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