate schemas that can be used with inarticulate participants. The delayed response task could be adapted for this purpose. For example, animals could see food hidden in one of two boxes, placed one above the other; then the boxes would be moved to a different location to remove environmental cues, and, after a delay, the animals could attempt to retrieve the food from one box. This requires dynamic binding of the food to a box, where the correct box is defined by its relation, above or below, to the other box. Thus, the spatial relationships within the set of boxes provide a coordinate system. There are potentially many variations on this paradigm, once the significance of dynamic binding to a coordinate system is recognised.

Another paradigm is the generativity test. A relational schema is induced by training on sets of isomorphic problems. Then elements of a new problem can be predicted by mapping into the schema. This is a form of analogical inference, and provides a good test for relational knowledge in humans (Halford & Busby 2007). The test can be applied to nonhuman animals using the learning set paradigm (Harlow 1949) comprising series of two-object discrimination tasks, in which the choice of one object is rewarded and the other is not. At the asymptote of training, typically after hundreds of isomorphic problems, discrimination between a new pair of objects is very rapid. In some higher primates it is close to perfect after one information trial (Hayes et al. 1953).

To illustrate, consider a new pair of objects. If A is chosen on the first trial and the response is rewarded (A+), A will continue to be chosen on a very high proportion of subsequent trials. If, however, B is chosen on the first trial, resulting in no reward (B−), there will be a reliable shift to A on subsequent trials (win-stay, lose-shift). This paradigm has not been widely interpreted as inducing relational knowledge, but it does have potential for that purpose (Halford 1993). At the asymptote of inter-problem learning, participants could acquire a representation of a relation between slots, one rewarded and the other not. When a new pair is encountered, following an information trial when one object is found not to be rewarded (B−) it will be mapped to the non-rewarded slot, and the other (A) will be mapped to the rewarded slot of the relation (by structural correspondence rules which provide, inter alia, that each object will be mapped to one and only one slot). This inference can be made before the participant has any experience with the second object (A) and is a form of analogical inference. This interpretation of learning set acquisition is supported by findings that participants learn less about specific objects near the asymptote of learning set acquisition than early in acquisition (Bessemer & Stollnitz 1971). This suggests a switch to a different mode of learning late in acquisition, consistent with our proposal that the ability to process relational schemas is acquired near the asymptote of learning set acquisition. This paradigm can be used with inarticulate species, because the types of stimuli presented and responses required remain the same as in simple discrimination learning. We propose that this paradigm has been under-utilised as a measure of relational knowledge in inarticulate species. It can also be applied to more complex concepts such as oddity and conditional discrimination (Halford 1993), as well as to structures based on mathematical groups (Halford & Busby 2007).

The difficulty in resolving controversies in animal cognition is partly attributable to limitations in the power of empirical methods, as Penn et al. note. The two paradigms that we propose might break this impasse. The generativity test is adaptable for inarticulate subjects and can be used to assess induction of relational schemas. Dynamic binding in the context of a coordinate system (relational schema) can be assessed with nonhuman animals, and it affords the missing conceptual link between externally driven, perceptually grounded representations and internally driven, structurally reinterpreted representations.

Ontogeny, phylogeny, and the relational reinterpretation hypothesis

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Abstract: If our knowledge of human cognition were based solely on research with participants younger than the age of 2 years, there would be no basis for the relational reinterpretation hypothesis, and Darwin's continuity theory would be safe as houses. Because many of the shortcomings cited apply to human infants, we propose how a consideration of cognitive development would inform the relational reinterpretation hypothesis.

Penn et al. propose a pervasive domain-general cognitive discontinuity that defines the difference between "us and them." In doing so, we believe Penn et al. have inadvertently argued something akin to cognitive recapitulation. In many ways, human ontogeny of the cognitive abilities they discuss appears to recapitulate phylogeny, as young human children seem to display the same lack of relational insight that the authors identify in nonhuman primates. Leaving debate about recapitulation theory aside, we wondered how we might apply their discontinuity hypothesis to development within our own species. Here, we examine whether the development of relational understanding is discontinuous within two domains mentioned by Penn et al.: spatial cognition (particularly, success on scale model tasks) and social cognition.

Children younger than age 3 years have difficulty using a scale model of a room as a source of information about the location of a hidden toy in the analogous, larger room (e.g., DeLoache 1989). In contrast, 3-year-olds succeed on the task as long as the locations are unique, but they fail when they cannot use object correspondences between the model and the room (Blades & Cooke 1994). Only by 5 years of age can children use the spatial relationships among identical locations in the scale model to find the toy in the room, thereby achieving the criteria set by Penn et al. One interpretation of the performance of 3-year-olds is that they are matching perceptual similarities between items in the model and the room, without understanding the relation between the two (Perner 1991). However, this seems unlikely. For example, 2-year-olds can match corresponding items in the model and room, even when they cannot find the hidden toy in the room based on the hiding event in the model (Troseth et al. 2007). Evidently, perceptual matching alone is not enough to promote success in the scale model task. Instead, accuracy in the model task, even with unique locations, might require at least some understanding of the relation between the room and the model.

Evidence from theory of mind tasks may potentially offer a similar developmental trajectory. After the 3 years of age, children start to show evidence of representing behavior in terms of mental states, and by 5 years of age they can understand another's false belief as a mental misrepresentation (Wellman & Liu 2004). Although traditionally children below the age of 3 have not been credited with reasoning about mental states, infants have shown success on tasks ranging from understanding goal-directed actions (Woodward 1998) to predicting behavior based on another's perception (Luo & Baillargeon 2007), as well as false belief (Onishi & Baillargeon 2005). We agree with Penn et al. that infant performance may be due to rule-based, rather than mental state, reasoning; however, given the breadth and flexibility displayed by infants in these tasks, it seems likely that such rules are organized within some sort of higher-order relational framework. Infants will respond similarly to a series of disparate goal-directed actions, including grasping, pointing, reaching, and looking (Woodward et al. 2001). Additionally, such responses seem to be modified correctly based on another's current and past visual access (Luo & Baillargeon 2007; Meltzoff & Brooks 2007), previous interactions with other individuals (Kuhlmeier et al. 2003), individual versus shared knowledge or preferences (Buresh & Woodward 2007; Song et al. 2005), and updated representations of otherwise meaningless actions based on context (Gergely et al. 2002; Kiraly et al. 2003). A rule-based account that did not allow for minimal relational reasoning would, in our view, struggle to explain such flexibility.

Yet, it appears that children under 3 years of age cannot achieve the level of relational insight put forward by Penn et al. as the hallmark of human cognition. Would we consider their abilities to be discontinuous with the abilities seen at age 5? Although achieving analogical thinking is a clear developmental change (Gentner 2003), it does not seem to qualify as discontinuous in a strong sense. Young children seem to be able to reason about unobservable explanatory mechanisms as well as map simple relations between a representation and reality, whereas more abstract relational understanding occurs later in development.

If, in this case, we are to claim that human ontogeny is continuous, how does that claim speak to phylogeny? In comparison, nonhuman primates achieve success on the same tasks in which we think children are using basic relational understanding. Kuhlmeier and Boysen (2002), for example, found that chimpanzees succeeded at using a scale model in the same task procedures that prove difficult for 2-year-old children, even though they, like 3-year-olds, seem to rely more on object correspondences. In the domain of theory of mind, Santos and colleagues have demonstrated flexible reasoning by rhesus macaques about a competitor's perceptual state, including responding correctly to changing perception across modalities (Flombaum & Santos 2005; Santos et al. 2006). We believe this suggests that nonhuman primates lie somewhere on a continuum of relational understanding, and they only fail at the later stages of higher-order relational reasoning that older children can achieve.

We pose two theoretical accounts for the development of cognitive architecture that might explain how older children, and not nonhuman primates, might come to conceptualize higher-order relations. Previously Povinelli (2001) has argued, at least within the domain of theory of mind, that humans have an additional system that sits side by side with evolutionarily older systems that simply activate earlier. Applied to the relational reinterpretation hypothesis, such a system might allow for analogical reasoning that is not constrained by superficial or context-specific correspondences and might be applied either across multiple specific domains or as a more domain-general "supermodule." In our view, the addition of such a system to the existing primate mind might explain conceptual change across development, yet it does not fully constitute a violation of Darwinian continuity, particularly if such a system engages actively with the older systems (as, for example, analogical reasoning builds upon the underlying understanding of perceptual correspondences; Gentner 2003). To account for discontinuity at the level that Penn et al. propose, we believe the authors would need to posit that the nonhuman and human minds each begin with unique mental architecture. In this case, it is only that the behavior evident in the first stages of human development looks strikingly similar to the capacities we see in other species. It is only in this latter case that we feel there would be evidence for true cognitive discontinuity.

Bottlenose dolphins understand relationships between concepts

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Abstract: We dispute Penn et al.'s claim of the sharp functional discontinuity between humans and nonhumans with evidence in bottlenose dolphins (*Tursiops truncatus*) of higher-order generalizations: spontaneous integration of previously learned rules and concepts in response to novel stimuli. We propose that species-general explanations that are "bottom-up" in approach are more plausible than Penn et al.'s innatist approach of a genetically prespecified supermodule.

The studies Penn et al. critique to discount nonhuman animal relational competencies are heavily weighted toward primates and birds, plus a few additional citations on bees, fish, a sea lion, and dolphins. Cognitive differences among nonhuman species are largely ignored, as if all were cut from the same mental cloth. Here, we focus on several findings on cognitive skills of the large-brained bottlenose dolphin (hereafter "dolphin") that suggest a capability for reasoning about higher-order relations through the spontaneous combination or concatenation of previously generalized concepts. Dolphin brain architecture is divergent from other large terrestrial mammals, such as the apes (Marino et al. 2007), giving pause to Penn et al.'s statement that "the substantive difference between human and nonhuman brains will be found in the prefrontal cortices" (sect. 11.1, para. 3). That structure (though not its functions) is lacking in the dolphin brain, but as a whole, the highly encephalized brain allows for levels of cognitive skills convergent with many of those demonstrated among apes (Herman 1980; 2006; Marino 2002). Refuting Penn et al.'s claims for functional discontinuity, the following examples illustrate dolphin relational competencies, as exhibited through laboratory studies of four dolphins, Akeakamai ("Ake"), Phoenix, Hiapo, and Elele.

Example 1. Herman et al. (1984) showed that Ake could learn to understand instructions conveyed gesturally within an artificial language system. A sequence of three gestures framed grammatically as *locative (L)* + *object (O)* + *action (A)* required Ake to take the signified action to the signified object that was at the signified location. A second three-gesture frame specified as *object1 (O1)* + *object2 (O2)* + *relational term (R)* required her to construct the signified role-specific relation between the two objects (e.g., by transporting *O2* to *O1*). Without further training, she immediately understood (on the first trial), all of the following four- and five-gesture frames: $O1 + L + O2 + R$; $L + O1 + O2 + R$; and $L_i + O1 + L_j + O2 + R$, where L_i and L_j may be the same or different locations (Herman 1986; Herman et al. 1984). Thus, she understood spontaneously the concatenation of these strings of symbols into a single instruction, and in so doing inferred the higher-order relation resulting from conjoined first-order relations. Additionally, when we substituted sequences of two deictic gestures for the symbolic gestural references to those objects, by pointing *(P)* briefly at one distal object and then at a second distal object, followed by a relational term, that is, $P1 + P2 + R$, Ake spontaneously incorporated the inverse grammar used with symbolic gestures, $O1 + O2 + R$, into her interpretation of the deictic gestural sequence, by taking the object pointed to *second* to the object pointed to *first* (Herman et al. 1999). The abstract grammatical rule was transferred not merely to other object exemplars, or to extensions of the existing grammatical rules within a closed symbolic communication system, but to a completely different indexical communication system, in a manner refuting "particular specificity."

Furthermore, Ake, when presented with long anomalous strings of symbols that violated the familiar syntactic structure of the artificial language, spontaneously extracted subsets of items that comprised a legitimate grammatical rule, even combining nonadjacent items when necessary, and she carried out the instruction contained within that embedded subset (Herman et al. 1993a; Holder et al. 1993). Additionally, when given proper syntactic strings that violated a semantic rule, such as a request to transport an immovable object, she rejected the string, either offering no response at all or occasionally carrying out a substitution response by transporting a movable object. These responses to anomalous sequences show a profound understanding of implicit relations within the grammar of the imposed language, and an ability for reinterpretation as necessary of the relations between symbols and the real world.

Example 2. Ake could report accurately whether a symbolically referenced object was present or not in her tank, by pressing a *Yes* or *No* paddle, respectively (Herman & Forestell 1985). Later, on the first occasion that she was given an $O1 + O2 + R$ instruction in that context, with *O1*, the destination object, absent, she spontaneously (and thereafter) carried *O2* to the *No* paddle (Herman et al. 1993b). This, in effect, was a reinterpretation of the perceptual world and a conditional reassignment of the function of the *No* paddle as a destination object.

Example 3. Our work with all four dolphins shows that dolphins are generalized mimics, capable of faithfully imitating on command arbitrary artificial sounds (Richards et al. 1984), as well as copying the behaviors of others (humans, other dolphins, or themselves), either viewed live or on a television screen (Herman 2002b; Mercado et al. 1998; 1999). Behavioral imitation is a form of "sameness" comprehension in that it requires relating one's body image (see Herman et al. 2001) to the perceived image of another, and may require inferring analogies where imitation crosses species boundaries, such as the dolphin representing the human leg by the dolphin's tail.

Example 4. As described in Herman (2002b) the four dolphins were taught a gestural sign, *tandem*. When each of a pair of dolphins was given the tandem sign followed by a sign for a particular behavior, such as *back dive*, they joined together and carried out that behavior in exquisitely close synchrony. Each dolphin was also taught a sign *create*, which required it to perform any behavior of its own choice. Then, when a pair was given the two-item sequence *tandem* + *create*, they joined together and in close synchrony performed the same self-selected behavior. On a later formal test of Elele and Hiapo's responses to *tandem* + *create*, 79 different highly synchronized behaviors were recorded with 23 of them novel (i.e., they were not under control of established gestures). The tandem responses were very closely timed, and although careful video analysis could detect some slight asynchrony in timing in some cases, there was no consistent "leadership" by one dolphin or the other. These results reveal close collaboration, as well as the marrying of two abstract concepts, *tandem*, a social collaboration, and *create*, a self-determined behavioral innovation, into a higher-order abstract relationship. This collaborative capability likely finds expression in the wild, for example, in the fluid first-and second-order alliances formed in collaborative efforts by male dolphins to secure female consorts (Connor et al. 2000); interestingly, Penn et al. deny that nonhumans can participate in collaborative activities.

Penn et al. make a top-down claim for genetic pre-specification in humans alone of a module for higher-order cognition. However, bottom-up theories may offer better paths to understanding nonhuman animal cognitive potential – for example, the non-generativist image schemas (Clausner & Croft 1999; Lakoff & Turner 1989) that are claimed to create conceptual representations through cumulative sensorimotor experiences. The relational capabilities of the dolphins illustrated (as well as others described in Herman 2006) we believe derive in part from the cumulative cognitively challenging experiences provided within their long-term immersion in a varied and stimulus-rich educational environment (in contrast to many of the animal studies cited by Penn et al.). These experiences allow for the emergence of intellectual competencies that might not be realized otherwise (Herman 2002a).

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Taking symbols for granted? Is the discontinuity between human and nonhuman minds the product of external symbol systems?

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Abstract: The target article provides a convincing argument that nonhuman animals cannot process role-governed rules, relational schemas, and so on, in a human-like fashion. However, actual human performance is often more similar to that of nonhuman animals than Penn et al. admit. The kind of rule-governed performance the authors take for granted may rely to a substantial degree on language on external symbol systems such as those provided by language and culture.

Nonhuman and human brains are made of the same stuff. Yet, as Penn et al. point out, there appear to be deep discontinuities between them. Owing to nonlinear interactions between genotypes, environment, and the resulting phenotypes, functional discontinuities are a common product of continuous evolutionary tinkering. At issue is whether apparent discontinuities in human mental function result directly from biological adaptations such as the "supermodule" hypothesized by the relational reinterpretation (RR) hypothesis or whether human mental abilities – differing quantitatively from those of nonhuman animals – are made qualitatively different by external symbol systems made possible by language, culture, and education.

At the same time as Penn et al. present the evidence against symbolic thinking in nonhuman animals, they tacitly assume that human cognition is innately symbolic and propositional. For instance, they claim that the "propensity to evaluate [similarity] … based on causal-logical and structural characteristics … rather than on […] shared perceptual features appears quite early and spontaneously in all normal humans" (sect. 2.1, para. 1). Yet, one of the authors has himself argued that generating spontaneous analogies poses substantial challenges even for adults who can be easily misled by perceptual similarities (Gick & Holyoak 1980). Although subsequent work went on to provide numerous demonstrations of children's and adults' sensitivity to structural relations (e.g., Holyoak et al. 1984), it is not obvious that this type of reasoning arises spontaneously. For instance, Gentner and colleagues (Kotovsky & Gentner 1996; Rattermann & Gentner 1998b) have argued for the role of relational labels aligning object representations: Hearing three differently sized objects referred to as "daddy, mommy, and baby" seemed to highlight the size relationship among the objects, enabling the 4- to 5-year-old children to transfer the relation to new objects. Without the relational labels, the relationship among the objects remained opaque. Namy and Gentner (2002) further argued that hearing common labels for objects facilitates taxonomic choices, leading children to group objects in more abstract ways (although Penn et al. mention some of this evidence, their dismissal of it is perhaps premature). Importantly, there is evidence that language is not only used as a "training tool," but may continue to play an online role in relational thinking, as suggested by studies using patients with linguistic impairments. For instance, the patient LEW (Druks & Shallice 1996), whose primary impairment is severe anomia showed a similar pattern of performance to that of 4- and 5-year-old children on tasks requiring relational reasoning. The addition of meaningful labels for stimuli induced a similar increment in performance to that found in children (Davidoff & Roberson 2004). It seems that when external aids (here, words) are unavailable, performance becomes more concrete and, to a greater degree, driven by perceptual similarities.

Humans can certainly reason analogically and perform relational judgments. The critical question is where these abilities come from. Are they the natural outcomes of the human genome? Or are they made possible by external aids such as the use of relational language? Penn et al. correctly point out that "normal human cognition clearly depends on normal linguistic capabilities" (sect. 9.3.1, para. 1). It remains possible that human performance that is *qualitatively* different from nonhuman performance may depend on an immersion in human culture and language. The evidence discussed in the target article fails to rule out this possibility.

The authors' assumption of innate symbolic reasoning by humans is also apparent in the section on language in which Penn et al. claim that it is "widely recognized […] that the ability to freely generalize relational operations over role-based variables is a necessary condition for using human languages" (sect. 3, para. 1). Although many researchers do hold this view, there is substantial evidence to the contrary. Some of this evidence is reviewed in the very article used by the authors to support their contention: Gomez and Gerken (2000). For instance, both infant and adult learners become more sensitive to the invariant structure (long-distance dependencies) in an artificial-grammar learning task when the variability of the intervening elements is increased (Gomez 2002) – the kind of token-based performance Penn et al. argue is characteristic of the performance of nonhuman animals (e.g., sect. 2.2., para. 2). Penn et al.'s discussion of language acquisition also omits the work on construction grammars (Goldberg 2006) and item-based learning (Tomasello 2003), which have offered ample demonstrations that children's language learning is intensely shaped by specific examples both at the lexical and syntactic levels. Computational modeling provides sufficiency proofs that item-based learning can produce the appearance of abstract role-based categories (Elman 2004). Evidence also indicates that adult language comprehension, rather than demonstrating knowledge of abstract role fillers (e.g., noun and verb phrases) instead demonstrates fluid interactions between word-specific knowledge and syntactic frames (Hare et al. 2003; 2004). Thus, although it remains to be explained how humans formulate explicit theories about language, actual human language use may rely less on abstract rules than the authors admit.

The human ability to reason about unobservable causes, to draw inferences based on hierarchical and logical relations, and to formulate highly abstract rules is not in dispute. Much of this thinking is compatible on an intuitive level with Penn et al.'s RR hypothesis. But although it is indeed "highly unlikely that the human ability to reason about higher-order relations evolved de novo and independently with each distinctively human cognitive capability" (sect. 11, para. 7), it is not unlikely that such uniquely human abilities depend on the use of external symbol systems. The ability to invent such systems and benefit from them in turn may depend on quantitative improvements in a range of domains: memory, imitation, shared attention, sequence learning, and so on (Elman 2005). The hypothetical child magically kept alive by itself on a desert island will inherit these quantitatively superior abilities in a range of cognitive domains. But would this child have all the abilities Penn et al. list as being uniquely human in the absence of the scaffolding afforded by external symbol systems offered by language and culture more broadly? The evidence that Penn et al. offer is insufficient to dismiss the conclusion that such a child would "not differ very much" from other great apes (Tomasello & Rakoczy 2003). Although the authors provide a compelling demonstration for an insensitivity to structural relations and the use of symbols by nonhuman animals, in taking for granted the biological basis for these abilities in human animals, the very premise of a biologically based fundamental discontinuity between human and nonhuman minds remains unfulfilled.

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An amicus for the defense: Relational reasoning magnifies the behavioral differences between humans and nonhumans

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Abstract: Relational representation abilities are a crucial cognitive difference between human and nonhuman animals. We argue that relational reasoning and representation supports the development of culture that increases in complexity. Thus, these abilities are a force that magnifies the apparent difference in cognitive abilities between humans and nonhumans.

Penn et al. demonstrate the many ways in which humans and nonhuman animals are behaviorally similar. As they point out, despite these similarities, there are significant differences between human and nonhuman animals outside the lab. Penn et al. argue convincingly that nonhuman animals rely largely on situational cues (e.g., perceptual features and associations), whereas humans are able to reason using complex relational representations. We expand on this point, arguing that the ability to understand and reason with relational information magnifies the cognitive differences between humans and nonhuman animals. In particular, our ability to form role-governed categories expands our conceptual and linguistic repertoire, allowing us to transcend mere situational and perceptual cues and represent concepts as related to functions and goals (Markman & Stilwell 2001). In addition, our ability to construct analogies based on relational mappings between domains that are dissimilar on the surface makes representational change and conceptual innovation possible. Finally, these differences may help to explain the uniquely human phenomenon of cumulative culture (Tomasello et al. 2005). Role-governed categories allow humans to posit the existence of objects that fill a particular relational role regardless of the perceptual properties of that object.

Human concepts can be loosely divided into three types: feature-based categories, which are represented as collections of features; relational categories, which represent a particular relational structure; and role-governed categories, which refer to items that play a particular role within a relational structure (Markman & Stilwell 2001). Many nonhuman animals have feature-based categories. Feature-based categories require only representations of co-occurrences among features. Humans, however, are able to construct relational categories. Some relational categories refer to particular important relationships in the world (e.g., kinship terms, which specify relationships between people). In addition, verbs specify relationships among a set of items that are part of a sentence (Gentner & Kurtz 2005; McRae et al. 1997). Verbs are particularly interesting, because any given verb must be completed with a set of objects that play different roles within the relational structure named by the verb (Ferretti et al. 2001).

For example, in the sentence "The EMT treated the accident victim," the EMT and accident victim play particular roles within these scenes (Ferretti et al. 2001). These roles themselves can in turn be named by role-governed categories, of which the typical agents associated with a relation are members. So a (medical) patient is someone who is the object of the relation X treats Y. Having relational and role-based concepts allows humans to categorize entities based on goals and functions, and to associate entities that, based on surface features alone, would be considered very different. The role-governed category patient allows humans and hamsters to be part of the same category, provided they are both undergoing medical treatment.

Analogical mappings – relational mappings between two domains – are ubiquitous in human reasoning. They allow the detection of subtle relational similarities between domains. More importantly, perhaps, they also allow extension of the representation of one concept by virtue of its similarity to another. Information about one domain that is connected to the relational match can be carried over to the other domain as an analogical inference (Falkenhainer et al. 1989; Markman 1997; Spellman & Holyoak 1996). Thus, analogies provide a powerful mechanism of representational change. The importance of analogy in scientific innovation, for example, has been well demonstrated, both in historical and naturalistic settings. Gentner et al. (1997) provide a detailed analysis of the importance of analogy in Kepler's discovery of the elliptical motion of the planets, showing it was his knowledge of light and magnetism that suggested solutions to the problems that planetary motion produced for seventeenth-century scientists. Similarly, Dunbar (1997) found that molecular biologists frequently rely on analogical mappings to problems with familiar solutions to produce novel solutions. Finally, Christensen and Schunn (2007) find that analogies are crucial for the development of innovative ideas in engineering design teams.

As argued by the target article, role-governed categories and analogical reasoning are a result of straightforward differences in representational capacity between human and nonhuman animals. We suggest that these abilities serve to magnify the apparent cognitive differences between human and nonhuman animals, because they are crucial for the development of cultural systems that increase in complexity across generations. Animals who have only feature-based concepts have no way of escaping the attributes of existing objects to suggest similarities across items that are based on relational similarities or on the possibility that two objects or individuals play the same relational role. Once animals develop a representational capacity that allows them to represent that two items play the same relational role within a relational system, it becomes possible to envision additional objects that might also fulfill that relational role. Thus, if a rock is used to break a nut, this rock becomes just one kind of *breaker*. Finding other objects that could fill this same role (perhaps more effectively) is crucial to the development of a technology. Role-governed technologies are the ones that are central to cultures that increase in their complexity (Tomasello 1999). Thus, role-governed categories are crucial prerequisites to the development of human-like tool cultures.

This view helps to explain how the cognitive abilities of human and nonhuman animals could simultaneously appear to be very similar and very different. Small differences in representation ability support large differences in the available knowledge base that humans and nonhuman animals have to reason with. What this work does not explain is how the leap from feature-based representations to relational representations is made. Future work in cognitive science must examine the important influence of language on the development of relational representations for insight into the development of relational systems (Gentner 2003).

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Putting Descartes before the horse (again!)

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Abstract: The "rational bubble" stance espoused in the target article confounds cultural symbolic achievements with individual cognitive competences. With no explicit role for learning, the core rationale for claiming a major functional discontinuity between humans and other species rests on a hybrid formal model LISA (Learning and Inference with Schemas and Analogies) now overtaken by new models of cognitive growth and new empirical studies within an embodied systems stance.

That there is discontinuity as well as continuity in the (nonlinear) evolution of cognitive systems is hardly news. In the case of contemporary humans, it is also self-evident that a runaway culture of cognition has led to an exponential growth in knowledge way outside the time frame of classical Darwinian evolution. Externalised as in the third world of books (Popper 1972), these knowledge-gaining systems are the product of a society of minds, public, open to scrutiny, repair, refutation, and (collective) redevelopment. These demand in turn extended periods of top-down instruction to secure for individuals what Piaget once dubbed the status of an "epistemic agent" capable of participation in the rational world of the sciences. Within this domain there is no possibility by definition of a nonhuman entry. And if this is the central thesis of Penn et al., then we have no disagreement with them.

However, despite the near impossible challenge of separating human cultural products from individual competences (Wundt 1898), the authors seem bent on assessing the "evolutionary" and cognitive status of the individual. Motivated by an adult end-state PSS (physical symbol system) -type model, they seek to explain discontinuity in terms of the individual's possession of a "supermodule." Installed in a space between more primitive nonhuman forms of cognition (and even human natural language), such a module is used to claim a special biological uniqueness for humans (but not Neanderthals), allegedly with a representational capability that forever separates us even from our closest simian relatives.

One difficulty in following this thesis is that when espousing their case for human structural superiority, the authors veer between task criteria which are adult end-state, context free, and formal, such as "systematicity," omnidirectionality, and "analogy" considered in isolation from content – and those which are embedded in "world knowledge" – such as functional analogy, theory of mind (ToM), and higher-order structural apprehension of perceived relations of similarity and difference. These heterogeneous domains are bridged with words such as "cognising," "abstraction," and "re-representation," giving rise to the impression these all share the property of an in-the-head compliance between formal structures and individual agents.

This not only conflates private with cultural constructions as templates for the individual mind, it also ditches in the process those elements of human cognition regarded by many as core and normative, namely, commonsense reasoning, bounded rationality, choice transitivity, and subjective scales of judgement (based on adaptive value rather than truth) as well as other sources of knowledge derived from perception and action – all of which are subject to principled influences of learning and development. In contrast, Penn et al.'s own characterisation of human cognition both diminishes the role of development and eliminates completely the role of learning. This is despite the fact that many of the authors they cite are at pains to point out that the human competences they describe are often the product of many years of human development (Halford 1993; Piaget 1970) and/or considerable explicit tuition (Kotovsky & Gentner 1996; Siegal et al. 2001) within a physical and social environment. To take just two examples, cross-dimensional analogy even at the concrete level and involving only three levels along a relational dimension (greatest, middle, least) are not "made reliably" until 8 years of age unless specific training is provided (Kotovsky & Gentner 1996). Similarly, symbolic transitive inference (not transitive choice) is slow to develop in the human child, despite claims to the contrary by the authors (Chalmers & McGonigle 1997; Clark 1969; Hunter 1957). The significance of the gradual acquisition of these core cognitive skills in humans for comparable studies in nonhumans is ignored by the authors in their review of equivalent comparative data. Where are the ground rules as suggested by, for example, Gentner, for training subjects to discount surface structure variation in favour of the underlying relational one?

And it is in this direction, that is, of "growing cognition" either in a model (Smith & Breazeal 2007) or assessing it in long-term learning-based studies with children and nonhumans (McGonigle & Chalmers 2006), that many now see the best prospect for providing an account of how we came to be what we now are (Griffiths & Stotz 2000). Clustered under the banner of "embodied cognition," furthermore, the scope of what constitutes a cognitive system within such programs reaches far beyond the formal horizons limiting that of Penn et al. Here action plays a crucial role in cognitive regulation, pointing up some of their most serious areas of neglect. In particular, new programs of research on serial ordering mechanisms and executive control with primates (McGonigle & Chalmers 2006; Terrace 2005b) open a window on the emergence of complex behaviors from simple relational primitives. These are already showing the growth of systematicity, compositionality, and the deployment of economic strategies with experience, which reduce cognitive costs (McGonigle et al. 2003); as well as an upward bound trajectory with a momentum that has not so far been limited by any glass ceiling on simian achievements. It is the study of these action grammars in the nonhuman, in fact, that may well reveal the genesis of the way we plan and think (Bloom 2000), providing in turn a platform for the human linguistic system (Hinzen, in press). As for evolutionary discontinuities, promising candidates from this research are not supermodules, but rather, the instruments for cognitive externalization through the superior fine motor control in the human which enable complex gesture (Corballis 2002), articulate speech (Pinker & Jackendoff 2005), and the ability to both manipulate objects and construct collections (Tallis 2003). In this way cognitive products are made available to agents as a result of their own activity and could prove crucial to the sharing of knowledge and cultural achievements (Donald 1991).

Already with a high prescriptive value, we need to maintain the momentum of systematic developmental and comparative programs of this sort. In an exciting area still largely in a vacuum created more by experimental neglect than animal failures, this rush to judgement by Penn et al. will put this fragile yet exciting new comparative agenda at risk.

NOTE

1. **Editorial Note:** We regret to inform readers that Professor Brendan McGonigle passed away on 29 November 2007.

Difficulties with "humaniqueness"

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Abstract: Explaining the transition from nonhuman to human behavior is a major scientific problem. Penn et al. argue for discontinuous evolution; they review many relevant papers but miss some that disagree with their stance. Given the shifting ground on which Penn et al.'s theories are based, and the likelihood of future studies providing additional information on continuities, a more open approach to continuity is warranted.

Penn et al. review a number of papers that demonstrate claims for human uniqueness and then proceed to a theoretical stance supporting this view. Given word limitations, I merely present data showing why Penn et al. should take care when arguing for lack of specific nonhuman capacities and for strong discontinuities between human and nonhuman competencies.

I begin with their discussion of same–different. Most of Penn et al.'s cited references do indeed fail to demonstrate nonhumans' comprehension of the relation; however, Penn et al. miss data from the Grey parrot study (Alex, *Psittacus erithacus*) that make a stronger case for human-like competence. Alex, who could observe two completely novel objects and respond to questions of both "What's same?" and "What's different?" with the label of an attribute that was same or different between the items ("color," "shape," "matter"; Pepperberg 1987) or with "none" if nothing was same or different (Pepperberg 1988), demonstrated, in Penn et al.'s words, a categorical distinction between displays with no item variability and those with any item variability at all. Furthermore, Alex, without any training, when queried "What color bigger?," transferred use of "none" to label absence of a size difference between two objects; thus he could transfer to an untrained format (Pepperberg & Brezinsky 1991).

Penn et al.'s discussion of transitive inference in nature is also limited in scope. They seem unfamiliar with studies on female great tits (*Parus major*), who decide whether to enter a male neighbor's territory (probably for extra-pair copulations) after eavesdropping upon experimentally manipulated, unobserved interactions between a stranger (an experimental playback) and her mate and the same stranger and said neighboring male. To succeed, the female has to distinguish her various neighbors from her mate and retain what she knows about the relative worth of her mate M, and each neighbor N. She must identify a new male, S, briefly listen and determine his rank in a contest versus M, and then do the same in another contest versus N. She must store and compare these two rankings and then infer the relative ranking of M and N based on their rankings with S, possibly updating her stored original memory. That is, the female tit makes her decision by inferring the ranking of the two resident males based on their respective abilities in dealing with the same intruder, and is more likely to enter the territory of the neighbor if he is inferred to be dominant to her mate (Otter et al. 1999; Peake 2005). Interestingly, because the relative rankings of males chosen for the experiment were unknown and the choice was random as to whether a given playback would simulate a dominant or a subordinate interaction, the information might counter what the female tit knows about previous interactions between her mate and her neighbor. Thus she is not simply making "an egocentric prediction about how to respond to a potential rival," but rather doing what Penn et al. argue is impossible for nonhumans.

A third case relates, albeit somewhat indirectly, to Penn et al.'s discussion of advantages that humans have on account of their capacity for symbolic communication as well as their ability to reason in a relational manner. Again, Penn et al. overlook research with the Grey parrot Alex (Pepperberg 2006). The study in question combined several of Alex's capacities. As noted earlier, he could label the color of the bigger or smaller object in a pair; he could also vocally quantify up to six-item sets (including heterogeneous subsets, i.e., quantify the number of blue blocks in a collection of blue and green balls and blocks; Pepperberg 1994). He was separately trained to identify the Arabic numerals 1 to 6 with the same vocal English labels, but was never trained to associate these Arabic numbers with their relevant physical quantities or to order the numerals or sets with respect to size. He was then shown pairs of Arabic numbers or an Arabic numeral and a set of objects and was asked for the color of the bigger or smaller numeral or set. Alex's high success rate showed he (a) understood number symbols as abstract representations of real-world collections, (b) inferred the relationship between Arabic numerals and their quantity via stimulus equivalence, and (c) understood the untrained ordinal relationship of his numbers. Obviously, Alex possessed skills not acknowledged by Penn et al. as being possible for nonhumans.

I wonder why Penn et al. fail to mention research by Timothy Gentner and colleagues (T. Gentner et al. 2006) demonstrating that recursive-style behavior, which Hauser et al. (2002a) claim is unique to humans, can be observed in starlings (*Sturnus vulgaris*). Now, many colleagues, including those cited by Penn et al., do not agree with the definition of recursion used by Hauser et al. nor do they believe that recursion is indeed the one defining factor that separates human and nonhuman communicative behavior. Nevertheless, Gentner et al. do provide evidence for an advanced nonhuman capacity that Penn et al. might well have discussed.

In sum, although Penn et al. do indeed present cases for which no good data as yet exist to demonstrate equivalent capacities for humans and nonhumans, I disagree with their insistence that the present lack of such data leads to a theoretical stance requiring a sharp divide between human and nonhuman capacities. Absence of evidence is not a sure argument for evidence of absence. A continuum appears to exist for many behavior patterns once thought to provide critical distinctions between humans and nonhumans; I discuss some such instances missed by Penn et al., others also exist, and I suspect that, over time, researchers will find more continua in other behavior patterns. Moreover, although I suspect that some of the papers that I cite were not published when this target article was written, their recent appearance only supports my point – that new data may require a reappraisal of purported certainties. One may argue about definitions of discontinuity – for example, how to reconcile some societies' advanced tool creation and use with those of primitive societies whose tools are not much better than those of corvids (Everett 2005; Hunt & Grey 2007) – and I do not deny the many differences that indeed exist between humans and nonhumans, but I believe future research likely will show these to be of degree rather than of kind.

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Quotidian cognition and the human-nonhuman "divide": Just more or less of a good thing?

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Abstract: We make three points: (1) Overlooked studies of nonhuman communication originally inspired, but no longer support, the blinkered view of mental continuity that Penn et al. critique. (2) Communicative discontinuities between animals and humans might be rooted in social-cognitive discontinuities, reflecting a common lacuna in Penn et al.'s relational reinterpretation mechanism. (3) However, relational reinterpretation need not be a qualitatively new representational process.

We wholly endorse Penn et al.'s unsentimental critique of the current zeitgeist in comparative cognition. One area they gloss over in their review is the natural communication systems of primates and other nonhumans. This omission is unfortunate because, following Don Griffin's spirited prescriptions (e.g., Griffin 1978), studies of animal communication in particular have been a key driver of the field's blinkered focus on only continuity between animal and human minds – the focus that Penn et al. are now at pains to exorcise. A paradigmatic example is research on vervet monkey communication by Seyfarth et al. (1980), which documented a small repertoire of alarm calls specific to different kinds of predator that prompt functionally different escape responses. The apparent referential quality of these alarm calls encouraged comparison to the symbolic properties of human words and provided a timely confirmation of Griffin's instinct that communication behaviors offered privileged insight into animal minds and that continuity with human minds would be revealed in proportion to their language-like qualities. The vervet monkey work thus catalyzed a generation of research aimed at identifying additional language-like phenomena in nonhuman communications. It also inspired research on continuity in other cognitive domains (e.g., transitivity, numerosity, causality, etc.) on the assumption that the manifest continuity between animals and humans in our own most vaunted ability – language – must foreshadow continuity in almost everything else; hence, the inference that some (perhaps many) nonhumans might be teetering on the brink of humanity.

Subsequent research on intentionality (qua theory of mind, ToM) seriously undercut these inferences. Additional field studies of communication showed that, contra language, primate vocalizations were not produced flexibly to contact and manipulate the intentional states of others. Indeed, signalers proved remarkably oblivious to the audience to which their vocalizations were "addressed." Laboratory studies of ToM pointed to the same social-cognitive lacuna. Results of ape language studies were corroborative: despite sometimes impressive symbol learning abilities, apes' use of artificial languages proved almost entirely instrumental and solipsistic. Because human language and its sine qua non – meaning – hinges on the intentionality of communications (mutual, implicit mental attributions; Grice 1957), it is increasingly difficult to see primate (and other animal) communications as very much like language in this fundamental respect (Notman & Rendall 2005; Owren & Rendall 2001). Thus, as Cheney and Seyfarth themselves now argue, although the functional behavioral outcomes that animal signals support might sometimes seem superficially language-like, the underlying psychological mechanisms are profoundly different (Cheney & Seyfarth 2005).

The upshot here for Penn et al. is that, in their efforts to correct the increasingly blinkered view that threatens comparative cognition, they have missed an opportunity to do so using results from the very research programs on communication that inspired that blinkering to begin with.

At the same time, however, we ask whether the profound functional gulf between humans and nonhumans in these and other domains need be underwritten by the fundamentally different psychologies that Penn et al. trace to our ability for "relational reinterpretation." True, the functional limitations in nonhuman communication and intentionality that we emphasize might well reflect a common lacuna in relational reinterpretation: truly symbolic communication requires understanding not just the (observable and local) referential connection between particular symbols and their real-world referents, but also the broader (but unobservable) relational system that they instantiate; similarly, ToM requires seeing through specific (observable and local) behavior-context associations to the broader (but unobservable) relational mentalistic system that they reflect.

However, it is not clear that either ability requires any qualitatively new representational process. For example, Landauer has shown that, starting only with a large corpus of (experienced) words and the discursive contexts in which they occur, and no other pre-existing knowledge, singular value decomposition followed by dimension reduction can distill from their local (first-order) associations the latent relational dimensions (i.e., second-order associations) among them that yield functional semantic comprehension (latent semantic analysis; e.g., Landauer & Dumais 1997). In principle, with sufficient and appropriate dimensions and observations, similar associative processes could produce the latent relational dimensions among individuals, behaviors, and contexts that would give the functional appearance of a theory of mind.

In other words, is it possible that relational reinterpretation is not a distinct and qualitatively novel, abstract representational process, but rather, a theoretical approximation for the under-appreciated (and still insufficiently explored) returns of (taxonomically widespread) associative processing? And is it therefore possible, at least in quotidian contexts, that humans too might have a mostly behavioristic understanding of the world that is driven primarily by perceptions of concretes, not by hypothesized unobservables, no matter how much our scientific theorizing spirits heuristic mentalistic constructs into our heads: that what is frequently seen to be necessarily analytic is in reality the result of nonanalytic cognition (Brooks 1978)?

There are two obvious objections. The first is that, compared to the representational account, the associative/nonanalytic account would be far more memory intensive, computationally extensive, and therefore processually inefficient. To which we respond, "Just exactly what defines the human brain and what our theories of comparative cognition need to account for: a tissue profligate, massively interconnected, parallel processor." A second objection is that the associative/nonanalytic account does not actually produce semantic knowledge or a mentalistic understanding of others, only the functional appearance of them. To which we respond, "And what else is there?"

Ultimately, then, we completely agree with Penn et al. that the current zeitgeist in comparative cognition is wrong; however, the mistake maybe lies not in emphasizing mental continuity, but rather in the kind of mental continuity emphasized. Animals and humans are probably similar: however, similar not because animals are regularly doing cognitively sophisticated things, but because humans are probably doing cognitively rather mundane things more often than we think. This assertion does not mean that there are not qualitative phenomenological differences between humans and animals. There are, and Penn et al. rightly foreground these in their opening statements. But, these phenomenological novelties need not be underwritten by a qualitatively different psychology. Rather these functional novelties might emerge naturally from humans' exaggerated tendency to put things in the world (sensu Clark 1997) and then to re-perceive them again, repeatedly. And then also to crunch the vast perceptual datasets created from this habit with exponentially more associative power. Paradoxically, and contra part of Penn et al.'s proposal, these habits might also make us more, rather than less, perceptually-driven than nonhumans.

Language as a consequence and an enabler of the exercise of higher-order relational capabilities: Evidence from toddlers

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Abstract: Data on toddler language acquisition and use support the idea of a cognitive "supermodule" that can resolve contradictory claims about human-animal similarities. Examples of imagination, aesthetic evaluation, theory of mind (ToM), and language learning reveal higher-order, relational, abstract capabilities early on. Although language itself may be a consequence of exercising this supermodule, it enables further cognitive operations on indirect experience to go far beyond animal accomplishments.

Here is a paradox: Whatever urges we humans have to declare we are special and to identify with the superhuman, these are balanced by the desire to believe animals are just like us. For millennia, arguments grounded in claims of unique relations to God, or gods, have stipulated that humans are different from animals. Against these stand pet owners extolling their charges' abilities, stories portraying animals as talking, thinking, acting, and interacting as humans do, and scientists offering evidence of remarkable feats by the animals they study. Even Furbies arouse in us a sense of commonality (Green 2007).

In the post-Darwin era, scientists try to resolve this paradox by addressing whether humans should persist in claims of uniqueness and on what basis. The authors of "Darwin's mistake" are not the first to defend "pro-difference" positions. Taking on a less formidable foe in a book titled *Dr. Doolittle's Delusion*, Anderson (2004) argued that only humans truly have language. And I, after years of dealing with undergraduates enamored of the abilities of animals like Sarah, Koko, and Alex, who had achieved fame if not language, argued that toddlers are already distinguished by language, self-reflection, and understanding of mind (Shatz 1994).

Neither Anderson nor I, however, proposed anything like a "supermodule" of cognitive ability to account for the learning and organization of human language as well as other cognitive skills. Penn et al. take that courageous step, arguing both against the adequacy of earlier proposed "supermodules" and for a broader alternative, although they admit to leaving as yet unspecified how it would function in a "neurally plausible cognitive architecture" (sect. 10.1, para. 3). Nonetheless, with their proposal, they offer new grounds for human-animal disparities and an intriguing explanatory basis for human language as essentially different from animal communication systems but not wholly unique among human cognitive systems. Notwithstanding their title, they do this while agreeing with the undeniability of evolution.

Penn et al. offer evidence for their claim based largely on what animals *cannot* do. An even stronger case could be made with more evidence of what human toddlers *can* do that sets them apart so early from even our closest relatives. My "pro-difference" stance followed from close observations of a toddler who, before age 3, had revealed through his talk that he could do higher-order, relational abstract reasoning about reality and fantasy, the artistic abilities of self and other, and his own knowledge and the false beliefs of another. Donning rain boots and saying, "These are my fireman's boots" [...] "I use them as my fireman's boots," the toddler showed he could imagine something to be what it was not. Upon viewing a cat painted by an adult, he opined that the cat he had painted was "lousy." And, after appearing naked before his grandmother and telling her he had left his pajamas in the bathroom (she had retrieved them and found them dry), he said, "You thought these were wet" (Shatz 1994).

Of course, children do not demonstrate higher-order cognitive capabilities like theory of mind (ToM) in every situation (Wellman 2002), and this counts as evidence that such abilities develop gradually. Overall cognitive complexity of the tasks requiring such reasoning is surely one explanation for this (Andrews et al. 2003). However, cognitive complexity alone cannot account for all human-animal differences. As Penn et al. note, animal behavior can hardly be deemed cognitively simplistic. Not long ago, I had the chance to reconsider my earlier position in light of recent claims for animals; my review of the new evidence, on both corvids and children, convinced me not to change my views (Shatz 2007). Animal cognitive sophistication is not qualitatively comparable even to toddlers' rudimentary knowledge about imagination and mind.

Admittedly, much (but not all) of the evidence for early ability is based on talk, and animals cannot talk. A dog shaking his blanket between his teeth with the violence that he might use on an unfortunate squirrel *may* be playing symbolically; still, we have no basis for attributing to him an awareness that reality and fantasy differ. In contrast, toddlers use language to show they can think about such a difference and so much more.

Crucially, even as they are acquiring a specific language, toddlers reveal they are using higher-order relational capacities to do so. For example, they begin to organize their lexicon even before having full knowledge of specific word meanings (Shatz & Backscheider 2001). And a toddler was observed reciting to himself a series of personal pronouns, apparently organizing them into a category, although his basis for doing so remained obscure (Shatz 1994). The research on the distributional properties of child-directed language suggests a basis for such behavior: The input feasibly offers adequate material for category creation to an organism *predisposed* to create categories of items related on abstract bases (Mintz et al. 2002; see also Tare et al. 2008). Additionally, experiments have shown that hierarchical organization is within the ken of toddlers (Diesendruck & Shatz 2001; Lidz 2007). These findings show that not only is language a means to revealing higher-order human capacities, but its acquisition may indeed be the consequence of exercising those capacities, as Penn et al. argue.

Finally, it may not be surprising that animals, clever though they are, remain mired in re-description of perceptually based data. Without having the higher-order capacities to learn language, they have no means to learn from testimony (Harris 2002) or to use language to learn more (Shatz 1994; 2007). Much of the immense power of language stems from the ability of the language user to engage in conversations with other like-language users to obtain more material on which to exercise one's higher-level cognitive abilities. Language may not be unique as an instantiation of the capacity Penn et al. grant humans, but its use may be the one that allows humans to go ever farther in bridging domains of knowledge in new ways. Penn et al.'s proposal is wholly compatible with the idea that the most important consequence of human uniqueness is the extension beyond clever animal exploitation of perceptions to the creative, imaginative re-description of both direct *and indirect* experience through language itself.

If we could talk to the animals

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Abstract: The thesis of discontinuity between humans and nonhumans requires evidence from formal reasoning tasks that rules out solutions based on associative strategies. However, insightful problem solving can be often credited through talking to humans, but not to nonhumans. We note the paradox of assuming that reasoning is orthogonal to language and enculturation while employing the criterion of using language to compare what humans and nonhumans know.

According to Penn et al., there is substantial evidence for discontinuity between human and nonhuman minds. They claim that "a distinctively human, modular system for approximating a LoT [language of thought] – that is, one that subserves higher-order, role-governed relational representations in a systematic and domain-general fashion – has evolved on top of and reinterprets the output of the *proto-symbolic* systems we still share with other animals" (sect. 11, para. 9, emphasis in original). A good part of their article aims to show that research pointing to nonhuman symbolic functioning in areas such as the ability to make transitive inferences or to demonstrate theory of mind reasoning can be best interpreted in terms of associative rule learning rather than evidence for insightful understanding similar to that of humans. The problem, though, is that their only apparent criterion by which nonhumans could be credited with higher cognition is through language. This criterion creates a paradoxical circularity in their argument, one that is not restricted to comparative psychology but has been long noted to be present in research on human cognitive development.

In this sense, the circularity of Penn et al.'s position resembles that in Piaget's theory (see Lourenço & Machado 1996; Siegal 1999; 2008). In Piaget's clinical method, thinking is assessed through language even though thinking is held to be genetically prior to language. According to this account, children who cannot justify their answers on measures such as those involving transitive inferences cannot be credited with having the necessary knowledge that the premises, if $A > B$ and $B > C$, must lead to the conclusion that $A > C$, and that this conclusion is a logical one which is independent of empirical verification. This standard of evidence means that children need to demonstrate proficiency in verbal ability to be counted as having the ability to respond correctly. So support for Piaget's theory has often been subject to the criticism that it is riddled with false negative results, of demonstrating that children lack logic and symbolic functioning when they often do show it in their everyday behavior. Similarly, adults in developing cultures may also appear to demonstrate a lack of competence on some formal tests that does not correspond to their highly adaptive intelligence.

Penn et al. describe evidence based on experiments and observations of nonhumans that would seem to be consistent with Darwin's continuity thesis. For example, crows, pigeons, and fish all show behavior that would seem to indicate a grasp of transitive inferences. However, Penn et al. prefer to dismiss this evidence in terms of training, reinforcement history, and low-level associational learning mechanisms that are independent of an understanding of logical relations. But on this basis, we could not credit the ability to perform transitive inferences to many humans. In common with crows, pigeons, and fish, children at an early age very clearly do show behavior that would seem to indicate a grasp of transitive inferences. However, they do not have the means to justify this behavior. Instead, they may order objects "logically" based on spatial imagery strategies and without the explicit use of logic (Pears & Bryant 1990). Although Penn et al. and Piagetians may not be ready to credit children and many adults with the abilities to solve transitive inference tasks unless they can verbalize a rationale to the effect of "because A is greater (or taller or longer) than B and B is greater than C, then A *must* be greater than C," it is seems entirely acceptable that the use of spatial imagery is a valid way to solve such tasks. It amounts to an alternative adaptive solution that serves the organism very well in a range of domains.

Similarly, birds such as scrub-jays and certain nonhuman primates show behavior that would seem to indicate a theory of mind reasoning in the form of understanding how conspecifics can be misled after having been imbued with false beliefs about the location of food. However, Penn et al. dismiss this evidence as falling short of their criterion for genuine theory of mind reasoning: requiring a demonstration that the animal can attribute mental state content to other agents and use this content in a "theory-like fashion" to predict behavior based on agents' mental states. Without providing a way for animals without language to demonstrate the possession of this theory, Penn et al. again prefer to interpret evidence for theory of mind (ToM) in nonhumans as evidence for a pattern of behavior created through training and reinforcement instead of based on insightful reasoning. This interpretation is close to that provided by Perner and Ruffman (2005) in dismissing the depth of nonverbal infants' ToM understanding as shown through patterns of visual attention devoted to the unexpected behavior shown by an agent with a false belief (Onishi & Baillargeon 2005).

Despite all this, it is abundantly clear that human infants have a substantial understanding of reality and the phenomenal world of reality as through the rational imitation of an agents' behavior (Gergely et al. 2002) – an ability shared to some substantial extent by chimpanzees (Buttelmann et al. 2007). Penn et al.'s proposal that humans are likely to undergo some sort of radical restructuring in their thinking and reasoning that does not occur in nonhumans needs to be reassessed. There are many other possibilities. For example, both humans and nonhumans could instead undergo some sort of "executive functioning" (EF) development. At a certain point, they now attend to the correct response – but humans, unlike nonhumans, can give verbal justifications to an experimenter for why this response is correct. It may of course be that humans undergo a more sophisticated EF development than do nonhumans. They also have access to language that alerts them to the pragmatic nature of the inferential reasoning that is required for task success. Ultimately, advances in brain scanning and eye-tracking techniques, as well as in the use of miniaturized video cameras for studying undisturbed behavior in natural surroundings (Rutz et al. 2007), may substantiate further both what young children and nonhumans know. In the meantime, Penn et al.'s verdict, "nonhuman animals didn't (and still don't) get it" (sect. 11.2, para. 4) is clearly premature.

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Explaining human cognitive autapomorphies

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Abstract: The real reason for the apparent discontinuity between human and nonhuman minds is that all closely related hominids have become extinct. Nonetheless, I agree with Penn et al. that comparative psychology should aim to establish what cognitive traits humans share with other animals and what traits they do not share, because this could make profound contributions to genetics and neuroscience. There is, however, no consensus yet, and Penn et al.'s conclusion that it all comes down to one trait is premature.

Every species is unique. Humans are no different. In taxonomy, the derived traits that are differentiating a species from even its closest relatives are called autapomorphies. Humans appear to have various such autapomorphies (e.g., menopause, concealed ovulation, and, for what it is worth, our varied hair that often is ever-growing). Penn et al. put forward an interesting account that tries to explain what is unique about the human mind – what we hence might call *human cognitive autapomorphies*. Such proposals often attract scepticism from comparative psychologists, as there is a suspicion that they are designed to justify human moral superiority (and hence how we allow ourselves to treat nonhumans), rather than to advance science (e.g., Cartmill 1990). On the other hand, Penn et al. charge that comparative cognitive psychologists have long been biased towards emphasising continuity.

Whatever the past motives, there are compelling new reasons why comparative psychologists ought to care about identifying human cognitive autapomorphies, as well as identifying what precisely are the traits that humans and other species share. Establishing this information can seriously narrow down the search space for identifying the neural and genetic underpinnings of these cognitive traits. Chances are that humans' cognitive autapomorphies have something to do with our brain autapomorphies. Subsequently, this knowledge would also inform us about when animal models of human conditions are useful and when they are not (Suddendorf & Corballis 2007b). I therefore believe that these questions about human cognitive autapomorphies are important to keep on the agenda.

Penn et al. may well be right when they claim that only humans can reason about "higher-order relations in a structurally systematic and inferentially productive fashion" (sect. 11, para. 10). They come to this conclusion after critically reviewing comparative data on a selection of what they regard as fundamental human abilities. There is merit in the general approach of identifying where and how other animals fail on tasks that humans master, and in seeking out what the limits have in common (cf. Premack 2007). This approach is not new, of course, and Penn et al.'s proposal is not the only non-modular account to pursue it. In fact, recursion (Corballis 2007b), meta-representation (Suddendorf 1999), and reasoning about ternary relations (Halford et al. 1998a) have previously been argued to go a long way towards explaining what sets human cognition apart. There seem to be structural similarities in the limits of nonhuman competence across domains. But whether these, or the current version of these proposals, really reflect one trait, and to what extend nonhuman animals' performances can be explained by their lacking this trait, is yet to be established.

There is ongoing debate about animal competence in each of the domains discussed, and what Penn et al. single out as *the best current evidence* is by no means uncontroversial. For example, citing Dally et al. (2006) as the best evidence for theory of mind in animals is a questionable choice, given that these authors themselves state that what they described need not require theory of mind (cf. Suddendorf 2006). There are also concerns about Povinelli's reinterpretation hypothesis (see Suddendorf & Whiten 2003 for a detailed discussion) that equally apply to the present incarnation. But I would like to take this opportunity here to comment on a missing piece to any explanation of the apparent discontinuity between human and nonhuman minds.

The authors assert that standard evolutionary mechanisms produced the human mind (e.g., Note 1 of the target article). So there is no special pleading to explain the human case. The extant uniquely human traits, however, are as much a function of whatever drives the evolution of the human capacities, as they are a result of what the minds of related species are like, and which of them happened to have survived. A gap is defined by both its sides. Only 40,000 years ago, that gap between the human and nonhuman mind would have been a lot smaller as we shared the planet with *Homo neanderthalensis* and *Homo floresiensis*. In an important sense, then, to *explain* today's apparent discontinuity, is to explain why these species went extinct and only ours survived. This is, of course, a fundamentally different kind of enterprise than the one Penn et al. pursue, but it goes to the heart of the mystery of human uniqueness. To be sure, it remains unclear why the other hominids perished and the gap between human and nonhuman mind widened, but given our historical violent tendencies, an active role of *Homo sapiens sapiens* in their demise cannot be ruled out.

Today, our closest living relatives, the apes, are also all at the verge of extinction (and humans no doubt have had a hand in that). To our great grandchildren the discontinuity between human and nonhuman minds may be even wider when their closest living relatives are monkeys, not apes. Penn et al. pay little attention to differences in competence between extant primate species. There is, however, strong evidence that great apes share with humans some sophisticated cognitive abilities that other primates do not (Suddendorf & Whiten 2001). For example, great apes can entertain secondary representations as evident in their competence in numerous domains ranging from mirror self-recognition (e.g., Povinelli et al. 1997) to understanding invisible displacement (e.g., Collier-Baker & Suddendorf 2006). This is evidence for continuity, and phylogenetic reconstruction allows us to trace the evolution of these capacities to our common great ape ancestor (Suddendorf & Whiten 2001).

Systematically mapping what cognitive faculties humans share with which other primate relatives may be as important as identifying what traits are human cognitive autapomorphies. Penn et al. briefly acknowledge that there might be other discontinuities in the contexts of cooperation (Sterelny 2003), numeracy (Deheane 1997), and mental time travel (Suddendorf & Corballis 2007a), but they hint that their proposal might explain what is unique about these too. Perhaps so. But a lot more work needs to be done to establish this, or its role in other potentially autapomorphies-harbouring contexts such as culture (Herrmann et al. 2007) and imagination (Whiten & Suddendorf, 2007), or aesthetics, morals, and humour. A systematic and sober approach might eventually lead us to consensus. This could enable comparative psychology to live up to its potential of making a seriously enlightening contribution to identifying the neural and genetic underpinnings of cognition.

Languages of thought need to be distinguished from learning mechanisms, and nothing yet rules out multiple distinctively human learning systems

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Abstract: We distinguish the question whether only human minds are equipped with a language of thought (LoT) from the question whether human minds employ a single uniquely human learning mechanism. Thus separated, our answer to both questions is negative. Even very simple minds employ a LoT. And the comparative data reviewed by Penn et al. actually suggest that there are many distinctively human learning mechanisms.

Penn et al. conflate two issues: one is the degree to which human and animal minds approximate a LoT (language of thought)-based system, and the other concerns the underpinnings of distinctively human learning and reasoning capacities.

A LoT requires a combinatorial syntax and semantics, and syntax-sensitive processes. The LoT hypothesis is *noncommittal* both about the details of the syntax and semantics of an organism's thoughts and about whether any particular process or rule is implemented as "hardware," "software," or something in-between (Fodor 1987). Certainly, it does not address what specific information the organism can learn or reason about. Thus, even the thought capacities of a very simple mind could approximate *one* LoT-based system to the same extent as a human's could approximate *another*.

The evidence suggests that the minds of honeybees approximate a LoT-based system to a high degree (Tetzlaff 2006). First, honeybee navigational capacities exhibit systematicity. The effects of panoramic context on the performance of route flight segments and the ability of bees to learn sequences of route segments provide one of many examples (M. Collett et al. 2002; T. S. Collett et al. 1993): If a bee has the capacity to learn the route sequence [distance *n* to landmark *L*, then distance *m* to landmark *K*], then it thereby also has the capacity to learn any of the route sequences (1) [distance *m* to *L*, then distance *n* to *K*], (2) [distance *n* to *K*, then distance *m* to *L*], and (3) [distance *m* to *K*, then distance *n* to *L*].

The vector-navigational capacities of bees are extremely difficult to explain without positing algebraic rules (Collett & Collett 2000; Gallistel 1998; Menzel et al. 2005). Moreover, the capacity to freely generalize universally quantified one-to-one mappings requires the use of algebraic rules (Marcus 2001). Honeybees are able to freely generalize the solar ephemeris for their locale: Based on minimal exposure to the sun, their solar-ephemeris learning mechanism produces a record that allows them to estimate the sun's azimuthal position at times when they have not seen it or can never see it (Dyer & Dickinson 1996). Also, recent Y-maze experiments show that bees can solve a delayed-matching-to-sample task, where their solution allows them to generalize to novel stimuli across sensory modalities (Giurfa et al. 2001). This suggests that bees can acquire novel rules such as [choose the *x*-marked arm if *x* was at the entrance].

Finally, honeybees seem able acquire non-perceptually based information about particulars. Path integration requires a global accumulator that tracks distance and direction from the hive. But there is also a need to posit one or more local accumulators that tie distance and direction information to specific locations, such as the place of release after displacement by an experimenter (Collett et al. 2002). Significantly, a bee's local-flight-segment learning mechanism can be active without being tied to any specific perceptual features. This could occur, for example, when a displaced bee, after playing out its feeder-to-hive vector (say), arrives at a perceptually uniform location that would have been the location of the hive in the absence of displacement (Menzel et al. 2005; Riley et al. 2003). It appears, then, that a bee can acquire information akin to [distance *n* and direction *d* from *o*], where *o* represents a particular location (the origination point) independently of any of its perceptual features.

Because humans are by no means unique in possessing a LoT, the real issue is how many distinctively human learning/reasoning mechanisms there are. Penn et al. claim that there is just one, for reasoning about higher-order relations. An objector whom they never properly address would claim that there are many distinctively human learning mechanisms, for "theory of mind" (ToM), for intuitive physics, for natural language, and more (Barrett & Kurzban 2006; Carruthers 2006). Penn et al.'s brief argument against this "multiple-module" hypothesis is that it can't explain the commonalities they claim to have identified across the various domains of distinctively human thinking. (Other than this, all of their arguments presuppose a single-module opponent, e.g., the claim that language is what explains all the cognitive differences between humans and other animals or that ToM does so.) But this presumes, of course, that there *are* such commonalities. We deny that there are.

Penn et al. claim that the distinctive thing common to all the phenomena they examine is that humans are reasoning about relations among relations in ways that are not available to nonhuman animals. But when one looks closer at the details of what humans are doing, it is impossible to make this description fit all (or even the majority) of the data. The ToM domain, for example, has nothing to do with relations among relations. It is a matter of identifying and drawing inferences involving the causal variables underlying observed behavior (beliefs, desires, and the rest). Likewise in the case of intuitive physics: this is about identifying and drawing inferences about the unperceived causal forces that govern the physical world (notably gravity and momentum). In contrast, the capacity to engage in transitive inference is not about underlying causal structure at all; nor is it about relations among relations. It is a matter of identifying those relations in respect of which transitive inference is valid, and reasoning accordingly. And the ability to learn category-based rules such as "noun-noun-verb" or "noun-verb-noun" is surely something else again. The only cases that clearly fit Penn et al.'s "relations-between-relations" interpretation are analogical reasoning and higher-order spatial reasoning (although the latter probably depends more crucially on ToM abilities).

On closer consideration, there is no reason whatever to think there could be a single learning mechanism that can engage in all of the distinctively human forms of learning that Penn et al. discuss. The only possibility that they present for consideration is LISA (Learning and Inference with Schemas and Analogies). But this takes semantically interpreted sentences as input and does analogical discovery and reasoning. No arguments are given for thinking that LISA (or anything like it) could also discover the mental variables underlying observed behavior, or the causal forces at work in the perceived physical world. Indeed, it seems most implausible that LISA could be extended into these domains without becoming an entirely different sort of learning mechanism.

At the end of the day, then, the multiple learning mechanisms hypothesis remains, not only unscathed, but as the best extant explanation of the comparative data.

Analogical apes and paleological monkeys revisited

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Abstract: We argue that formal analogical reasoning is not a uniquely human trait but is found in chimpanzees, if not in monkeys. We also contest the claim that the relational matching-to-sample task is not exemplary of analogical behavior, and we provide evidence that symbolic-like treatment of relational information can be found in nonhuman species, a point in contention with the relational reinterpretation hypothesis.

Analogical apes and paleological monkeys revisited. Thompson and Oden (2000) concluded that monkeys are *paleologicians*; their conceptual categories are based on shared predicates – absolute and relational features bound by perceptual and/or associative similarity, whereas symbol trained apes are *analogical* in the sense that they perceive abstract propositional similarities spontaneously. Moreover, symbol systems provide the representational scaffolding for manipulation and expression of propositional knowledge in relational matching-to-sample (RMTS) and related nonverbal analogy tasks (Gillan et al. 1981; Oden et al. 2001). However, the authors of the target article dismiss this distinction, essentially arguing that only humans are truly analogical organisms, whereas all other animals are paleological in their conceptual abilities.

We suggest that the authors' necessary criteria as to what constitutes an analogy may be overly exclusive. As they note, when Sarah, a chimpanzee, under conditions of non-differential reinforcement, constructed both the base and target relations of an analogy from four of five elements (Oden et al. 2001, condition 4), she did so by equating the *number* of within-pair featural differences, independently of the physical nature of those differences. We believe that Sarah's performance is evidence of her ability to construct a *formal*, if not *material*, analogy in which properties (i.e., number of featural changes) of one set of objects X are mapped onto those of another set Y according to the principles of mathematics (Rothbart 2007).

In this regard Sarah is perhaps not alone in her formal analogical abilities, given the ability of other primates and birds to match entropy levels regardless of the physical icons used to instantiate this mathematical property (e.g., Fagot et al. 2001; Wasserman et al. 2001; Young & Wasserman 1997). However, Sarah's performance on functional analogy problems (Gillan et al. 1981) provides for now – the authors' concerns notwithstanding – the sole evidence of a nonhuman recognizing a *material* analogy by, "observing similarities between materials or types of phenomena" (Rothbart 2007, p. 24).

Is the relational matching-to-sample task exemplary of analogical reasoning? There is compelling evidence of relational conceptual capabilities in nonhuman animals (for reviews see, eg., Wright & Katz 2006, Zentall et al., in press). Macaque rhesus monkeys, for example, exposed to the same "symbol" training procedures as chimpanzees in a RMTS task (Thompson et al. 1997) learned to generalize their responses to a circle whenever the two items in the discriminative cue matched (e.g., AA, etc.), and to a triangle whenever they did not (Washburn et al. 1997).

Flemming et al. (2007) also found that rhesus monkeys (*Macaca mulatta*) not only correctly chose novel identical/nonidentical relational pairs in the presence of discriminative color cues, but they also correctly chose the color itself in the presence of the relational pairs. Importantly, however, unlike chimpanzees (Thompson et al. 1997), none of the monkeys in these experiments (Flemming et al. 2007; Washburn et al. 1997) responded above chance on the RMTS task over literally thousands of trials.

The authors argue that, "a cognizer could pass a classic S/D [same-different] task by calculating an analog estimate of the variability between items in the sample display and then employ a simple conditional discrimination to select the appropriate behavioral response to this chunked result" (sect. 2.2, para. 4). But, given that monkeys can learn two-item conditional relational judgment tasks as described earlier, should they not then also acquire the relational matching task if judgments of sameness and difference may be reduced to the discrimination of between-item variability or entropy? Yet, clearly the monkeys do not.

Moreover, results obtained by Flemming et al. (2007) from rhesus macaque monkeys further suggests that categorical same/different judgments, although not necessarily prevalent in early stages of relational discriminations, can be learned and applied through the implementation of entropy-infused displays. Monkeys were not only successful in making a two-choice discrimination between sets of six identical or nonidentical stimuli, but also with *pairs* of novel stimuli. When the number of items in the display was systematically reduced to two, the monkeys' performance levels neither declined nor revealed asymmetric effects (on same vs. different trials), as would be expected if the animals' judgments were still under perceptual control of entropy. Flemming et al. (2007) argued that same/different judgments are not entirely based on entropy-infused displays, but rather that conceptual categorical judgments can emerge and overcome the initial dominance of perceptual-based responding.

A conditional cue is proto-symbolic. Nevertheless, as noted, these same monkeys still failed to acquire the RMTS task. Why might this be? As described by Thompson and Oden (1996; 2000), conditional S/D tasks can be "solved" following application of a single matching operator, whereas for success in the RMTS task the animal must not only apply the matching operator to the sample and alternatives, but also to the abstract encoded outcomes.

The "profound disparity" in the performance of chimpanzees and monkeys in the RMTS task lies then in the chimpanzee's capacity – like that of children (Rattermann & Gentner 1998b) – to symbolically recode abstract relations into iconically equivalent symbols, thereby reducing relational matching to a task that is functionally equivalent to physical/perceptual matching (Thompson & Oden 1996; 2000; Thompson et al. 1997; 2001), a process, "akin to acquiring a new perceptual modality" (Clark 1998, p. 175).

Penn et al. suggest that, in part, the ability to label relational information is unique to the human mind and responsible for the discontinuity implicated by the relational reinterpretation (RR) hypothesis. In fact, we believe there is comparative evidence to suggest that similar symbolic systems also apply to our nearest primate relatives. In the case of other animals, like monkeys, however, no evidence as yet indicates that a conditional cue can acquire the full status of a symbolic label, although it would seem that symmetric treatment of a conditional cue lays the foundation for a recoding of relational information as set forth by the RR hypothesis.

Monkey see, monkey do: Learning relations through concrete examples

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Abstract: Penn et al. argue that the complexity of relational learning is beyond animals. We discuss a model that demonstrates relational learning need not involve complex processes. Novel stimuli are compared to previous experiences stored in memory. As learning shifts attention from featural to relational cues, the comparison process becomes more analogical in nature, successfully accounting for performance across species and development.

Penn et al. present an encompassing argument on why nonhumans are not able to reason relationally. Their point is well made, yet they fail to adequately address the basis of performance in the relation-like reasoning tasks in which animals do succeed, such as same-different learning (Young & Wasserman 1997), match to sample, and primitive grammatical learning (T. Q. Gentner et al. 2006; Hauser & Weiss 2002). Although these tasks do not necessarily require a relational reasoning system, they are instances of relational responding. If animals do not possess a perceptual symbol system, how do they respond relationally?

We offer an explanation for the ability of animals in the form of a computational model that learns to respond to categories defined by relations by making structured comparisons to concrete examples stored in memory. The model, BRIDGES (Building Relations through Instance Driven Gradient Error Shifting), provides an account of how animals (and people) learn to respond relationally. The model does not posit elaborate processes or representations.

BRIDGES combines two popular approaches to cognition, exemplar-based category learning (Kruschke 1992) and structure mapping theory (D. Gentner 1983). Exemplar-based models store every experienced stimulus in memory. When a novel stimulus is encountered, the similarity between the stimulus and each stored exemplar is calculated. The novel item is assigned to the category whose members have the highest summed similarity. A learning process adjusts the attention allocated to the various stimulus dimensions, which affects the model's notion of similarity. For instance, if small red stimuli and big red stimuli belong to category A, and small blue stimuli and big blue stimuli belong to category B, the model will learn to weight color more than size.

Structure mapping theory expands on this notion of similarity. The similarity between two scenes is determined by aligning the objects and relations present within one scene with the objects and relations in the other scene (Markman & Gentner 1993). The quality of the alignment determines similarity.

BRIDGES extends the notion of similarity used in exemplar models to an attention-weighted form of structure mapping theory. This allows relational similarity, the degree to which mapped objects play the same role in their corresponding relations (Jones & Love 2007), to play a variable role in the alignment process. Attention can shift between the features (e.g., red) and the relations (e.g., redder). This allows for abstraction away from the features and toward the relations, but only so far as the statistics of the environment warrant. Attention is updated according to a supervised or unsupervised gradient descent algorithm. The result is that BRIDGES is able to learn to respond differentially to the presence of relations, but that responding is still affected by the features of the stimuli.

BRIDGES has successfully simulated (Tomlinson & Love 2006) relational responding in a number of situations, including same-different learning in pigeons (Young & Wasserman 1997) and infant grammar learning (Marcus et al. 1999). Like the participants in these experiments, BRIDGES generalizes to presentations of the relations with novel objects. Also, these relations are still clouded by the featural similarity of the individual stimuli since attention shifting is rarely complete. BRIDGES's operation is consistent with observed relational shifts (from concrete to abstract) in children and experts (Chi et al. 1981; Gentner & Rattermann 1991).

In contrast to BRIDGES, Penn et al. explain the match-to-sample tasks and same-different learning as a result of entropy detection (see Young et al. 2003), which does not require a relational competency. Entropy explanations and BRIDGES both do equally well in accounting for a number of phenomena. However, BRIDGES is distinguished from an entropy explanation by its sensitivity to experienced examples (i.e. attention does not fully shift to relations). In support of BRIDGES, Gibson and Wasserman (2004) found that pigeons adjust their responding when the featural similarity of the test arrays is put at odds with the relational similarity of the arrays.

BRIDGES suggests that animals and humans at various stages of development can be understood as lying along a continuum. When modeling the simple behavior of animals or infants, attention shifting is rarely complete and a representation with only simple features and a type-token relation is sufficient. The type-token relationship assumes that the individual is able to recognize objects present in the input as members of a larger category. In other words, when pigeons are presented with an array of shapes, they are able to represent the squares as members of an abstract type, square. In contrast, when modeling more complex behavior, in children or adults, a representation using other relations (e.g., cause) or high-order relations (i.e., relations between relations) is often required. Additionally, attention shifting occurs faster and is more complete. BRIDGES provides a tool to talk about these and other differences in a quantitative way.

Animals might not be able to succeed at complex relational reasoning tasks, but they can compare current examples to previous examples in a structured way, and from this respond in a manner consistent with an understanding of abstract relations. BRIDGES is a computational model of how this relation-like behavior can be learned. By comparing concrete examples of the relations in a structured manner, one can learn to respond in a manner consistent with the relations, without true abstract knowledge.

On possible discontinuities between human and nonhuman minds

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Abstract: The history of comparative psychology is replete with proclamations of human uniqueness. Locke and Morgan denied animals relational thought; Darwin opened the door to that possibility. Penn et al. may be too quick to dismiss the cognitive competences of animals. The developmental precursors to relational thought in humans are not yet known; providing animals those prerequisite experiences may promote more advanced relational thought.

They cannot speak. Their movements are limited and clumsy. And, their sensory systems are barely functional. Evidence of habituation and associative learning can be obtained only when the most sensitive and creative behavioral testing methods are deployed. Of course, there are no signs that they reason about higher-order relations between events. Should the absence of evidence of reasoning about higher-order relations be counted as incontrovertible evidence of absence in these creatures?

This is a trick question! We might be talking about a newly hatched pigeon or we might be talking about a newborn human infant. These two organisms traverse dramatically different developmental trajectories to adulthood. As adults, pigeons fail some of the tests of higher-order relational cognition – like the forming of analogies – that humans pass. Why? Penn et al. point to the inherited information processing systems of the respective organisms; humans are born with neural systems which pigeons lack.

Penn et al.'s proposal is certainly plausible. But precisely what are these neural systems? Do these systems merely mature as the child approaches adulthood? Or must these systems be carefully cultivated by enriching experiences to fully flower? Suppose that these experiences are not a part of pigeons' usual upbringing; could providing pigeons with these experiences promote still loftier levels of cognitive achievement? Is it not reasonable to take these questions seriously before yet again proclaiming an evolved human uniqueness?

The history of comparative psychology is replete with confident proclamations of human exclusivity. Most famous and germane here is that of John Locke, who in his 1690 volume, *An Essay Concerning Human Understanding*, assuredly opined: "I think, I may be positive . . . That the power of Abstracting is not at all in [Brutes]; and that the having of general Ideas is that which puts a perfect distinction betwixt Man and Brutes; and is an Excellency which the Faculties of Brutes do by no means attain to" (Locke 1690/1975, p. 159).

Nearly two centuries later, the faculty of abstraction was a focal point of Charles Darwin's consideration of animal and human intelligence in *The Descent of Man*: "[T]he greatest stress seems to be laid on the supposed entire absence in animals of the power of abstraction, or of forming general concepts" (Darwin 1874/1896, p. 83). Unlike Locke, Darwin left the door open to abstraction in animals. Darwin observed that:

> It is generally admitted, that the higher animals possess memory, attention, association, and even some imagination and reason. If these powers, *which differ much in different animals*, are capable of improvement, there seems no great improbability in more complex faculties, such as the higher forms of abstraction, and self-consciousness, &c., having been evolved through the development and combination of the simpler ones. (Darwin 1874/1896, pp. 83–84, emphasis added)

Hence, abstract thinking might only emerge in species possessing a requisite ensemble of other, foundational cognitive skills.

Perceptively linking evolutionary and developmental considerations, Darwin anticipated and countered an obvious criticism: "It has been urged against the views here maintained that it is impossible to say at what point in the ascending scale animals become capable of abstraction, &c.; but who can say at what age this occurs in our young children? We see at least that such powers are developed in children by imperceptible degrees" (p. 84). It must be acknowledged that Darwin knew of no compelling or even suggestive evidence of abstraction in animals; his aim was to merely to remain receptive to evidence of abstraction in animals, even if rather rudimentary forms of abstraction were to be exhibited compared to the more highly advanced relational skills of human adults.

A quarter century later, C. Lloyd Morgan denied animals the ability to behave conceptually. Conceptualization, he wrote in *An Introduction to Comparative Psychology*, requires that we "neglect all that is variable and focus the attention on the uniform relation. [Then] we have reached a conception, and this conception is not concrete, particular, and individual, but abstract, general, and of universal application" (Morgan 1894/1896, p. 263). Morgan believed that only adult humans (not even children) are capable of conceptualization. He rejected the hypothesis of relational conceptualization in animals, "in no dogmatic spirit, and not in support of any preconceived theory or opinion, but because the evidence now before us is not . . . sufficient to justify the hypothesis" (p. 377).

What would that evidence be? Here, we hit a sticking point. Locke, Darwin, and Morgan were not at all helpful in saying just what evidence would convincingly document abstract relational behavior, particularly in nonhuman animals. Nor do Penn et al., although they do dismiss all prior claims of relational learning in nonhumans. Physical matching-to-sample, same-different discrimination, relational matching-to-sample, and both physical and functional analogy completion are all tossed aside, either because the tasks are deemed to be inadequate or because the behaviors of animals on these tasks do not meet the authors' standards. I do wish that Penn et al. had described clear behavioral tests of human and nonhuman minds that would enable investigators to see if nonverbal creatures can exhibit cognitive performances that all would agree are "truly" higher-order, relational, and systematic. Doing so would have represented a positive proposal in contrast to the rather bleak assessment of animal cognition that Penn et al. now provide.

This negative assessment prompts Penn et al. to assert that Darwin was mistaken when he proposed that intellectual differences between animals and humans are quantitative and not qualitative. I trust that the earlier quotations document that Darwin held a fuller and more nuanced position concerning species differences in intelligence than is suggested by his oft-cited "continuity" claim.

Finally, Penn et al. should clarify what appears to be a striking anomaly in their logic. After strenuously arguing that human and animal minds differ in kind, Penn et al. curiously suggest that human and nonhuman minds differ in the degree to which they approximate the relational capabilities of a physical symbol system. Can they have it both ways?

Minding the gap: Why there is still no theory in comparative psychology

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Abstract: The prevailing view that there is significant cognitive continuity between humans and other animals is a result of misinterpretations of the role of evolution, combined with anthropomorphism. This combination has often resulted in an over-interpretation of data from animal experiments. Comparative psychology should do what the name indicates: study the cognitive capacities of different species empirically, without naive evolutionary presuppositions.

Darwin's insistence that there was "no fundamental difference between man and the higher mammals in their mental faculties" (Darwin 1871, p. 35) may be counted one of his few significant mistakes. Comparative psychology has been bedevilled for over a century by the need to reconcile the obvious cognitive gap between the human and nonhuman mind with Darwin's identity thesis. We commend Penn et al. for bringing this issue to the fore. We suggest that the adoption of models based on a mistaken view of evolution, combined with a tendency to anthropomorphise, has led to a widespread perpetuation of Darwin's mistake (cf. Wynne 2005). The form of evolutionary continuity between man and beast that many contemporary researchers seek is, in fact, a tacit perpetuation of the old *scala naturae* concept (Hodos & Campbell 1969). This is seen in the search for cognitive homologies in our closest relatives. In contrast, others have suggested that there is convergence of cognitive capabilities, such that birds or dogs may be more similar to humans than apes. We will discuss the different evolutionary scenarios in turn.

As the target article makes clear, many researchers still seek to extend homology to cognition. One example not considered by Penn et al. is the evolution of morality. De Waal and collaborators claim to have identified cognitive capacities in nonhuman primates that they consider signs of proto-morality, or at least cognitive traits such as empathy and unfairness avoidance, that are prerequisites for moral behaviour (de Waal 2006). Concurrently, de Waal (1999) has advocated the use of what he calls "animal-centered anthropomorphism." Thus, chimpanzees were said to "console" each other after fights (de Waal & van Roosmalen 1979), and capuchin monkeys and chimpanzees were reported to be averse to unfairness (Brosnan & de Waal, 2003; Brosnan et al. 2005). De Waal (2006) has suggested that "if closely related species act the same, the underlying mental processes are probably the same too" (p. 62), and hence it is assumed, anthropomorphically, that when apes and monkeys show behaviours that resemble certain human behaviours, they are thinking what we think under similar circumstances. Subsequent research, however, has revealed that there is in fact no evidence for "consolation" in chimpanzees (Koski & Sterck 2007) or for inequity avoidance in capuchin monkeys (Dubreuil et al. 2006; Wynne 2004b) or chimpanzees (Bräuer et al. 2006).

In contrast to the search for cognitive homologies in human's closest relatives, other researchers have sought evidence for evolutionary convergence in species distant from humans, such as birds and dogs (e.g., Emery & Clayton 2004b; Hare & Tomasello 2005). The principle behind convergence is that evolutionary remote taxa may have reached similar solutions to certain cognitive problems because they have experienced similar selection pressures. The trouble for a comparative analysis is that we do not know what these selection pressures were. All we can observe is current behaviour. We may make guesses as to what kind of selection pressures there may have been, but these are only guesses, not testable hypotheses. Only the current behaviours (and their underlying mechanisms) are available to experimental investigation. Bolhuis and Macphail (2001; 2002) have argued that the functional similarities between species, and the possible similarities in evolutionary history, could provide clues to the cognitive and neural mechanisms involved. But these cannot be more than clues – evolution cannot explain the mechanisms.

Take vocal learning, for example. For a long time, comparative psychologists studied apes in their quest for animal models of human speech and language acquisition. This seemed reasonable from the point of view of evolutionary homology – apes are our closest relatives (Wynne 2007). It has subsequently become clear that songbirds and marine mammals are better models for human vocal learning (Bolhuis & Gahr 2006; Fitch 2000; Hauser et al. 2002a). There are behavioural and neural similarities between bird song learning and speech acquisition (Bolhuis & Gahr 2006; Doupe & Kuhl 1999; T. Q. Gentner et al. 2006; Gobes & Bolhuis 2007). But there is no evolutionary principle from which these similarities could be deduced: they had to be discovered by experiment. Nor can we predict how far the similarities will stretch: If we want to know the nature of the neural or cognitive mechanisms of birdsong or human speech, we need to study them directly. Evolutionary convergence may give us clues concerning these mechanisms, but we need to investigate them to see whether these clues prove useful (Bolhuis 2005). It may be that the ancestors of modern songbirds and humans experienced comparable selection pressures that led to the evolution of vocal learning mechanisms. Or the apparent similarities in these two communicative systems may turn out to be superficial and adventitious. Unfortunately, evolutionary theory offers little guidance on this point.

Penn et al. have performed a great service in so clearly illuminating the cognitive gap between humans and other animals – a gap that we have emphasized elsewhere (e.g., Macphail 1998; Macphail & Bolhuis 2001; Wynne 2004a; 2004c; 2007). The target article attempts to delineate where human cognition differs from that found in other species. It does not, however, offer a program of research for comparative psychology. Such a program would need to take cultural evolution into account, which may have been far more important than genetic evolution in the emergence of human cognition (Laland & Brown 2002). Increasing costs and a greatly increased regulatory burden have led to a reduction in the range of species studied by psychologists in recent decades (Wynne & McLean 1999). Given that evolutionary considerations are of limited value when it comes to understanding the mechanisms of cognition, we believe a systematic program of reinvigorated comparative psychology is essential to understand the uniqueness of the human condition.

Authors' Response

Darwin's triumph: Explaining the uniqueness of the human mind without a *deus ex machina*

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Abstract: In our target article, we argued that there is a profound functional discontinuity between the cognitive abilities of modern humans and those of all other extant species. Unsurprisingly, our hypothesis elicited a wide range of responses from commentators. After responding to the commentaries, we conclude that our hypothesis lies closer to Darwin's views on the matter than to those of many of our contemporaries.

R1. Introduction

In our target article, we argued that there is a pervasive functional discontinuity between the cognitive abilities of modern humans and those of all other extant species due, in large part, to the significant difference in degree to which human and nonhuman minds are able to approximate the higher-order relational properties of a physical symbol system (PSS). Unsurprisingly, our relational reinterpretation (RR) hypothesis elicited a wide range of responses from commentators. We thank all of our commentators for taking the time to suggest where we went wrong (or right) and for numerous perspicacious suggestions. We will address the issues our commentators raised in roughly the same order as the corresponding topics were introduced in the original target article.

R2. Is there, in fact, a functional discontinuity between human and nonhuman relational cognition?

To some commentators, our hypothesis that there is a functional discontinuity between human and nonhuman minds seemed self-evident (e.g., **Bickerton**; **Bermúdez**; **Gentner & Christie**; **Halford, Phillips, & Wilson** [**Halford et al.**]; **Lupyan**, **Markman & Stilwell**; **Shatz**; **Wynne & Bolhuis**). To many others, however, particularly those coming from a comparative perspective, our hypothesis appeared unfounded, ill-conceived, anti-Darwinian, or at least premature (e.g., **Burghardt**; **Emery & Clayton**; **Gardner**; **Hallinan & Kuhlmeier**; **Herman, Uyeyama, & Pack** [**Herman et al.**]; **McGonigle & Chalmers**; **Pepperberg**; **Siegal & Varley**; **Tetzlaff & Carruthers**; **Thompson & Flemming**; **Wasserman**). Several commentators also argued that our hypothesis is unfalsifiable. Emery & Clayton, for example, complained that the cognitive differences we postulated between human and nonhuman minds "are without exception impossible to quantify because of the reliance on language in experiments of human cognition." Similarly, Wasserman argued that we failed to provide "clear behavioral tests" that would "enable investigators to see if nonverbal creatures can exhibit cognitive performances that all would agree are 'truly' higher-order, relational, and systematic."

In the Appendix (sect. R7), we propose an extensive set of nonverbal experiments that should erase any doubts as to the falsifiability of our hypothesis. Hereinbelow, we address the various objections commentators raised against our claim that there is a functional discontinuity between human and nonhuman cognition.

R2.1. The discontinuity in the continuum

Many commentators argued that there is no discontinuity between human and nonhuman minds because the cognitive abilities of human and nonhuman animals exist along a "continuum" (e.g., **Burghardt**, **Hallinan & Kuhlmeier**, **Herman et al.**, **McGonigle & Chalmers**, **Pepperberg**, **Siegal & Varley**, **Tomlinson & Love**, **Wasserman**). We tried to forestall this objection by clearly defining up front what we meant by the term "discontinuity" in our target article (see Note 1). But it seems our definition of this term got lost in the rush to defend Darwin's honor. We therefore begin this reply by pointing out, once again, that our claim that there is a significant gap (a.k.a. "functional discontinuity") between the relational abilities of modern humans and those of all other extant nonhuman species is completely consistent with the fact that the relational abilities of all extant species undoubtedly evolved along a multidimensional continuum and can still be distributed along that continuum.

According to the framework laid out in our target article, relational cognitive processes run the gamut from simple conditional discriminations based on the perceptual similarity between objects (e.g., same–different tasks) to systematic inter-domain inferences based on higher-order structural correspondences (e.g., analogical inferences). At the simplest end of the spectrum, relational discriminations can be made by encoding relations into analog measures of perceptual variability. At the most complex end of the spectrum, relational inferences can only be made using explicitly structured representations of roles, relations, and fillers. In *both* human and nonhuman animals, relational problems at the simplest end of the spectrum are typically solved using "embedded" perception and action routines (see **Barrett**). Relational problems at the most complex end of the spectrum require increasingly abstract, non-domain-specific representations including, at the limit, extensive linguistic scaffolding (see **Bermúdez**, **Gentner & Christie**).

As Clark and Thornton (1997) pointed out in this journal a decade ago, relational problems are "rife" in biologically realistic settings, but animals regularly solve them – typically quite well. Therefore, it is apparent that (almost) all biological cognizers are capable of "reasoning" about relations to some degree. Indeed, if every organism that had ever lived on this planet still existed today, there would be no functional discontinuity to speak of and the immense interval between the two ends of this relational spectrum would be filled with "numberless gradations" (Darwin 1871, p. 35). But, based on the available empirical evidence, there appears to be a significant gap between the relational abilities of modern humans and all other *extant* species – a gap at least as big, we argued, as that between human and nonhuman forms of communication. Among extant species, only humans seem to be able to reason about the higher-order relations among relations in a systematic, structural, and role-based fashion. *Ex hypothesi*, higher-order, role-based relational reasoning appears to be a uniquely human specialization, or "human cognitive autapomorph[y]" (our thanks to **Suddendorf** for reminding us of this excellent term; see extended discussion in Povinelli & Eddy 1996, Ch. 1).

R2.2. Is our hypothesis "premature"?

Many commentators claimed that our hypothesis is "premature" (e.g., **Emery & Clayton**, **Hallinan & Kuhlmeier**, **Lupyan**, **Pepperberg**, **Siegal & Varley**, **Wasserman**). Now, it would clearly be premature (indeed daft) to claim that we have definitively refuted all alternative hypotheses, or that our RR hypothesis is the last word on the issue of what makes the human mind human. But it hardly seems premature to postulate the *possibility* that human cognition is, indeed, unique in certain ways and to make some attempt to specify how and why. In our eyes, postulating plausible, falsifiable hypotheses and then trying to verify those hypotheses empirically is the *sine qua non* of any experimental science. If our target article serves no other purpose than to motivate our critics to go forth and prove us wrong, our efforts will not have been in vain. We are happy to be hostage to empirical fortune.

R2.3. Same–different relations

Thompson & Flemming cite a list of studies showing that nonhuman animals can acquire a "categorical" understanding of sameness and difference relations. **Pepperberg** makes a similar claim on behalf of the Grey parrot, Alex. We agree that a "categorical" understanding of perceptual similarity is not a uniquely human capability. We made the same point in our target article. The crucial and persistently overlooked issue, however, is that the *kind* of cognitive operation required to pass same–different (S/D) and relational match-to-sample (RMTS) tasks is not the same *kind* of operation required to reason about higher-order relations in a systematic, structural, role-based fashion. The fundamental problem is that the relations at stake in S/D and RMTS tasks involve symmetrical and interchangeable roles and are therefore reducible to analog measures of variability, such as entropy. Therefore, the ability to make a categorical distinction between displays above and below a certain entropy threshold is not evidence for higher-order relational reasoning in the structural or role-based sense posited by our hypothesis.

Gentner & Christie claim that although RMTS tasks involving multiple items per set can be solved by perceptual variability alone, tasks involving only two items per set cannot. This is incorrect. Using the definition of categorical entropy proposed by Young and Wasserman (1997), "same" pairs such as AA have an entropy of 0, whereas "different" pairs such as AB have an entropy of 1. The difference in entropy between all-same and all-different displays is certainly smaller in two-item sets than in multiple-item sets; but there is a non-zero difference nonetheless. Training with same–different symbols may improve subjects' ability to pay attention to these small differences in entropy (a form of perceptual learning) or may align the threshold for their responses more closely to that of humans. However, once the possibility that RMTS tasks can be solved using an analog measure of variability is admitted, it must also be admitted the task lacks the power, even in principle, to demonstrate that a subject is reasoning about the kind of higher-order, structurally explicit relations that Gentner and her colleagues have rightfully claimed to be the centerpiece of human cognition (e.g., Gentner 2003).

Thompson & Flemming point out that there is a disparity between the responses of nonhuman apes and monkeys on RMTS tasks. Thompson & Flemming ask why such a disparity exists if (as we argue) the RMTS task is solvable using entropy values.

There are many possible reasons for this disparity. That there is a significant gap between the relational abilities of human and nonhuman subjects does not imply that the relational abilities of all other extant species are identical or even homogeneous. The RMTS task may be more computationally complex than the S/D task for primates. And the two-item RMTS task may require a greater sensitivity to variability than the multi-item RMTS task does. These are all plausible hypotheses that deserve further experimental scrutiny. But the fact that only certain species possess the evolved heuristics and/or processing capacity necessary to solve two-item RMTS tasks does not imply that the RMTS task requires subjects to reason about higher-order structural relations. To make this latter claim, **Thompson & Flemming** would need to show that the RMTS task requires subjects to reason about higher-order relations in a structurally sensitive fashion. And this, they have not done.

R2.4. Analogical relations

We defined "analogical reasoning" as the ability to draw inferences about a target domain based on systematic, structural similarities between a source domain and the target domain. Importantly, the relevant similarities in analogical inferences are based on the roles various entities play in their respective relations, and on structural similarities between the relations, rather than (and distinct from) perceptual similarities between the entities involved in the relations (Gentner 1983; Gentner & Markman 1997; Holyoak & Thagard 1995). Like any other form of relational reasoning, analogical inferences vary in their degree of abstraction, structural sophistication, and domain specificity. Even 4-year-old children understand simple analogies involving familiar visuospatial relations – for example, "If a tree had a knee, where would it be?" (Gentner 1977). But it takes quite a bit of linguistic scaffolding, inter-domain mapping, and content-specific enculturation to make sense out of Donald Rumsfeld's assertion that installing democracy in Iraq is like teaching a child to "ride a bike" (Silverstein 2007). According to our RR hypothesis, reasoning about even the simplest, most modality-specific analogies is a human cognitive autapomorphy.

Many commentators agree with us that analogical reasoning is a distinctively human capability (e.g., **Bermúdez**, **Gentner & Christie**, **Hallinan & Kuhlmeier**, **Markman & Stilwell**). **Thompson & Flemming**, however, argue that at least one chimpanzee, Sarah, is also capable of comprehending some analogies. We have considerable sympathy with their point of view, as one of us (Holyoak) reached similar conclusions at one time (see Holyoak & Thagard 1995). However, more recent findings (i.e., Oden et al. 2001) have shown that Sarah's performance does not merit this conclusion.

Thompson & Flemming admit that Sarah's performance on Oden et al.'s (2001) replication does not qualify as a "material analogy" and acknowledge that Sarah's performance was functionally equivalent to the performance of other primates and birds on S/D tasks. Thompson & Flemming nonetheless claim that Sarah's performance counts as a "formal analogy," and they find our own definition of analogy "overly exclusive."

Researchers clearly use the term *analogy* to refer to a wide variety of relational inferences (see, e.g., **Gentner & Christie**, **Halford et al.**, **Herman et al.**, **Lupyan**, **Markman & Stilwell**). But **Thompson & Flemming's** definition of a "formal analogy" is exceptionally idiosyncratic. In the philosophical literature (e.g., Hempel 1965), a formal analogy is defined as an isomorphism between systems of relations (e.g., the analogy between groups in algebra and topological manifolds in geometry). Sarah's strategy for solving geometric "analogies" – equating number of featural changes – does not establish an isomorphism, and hence does not exemplify an analogy under any established definition. If the term *formal analogy* is now to be used to refer to relational tasks that can be solved by comparing analog measures of variation, then indeed Sarah is capable of solving "formal analogies" – but so are many other species, including pigeons (Cook & Wasserman, in press). Thompson & Flemming's change in terminology simply shifts the semantics, not the substance, of the debate.

The substantive debate is not about how to define the term *analogy* but about whether or not there is a discontinuity in the cognitive mechanisms that human and nonhuman animals employ to make relational inferences. **Thompson & Flemming** propose that there is a discontinuity between the symbolic-relational abilities of apes and all other species (see also Thompson & Oden 2000). We believe this "analogical ape" hypothesis fails twice: It severely underestimates the symbolic-relational abilities of other non-primate species (see, e.g., the commentaries by **Herman et al.** and **Pepperberg**). And it glosses over the fundamental, qualitative difference between the feature-based strategy employed by Sarah and the non-domain-specific, role-based analogies made universally by modern humans. Even Thompson & Flemming admit that the sole evidence of a nonhuman animal having solved a "material analogy" is Sarah's unreplicated performance on Experiment 3 reported by Gillan et al. (1981). As we pointed out in our target article, Sarah's remarkable and unreplicated success in this experiment constitutes exceedingly thin support for the "analogical ape" hypothesis. (See our Appendix [sect. R7] for examples of experimental protocols that could provide evidence for various kinds of analogical reasoning in nonverbal subjects.)

R2.5. Rules

Tetzlaff & Carruthers are right to emphasize the fact that rule learning (or, at least, rule-like learning) can be found among minds as distantly related to humans as those of honeybees and desert ants. We made the same point in our target article. But we hypothesized that only humans possess the ability to learn rules that involve non-perceptual, structural relations among role-based variables. Tetzlaff & Carruthers provide no reason to doubt this hypothesis.

For example, the location of a particular object with respect to specific landmarks is the epitome of a perceptual (i.e., spatial) relation between observable stimuli. Therefore, the fact that honeybees' path integration mechanisms use the distance and angle between arbitrary landmarks is evidence that they can represent these spatial relations in a rule-like fashion; but it hardly counts as evidence that honeybees are able to reason in terms of "non-perceptually-based information" as **Tetzlaff & Carruthers** claim.

R2.6. Higher-order spatial relations

Hallinan & Kuhlmeier do not challenge our claim that reasoning about higher-order spatial relations is a uniquely human specialization, nor our interpretation of the chimpanzees' performance on Kuhlmeier and Boysen's (2002) scale-model task. Instead, they point out that human children younger than 5 years of age sometimes fail a fully relational version of this task, as well; and they argue that the "continuous" nature of human ontogeny implies a similar continuity in phylogeny.

We will return to question the analogy between ontogenetic and phylogenetic continuity further on. For now, let us simply note just how marked the gap is between human children and all other animals on this planet. All normal 5-year-old children reason about three-dimensional scale models in a systematic fashion, as **Hallinan & Kuhlmeier** fully admit. Moreover, there is even evidence that children as young as 3 years of age can use distance information from a map to find a point in the real world along a single dimension, and, by 5 years of age, can find objects using a two-dimensional map where the objects are located some distance away from any mapped landmarks (Huttenlocher et al. 1999; Vasilyeva & Huttenlocher 2004). Needless to say, there is no evidence that any nonhuman animal could use a one- or a two-dimensional map in this fashion (but see the Appendix for a protocol that could be used to test for this ability in nonhuman subjects).

R2.7. Transitive inference

We singled out Lazareva et al.'s (2004) test of "transitive responding" in hooded crows as a recent example of an experimental protocol that lacks the power, even in principle, of providing evidence for logically underpinned transitive inferences (TI). Notably, **Wasserman** did not challenge our analysis of these results; instead he claimed that we failed to provide any examples of experimental protocols that could falsify our hypothesis. In the Appendix, we suggest a lab-based protocol that could be used to test for TI in a nonverbal species.

We also criticized two recent "naturalistic" experiments that claimed to have demonstrated TI in male pinyon jays and small African cichlids (Grosenick et al. 2007; Paz et al. 2004). **Pepperberg** did not defend the validity of these experiments but instead cited two sets of experiments with great tits (Otter et al. 1999; Peake et al. 2002) that we had overlooked. These experiments do, indeed, provide additional evidence that the ability to reason about tertiary social relations is not limited to primates (cf. Tomasello & Call 1997). But they provide no evidence that great tits are capable of TI.

In Otter et al.'s (1999) experiment, for example, it suffices for the female subject to keep track of the dominance relation between her mate and any males she has heard in her current mate's territory and then follow the procedural rule <*look for males that have dominated my current mate*>. As we explained in our target article, the ability to recognize the social relation among conspecifics based on certain perceptual cues and to rank conspecifics relative to some egocentric benchmark (e.g., my own dominance ranking, my current mate, my matriline) is widely available in the animal kingdom (e.g., Grosenick et al. 2007; Paz et al. 2004; Silk 1999). What appears to be missing among extant nonhuman species is the ability to systematically generalize information about observed relations to *unobserved* tertiary relations in a transitive fashion. Although neither of the experiments with great tits provides any evidence for this ability, in the Appendix we show how Otter et al.'s (1999) protocol could be adapted to provide a valid test of TI.

R2.8. Hierarchical relations

Reasoning about hierarchical relations is a universal feature of human cognition and, as **Shatz** points out, well within the repertoire of toddlers. Contrary to persistent claims by comparative researchers over the years (e.g., Bergman et al. 2003; Greenfield 1991; Matsuzawa 1996; Pepperberg 2002), we argued that reasoning about hierarchical relations is outside the scope of the capabilities of any extant nonhuman species. None of our commentators directly challenged our analysis of this evidence.

Instead, **Pepperberg** mentions an experiment by T. Q. Gentner et al. (2006) that purports to show that European starlings can learn a recursive, center-embedded grammar. But it is far from clear that the particular grammar mastered by the starlings in this experiment requires a hierarchical or recursive computation (see Corballis 2007a). In addition, there is no evidence that starlings can generalize the patterns they did learn to novel vocabularies – the essential feature of cognizing hierarchical relations in a language-like fashion (Marcus 2006). It is worth noting that even **Herman et al.**'s dolphins never demonstrated the ability to process sentences involving hierarchically embedded constructions. Herman et al. (1984) once claimed that the dolphins responded appropriately to "recursive forms including conjoined constituents and conjoined sentences" (p. 188); however, the tests given were, at best, examples of "tail recursion" and therefore did not involve embedded structures or hierarchical relations.

McGonigle & Chalmers cite an experiment (McGonigle et al. 2003) purporting to show evidence for "hierarchical classification" in monkeys and claim that this experiment sheds light on the "genesis" of human thought and language. In the cited experiment, McGonigle et al. (2003) presented four capuchin monkeys with nine icons that were to be selected on a touch screen in a predefined order: for example, first by shape and then in order of increasing size. After thousands of trials, the capuchin monkeys succeeded in selecting the nine icons in the correct order at least 75% of the time over 20 consecutive trials. McGonigle et al. (2003) interpret these results as "evidence for hierarchical processing based on branching procedures." Indeed, McGonigle et al. (2003) claim that the monkeys acquired rules "similar to those operating in a phrase structure grammar," and they explicitly challenge Hauser et al.'s (2002a) hypothesis that hierarchical and recursive computations are uniquely human.

Given the exhaustive task-specific training McGonigle et al. (2003) employed, it is hard to interpret the cognitive significance of these results. But one thing is clear: The manifest behavior of the capuchin monkeys in this experiment has very little bearing on whether or not they are capable of reasoning about hierarchical relations in a human-like fashion. What makes hierarchical and recursive operations such a powerful component of the human language faculty is that they enable human subjects to generatively combine a finite number of linguistic elements into an unlimited range of novel combinations.

McGonigle et al. (2003) provide no evidence that capuchin monkeys are able to recombine hierarchically organized sequences in a systematic or generative fashion. For example, there is no evidence that the monkeys would be able to switch from sorting on the basis of shape and then size, to sorting on the basis of size and then shape, without learning the entire sequence over from scratch. If it took human language learners thousands of trials to acquire a single invariant sentence, human language would be of little interest.

R2.9. Causal relations

A key claim in our target article is that the ability to reason about unobservable causal mechanisms is a uniquely human capability (see also Penn & Povinelli 2007a; Povinelli 2000; Vonk & Povinelli 2006). We interpreted Seed et al.'s (2006) results as further evidence for this hypothesis. **Emery & Clayton** claim that we were guilty of "misinterpretations, absences, and misrepresentations" in our portrayal of Seed et al.'s (2006) experiment. What is "at issue," Emery & Clayton write, is the performance of a single rook, Guillem, which passed the crucial transfer test.

We fail to see where the alleged "misrepresentations" are to be found. Indeed, our interpretation of Guillem's singular behavior is the same as that proposed by the authors of the original paper:

> Given that six of the seven rooks failed to transfer to Tubes C and D which had no visual features in common with the first task, it seems unlikely that they had an understanding of the unobservable causal properties of the task at their disposal. . . . The surprising performance of Guillem, who solved all four tasks despite the lack of a constant arbitrary visual cue, deserves further attention. . . but the result of one bird among seven must be interpreted with caution. (Seed et al. 2006, p. 700)

We certainly agree that Guillem's behavior deserves "further attention," but Tebbich et al. (2007) subsequently replicated the same task on seven new rooks and found that only three out of seven passed the perceptual transfer task, and none of them passed the crucial nonperceptual transfer task. In the Abstract to this paper, Tebbich et al. (2007) write:

> We found no evidence compatible with the formation of a mental representation of physical problems given that none of these 3 birds passed the transfer tasks. This is not surprising given that there is no evidence to date that any tool-using animal has a causal understanding of the trap-tube problem.

If anything, our interpretation of Seed et al.'s (2006) results seems to be more generous than that of the original authors: Contra Tebbich et al. (2007), we posit that rooks as well as other nonhuman animals do, indeed, have a "mental representation of physical problems" and a "causal understanding of the trap-tube problem" – albeit not one that involves unobservable causal mechanisms (see again Penn & Povinelli 2007a; Povinelli 2000).

Emery & Clayton also argue that the rooks' performance on the two-tube task could not be due to "domain-specific expectations" because rooks do not use tools in the wild. Here, we suspect that both we and Emery & Clayton were tripped up by the protean term "domain-specific." Emery & Clayton interpreted our use of the term as meaning "tool-specific." We meant the term to refer to the domain of physical causal reasoning in general, not tools in particular. Many cognitive psychologists believe that human subjects reason about the physical world using formal and substantive assumptions such as temporal priority, causal directionality, and Michottean perceptual causal principles that are specific to the domain of physical causality, but not specific to tool use per se (see Gopnik et al. 2004; Lagnado et al. 2005). There is abundant evidence that nonhuman animals make many of the same causal assumptions as humans (see Penn & Povinelli 2007a for a review). In our view, the fact that a non-tool-using species such as rooks was able to quickly master the initial version of Seed et al.'s (2006) task is compelling evidence that at least some nonhuman animals are able to reason about novel tool-use tasks using knowledge and expectations that are specific to physical causal relations but not to tool use per se (see also Santos et al. 2006).

R2.10. Theory of mind

In our target article, we criticized Dally et al.'s (2006) experiment with scrub-jays as providing no new positive evidence for theory of mind (ToM) abilities. **Emery & Clayton** did not challenge our interpretation of Dally et al. (2006). Instead, they reasserted that scrub-jays are capable of "experience projection" based on evidence reported by Emery and Clayton (2001).

In these experiments, **Emery & Clayton** investigated the propensity of scrub-jays to re-cache food that they had previously cached in front of a conspecific, and found that scrub-jays only re-cached food when they had had prior experience stealing another bird's caches. "This result raises the exciting possibility," Emery (2004, p. 21) wrote, "that birds with pilfering experience can project their own experience of being a thief onto the observing bird, and so counter what they would predict a thief would do in relation to their hidden food" (see also Emery & Clayton 2004b).

As noted by Penn and Povinelli (2007b), this may be an "exciting possibility"; but it is certainly not the only, or even the most cogent, explanation. Unfortunately, the existing evidence sheds almost no light on the internal mental representations or cognitive processes being employed by the birds in question. For example, all of the birds involved in this experiment had had previous experience being pilfered (see discussion in Emery & Clayton, in press). But **Emery & Clayton** do not explain how scrub-jays could have the cognitive prowess necessary to reason by analogy to their own subjective experience as pilferers but not have the cognitive wherewithal to realize they should start caching once they have been victims of pilferage themselves. Indeed, Emery & Clayton do not explain why a species with the ability to reason by analogy cannot understand, prior to pilfering another's cache, that caching food from potential competitors might be a good idea.

To make matters worse, the existing evidence has not ruled out the obvious possibility that pilfering changes the subjects' *motivation* to cache their own food rather than change their cognitive understanding of the functional value of caching per se. This is the point of our analogy to redirected aggression in primates (see Penn &

Povinelli 2007b): after conflicts, monkeys sometimes behave more aggressively towards groupmates not involved in the original conflict. This evolved behavior seems to be adaptive, both because it reduces monkeys' stress hormones and because it lessens their chance of being victims of further harassment (Silk 2002b). But there is no reason to conclude that monkeys are reasoning by analogy to their own subjective experience as "victims." The same evolutionary and ecological analysis, *mutatis mutandis*, might shed some light on why scrub-jays only cache their food once they have had experience pilfering. In the meantime, the claim that scrub-jays are capable of "experience projection" would seem to require considerably more empirical support before this "exciting possibility" could be qualified as anything more than that (see our Appendix [sect. R7] for an example of how such evidence might be produced).

Herman et al. cite the example of bottlenosed dolphins responding to "tandem + create" commands as an example of "collaboration." In fact, as Herman (2006) himself acknowledges, responding to the "tandem + create" command need not require explicit collaboration or intentional communication. It suffices for one of the two dolphins in the pair to understand that the command requires it to mimic the behavior of the other dolphin. To be sure, this is no mean cognitive feat; and we know of no other nonhuman subject that has ever manifested this degree of symbolic-relational sophistication. At the very least, one of the dolphins on each trial interpreted the argument "create" in the context of a "tandem" command in a radically different manner than it had in the past. But the available evidence is still a long way from demonstrating that dolphins understand each other's roles in a collaborative fashion or are capable of intentional communication. In the Appendix, we propose a modified version of Herman et al.'s "tandem + create" command that could provide definitive evidence for role-based collaboration and intentional communication among dolphins, as well as a nonverbal "false belief" task that could provide positive evidence, at least in principle, that there is another species on this planet that possesses a ToM.

R2.11. A LoT for every species

After reviewing the comparative evidence across a variety of domains, we (like **Bermúdez**) concluded that extant nonhuman species do, in fact, possess representational systems that are "syntactically structured," "functionally compositional," and "featurally systematic" to some degree (we thank Bermúdez for suggesting this last term). Therefore, as we pointed out, our RR hypothesis should not be reduced to the claim that human minds alone approximate a language of thought (LoT), whereas nonhuman minds do not. Quoting Bloom (2000), we argued that "every species gets the syntax it deserves."

Notwithstanding our efforts to forestall this very misunderstanding, **Tetzlaff & Carruthers** make the same point as if they are disagreeing with us: "[E]ven the thought capacities of a very simple mind could approximate *one* LoT-based system to the same extent as a human's could approximate *another*." To reiterate: We believe that minds as "simple" (*sensu* Carruthers) as those of honeybees employ internal mental representations that are syntactically structured, functionally compositional, and featurally systematic to some degree. Because human minds are by no means unique in approximating a LoT, the real issue is what distinguishes the human species of LoT from all the others that remain on this planet. Carruthers has argued elsewhere (see Carruthers 2002; 2005a) that there are certain features of human thought – particularly our ToM and faculty for language – that are distinctively human. So it would seem that Tetzlaff & Carruthers would have to agree with us that there is something uniquely human about the modern human LoT. Unfortunately, Tetzlaff & Carruthers do not suggest what this might be.

Wasserman finds our claim that there is a difference in "kind" between the manifest cognitive abilities of human and nonhuman animals to be inconsistent with our claim that there is a difference in "degree" between human and nonhuman animals' ability to approximate the relational capabilities of a PSS. The problem here is not an "anomaly" in our logic – the problem is that Wasserman does not acknowledge the difference between a functional-level and a representational-level analysis (Marr 1982). In our target article, we use the construct of a PSS as a heuristic framework for decomposing the relational operations manifested by biological cognizers at a *functional level of analysis* into distinct representational-level components (i.e., symbols, compositionality, types and tokens, etc.). As we point out, different species approximate these multifarious features of a PSS to varying degrees. *Ex hypothesi*, the difference in degree to which various species approximate the features of a PSS at a representational level produces a difference in the kinds of relational reasoning these species manifest in their cognitive behaviors. In particular, although all biological cognitive architectures approximate the features of a PSS to some degree, only those cognizers that closely approximate the higher-order, structural properties of a PSS manifest the kinds of relational reasoning that are characteristic of human cognition (e.g., ToM, analogical inferences, hierarchically structured languages, reasoning about unobservable causal mechanisms).

Halford et al. propose that dynamic binding to a coordinate system in working memory is the fundamental prerequisite for any form of relational reasoning. We agree. And, in our view, Halford et al.'s proposal provides a more plausible and cogent framework for understanding the LoT-like abilities of honeybees and desert ants than does the classical version of a LoT espoused by **Tetzlaff & Carruthers**. Halford et al.'s proposal also puts a hard lower limit on the kinds of computational architectures that constitute plausible models of animal cognition (cf. **Lupyan**).

Halford et al. propose two protocols for testing the compositionality and systematicity of nonhuman mental representations, using a delayed response task and "generativity tests" based on learned relational schemas. Our prediction is that nonhuman animals of many taxa will *pass* both of these tasks but that many connectionist-style models will have great difficulty with them. Of course, it is important to keep in mind that Halford et al.'s proposed tasks test only whether a subject can form implicitly structured relations by binding an object to a "slot" in working memory. This is a necessary prerequisite for functionally compositional and syntactically structured representations (Horgan & Tienson 1996). But Halford et al.'s tasks do not test the capacity to reason about higher-order relations or relational roles in the fashion that we have posited is unique to modern humans. In their past research, Halford and colleagues have employed a wide variety of protocols to test higher-order, role-based relational capabilities in human subjects (e.g., Andrews & Halford 2002; Andrews et al. 2003; Halford 1984; Halford et al. 2005; Halford & Busby 2007). Many of these protocols can (and should) be adapted to probe the similarities and differences between human and nonhuman LoTs (see our Appendix for examples).

R3. Who gets to become human?

As **Shatz** points out, the cognitive abilities of even the most highly encephalized and enculturated nonhuman pale in comparison with the typical human child. Some of our commentators, however, tried to use the ontogenetic evidence against us (e.g., **Hallinan & Kuhlmeier**, **McGonigle & Chalmers**, **Siegal & Varley**, **Wasserman**): If human infants start out with cognitive abilities less sophisticated than that of some adult nonhuman animals, they argued, how can we claim that there is an innate, genetically-prespecified "discontinuity" between human and nonhuman animals? Darwin, of course, relied on a similar argument to bolster his case for the mental continuity between humans and other animals (Darwin 1871, p. 84; cited approvingly by Wasserman). Let's take apart this venerable argument piece by piece.

R3.1. Nature and nurture (and more nature)

Many of our commentators (e.g., **Hallinan & Kuhlmeier**, **Lupyan**, **McGonigle & Chalmers**, **Siegal & Varley**, **Wasserman**) assumed that because we postulated an "innate" or "genetic" basis for the discontinuity between human and nonhuman cognition, we were necessarily denying the importance of ontogeny, environment, language, enculturation, and everything else. For example, Wasserman acknowledges that the neural systems of humans may differ from those of nonhumans but asks, "Do these systems merely mature as the child approaches adulthood? Or must these systems be carefully cultivated by enriching experiences to fully flower?"

Wasserman's rhetorical question poses a false dilemma. There is no either/or when it comes to nature and nurture. No biological system, least of all a neural one, "merely" matures on its own. The ontogeny of any biological system is substantially modulated by its environment. But this does not mean that genetic factors play no role in shaping an organism's ontogeny. There is a complex, nonlinear, epigenetic relationship between genes and the environment that plays out over the entire lifespan of an organism – even an enculturated organism.

R3.2. Does primate phylogeny recapitulate human ontogeny?

Hallinan & Kuhlmeier argue that there would be a true cognitive discontinuity between human and nonhuman minds only if the behavior evident in the first stages of human development looked strikingly different from the capacities we see in other species. But the fact that nonhuman primates perform as well as 3-year-old children on some (but not other) tasks has little bearing on our claim that there is a fundamental discontinuity between human and nonhuman minds. The monumental fact of the matter – a fact which Hallinan & Kuhlmeier do not deny – is that the ontogenetic trajectory of one particular primate species' relational abilities distinguishes itself from that of all other extant species on the planet. As **Shatz** points out, by the second year of life, the cognitive differences between humans and other primates are unmistakable. And by age 5, the functional discontinuity is so enormous that even the most generous comparative psychologist cannot deny the disparity.

Hallinan & Kuhlmeier end up proposing a theoretical account for the disparity between human and nonhuman relational cognition that appears to be the same as our own. Citing Povinelli (2001), they postulate that humans possess "an additional system that sits side by side with evolutionarily older systems" and that this additional system allows for analogical reasoning that is "not constrained by superficial or context-specific correspondences." To our ears, that sounds a lot like our hypothesis (see also Povinelli 2000; Povinelli & Bering 2002; Povinelli et al. 2000). Like Hallinan & Kuhlmeier, we believe that our uniquely human system for higher-order, role-based relational reasoning continues to interact with cognitive systems that are evolutionarily more ancient and that come on-line earlier in normal human ontogeny (the second 'R' in our RR hypothesis stands for "reinterpretation," not "replacement"). But Hallinan & Kuhlmeier are mistaken, in our opinion, to believe that our "reinterpretation" hypothesis is inconsistent with the claim that there is a fundamental discontinuity between human and nonhuman minds. Both we and Hallinan & Kuhlmeier postulate that there is an "additional system" responsible for subserving our uniquely human ability to reason about higher-order relations and that the emergence of this additional system is unique to the ontogeny of members of our species. Unless Hallinan & Kuhlmeier want to argue that the profound disparity between the cognitive ontogenies of human and nonhuman primates is solely the result of environmental factors, there must be something unique about the potential of the human mental architecture from day one.

R3.3. Constructing the human mind

Lupyan seems to believe that we consider the human mind to be "innately symbolic and propositional." Our RR hypothesis could not be farther from this strawman. We explicitly denounced the classical view of the mind as biologically implausible and functionally impoverished. To argue that humans and nonhumans differ in their potential for symbolic-relational cognition from conception forward does not entail – or even suggest – that the human cognitive architecture is born with its adult-state symbolic-relational abilities all wired up and ready to go. Our claim is that the human genotype has the unique *potential* to produce a neural architecture capable of higher-order relational reasoning. Without the appropriate internal and external inputs, however, this genetic potential is sure to be thwarted.

Lupyan goes on to point out that some of the authors we cited on the subject of human language learning do not support the view that adult syntactic competence is prewired into the human brain (e.g., Gomez & Gerken 2000; Tomasello 2000). We cited these authors for a reason: Unlike a Chomskyan view of language, our RR hypothesis does *not* posit that human beings are born with adult syntactic competence. Again, our claim is simply that there must be something different about the human cognitive architecture in order to explain why only human children have the *potential* to learn grammatically-structured languages, develop a ToM, participate in collaborative activities, acquire culturally-transmitted knowledge, and employ external symbol systems to scaffold their cognitive achievements.

R3.4. Equal opportunity for pigeons?

Gardner objects to comparative researchers' tradition of "nondiscoveries" of "noncontinuity" based on "nonexperiments." Gardner is right to remind readers that comparative psychology has been guilty of some rather embarrassing methodological blunders in its short history. Gardner is also certainly correct that differences in rearing conditions and training procedures have a significant impact on the cognitive performance of both human and nonhuman animals. But the claim that human cognitive uniqueness is solely and merely the product of human enculturation is difficult to sustain. The research cited by **Herman et al.** and **Pepperberg** are notable examples both of what nonhuman species can achieve with intensive training – and also of how vast a functional discrepancy there is between even the most highly enculturated nonhuman animal and the average human subject. **Wasserman**'s plea to withhold judgment on the cognitive abilities of pigeons until a member of that species has been given the same cultural opportunities as those provided to human children strikes us as particularly extreme. Unless pigeons harbor some heretofore unrealized potential for relational reasoning that surpasses that of chimpanzees, bottlenosed dolphins, and African grey parrots, we doubt the discontinuity between human and nonhuman minds will be challenged by an enculturated pigeon.

R4. Does a discontinuity in relational reasoning actually explain the functional discontinuity between human and nonhuman minds?

If it weren't so widely and stubbornly contested, the claim that there are significant discontinuities between the functional capabilities of human and nonhuman minds would seem self-evident and banal. We have great sympathy with those commentators who believe that the interesting debate is not over whether there are any human cognitive specializations, but over what these specializations are and what best explains their origin.

R4.1. Are we just the "massively lucky" species?

Tetzlaff & Carruthers, for example, disagree with our claim that higher-order relational reasoning lies at the core of the many uniquely human forms of cognition. Instead, they argue that there are "many distinctively human learning mechanisms."

To our eyes, it seems wildly implausible that one species happened to be the only one lucky enough to have evolved separate and independent "learning mechanisms" for each distinctively human form of cognition (in a few million years to boot), whereas no other species evolved any of them. Moreover, as we argued in our target article, the massively modular explanation for human cognitive uniqueness is undermined by the fact that each distinctively human cognitive ability seems to rely on a common set of relational competences. **Suddendorf** acknowledges that we might be on the right track in looking for deep structural similarities across domains. **Tetzlaff & Carruthers**, however, flatly deny that there are any such "commonalities."

Tetzlaff & Carruthers' assertion that our human ToM, language faculty, and "intuitive physics" have "nothing to do with relations among relations" runs counter to a large body of existing research and theory (as well as the points of view of many of our other commentators; see, e.g., **Bermúdez**, **Gentner & Christie**, **Halford et al.**, **Markman & Stilwell**, and **Suddendorf**). Numerous researchers have demonstrated a compelling empirical relationship between higher-order relational reasoning and ToM performance (e.g., Andrews et al. 2003; Zelazo et al. 2002) and most theoretical models of ToM require some degree of higher-order, role-based relational reasoning (see, e.g., the theories proposed in Carruthers & Smith 1996). With respect to causal reasoning, the one point on which most contemporary researchers agree is that the ability to recognize and reason about the network of relations among causes and effects in a systematic and allocentric fashion is the bedrock of human causal cognition (e.g., Gopnik et al. 2004; Lagnado et al. 2005; Tenenbaum et al. 2006). Tetzlaff & Carruthers even claim that transitive inferences are not about the relations amongst relations, dismissing a long tradition arguing exactly the contrary (e.g., Halford et al. 1998a; Inhelder & Piaget 1964). Ditto for language (e.g., Gomez & Gerken 2000; Hauser et al. 2002a; Pinker & Jackendoff 2005).

Perhaps everybody else is wrong. We would certainly be the last ones to claim that a "consensus" (no matter how large) is any guarantor of truth. But at the very least, it seems incumbent on **Tetzlaff & Carruthers** to provide a far more substantive and convincing refutation of our argument that ToM, causal reasoning, transitive inference, and language all involve higher-order relational reasoning of various kinds before dismissing it out of hand.

To clarify our own position: We never claimed (contrary to what **Tetzlaff & Carruthers** write) that "there is just one" mechanism that distinguishes human and nonhuman learning mechanisms. Reasoning about the relation between relations is not sufficient to account for any of our human cognitive capabilities. Additional cognitive and morphological adaptations are also necessary to subserve our distinctively human capabilities in ToM, language, and abstract causal reasoning. Nor are we arguing against the *functional* modularity of human cognition (Barrett & Kurzban 2006). We are merely arguing that higher-order, role-based relational reasoning is one core component of all of these distinctively human capabilities, and that the functional supermodule that subserves this form of reasoning in humans is necessary (but not *sufficient*) to enable these capabilities.

R4.2. Is there a discontinuity in executive functioning?

After producing a seminal body of research showing that many distinctively human forms of thought are preserved despite severe linguistic impairments (e.g., Siegal et al. 2001; Varley et al. 2005; Varley & Siegal 2000), **Siegal & Varley** nevertheless make the surprising suggestion that the differences between human and nonhuman cognition may be solely the result of a difference in "executive functioning" rather than a "radical restructuring" of human thinking and reasoning.

We are grateful that **Siegal & Varley** raised the issue of executive functioning. Variations in executive functioning clearly have a direct impact on the kind and quality of relational reasoning a subject can perform (Andrews et al. 2003; Halford et al. 1998a; Robin & Holyoak 1995; Waltz et al. 2004). For example, uniquely human forms of executive control probably subserve the uniquely human forms of planning and practical decision-making highlighted by **Bridgeman**. And Hadley (1999) has argued that some form of a classical computational architecture may be necessary to account for the unique patterns of information flow manifested by human reasoners. Therefore, there are undoubtedly significant differences between the executive functioning capabilities of human and nonhuman animals that contribute to the significant difference in degree to which human and nonhuman minds are able to approximate the computational properties of a PSS.

But positing a difference in executive functioning between human and nonhuman subjects does not somehow undermine our RR hypothesis. Rather, it simply points to one more facet of our supermodule for higher-order relational reasoning that may be uniquely human. Unless **Siegal & Varley** believe that all the distinctively human forms of cognition they have documented in agrammatic subjects can be performed using the same representational structures as those employed by nonhuman animals, they should agree with us that there is something distinctively human about both the architecture of human relational representations and the executive processes that operate over those representations.

R4.3. Is the discontinuity due to language alone?

In our target article, we argued that language is not solely and completely responsible for the differences between human and nonhuman cognition. Many commentators took issue with this argument (e.g., **Bermúdez**, **Bickerton**, **Lupyan**, **Gentner & Christie**). In some cases, the disagreements are due to a difference of emphasis rather than a difference in substance. Gentner & Christie, for example, agree with us that our "extraordinary relational ability" is a central reason "why we're so smart" (Gentner 2003); yet they believe they are disagreeing with us when they accord "central importance to language and other symbol systems" as well. Not only do we *not* disagree with Gentner & Christie on this point, we find their description of the relationship between language and higher-order relational reasoning in their commentary to be succinct and eloquent:

> In our view, human cognitive powers stem from both inborn relational ability and possession of a symbol system capable of expressing relational ideas. These two capacities form a positive feedback cycle. Analogical processes are integral to language learning . . . and relational language fosters relational ability.

In our target article, we freely acknowledged the "instrumental role" that relational language plays in facilitating human learners' sensitivity to relational similarities and potential analogies. We simply focused the bulk of our argument on the other part of the "positive feedback cycle" – that is, the internal cognitive architecture necessary to support relational learning and reasoning to begin with. To borrow and rephrase **Gentner & Christie**'s closing sentence, our claim is that language, culture, and normal human enculturation are required to fully realize our species' potential for higher-order, role-based relational thought; but that humans alone are born with this potential.

We also find **Bermúdez**'s "rewiring hypothesis" to be largely consistent with our own (see also Bermúdez 2005). According to this hypothesis, language played a crucial role in "rewiring" the architecture of the human mind during our evolution as a species. We believe Bermúdez's rewiring hypothesis is plausible and cogent. The only point we tried to make in our target article concerning this evolutionary hypothesis was that language may not have been the *only* factor that played a role in pushing the architecture of the human mind in a relational direction. Given the enormous adaptive value that abstract causal reasoning, ToM, spatial reasoning, and analogical inferences have in the ecological niche occupied by humans, it is at least possible that one or more of these other relational abilities *also* played a part. We remain agnostic as to the relative importance of these various cognitive abilities. If our RR hypothesis is correct, all of these specializations coevolved with our capacity for higher-order, role-based relational reasoning in such an inextricable and nonlinear fashion that any linear ordering of their relative importance would be both unverifiable and meaningless.

The evolutionary version of the "rewiring" hypothesis championed by **Bermúdez** should be distinguished from the kind of ontogenetic "rewiring" alluded to by **Gentner & Christie** and others (e.g., Dennett 1996). We do not doubt that language played and still plays a crucial role in rewiring the human brain in both its evolution and its ontogeny (i.e., both Bermúdez and Gentner & Christie are right). But any "rewiring" that was performed on the human brain over evolutionary timescales is an entirely different process (both at a representational and at a physical level) than any "rewiring" done during ontogeny. Therefore, it is important to emphasize that the rewiring effects of language learning do not "recapitulate" the rewiring effects of language evolution (i.e., newborn human brains do not start off at the same place as our prelinguistic ancestors or our nonhuman cousins do). We would only have to take issue with Bermúdez and Gentner & Christie if they were to claim that language and cultural learning are the *only* factors that distinguish modern human minds from those of extant nonhuman species. To our knowledge, they would not make this claim (but see **Lupyan** or **Wasserman** for scholars who might).

Our disagreement with **Bickerton** is more substantial. Bickerton acknowledges the functional discontinuity between human and nonhuman minds and the importance of higher-order relational reasoning in this discontinuity. He even gives us four kudos for confronting the comparative consensus on this contentious issue. But he gives us only a single kudo for our representational-level account of the discontinuity, preferring his own story about how language "rewired" the human brain.

We are grateful for any kudos we can get. But we believe we deserve an extra point for effort. The point of our target article was not to tell an evolutionary story. The point of our target article was to argue that the modern human brain is quite distinctive in its representational capabilities and that our unique capacity for higher-order relational reasoning is not entirely and solely a function of language or enculturation. Here, **Bickerton** would seem to be forced to agree with us. He acknowledges in his commentary that once language wrought its rewiring effects on the human brain, human mental representations became qualitatively different from those of other animals and continue to be so today even in the absence of occurrent verbal labels. But Bickerton does not provide a formal description of the representational changes wrought by language, nor does he provide a computational model of how those changes subserve the extra-linguistic cognitive abilities that distinguish modern human from extant nonhuman cognition. We are a long way from providing a complete representational-level account ourselves; but this is where we think we deserve that extra kudo for effort (see also our reply to **Bermúdez** in sect. R5.3, para. 2, further on).

Ironically, the weakest part of **Bickerton**'s story is his assessment of the cognitive abilities of nonhuman animals. Bickerton claims that "all nonhuman representations are distributed." And he challenges us to present evidence inconsistent with this proposal. We think Bickerton would do well to consult the commentaries by **Emery & Clayton**, **Herman et al.**, **Pepperberg**, **Suddendorf**, and **Tetzlaff & Carruthers**. These commentaries provide ample evidence that nonhuman representations are, indeed, functionally compositional and syntactically structured (see also Bermúdez 2003; Horgan & Tienson 1996). Furthermore, Bickerton's claim that nonhuman representations are tightly coupled to occurrent stimuli flies in the face of abundant comparative evidence to the contrary (see, e.g., Suddendorf & Whiten 2001).

The problem for **Bickerton** is that if language is not necessary to subserve "permanent, focused representations" in nonhuman animals, then Bickerton's evolutionary story does little explanatory work. In our view, language had and still has a substantial role in rewiring the human brain; but language's distinct evolutionary and ontogenetic impact on human reasoning falls more along the lines described by **Bermúdez** and **Gentner & Christie,** respectively, than that proposed by Bickerton.

R4.4. Are the differences only in our heads?

Barrett concurs with our reassessment of the comparative literature, but takes us to task for neglecting the role of the environment in supporting higher cognition in humans (see also **Rendall, Vokey, & Notman** [**Rendall et al.**]). Her point is well-taken. Many human and nonhuman cognitive abilities clearly rely on organisms' ability to make use of their bodies and the world in highly evolved, species-typical ways. For example, early work on the development of analogical problem solving in children called attention to its close parallels with symbolic play using physical objects (Holyoak et al. 1984; see also **Shatz**). And our discussion of the "seriated cups" test of "hierarchical reasoning" relied heavily on Fragaszy et al.'s (2002) demonstration that this task is more a test of subjects' sensorimotor skills in the world than of their ability to reason about hierarchical representations in their heads. If we had given due consideration to all the myriad of ways in which human and nonhuman animals leverage the world and their bodies in order to solve relational problems, our target article would have been considerably longer.

This said, there is reason behind our gloss. The purpose of our target article was to suggest an explanation for why human and nonhuman cognition differ so radically. And here, contrary to **Barrett**'s contention, the answer cannot be solely or even primarily "outside the head." One obvious problem with an "it's all outside the head" stance is that it does nothing to explain why humans, and no others, are able to leverage the world in their species-unique ways. Clark's (2001) hybrid stance seems more promising: Certain cognitive tasks are, to borrow Clark's apt phrase, more "representation hungry" than others. One class of representation-hungry problems of central importance to all biological cognizers is relational problems (Clark & Thornton 1997). Figuring out why human cognizers alone are able to use knowledge-rich artifacts and symbol systems to help them solve higher-order relational problems requires figuring out, among other things, what is distinctive about the internal representational processes humans bring to bear on these problems. As **Suddendorf** puts it, "chances are that humans' cognitive autapomorphies have something to do with our brain autapomorphies."

R5. Which computational models earn their explanatory keep?

R5.1. Computational models that aim too low

Rendall et al. suggest that "associative processes" could, at least in principle, provide sufficient representational power to subserve higher-order relational reasoning (see also **Lupyan**). We agree. We certainly do not rule out connectionist mechanisms as possible implementations of higher-order relational reasoning in humans. We merely believe that anyone who wishes to model human cognition needs to take Smolensky's (1999) "Symbolic Approximation" hypothesis very seriously. As we reviewed in our target article, connectionist models that fail to acknowledge the necessity of approximating the higher-order, structural properties of a PSS consistently fall short precisely where higher-order relational reasoning is required. And, at least at present, it seems doubtful that traditional "parallel distributed processing" (PDP) connectionist models can approximate the higher-order structural properties of a PSS without the addition of qualitatively new representational processes (see also Doumas & Hummel 2005; Holyoak & Hummel 2000; Wilson et al. 2001b).

R5.2. Computational models that aim too high

Tomlinson & Love pose an excellent question: If animals cannot approximate a full-fledged PSS, what kind of computational architecture do they have? There is a conspicuous dearth of biologically plausible, computationally feasible, behaviorally adequate answers to this question. Indeed, there are so few researchers willing to even ask this daunting question that we happily accord two kudos to Tomlinson & Love just for showing up and making the effort.

This said, the BRIDGES (Building Relations through Instance Driven Gradient Error Shifting) model touted by **Tomlinson & Love** begs the question at issue in our target article. The BRIDGES model solves S/D and RMTS tasks by combining exemplar-based category learning (what we call perceptual relational learning) with structured relational mapping (which we claim is unique to humans). No one doubts, of course, that S/D and RMTS tasks *can* be solved by structured relational mapping – human subjects may very well solve RMTS tasks in this manner under certain conditions. But the issue at stake in our target article is whether or not there is any evidence that other extant species employ this particular mechanism as well.

Tomlinson & Love point out that an explanation based on sensitivity to categorical entropy alone does not explain the degree to which pigeons are influenced by the featural similarity between the test array and previous arrays the animal has been trained with. We agree. Categorical entropy is certainly inadequate to account for all of the patterns of relational responding manifested by pigeons or any other animal (as Cook and Wasserman [2006] themselves point out). But all of the additional influences on pigeons' relational responses, including those documented by Gibson and Wasserman (2004), are further examples of *feature-based* relations, not the higher-order structural relations we have argued are unique to humans. And Tomlinson & Love give no reason to believe that pigeons or any other nonhuman animals employ higher-order mappings between structured relations in order to solve S/D or RMTS tasks.

R5.3. Does LISA earn its explanatory keep?

We discussed the LISA (Learning and Inference with Schemas and Analogies) model of analogical reasoning proposed by Hummel and Holyoak (1997; 2003) as one possible representational-level model for how higher-order relational reasoning might be implemented in a neurally plausible architecture. But **Tetzlaff & Carruthers** are not unjustified to point out LISA's numerous limitations. To put it bluntly, LISA is a rudimentary, highly stylized model of analogical reasoning that accounts for only a small part of what makes human cognition human (although it is getting better; see Doumas et al. 2008). In our view, LISA is the worst model of higher-order reasoning currently on offer, except for all the others. If Tetzlaff & Carruthers have a better model to suggest, we are all ears.

Bermúdez largely concurs with our analysis of the discontinuity between human and nonhuman minds but argues that the LISA model simply "appears to recapitulate" our functional-level description and does not "explain" how this discontinuity evolved in the first place. It is true that we did not provide an "explanation" for how higher-order relational reasoning evolved in the human brain; but simply invoking a story about how language "rewired" the human mind (see also **Bickerton**) leaves most of the interesting representational-level questions unanswered as well. It is one thing to identify the functional characteristics of the discontinuity between human and nonhuman cognition. It is quite another to explain how the functional abilities specific to human cognition are implemented in the neural matter of the human brain.

Representational-level computational models such as LISA (see also **Tomlinson & Love**) have an invaluable but undervalued role to play in cognitive science. It is all too common for psychologists and philosophers to create high-level models of a given cognitive behavior without giving due consideration to whether such models are computationally feasible or biologically plausible. Although there are clearly multiple distinct "levels" of explanation in cognitive science, even Marr (1982) did not countenance ignoring all but the highest level of analysis. Working implementations of a cognitive capability have the potential to challenge or support the plausibility and coherence of higher-level specifications, to provide new insights into the operational characteristics of that cognitive capability, and to serve as models bridging the (often quite large) gap between functional-level and neural-level descriptions.

The bulk of our target article focused on identifying the functional characteristics of the discontinuity between human and nonhuman cognition. Developers of symbolic-connectionist computational models such as LISA are trying to understand what kind of rewiring changes are necessary in order to subserve the higher-order relational capabilities that both we and **Bermúdez** believe are unique to the human mind – including those that are necessary for language itself. LISA, in particular, provides one possible example of how the higher-order relational capabilities of the human mind might be implemented on top of the lower-order, perceptually grounded capabilities of the nonhuman mind. At the very least, then, LISA provides some confirmation that our RR hypothesis is neither computationally infeasible nor neurally implausible.

But LISA's explanatory neck is stuck out a good deal farther. If LISA is correct, the substantive discontinuity between human and nonhuman cognition came about because only the hominid lineage evolved the ability to use synchronized activity among prefrontal neural populations to support dynamic-binding among roles, fillers, and structured relations. Although neural synchrony is used by many species for coding contextual associations of various sorts (see Fries et al. 2007), LISA suggests that co-opting this mechanism for role-based relational coding was responsible for the "Great Move" (Newell 1990) in human cognition. Certainly, neural synchrony is not the only possible mechanism by which the human brain might approximate the higher-order properties of a PSS (for other possibilities, see Smolensky 1999; Wilson et al. 2001a). And the hypothesis that some form of neural synchrony is the critical innovation subserving higher-order human cognition requires much further empirical support before it can be deemed anything more than a plausible possibility (but see Uhlhaas & Singer 2006 for a start). Nevertheless, **Bermúdez** is surely mistaken to argue that LISA is merely a "redescription" of the functional-level facts.

Bermúdez challenges us to explain why the ability to represent higher-order relations, abstract roles, and functions is such a rarity among animals. Here again, LISA suggests one possible story that would not have been apparent otherwise: One of the most interesting and provocative findings to arise out of symbolic-connectionist research is that it is, in fact, quite hard to approximate the higher-order features of a PSS in a neurally plausible fashion. Although higher-order relational reasoning may come naturally to modern humans, it does not come naturally to neural networks. By contrast, it is much easier for neural networks to approximate the kinds of perceptual reasoning that characterize nonhuman cognition. Indeed, traditional PDP-style networks are clearly quite good at approximating many of the basic capabilities of animal cognition. And tweaking these models with various task-specific tricks, ploys, and heuristics (Clark & Thornton 1997) allows these networks to approximate fairly complex relational tasks, as well. But there is no simple "next step" that will transform a clever PDP model into a full-fledged PSS complete with dynamic role-filler binding and higher-order relational structures. To cross the gap between a PDP network and a PSS, LISA suggests that a neural system needs to make a much more fundamental and costly change in its architecture. From an evolutionary point of view, then, LISA suggests that nonhuman cognitive species have evolved into various "local minima" in the space of biological neural systems, and that the cost of moving out of these local minima has been prohibitive for all but one species on this planet.

R6. So who was mistaken?

The editors of this journal warned us that the title, "Darwin's Mistake", might distract some commentators from the substantive issues at stake in our article. They were right. **Burghardt** compares our hypothesis to the metaphysical arguments proposed by Mortimer Adler and Will Gaylin and warns that we have opened a "wedge" that creationists will exploit. **Gardner** aligns us with Alfred Russell Wallace and claims that "virtually all" of the experimental evidence we cited commits the same methodological error as Pfungst's work with Hans the horse. **Wasserman** challenges our hypothesis not by rebutting any of our empirical claims but by comparing our "bleak assessment of animal cognition" to that of John Locke and C. Lloyd Morgan.

Unfortunately, the reaction of these commentators is not atypical. Many contemporary comparative psychologists reflexively treat any suggestion of a cognitive discontinuity between human and nonhuman species as a heresy equivalent to defending creationism, or, worse, anthropocentrism. For the record, we never suggested either that some *deus ex machina* played a role in the evolution of the human mind or that animals lack the power of abstraction; and we never called for Darwin to surrender his place in the pantheon of great scientists. Indeed, our hypothesis is entirely Darwinian in its inspiration. Was not the entire point of Darwin's (1859) *magnum opus* that the "Divergence of Character" combined with the principles of "Natural Selection" and the "Extinction of less-improved forms" would, by their very nature, create functional differences between extant organisms, some so great as to differentiate one kind (i.e., "species") of organism from another? **Lupyan** puts it perfectly: "Owing to nonlinear interactions between genotypes, environment, and the resulting phenotypes, functional discontinuities are a common product of continuous evolutionary tinkering." Our claim that continuous evolutionary processes have produced a radical functional discontinuity between the cognitive abilities of extant species is not an affront to Darwin's legacy (cf. **Burghardt**, **Wasserman**) – it is what Darwin's own theory predicts.

Burghardt uses the bulk of his commentary to debate the semantics of the term "difference in kind." According to Burghardt's analysis, which he attributes to Adler (1968), any gap compatible with evolution is *ipso facto* no more than a "superficial" difference in kind, illustrated by the state change from water to ice that results when a continuous variable – that is, temperature – reaches a certain threshold. Burghardt illustrates Adler's stronger "radical difference in kind" by the distinction between living and nonliving entities, which Adler himself apparently viewed as a gap too great to be crossed by material processes.

It is hard to see how any interesting biological differences are cogently captured by **Burghardt**'s taxonomy. Is the difference between eukaryotic and prokaryotic organisms a "superficial" or a "radical" difference in kind? Even Darwin's concept of a "species" seems to run afoul of this simplistic taxonomy. Burghardt's semantic analysis is even less enlightening with respect to the evolution of human cognition. The differences between human and nonhuman brains are clearly not limited to an incremental change along some single continuous quantity, such as number of neurons or brain size (Preuss 2000). Yet everybody (reasonable) agrees that there is no need to posit any special kind of nonmaterial mental stuff. Whatever differences there are between human and nonhuman minds, they are certainly more than "superficial" in Adler's sense but definitely less than "radical," and in any case are completely compatible with and predicted by Darwin's materialist theory of evolution.

So did Darwin make a mistake? His liberal use of secondhand anecdotes and anthropomorphic attributions in the opening chapters of *The Descent of Man* (1871) did not mark his finest scientific moment. His infatuation with the mental and moral virtues of domesticated dogs illustrates the problem. Dogs, Darwin argued, exhibit "a sense of humour, as distinct from mere play" and "possess something very like a conscience." "There can be no doubt," he goes on to write, "that a dog feels shame, as distinct from fear, and something very like modesty when begging too often for food" (Darwin 1871, p. 40).

Admittedly, Darwin's emphasis on the mental continuity between human and nonhuman minds was politic in his time – as it still is today. And whatever mistakes Darwin made, he made them almost a hundred years before the rise of modern linguistics, computational theory, genomics, and the cognitive "revolution" in psychology. So after considering the commentaries on our target article, we admit our original title may have been too harsh.

As **Wynne & Bolhuis** remind us, the stance taken by many comparative psychologists today is even more anthropomorphic than Darwin's. **Burghardt**'s commentary confirms those suspicions: "Research over the last 40 years," Burghardt writes, "has shown that Darwin actually underestimated the mentality of apes, for example, in tool making, numerosity, and communication." Indeed, in many respects, the hypothesis we proposed in our target article lies closer to Darwin's views on the matter than to those of many of our contemporaries. Darwin (1871) at least acknowledged the "immense" and "enormous" difference between "the lowest savages" and even the "most highly organised ape" – whereas many comparative researchers today believe that a human child magically kept alive alone on a desert island would "not differ very much" from other great apes (Tomasello & Rakoczy 2003; see also **Gardner**, **Lupyan**, **Wasserman**). And unlike some researchers (e.g., **Bickerton**) who believe that language alone can explain what is distinctive about the human mind, Darwin argued – as we do – that "the mental powers of some early progenitor of man must have been more highly developed than in any existing ape, before even the most imperfect form of speech could have come into use" (Darwin 1871, p. 57).

In short, any differences we may have with Darwin concerning the cognitive limitations of nonhuman animals pale in comparison to the differences we have with most of our contemporaries in comparative psychology. And any mistakes Darwin may have made over the course of his career seem trivial when weighed against the monumental insights he provided into the evolution of life in general and the origins of the human mind in particular. In hindsight, we erred: "Darwin's Triumph" makes a better title.

R7. Appendix: Falsifying the relational reinterpretation hypothesis

Hereinbelow, we sketch examples of experimental protocols capable of falsifying our functional-level claims for each of the distinctively human relational capabilities discussed in our target article.

R7.1. Analogical relations

R7.1.1. Experiment 1: Formal analogies. Raven's Standard Progressive Matrices Test (Raven 1941) provides a well-studied template for developing nonverbal measures of formal analogical reasoning. This protocol can be easily adapted to nonhuman subjects. According to our RR hypothesis, many nonhuman animals are capable of solving Raven-like problems involving zero relations (even non-enculturated pigeons!) and some may be capable of solving one-relation problems; but no nonhuman animal is capable of solving Raven-like problems involving two or more relations (see discussion by Waltz et al. 1999).

R7.1.2. Experiment 2: Visuospatial analogies. The dolphin's prowess at mimicry (see Herman 2006 for a review) provides an opportunity to test this species' ability to reason about simple visuospatial relations in an analogical fashion. Our proposed test of visuospatial analogies employs the "progressive alignment" strategy that Kotovsky and Gentner (1996) used to "train" children to recognize relational mappings – that is, subjects begin by recognizing highly similar examples of a relation and are progressively encouraged to compare more and more disparate instances. Then, on each test trial, role-based and perceptual similarity are pitted against one another.

Train a dolphin to mimic the relational action demonstrated by a trainer as closely as possible given the set of objects available to the dolphin in the pool. In the beginning, the objects in the pool should allow the dolphin to mimic the trainer's actions quite closely: for example, the trainer touches a stick to a Frisbee, and the dolphin has available a different but identical stick and a different but identical Frisbee. Then, the dolphin can be trained on more and more challenging problems by using objects that can no longer serve, literally, to imitate the trainer's actions. For example, when the trainer touches a stick to a Frisbee, there is only a stick and a ball in the pool; when the trainer puts a ball in a box, there is only a Frisbee and a basket in the pool.

Once the dolphin has learned to mimic the relevant relations using perceptually disparate objects, the dolphin can be tested on tasks in which perceptually similar objects play conflicting roles. For example, the trainer could put a ball in a basket; and the dolphin could be given a small basket, a larger box, and an even larger ball (where the ball is too large to go in the box and the box is too large to go in the basket, so that the "analogous" solution is for the dolphin to put the basket in the box). Or the trainer might blow a ping-pong ball through a cylinder with her mouth; and the dolphin could be given an identical cylinder, a hoop, and a ball (where the ball is too large to pass through either the hoop or the cylinder, so that the analogous solution is for the dolphin to push or blow the cylinder through the hoop with its mouth).

Of course, success on any one test trial is of little significance. Any given trial could be passed using some feature-based heuristic, or indeed, simply by chance. In order to provide convincing evidence of analogical reasoning, subjects must demonstrate their ability to systematically mimic the trainer's actions across a variety of visuospatial relations.

R7.1.3. Experiment 3: Analogical problem solving. Tests involving "artificial fruits" – that is, containers that can be opened only using a specific sequence of movements – have been a staple of comparative research ever since they were introduced by Whiten et al. (1996). In the past, these experiments have focused on testing an animal's ability to "imitate" the actions taken by a demonstrator. The following experiment uses the "artificial fruit" apparatus to test for a much more cognitively demanding ability: the ability to gain insight into how to solve a novel problem by observing a demonstrator solve a different but analogous problem.

In our proposed experiment, there are pairs of artificial fruits. Both fruits in a pair are identical except that the combinations of movements necessary to open each fruit's "lock" are perceptually different but structurally analogous. For example, if one fruit's lock can be opened by pushing three buttons in the sequence 2-1-3, then the analogous fruit's lock can be opened by pulling three bolts out in the same 2-1-3 sequence. Alternatively, if one fruit's lock can be opened by setting three switches into the positions Up – Down – Down, then the analogous fruit's lock can be opened by turning three knobs to the positions Left – Right – Right. To test subjects' ability to solve novel problems by analogy to observed solutions, the demonstrator opens one fruit of a pair repeatedly in front of the test subjects, and then the subjects are given the opportunity to open the analogous fruit by themselves.

R7.2. Higher-order spatial relations

R7.2.1. Experiment 4: Scale-model comprehension. Kuhlmeier and Boysen's (2002) original experiments on scale-model comprehension among chimpanzees could be easily modified to provide a valid test of a nonverbal subject's ability to reason about higher-order spatial relations. First, any local perceptual similarity between miniature objects and full-sized objects must be eliminated (e.g., all landmarks should be perceptually identical). Second, the location of the scaled and full-sized versions of objects must be systematically varied on each trial.

R7.2.2. Experiment 5: Single-dimensional map comprehension. Huttenlocher et al. (1999) provide an elegant test of a simple form of spatial reasoning that is a necessary precursor for reasoning about higher-order spatial relations: finding an object based on the scalar correspondence between two surfaces along a single dimension. To adapt this protocol for nonhuman animals, subjects could be presented with a long, narrow tray that is an order of magnitude smaller than an adjacent sandbox but has the same aspect ratio as the sandbox. A marker is placed in one of ten possible locations equidistant along the length of the tray in full view of the subjects, and a reward is hidden at the equivalent location in the larger sandbox out of sight of the subjects. The subjects are trained to find the reward based on the location of the marker in the first five distinct locations in the tray (i.e., locations 1, 2, 3, 4, 5). Once they have mastered this correspondence, they are tested on whether or not they are able to find the reward in the remaining five, novel locations (i.e., 6, 7, 8, 9, 10).

If any nonhuman species succeeds in passing this one-dimensional task, it should then be tested on whether this ability generalizes to two-dimensional surfaces without additional training (see Vasilyeva & Huttenlocher 2004). Passing a systematic, two-dimensional version of this task on a first-trial basis would provide definitive evidence for higher-order relational reasoning in the spatial domain.

R7.3. Transitive inference

The key criteria for demonstrating transitive inference (TI) experimentally are the following: (1) subjects must be given relational information alone (e.g., $A > B$) without any cues as to the absolute values of the arguments (e.g., $A = 5$, $B = 3$); (2) the relation involved must be logically transitive and the fact that the relation is transitive must be necessary to make the inference; (3) the transitive relation between stimuli must not be inferable from reinforcement or associative history; (4) the transitive inference must be made on a one-shot, first-trial basis (for further details, see Halford 1984; Halford et al. 1998a). Below are two examples of a valid test of TI.

R7.3.1. Experiment 6: Balance-scale test of transitive inference. Let the subjects freely play with a balance-scale that has two fixed platforms for holding objects equidistant from the fulcrum. (NB: Unlike the traditional Piagetian version of this task, only weight is a variable.) Once the subjects have experienced placing objects of various weights on each platform and observing that the heavier object tips the balance down, train them to indicate which platform will tip down (e.g., by pointing or moving a marker) using a set of balls of various sizes, colors, and weights. Once the subjects can reliably predict which platform will be tipped down for any given pair of balls in the training set, test the subjects on a novel set of identically-sized balls of different colors (e.g., A through E), as follows: Without letting them touch the balls and without any differential reinforcement, repeatedly show the subjects the behavior of adjacent pairs of balls on the balance-scale, so that they can observe that $A > B$, $B > C$, $C > D$, and $D > E$. Then test the subjects on non-adjacent, unobserved pairings, for example, D and B. Subjects who can systematically predict the behavior of the balance-scale for non-adjacent, unobserved pairs will have manifested principled evidence for TI.

R7.3.2. Experiment 7: Transitive inference in great tits. In our response, we have argued that Otter et al.'s (1999) experiment with great tits does not qualify as evidence for TI. But their protocol could be modified as follows: Allow female great tits to eavesdrop on simulated agonistic encounters between pairs of unfamiliar males selected from a set of five, with outcomes that imply the dominance ordering $A > B > C > D > E$. Then remove the female's current mate and test whether or not the subject shows a systematic preference for the dominant male in any given pair when given a choice of a new mate (e.g., preferring B over D).

R7.4. Rules

R7.4.1. Experiment 8: Structural rule learning using an AGL protocol. The literature on artificial-grammar learning (AGL) with humans provides a rich mine of experiments that can be used to test nonhuman animals' ability to infer structural rules between non-repeating elements and to generalize this knowledge to novel vocabularies. Tunney and Altmann (2001), for example, presented subjects with sequences of eight graphic symbols (A to H) generated from a grammar that allowed any of the elements E to H to occur in positions 1, 2, 5, and 6 in a uniform, random distribution, and allowed either the pair A and B, or the pair C and D, to appear (in either order) in positions 3 and 4. They then evaluated the subjects' assessment of the grammaticality of 96 unique sequences drawn from an entirely novel vocabulary of eight nonsense syllables ordered according to the same structural rules. Tunney and Altmann (2001) showed that human subjects were able to transfer grammaticality discriminations from graphic symbols to novel nonsense syllables despite an arbitrary mapping between the two domains, and without any repetitions or other salient perceptual relations between elements in a given sequence. The same test can be readily adapted to nonverbal animals.

R7.4.2. Experiment 9: Structural rule learning using a contingency learning task. The following experiment is adapted from a contingency learning task first employed by Shanks and Darby (1998) with human subjects. During the initial training, subjects are presented with cues (e.g., lights, tones) and outcomes in the following combinations: AB+, A-, B-, CD-, C+, D+, E+, F+ and GH- (where *X*+ means that presentation of the cue *X* is paired with a reward, and *X*- means that presentation of the cue *X* is not paired with any reinforcer). At test, the subjects are presented with the novel cue-outcome combinations EF, G, and H.

In Shanks and Darby's (1998) original experiment, human subjects who learned the patterns shown during training anticipated that EF would *not* be paired with a reward, whereas cues G and H presented separately *would* be paired with a reward. In other words, these subjects learned the "rule" that the likelihood of the outcome after a compound of two cues is the inverse of the likelihood of the outcome when those same cues are presented separately. Shanks and Darby (1998) concluded, and we concur, that success on this protocol demonstrates that the subject can learn structural rules about contingencies that are distinct from (and even contrary to) the outcomes predicted by associative conditioning.

R7.5. Hierarchical relations

R7.5.1. Experiment 10: Hierarchically structured sentences. Herman et al. (1984) report that bottlenosed dolphins comprehend sentential constructions such as "LEFT FRISBEE FETCH RIGHT HOOP," which can be glossed as "take the Frisbee to your left to the hoop located to your right." To test whether or not dolphins can understand hierarchically structured, recursive constructions, one could test their ability to comprehend sentential constructions of the following form: NP + V + NP, where V is an action such as FETCH, and NP is a noun phrase that can be either an object (e.g., FRISBEE), or a location modifier and an object (e.g., LEFT FRISBEE), or another noun phrase followed by a location modifier and an object (e.g., RIGHT FRISBEE LEFT BALL). For example, the construction "RIGHT FRISBEE LEFT BALL FETCH SPIGOT" instructs the dolphin to take the ball that is to the left of the Frisbee that is to the right of the subject over to the water spigot. If dolphins – or any other nonhuman animal – could comprehend and act on constructions such as these in a systematic fashion, this would constitute definitive evidence that they are able to comprehend hierarchically structured grammatical relations.

R7.5.2. Experiment 11: Hierarchical representation of dominance relations. In our target article, we criticized Bergman et al.'s (2003) claim to have found evidence for hierarchical social classifications among wild savannah baboons. But it would not be hard to adapt their protocol to provide compelling evidence for hierarchical representations. Given matrilines A > B>C with offspring $a_1..a_n$, $b_1..b_n$, $c_1..c_n$, respectively, and using the artificial playback protocol described by Bergman et al. (2003), present subjects not in the A, B, or C matrilines with unexpected rank reversals between the dominant members of the A and B matrilines and the B and C matrilines (i.e., C > B and B > A but not C > A). Subjects that are capable of reasoning about social dominance relations in a hierarchical fashion should be more "surprised" at hearing $c_x < a_y$ than at hearing $c_x > a_y$ for any arbitrary member of the two nonadjacent matrilines. Furthermore (contrary to the results reported by Bergman et al. [2003], the subjects should be more "surprised" by rank reversals between subordinates in more distant matrilines (e.g., $a_x > c_y$) than by rank reversals in more closely ranked matrilines (e.g., $b_x > c_y$).

R7.6. Causal relations

R7.6.1. Experiment 12: Nonhuman primates' understanding of weight. One of us (Povinelli) has already proposed numerous experiments capable of testing a nonhuman primate's ability to reason about unobservable causal mechanisms (see Povinelli 2000). Here we suggest one further experiment that would be probative.

Nonhuman primates are quite familiar with the effort required to lift objects. Chimpanzees in particular have been shown to use the weight of an object instrumentally. For example, free-ranging chimpanzees learn to use the weight of heavy stones to crack open hard nuts and lighter stones to crack open softer nuts, in a population-specific fashion. The following experiment tests whether nonhuman primates actually reinterpret the effort required to lift objects and the accompanying sensorimotor cues into a causal notion of "weight" (for more details, see Povinelli, in press). First, present subjects with two balls that are visually identical but of radically differing weights (one is heavy, the other is very light). Train the subjects to sort the balls into one of two containers based on the "weight" of the balls (e.g., "heavy" ball goes in the container to the left, "light" ball goes in the container on the right). Separately, allow the subjects to freely play with the ramp apparatus shown in Figure R1, allowing them to launch balls of various weights down the ramp without the reward apple being present.

Figure R1. Ramp apparatus used to determine if chimpanzees understand that a heavy, but not an extremely light projectile (ball) can be used to dislodge a desired reward apple.

Then, after placing the apple, allow the subjects (a) to dislodge the apple with their hands and (b) to observe trainers launch heavy and light balls down the ramp, thereby letting them see that only some balls, not all, dislodge the apple. Finally, at test, present the subjects with the two visually identical but differentially weighted balls and the ramp/apple apparatus, and observe whether or not the subjects choose the heavier ball on the first trial.

One of us (Povinelli) has already run several experiments like the one just described on a group of captive chimpanzees (see Povinelli, in preparation). Subjects chose to use the heavier ball to dislodge the apple at chance levels on the critical test trials – even though they were still able to sort the balls correctly.

R7.6.2. Experiment 13: Using interventions in an epistemic fashion. The following protocol tests an animal's ability to use the knowledge gleaned from its own interventions to form a systematic, allocentric representation of a causal model. Subjects are presented with four levers. Each lever triggers one of four distinct cues: L1, L2, T1, or T2, where the L cues are of one kind (e.g., lights) and the T cues are of another kind (e.g., tones). Pressing the lever corresponding to a given cue triggers that cue for 10 seconds. A food reward is delivered if within 10 seconds the subject triggers cues L1 and T1 or triggers cues L2 and T2. Any other combination of cues (e.g., L1 and L2; L1, T1, and T2) results in a time-out and no reward. Subjects are allowed to freely play with the levers until they discover the two ways of producing the reward (pressing L1 and T1 or pressing L2 and T2). Once the subjects have made that discovery, no rewards are presented in the subsequent test sessions.

For the first test session, the levers corresponding to the L cues are removed, leaving only the levers corresponding to the T cues available. Then at random intervals, cues L1 and L2 are presented for 10 seconds each. If the subjects understand that they can intervene to produce the cue that completes a pair of cues that was previously rewarded, they should press the lever corresponding to T1 while L1 is illuminated, and press the lever corresponding to T2 while L2 is illuminated. During a second test session, the levers corresponding to the T cues are removed, leaving only the levers corresponding to the L cues available. Then the analogous protocol is followed for presentations of T rather than L.

A subject that responds with the appropriate instrumental action in response to all of these combinations of cues will have demonstrated that it can learn and then access the structure of a simple causal model in a systematic, allocentric fashion across both observations and interventions.

R7.7. Theory of mind

R7.7.1. Experiment 14: Experience projection. The following test of "experience projection" is adapted for scrub-jays from an experiment originally proposed by Heyes (1998), adapted by Povinelli and Vonk (2003), and defended by Penn and Povinelli (2007b). Allow subjects to witness food being cached by a competitor behind two different barriers of different colors. One barrier is transparent to the subject because it is made of one-way glass and allows the subject to see through the barrier; the other barrier is opaque to the subject. There are multiple potential cache sites behind each barrier. If the competitor caches food behind the transparent barrier, the subject can see precisely where the food was cached. If the competitor caches food behind the opaque barrier, the subject cannot see precisely where the food was cached. From the cacher's point of view, the barriers are of different colors but otherwise are perceptually identical (i.e., both look like mirrors). After the competitor has cached food behind both kinds of barriers, allow the subject to retrieve the caches it saw the other bird make (i.e., behind the one-way barrier). Then, at test, allow the subject to make its own caches either in front of or behind both kinds of barriers in the presence of a novel competitor. If the subject preferentially caches behind the opaque barrier rather than the one-way glass barrier, this would be strong evidence for "experience projection."

R7.7.2. Experiment 15: Understanding role reversals. The following experiment tests for evidence of role-based collaboration based on a protocol first proposed by Povinelli et al. (1992). A pair of subjects is trained to operate an apparatus that has four pairs of food trays. One of the two subjects (the *informant*) can see which of the four pairs of food trays is baited. The other subject (the *operator*) cannot see which trays are baited but can pull on one of four handles to bring the corresponding pair of trays within reach of both participants. The participants are separated by a clear partition. The informant is trained to designate which pair of trays is baited by placing a marker over the appropriate trays. The operator is trained to pull on the handle associated with the pair of trays that has been marked by the informant. Both subjects can fully observe the actions of the other during this training procedure. Once both subjects have mastered their respective roles, the apparatus is rotated in full view of the subjects, thus switching the roles to be played by the subjects. If both subjects can immediately take the appropriate actions (i.e., marking the baited trays and pulling on the handle that has been marked), they will have shown an ability to reason about a collaborative activity in a role-based fashion.

R7.7.3. Experiment 16: Role-based collaboration and intentional communication. The following protocol is based on the capabilities reported by Herman (2006). Train dolphins to respond to the command "Tandem X Y" by having one dolphin perform behavior X and the other dolphin perform behavior Y in tandem, where X and Y are selected randomly on each trial from a set of suitable behaviors (e.g., back flip, jump). Designate which dolphin is to perform which behavior by pointing at the appropriate subject. Once the dolphins have mastered this command, isolate the two dolphins so that only one of them (i.e., the *communicator*) can see the gestures being made by the trainer. Give the "Tandem X Y" command only to the dolphin designated as the communicator. Then allow the two subjects to rejoin each other and perform the designated behaviors. If both subjects are now able to execute the appropriate X and Y behaviors correctly, this would provide the first definitive evidence of intentional communication and role-based collaboration in a nonhuman species.[1]

R7.7.4. Experiment 17: An acid test of "false belief" understanding. The "acid test" of a theory of mind (ToM) has long been taken to be the ability to reason about the cognitive effects of another subject's counterfactual representations about the world (for recent discussions of what should and should not count as evidence for "false belief" understanding, see Penn & Povinelli 2007b; Perner & Leekam 2008). Pack and Herman (2006) suggest that dolphins may be capable of understanding "false beliefs" (see also Tschudin 2006). If so, dolphins should be able to pass the following test, adapted from a task that Call and Tomasello (1999) first employed with children and nonhuman apes (the nonhumans failed).

In the initial training phase, an experimenter hides a reward object in one of two identical containers in the pool while being observed by one dolphin (the *observer*) but out of sight (and earshot) of the other dolphin (the *retriever*). The retriever is released back into the common pool area and the observer is trained to inform the retriever in which container the reward is hidden (e.g., by "pointing" at the container with its echolocation "beam" or by any other species-natural behavior).

Once the two dolphins have mastered their respective roles in the initial training phase, each trial in the second training phase occurs in the following steps: (1) the retriever is removed from the pool area; (2) the reward is hidden in one of the two containers in view of the observer; (3) the observer is removed from the pool area; (4) the retriever is released back into the pool area; (5) the observer is also returned to the pool area; (6) the observer is allowed to indicate in which one of the two containers the reward is; and (7) the retriever is allowed to retrieve the reward. In the initial baseline training condition, the locations of the two containers remain unchanged over the course of all steps. In the second baseline training condition, the locations of the two containers are switched during step 2, in full view of the observer but not in view of the retriever. In the third baseline training condition, the locations of the two containers are switched after step 5 – that is, in full view of both the observer and the retriever. Note that in all three baseline training conditions, the observer is correctly informed as to the location of the reward but the retriever is not.

Once the retriever can reliably find the hidden object in all three baseline training conditions, the crucial test sessions can begin. On successive trials, the following "false belief" conditions are randomly interspersed with the three baseline training conditions: (1) switch the location of the two containers after step 4 in view of the retriever but not the observer; and (2) hide the reward before step 1 in full view of the retriever and the observer, then switch the locations of the containers during step 2 in view of the observer but not the retriever. In the first of these "false belief" conditions, the observer is misinformed as to the true location of the reward and the retriever must infer that the correct location is the one the observer does not point out (this is essentially the same test as reported by Call & Tomasello 1999). In the second "false belief" condition, the retriever believes it knows the location of the reward but is misinformed, and the observer must inform the retriever that the containers have been switched and/or that the retriever is misinformed.

Additional control conditions are of course necessary. These include interspersing a condition in which the retriever sees the placement of the reward but the locations of the containers are *not* switched; and normalizing the delays between all steps (see Call & Tomasello [1999] for additional controls). But if dolphins could pass both of these "false belief" conditions, this would constitute the first compelling evidence for ToM abilities in a nonhuman animal.

NOTE

1. Our proposed "Tandem X Y" task is qualitatively different from the kind of communication purportedly performed by bees with their "waggle dance" (De Marco & Menzel 2005). In the case of bees, the information is a simple broadcast; the assignment of different roles to different recipients is not encoded in the dance in a systematic fashion.

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[The letters "a" and "r" before author's initials stand for target article and response references, respectively.]

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