

Published in final edited form as:

Neurosci Biobehav Rev. 2012 November ; 36(10): 2355–2369. doi:10.1016/j.neubiorev.2012.09.003.

Implicit and Explicit Categorization: A Tale of Four Species

J. David Smith^{a,1}, Mark E. Berg^b, Robert G. Cook^c, Matthew S. Murphy^c, Matthew J. Crossley^d, Joe Boomer^a, Brian Spiering^e, Michael J. Beran^f, Barbara A. Church^a, F. Gregory Ashby^d, and Randolph C. Grace^g

J. David Smith: psysmith@buffalo.edu; Mark E. Berg: bergm@stockton.edu; Robert G. Cook: Robert.Cook@tufts.edu; Matthew S. Murphy: Matthew.S.Murphy@tufts.edu; Matthew J. Crossley: crossley@psych.ucsb.edu; Joe Boomer: jboomer@buffalo.edu; Brian Spiering: bspiering@gmail.com; Michael J. Beran: mjberan@yahoo.com; Barbara A. Church: bchurch@buffalo.edu; F. Gregory Ashby: ashby@psych.ucsb.edu; Randolph C. Grace: randolph.grace@canterbury.ac.nz

^aDepartment of Psychology, University at Buffalo, The State University of New York, Buffalo NY 14260 USA

^bDepartment of Psychology, Richard Stockton College of New Jersey, Galloway, NJ 08205-9441 USA

^cDepartment of Psychology, Tufts University, Research Building, 530 Boston Ave, Medford, MA 02155 USA

^dDepartment of Psychological and Brain Sciences, University of California Santa Barbara, Santa Barbara, CA 93106 USA

^eDepartment of Psychology, 1147 Biology/Psychology Building, University of Maryland, College Park, MD 20742 USA

^fLanguage Research Center, Georgia State University, University Plaza, Atlanta, GA 30302 USA

^gDepartment of Psychology, University of Canterbury, Christchurch, Private Bag 4800, Christchurch NZ

Abstract

Categorization is essential for survival, and it is a widely studied cognitive adaptation in humans and animals. An influential neuroscience perspective differentiates in humans an explicit, rule-based categorization system from an implicit system that slowly associates response outputs to different regions of perceptual space. This perspective is being extended to study categorization in other vertebrate species, using category tasks that have a one-dimensional, rule-based solution or a two-dimensional, information-integration solution. Humans, macaques, and capuchin monkeys strongly dimensionalize perceptual stimuli and learn rule-based tasks more quickly. In sharp contrast, pigeons learn these two tasks equally quickly. Pigeons represent a cognitive system in which the commitment to dimensional analysis and category rules was not strongly made. Their results may reveal the character of the ancestral vertebrate categorization system from which that of primates emerged. The primate results establish continuity with human cognition, suggesting that nonhuman primates share aspects of humans' capacity for explicit cognition. The emergence of dimensional analysis and rule learning could have been an important step in primates' cognitive evolution.

¹To whom correspondence should be addressed. J. David Smith, 346 Park Hall, University at Buffalo, The State University of New York, Buffalo, NY 14260 USA, psysmith@buffalo.edu, 716-645-0229 (voice), 716-645-3801 (fax).

Keywords

category learning; cognitive neuroscience; implicit/explicit cognition; primate cognition; comparative cognition

1. Introduction: Multiple Systems for Categorization

Learning and using psychological or behavioral equivalence classes—categories—is an essential cognitive function. For this reason, categorization is a sharp focus of human and animal research (humans—e.g., Ashby and Maddox, 2011; Brooks, 1978; Knowlton and Squire, 1993; Medin and Schaffer, 1978; Murphy, 2003; Nosofsky, 1987; Smith and Minda, 1998; animals—e.g., Herrnstein et al., 1976; Jitsumori, 1994; Lazareva and Wasserman, 2010; Lea and Wills, 2008; Pearce, 1994; Smith et al., 2008; Thompson and Oden, 2000; Vauclair, 2002).

Categorization might even be important enough to receive multiple expressions within the cognitive system. For example, when organisms must identify their mate or their own-group members, categorization should have a particularizing emphasis. Research has shown that something like individuated exemplar memory sometimes underlies categorization (e.g., Nosofsky, 1987; Medin and Schwanenflugel, 1981; Smith and Minda, 1998). In contrast, when organisms must respond equivalently to whole classes of objects (e.g., a prey species), categorization should have a generalizing emphasis. Research has also shown that something like general rules or abstractions sometimes underlies categorization (Ashby and Maddox, 2005; Aydin and Pearce, 1994; Jitsumori, 1996; Homa et al., 1981; Knowlton and Squire, 1993; Smith et al., 2008; Reber et al., 1998; Reed, 1972; von Fersen and Lea, 1990; White et al., 1993).

Moreover, research has begun to document the tradeoffs among different representational systems in categorization. For example, different processes control categorization early and late in learning (Cook and Smith, 2006; Reed, 1978; Smith et al., 2010b; Wasserman et al., 1988), when categories have small or large exemplar-set sizes (Blair and Homa, 2003; Homa et al., 1981; Katz et al., 2002; Minda and Smith, 2001; Wright and Katz, 2006), when categories are coherent or incoherent perceptually (Blair and Homa, 2003; Smith et al., 1997), and when the categorization rule is easy or difficult to verbalize (Ashby and Maddox, 2005).

Consequently, a multiple-systems theoretical perspective has become an important part of the human categorization literature (Ashby and Ell, 2001; Ashby et al., 1998; Ashby and Valentin, 2005; Cook and Smith, 2006; Erickson and Kruschke, 1998; Homa et al., 1981; Minda and Smith, 2001, Rosseel, 2002; Smith and Minda, 1998), based on the idea that organisms have multiple categorization utilities that learn different statistical aspects of the environment. The multiple-systems perspective has profoundly enriched the human categorization literature.

Little is known of the phylogenetic roots of humans' multiple-system capacity for category learning—its evolutionary origins, its phylogenetic breadth and depth, and its cognitive affordances that differentiate human cognition from that of other species. Introducing these issues to readers is the overarching goal of our article. By doing so, we hope to foster a dialog among cognitive, neuroscience, and comparative researchers of category learning. We believe it is fruitful to compare humans' and animals' categorization competencies and limitations and to correlate these with the differential development across species of the brain systems that serve category learning. We also believe it is a deficiency in these allied

disciplines that there continues to be so little cross-talk between human and animal studies (Ashby and Maddox, 2005).

2. Implicit and Explicit Systems of Categorization

In the multiple-systems literature, a core distinction is made between implicit and explicit utilities serving categorization. The implicit utility appreciates stimuli using broad, diffuse, attentional processes that encompass multiple stimulus features in parallel. It learns by slowly associating behavioral responses to whole (unanalyzed) stimulus configurations. Participants lack conscious access to the reasons for their behavioral responses following implicit category learning, and they cannot declare their solutions to category problems to others.

The explicit utility appreciates stimuli using narrow, focused attentional processes that single out individual stimulus features. It learns by testing hypotheses about stimulus dimensions that might be relevant to the category problem. It relies on working memory and executive attention to test and replace hypotheses. It provides conscious access to and declarative reports of its solutions to category problems. Many have granted explicit rules an important role in human categorization (Ahn and Medin, 1992; Ashby and Ell, 2001; Erickson and Kruschke, 1998; Feldman, 2000; Medin et al., 1987; Nosofsky et al., 1994; Regehr and Brooks, 1995; Shepard et al., 1961).

Brooks (1978) first made the implicit-explicit distinction during his debate with Reber (1967) about unconscious cognition. Brooks found that unintentional category learning—fostered by incidental, mere exposure to category members—was nonanalytic and nondeclarative. However, intentional category learning—fostered by explicit instructions to participants to learn the nature of the categories—was analytic and rule-based. Kemler Nelson (1984) supported Brooks's distinction using an elegant paradigm in which categories were learnable by either holistic, unanalyzed family resemblance or by single-dimensional rules. Incidental learners learned by overall family resemblance; deliberate learners learned by dimensional rules. Love (2002) found that incidental learning conditions selectively impaired rule-based category learning. Waldron and Ashby (2001) showed that a cognitive load that competed for working-memory resources selectively disrupted rule-based category learning. Maddox and Ashby (2004) contributed a seminal review in this area, in which they described many of the implicit-explicit dissociations in humans' category learning. In humans, the implicit-explicit framework is well established. The framework extends to the domain of clinical psychology. For example, Smith et al. (1993) showed that depression spared multi-dimensional, family-resemblance category learning while severely disrupting rule-based category learning. Depression saps the deliberate commitment of working-memory resources to rule-based category-learning problems that depend upon them. The framework also extends to explain the strengths and weaknesses in category learning of different neuropsychological patient populations (Ashby et al. 2003; Schnyer et al., 2009).

The implicit-explicit distinction also draws on research and theory in cognitive development. Research using Garner's (e.g., 1974) classification tasks showed that young children, impulsive children, and children with mental retardation dimensionalize their perceptual worlds less strongly than adults do. They appreciate stimuli more holistically. They group items more often based on unanalyzed, multidimensional similarity, and less often by a single, sharply attended feature that all the stimuli share. Formally, they treat separable dimensions (potentially decomposable by selective attention) as more integral or configural (not attentionally separated). They produce a less dimensionalized, more holistic metric of psychological similarity (Kemler, 1982a,b; Shepp et al., 1980; Smith and Kemler Nelson, 1984, 1988; Ward, 1983). The organizing theme in this literature was that those

populations—lacking the mature complement of rule-based and analytic-dimensional cognitive utilities—were reliant on an implicit, immature mode of nonanalytic cognition. This theme has a strong resonance as one considers across species the evolutionary emergence of analytic-dimensional systems of categorization.

Ashby, Maddox, and their colleagues placed the implicit-explicit distinction into a cognitive-neuroscience framework—the COVIS (Competition between Verbal and Implicit Systems) theory of category learning (Ashby et al., 1998; Maddox and Ashby, 2004; Ashby and Waldron, 1999). COVIS describes an implicit, nonanalytic categorization system that relies on the striatum and is based on conditioning-like mechanisms—that is, the reinforcement-mediated strengthening of dopamine-related synapses (Ashby et al., 2007). It describes an explicit, analytic categorization system that relies on the anterior cingulate gyrus, the prefrontal cortex, the head of the caudate nucleus, and medial temporal-lobe structures that also serve declarative memory. The explicit system seems to engage the same neural complex that affords the executive control of attention (Rossi et al., 2009). This article explores the phylogenetic breadth and depth of this division of labor between implicit and explicit systems of categorization.

3. An Illustrative Methodology

We describe evidence from four species that was produced over many experiments in independent articles (Smith et al., 2010a, 2011a, 2012). Collectively, the results document the evolutionary emergence of dimensional-analytic categorization within the line of the primates.

The experiments used rule-based (RB) and information-integration (II) category tasks, like those illustrated in Figure 1. In the top panel of Figure 1, the vertical category boundary denotes that only X-axis variation carries valid information about category membership. The participant must discover this dimensional rule (Category A: $X < 50$; Category B: $X > 50$) based on successive presentations of single stimuli, with feedback given following each response. The top panel is an example of an RB task because the category bound can be discovered via logical reasoning and hypothesis testing and an analytic approach to the dimensional structure of the stimuli. The informative stimulus dimension should be attended sharply and selectively. The non-informative stimulus dimension should be completely ignored as it varies equivalently over its whole range within both categories.

In contrast, in the II categorization task illustrated in Figure 1's lower panel, the diagonal category boundary indicates that both stimulus dimensions carry partially valid category information. The participant must learn the dimensional-integration principle that allows correct category assignment, once again based on the presentation of single stimuli with feedback. Now one should not ignore either dimension. Now attention must broaden to encompass both aspects of each stimulus. Accuracy can be maximized only if information from both stimulus dimensions is integrated into the category decision. There is no simple rule by which to verbally describe this category boundary. Nor is there any gain from treating the stimulus dimensions separably and analytically. One could fare just as well in the II task by approaching stimuli holistically and configurally and learning what behavioral response is correct for them.

In the data sets summarized here, the stimuli were sine-wave gratings that varied on two dimensions: bar frequency (the spatial frequency of the disks' internal black-white striping pattern) and bar orientation (the tilt of the disks' internal striping pattern). Category exemplars were created using the randomization technique developed by Ashby and Gott (1988). Categories were defined by bivariate normal distributions along the two stimulus dimensions, within which each stimulus dimension ranged along a normalized 0-to-100

scale. In the RB task (Figure 1, top), Category A and B stimuli would have the same Dimension Y mean, but a contrasting Dimension X mean. A larger stimulus variance along dimension Y creates the elliptical shapes of the categories' exemplar clouds. The absence of any XY covariance ensures that the exemplar clouds orient vertically. In the II task, Category A and B stimuli would have contrasting Dimension X and Dimension Y means. In this case, a substantial positive XY covariance would be used to ensure that the category ellipses slant up the major diagonal of the stimulus space.

Each stimulus was created by drawing a random sample (x,y) from the Category A or Category B distribution. This process was repeated until the full set of Category A and Category B exemplars had been generated, with slight adjustments made to the exemplar sets in the end so that their sample means and sample covariance matched the desired population values for the two categories in the task. In a typical experiment, there could be up to 300 exemplars in each category of each task. A few of these are illustrated in Figure 1. Finally, a linear transformation was applied to each stimulus coordinate-pair to map its values from the original 0-to-100 scale to a space representing actual values of spatial frequency (the number of light-dark cycles per degree of visual angle) and orientation (the tilt of the light-dark bands expressed in radians) used in the experiment. For example, in Smith et al. (2010a), these mappings were: Spatial Frequency = $1.0 + x/30.0$; Orientation = $y \times \pi/200 + \pi/9$.

It is important to note that RB and II tasks like those shown in Figure 1 are matched for many important aspects of category structure, including category size, within-category exemplar similarity, and between-category exemplar separation. In a perceptual space composed of dimensions of about equal salience, the two tasks are also matched for the *a priori* perceptual difficulty of the categorization problem. In fact, the two category structures are essentially identical, except that one structure is rotated 45° through stimulus space. In a perceptual space composed of truly integral dimensions (e.g., the color dimensions of saturation and brightness, in which attentional processes cannot selectively target one dimension or the other), the two category structures would be precisely identical in every respect from the perspective of the perceiver, because there would be no privileged dimensional axes, and thus neither category task would be unidimensional or rule-based. Thus, in many senses, these two tasks serve as mutual controls. They differ only in the RB-II aspect that is crucial to the theoretical issues surrounding implicit-explicit categorization and crucial to the present cross-species comparisons.

The RB-II dissociative framework has the potential to make an elegant contribution to research across species. By rotating the dimensional axis of category tasks, from II to RB, one can ask whether the cognitive systems of different species are dimensionally polarized. If so, then the dimensional task orientation—the RB task—will admit strong and rapid learning, just as a polarizing filter will strongly admit light when it finds the axis of the light's polarization. If the cognitive system of the species is not dimensionally polarized, both II and RB tasks will be learned to the same level at the same speed. This discovery can be made regarding any species that can successfully perform in behavioral discrimination tasks.

4. Humans (*Homo sapiens*)

4.1. Method

Illustrating this dissociative methodology, Smith et al. (2010a) gave sixty humans the two-dimensional RB and II category tasks illustrated in Figure 1. Participants were told that they should decide whether each striped circle belonged to Category A or B. They were motivated by the prospect of cash prizes to be awarded to those who earned points most

efficiently by classifying the disks correctly. Humans received the RB and II tasks in counterbalanced order (RB-II or II-RB). Within each session, participants completed 600 trials that represented one random permutation of 300 Category A and 300 Category B stimuli. Each trial consisted of one disk presented in the center-top of a computer screen against a gray background. The response icons (A and B) were located on the screen's lower-left and lower-right. Humans responded by pressing keyboard keys, labeled and spatially positioned to correspond to the A or B on the screen. Humans received points for correct responses. They lost points for incorrect responses and incurred a 3-second penalty delay. The screen included a scorecard that presented their increasing (or decreasing) point total.

4.2. Accuracy-based results

Humans' proportion correct by 10-trial block is shown in Figure 2. Clearly, humans learned the RB task more quickly and to higher levels. They were .958 and .795 correct overall on the RB and II tasks, respectively, an overall performance advantage of .163. Over their last 100 trials, they showed an RB performance advantage of .140 (.968 vs. .828). This advantage characterized the terminal performance levels within both RB-II and II-RB task orders. Nonetheless, one sees that there is a period of stimulus acclimation and general domain learning that characterizes performance in the first task (RB or II) that an organism addresses. This acclimation period will also appear in the results from other species.

4.3. Model-based results

Formal models provide another analytic approach for understanding humans' categorization decision boundaries. For example, we can fit a rule-based model to ascertain whether humans really do create a vertical decision boundary in the RB task by attending only to variation along the spatial-frequency dimension and separating stimuli on that basis alone. The outcome of the modeling is to specify the vertical line drawn through the stimulus space that would best partition the participant's Category A responses from his or her Category B responses. One can also measure how accurate and complete that best partition is—that is, how good an explanation of the participant's categorization performance the model provides. In effect, the modeling examines whether humans' categorization system in the RB task is truly dimensionally polarized.

A rule-based model fit best the RB performance of 57 of 60 participants, indicating that their decision boundaries were strictly vertical. The three remaining humans were fit best by decision bounds that were nearly vertical. Moreover, these three participants performed essentially as well (93.5% correct) as did the participants whose decision boundaries were modeled as strictly vertical (95.9% correct), confirming that the categorization strategies of the two groups were essentially identical. Humans are strongly dimensionally polarized when facing RB tasks. They have a strong tendency to learn RB tasks by finding something close to the optimal decision bound that is aligned with the dimensional structure of the stimulus space and that essentially constitutes a unidimensional category rule grounded by sharply selective attention.

We can also fit an information-integration model to ascertain whether humans in the II task create a sloping decision boundary, indicating that they are successfully integrating stimulus information over both dimensions. Here the outcome of the modeling is to specify the line—*of any slope and intercept*—drawn through the stimulus space that would best partition the participant's Category A responses from his or her Category B responses.

An information-integration model fit best the II performance of 51 of 60 participants. This confirms that many humans can and do—when necessary because the task's structure makes

rule-based strategies insufficient and unworkable—adopt an information-integration strategy by which they broaden out attention and combine the partially valid category information offered by two stimulus dimensions.

However, some participants' data in the II task were still best fit by the rule-based model, indicating that their best-fitting decision bounds were strictly vertical and that their attention was allocated exclusively toward one stimulus dimension. This strategy did not serve these participants well. They performed much more poorly than their peers (.695 correct vs. .815 correct). These participants showed humans' tendency to sometimes choose dimensionally aligned, rule-based category-learning strategies even for tasks that are not actually structured according to unidimensional category rules. For interested readers, the Appendix gives more details on typical model-fitting procedures in this area.

4.4. Summary

Thus, humans show distinct behavioral differences in learning RB and II category tasks (review in Ashby and Maddox, 2005). They strongly dimensionalize these stimuli. They solve RB category tasks quickly through explicit-reasoning and hypothesis-testing processes. They declare verbally their solution. In contrast, they learn II category tasks slowly. They integrate the dimensions poorly and with difficulty because they perceive them so separably and uncommensurately. They cannot verbally describe their II task solutions.

These results raise many cross-species questions. Is the multiple-system, implicit-explicit organization uniquely human? Is the explicit system dependent on language and verbal rules, or on symbolic-logical mental representations that could be language independent and that might be possessed by animals as well as humans? Are there brain regions or kinds of brain organization that are particularly well-organized for the rule-based and hypothesis-testing processes of RB category learning? Does this mean that some species—because they do not have that brain organization—will not show the psychological privilege and preference toward RB tasks that humans clearly show? What was the phylogenetic origin of humans' multiple category systems during cognitive evolution? What is the phylogenetic depth of explicit, rule-based categorization in particular? What does the phylogenetic map of the multiple-systems organization look like, and what is the phylogenetic breadth of explicit categorization in particular? Is explicit categorization a human thing, an ape thing, a primate thing, a mammal thing, a vertebrate thing?

The matched and diagnostic RB and II tasks are well suited for addressing these questions. These tasks allow the comparison of rule-based and nonanalytic categorization within a carefully controlled empirical framework. So now we can go on to ask: if human minds are dimensionally polarized, then what about the minds of other species?

5. Rhesus Macaques (*Macaca mulatta*)

5.1. Introduction

We chose rhesus macaques—an Old World monkey species—as a test species to begin answering questions about the phylogenetic breadth and depth of privileged dimensional categorization. We approached this investigation with some skepticism. Macaques' capacity for explicit cognitive processing is not a salient feature of their overall cognitive adaptation. They have proportionally smaller frontal cortices (Semendeferi et al., 2002). They are compromised relative to humans on frontal tasks that offer response competition or require response inhibition (Stroop tasks, flanker tasks, etc.—Roberts, 1996; Washburn, 1994). Therefore, it was a reasonable hypothesis that they might have only a rudimentary explicit category-learning system.

Supporting this hypothesis, Smith et al. (2011b) gave macaques rule-based XOR (exclusive-or) category problems. (In an XOR task, Category A stimuli have either none or both of the two critical attributes; Category B stimuli have exactly one of the two critical attributes.) Macaques learned these tasks very slowly, accruing hundreds of errors as they reached terminal performance levels of only about .750. Now it is true that the XOR task requires the derivation of a two-dimensional rule that is more complex than the one-dimensional rules explored within the RB-II theoretical framework. However, Smith et al. (2004) showed that macaques learned even one-dimensional RB categories relatively slowly, over hundreds of trials, and with none of the sudden realizations and qualitative performance improvements that humans show upon discovering the category rule. Thus, it remained an open question whether macaques would bring to RB category tasks some preference or privilege toward dimensional-analytic categorization. Remember: if they do not, the RB and II tasks will be learned equally well and equally quickly, because the tasks are perfectly matched on every aspect of category structure and difficulty, unless the organism can apply dimensional attention and rule-based categorization to the RB task.

5.2. Method

Smith et al. (2010a) gave six macaques RB and II tasks like those that have been described. The macaques performed these tasks in counterbalanced order (RB-II; II-RB). They had been trained to respond to computer-graphic stimuli by manipulating a joystick that controlled a cursor. They were tested in their home cages at the Language Research Center of Georgia State University, with *ad lib* access to the test apparatus, working or resting as they chose during long sessions. They were neither food deprived nor weight reduced for the purposes of testing and they had continuous access to water.

Each trial began with a black square presented in the same position as the to-be-categorized stimulus. Animals moved the cursor to touch the square as a trial-start response, indicating their readiness to perform. The black square released to the disk and the two response icons were illuminated. The macaques received a food pellet for correct responses. They received a 20 s, trial-less timeout period for incorrect responses. Stimuli were presented in random permutations of the 300 Category A and 300 Category B stimuli available for a task.

5.3. Accuracy-based results

Macaques' proportion correct by 100-trial block is shown in Figure 3. In comparing the performance of macaques (Figure 3) and humans (Figure 2), remember the 10-fold difference in trial-block length and in total trials on task. Like humans, macaques clearly learned the RB task more quickly and to higher levels than the II task. They were .838 and .711 correct overall on the RB and II tasks, respectively, an overall performance advantage of .127. Over their last 1,000 trials, they showed an RB performance advantage of .126 (.906 vs. .780). This advantage characterized the terminal performance levels within both RB-II and II-RB task orders. In Figure 3A, the RB advantage was .084 over the last 1,000 trials, even though when they performed the RB task first the macaques were dealing with all of their general domain learning with the stimulus set. Despite that early period of acclimation to the stimuli, macaques improved to a very high, advantaged performance level late in the RB task. In Figure 3B, the RB advantage over the last 1,000 trials was .168.

The macaques' sharp preference for dimensionally focused tasks also revealed itself early in performance. Macaques were .915 correct on their first 1,000 trials when they completed the RB task as the second of two tasks. They were .654 in the first 1,000 trials when they completed the II task as the second of two tasks—a .261 performance disadvantage. Their appreciation of the RB task's dimensional structure in their second task was essentially

instantaneous, demonstrating in another way the privilege of dimensional analysis within their category-learning system.

Indeed, Figure 3 expresses this privilege in many ways. In Figure 3A, the RB1 task—terminally performed at very high levels—was replaced by the II2 task. Performance fell off drastically, and never recovered, giving every indication that the II task did not fit comfortably these macaques' category-learning systems. In Figure 3B, the II1 task—performed terminally at low levels—was replaced by the RB2 task. Performance improved instantaneously and immediately rose to very high levels, to levels essentially as high as our macaques ever show, giving every indication that the RB task fit very comfortably with these macaques' category-learning systems.

5.4. Model-based results

This psychological privilege was also revealed through modeling analyses. We fit the rule-based and information-integration models to each macaque's data from their last 1,000-trial block. The rule-based model fit best the RB performance of 4 of 6 subjects. Two macaques were best fit by an information-integration model, indicating that their best-fitting decision bounds were not strictly vertical. However, those bounds were nearly vertical. In actuality, all 6 macaques showed sharply focused selective attention and dimensional learning in the RB task.

This analytic strategy was clearly reflected within the II task as well. One macaque in the II task was best fit by a rule-based model, indicating that his best-fitting decision bound was rule-based and that his attention was allocated exclusively to one dimension. Three other macaques adopted decision boundaries that were essentially rule-based, though their data were fit slightly better by the information-integration model because their boundaries were not precisely vertical. Thus, the majority of the macaques showed a strong dimensional focus even in the II task that did nothing to encourage that strategy and that even punished that strategy by reducing the rate of correct responses and the ongoing rate of reinforcement. Macaques' category-learning system is dimensionally polarized similarly to humans' category-learning system, though one must bear in mind that macaques' system does not learn categories nearly as rapidly.

5.5. Summary

Macaques also showed distinctive behavioral differences in learning RB and II category tasks. They strongly dimensionalized the stimuli. They learned RB tasks faster and to higher terminal performance levels. In contrast, they learned II tasks slowly to lower levels, and, even here, they showed some tendency to adopt rule-based strategies that were highly non-optimal. These results suggest answers to several of the cross-species questions raised earlier. For example, it clearly is not the case that language is a necessary condition for the psychological privilege toward rules and dimensional analysis to emerge. In early formulations of multiple-system theories, from Shepard et al. (1961) to Ashby et al. (1998), theorists closely linked explicit categorization and category rules with verbal hypotheses and descriptions. The macaque results show that this link is not essential. There must be other ways for dimensional hypotheses to be represented in mind or expressed in cognition, perhaps as non-verbal, propositional proto-rules, or cortical loops of sustained activity, and so forth. However, humans use rules with great agility, and they learn RB tasks much faster than macaques. So, it is still possible that language and verbal hypotheses are an adaptive vehicle for holding rule-based hypotheses and for referring to them during categorization. Language may be able to crystallize the rule-based processes of categorization and accelerate category learning in that way. Of course the results also show that the privilege toward dimensional analysis and category rules is not a uniquely human thing. It extends

beyond humans, at least to some extent to other species in the order *Primates*. This implies that rule-based categorization had some earlier evolutionary origin than with the hominids, and it raises the questions of when that dimensionally analytic system of categorization emerged, and why it was adaptive.

6. Capuchin Monkeys (*Cebus apella*)

6.1. Introduction

Macaques are Old World Primates—anthropoid, cattarehine primates that in a sense represent or lie on the main sequence of primate-ape-hominid evolution. In addition, macaques are notoriously flexible, adaptive, opportunistic, and successful primates. They have the widest geographic range of any nonhuman primate. They occupy diverse ecologies. They are full-spectrum omnivores. For these reasons, macaques cannot by themselves support the inference that dimensionally analytic categorization is broadly privileged within the primate order.

Therefore, Smith et al. (2012) extended the survey of the primates in this domain by testing a New World primate—the capuchin monkey (*Cebus apella*). The New World (Platyrrhine) primates separated from the Old World primates about 40 million years ago. They represent another major branch of the primate family tree. They provide a second crucial data point in determining whether primates generally respond to dimensional, rule-based category tasks with preference and psychological privilege.

Capuchins themselves are adaptive and flexible learners in many tasks—to the point that some refer to them as the poor-person's chimpanzee. They are especially noted for their use of tools in the laboratory and in the wild, and for their general problem-solving abilities (D'Amato and Colombo, 1989; Evans and Westergaard, 2006; Flemming, 2011; Judge et al., 2005; Kennedy and Fragaszy, 2008; McGonigle et al., 2003; Wright and Katz, 2006). On the other hand, recent research from several independent laboratories has suggested that capuchins lack a capacity for metacognition, a capacity likely to be allied to executive attention and explicit cognition (Basile et al., 2008; Beran and Smith, 2011; Beran et al., 2009; Paukner et al., 2006). Therefore, for capuchins, too, it was a reasonable hypothesis that they might have only a rudimentary explicit category-learning system.

6.2. Method

Smith et al. (2012) gave four capuchins RB and II tasks in counterbalanced order (RB-II or II-RB). The capuchins had been trained to respond to computer-graphic stimuli by manipulating a joystick that controlled a cursor (Evans et al., 2008). They were tested under the conditions that have already been described for the macaques.

Each trial began with a black square presented in the same position as the to-be-categorized stimulus. Capuchins moved the cursor to touch the square as a trial-start response, indicating their readiness to perform. The black square released to the disk and the two response icons were illuminated. The capuchins received a food pellet for correct responses. They received a 20 s, trial-less timeout period for incorrect responses. Stimuli were presented in random permutations of the 300 Category A and 300 Category B stimuli available for a task.

In early testing, we found that capuchins strongly benefited from a method based on correction trials. By this method, time-out periods for errors were followed by correction trials in which the monkeys were presented the same stimulus from the previous trial, but their responses were not followed by reward or penalty. Correct responses for correction trials were followed by the next regular trial. Incorrect responses for correction trials were followed by a repetition of the correction trial. Only experimental trials (not correction

trials) were analyzed. Given the smaller number of animals tested, we present results for each individual.

6.3. Results: Logan (RB-II)

Figure 4A shows the results from Logan's RB and II tasks. Logan, despite needing to acclimate to the new stimulus domain, showed a strong RB acquisition. Over his last 2,000 RB trials, Logan was .914 correct. In contrast, over the last 2,000 II trials, Logan was .808 correct, a .106 performance disadvantage.

Logan's performance was modeled as described above. He placed his RB decision boundary optimally, choosing the vertical boundary that best differentiated the Category A and B stimulus classes. However, his II decision boundary was distinctively non-optimal. Logan kept a nearly vertical decision boundary. He continued to pursue a dimensionalized task strategy to the detriment of his II performance. This confirms in another way the salience that dimensional foci have for capuchin monkeys during categorization.

To rule out the uninteresting hypothesis that one salient dimension controlled Logan's perception, we gave him a third task, the RB task with a horizontal optimal decision boundary, so that now, the orientation of the bars in the disks were solely relevant. The elliptical stimulus ellipses in Figure 1A, if rotated 90° counterclockwise about the center of the stimulus space, would then illustrate the horizontal RB task. Now, Logan showed a flexible shift in his attention to emphasize the orientation dimension. Over his last 2,000 trials, he performed at 92.9%. Moreover, he now placed his RB decision boundary optimally—horizontally—through the stimulus space. Thus, Logan easily and flexibly moved his decisional boundary into the next dimensional polarity. What he did not accomplish well was to place his decisional boundary into a diagonal, information-integration polarity. All his results are consistent with the preference and psychological privilege that capuchin monkeys bring selectively to RB tasks.

6.4. Lily (RB-II)

Figure 4B shows the results from Lily's RB and II tasks. Despite needing to acclimate herself to the stimulus domain, she showed a strong RB acquisition, with performance levels that soon rose above 85%. Over her last trials in the RB task, Lily was .854 correct. In contrast, over her last II trials, she was .782 correct, a .072 performance disadvantage compared to the RB task.

Lily's modeling results were nearly identical to those of Logan. She placed her RB decision boundary optimally, using essentially the vertical decision boundary that best differentiated the Category A and B stimulus classes. She was definitely not decisionally optimal in her II task. Like Logan, she kept her decision boundary much too vertical to the detriment of her II performance.

6.5. Liam (II-RB)

Figure 4C shows the results from Liam's II and RB tasks. The II task was Liam's first acquisition. His II acquisition was very weak. Over the last 2,000 trials in the II task, Liam was .629 correct. In sharp contrast, Liam's appreciation of his second, RB task appeared to be almost immediate, and he learned to high levels by the RB task's end. Over the last 2,000 trials in the RB task, Liam was .894 correct, a .265 performance advantage compared to the II task.

Liam's performance was modeled using the procedures already described. Liam placed his II decision bound vertically, confirming that he performed the task as a rule-based task even

though it was not so constituted. This vertical decision boundary illustrates again the psychological privilege with which capuchin monkeys apply rule-based frameworks to category tasks. Eventually this near-vertical decision boundary came to serve Liam well, when he transitioned into his second, RB task.

6.6. Nala (II-RB)

Nala was the weakest learner of the four capuchins. Figure 4D shows her II and RB results. The II task was Nala's first acquisition. Her II acquisition was extremely weak. Over the last 2,000 trials in the II task, Nala was .528 correct. In contrast, Nala did progress with her RB acquisition. Over the last 2,000 RB trials, she was .686 correct, a .158 performance advantage compared to the II task.

Nala's performance was modeled using the procedures already described. Because Nala learned nothing in her II (first) acquisition, no decision boundary could be estimated. In her RB (second) acquisition, Nala did place her decision boundary vertically, appropriately to the structure of that task. Even though Nala was not the strongest performer, for her, too, the RB task was more psychologically approachable.

We gave Nala a second opportunity to master the II category structure. In her third task, the Category A and Category B stimulus ellipses straddled the minor diagonal of the stimulus space and there was an optimal decisional boundary extending from 10 o'clock down to 4 o'clock in the stimulus space. The elliptical stimulus ellipses in Figure 1B, if rotated 90° counterclockwise about the center of the stimulus space, would then illustrate this negatively correlated or minor-diagonal II task. She performed generally above chance in this task, and at .705 correct over her last 2,000 trials. However, modeling revealed that she set a vertical decision boundary, treating the task as rule-based even though it was not so constituted. That Nala failed her first II task, succeeded with her RB task, and construed her second II task dimensionally all reflect the general conclusion that capuchin monkeys, like humans and rhesus macaques, approach RB tasks with psychological privilege and greater learning potential, and sometimes apply RB strategies even when these are not optimal or warranted.

6.7. Summary

All in all, capuchin monkeys appeared to be somewhat less sharp and sensitive learners than macaques, who in turn were less sharp and sensitive learners than humans. Nonetheless, capuchins also learned RB tasks faster and to higher terminal performance levels. In contrast, they learned II tasks slowly to lower levels, and, even here, they showed some tendency to adopt rule-based strategies that were highly non-optimal. These results suggest that the tendency to approach RB category tasks with psychological preference and privilege extends broadly across the taxonomic tree of the primates, and perhaps therefore far back temporally into the earlier stages of the evolution of the primates, or perhaps beyond.

7. Pigeons (*Columba livia*)

7.1. Introduction

At this point, one might suppose that the privilege of dimensional categorization is distributed widely or even universally across vertebrate species. One wonders if there might be something inherent to the processing of sensory signals that forces a preferential psychological response to one-dimensional category regularities. This would be an important theoretical conclusion were it true, because it could suggest the universality of dimensional separability, stimulus analysis, and category rules. Thus, this possibility should be evaluated as broadly as possible. An important strength of the RB-II dissociative

technique is that it can be broadly applied to any vertebrate species that is capable of participating in structured experimental testing.

Accordingly, laboratories in New Zealand (NZ-Canterbury) and the United States (USA-Tufts) did evaluate this theoretical possibility by giving pigeons II and RB category tasks instantiated using the same sine-wave gratings varying in bar frequency and tilt. Upon discovering this convergence across laboratories, the independent investigations were combined (Smith et al., 2011a).

7.2. Method

Naïve pigeons (6-NZ; 11-USA), maintained at 80-85% of free-feeding weight, were tested in a two-alternative symbolic matching-to-sample choice procedure using touchscreen-equipped LCD monitors. To-be-categorized stimuli were presented through a window in each chamber's front panel. These stimuli were circular sine-wave gratings varying in bar spatial frequency and orientation as already described. Choice stimuli were located to each side of the stimulus. These choice stimuli were illuminated following observing responses to the to-be-categorized stimulus. Response assignments were counterbalanced across birds and tasks. A single response to the correct or incorrect choice produced food reinforcement or a timeout, respectively, followed by an inter-trial interval. A central food hopper in the front panel delivered the grain reinforcements for correct choices. White noise masked external sounds. Daily sessions contained approximately equal numbers of samples from each category that were selected randomly from the available pool. Training continued until each bird's performance reached criterion with 4 non-consecutive sessions $\geq .800$ correct (NZ) or with 6 non-consecutive sessions $\geq .850$ (USA).

Though structured similarly, the NZ-USA projects had many small procedural differences from one another (e.g., size of stimuli, number of stimuli per category, length of intertrial interval, and so forth; details in Table 1, Smith et al., 2011a). These procedural differences resulted from the independent planning and executing of the separate projects. The strongly converging results that were obtained—despite these differences—underscore the robustness of the results and strengthen the theoretical conclusion that the pigeon data recommend.

7.3. Accuracy-based results

Three NZ pigeons and six USA pigeons received the RB task. Two NZ pigeons experienced RB learning difficulty and one of these birds failed to learn. These results already suggest the non-privileged status of RB tasks for pigeons. On average, and excluding the RB non-learner, pigeons reached criterion in the RB task after 33.2 sessions. Three NZ pigeons and five USA pigeons received the II task. On average, pigeons reached criterion in the II task after 32.9 sessions. Even excluding the one RB non-learner, there was no RB advantage in the speed of learning.

Over all sessions, RB birds and II birds were .661 and .682 correct, respectively, again with the RB non-learner excluded. Over their last 10 sessions, RB birds and II birds were .829 and .820 correct, respectively, again with the RB non-learner excluded. There is no evidence of an RB performance advantage in these comparisons. Of course excluding the RB non-learner makes these analyses conservative.

Figure 5A shows performance by session from the onset of learning for the eight RB-learning pigeons and the eight II-learning pigeons. There is no evidence of an RB performance advantage in these forward learning curves. A problem with these curves is that the pigeons were removed from the task upon reaching criterion, leaving the weaker performing birds to be graphed alone in later sessions. This creates some waviness in the forward learning curves. Accordingly, Figure 5B shows the performance of the birds by

session backward from the criterial block. These backward-learning curves align better the main acquisition epochs of the birds. (The RB non-learner was excluded from both graphs in Figure 5). There is still no evidence of an RB performance advantage in these backward learning curves. To the contrary, there is a very close equivalence between II and RB performance leading up to the criterial block, as though the pigeons were performing two category tasks of just the same character and learnability.

This conclusion about pigeons' categorization is not constrained by statistical power. There were essentially no RB-II differences in learning rates or levels, though relatively large numbers of birds were tested in two independent experiments. There is no suggestion that a larger sample of pigeons would have produced any RB performance advantage, much less one the size seen in primates. In contrast, primates' RB performance advantages are easily identifiable, within small samples or even individual learners. The conclusion about pigeons' categorization is also not constrained by particular methodological choices. There were many methodological differences between the NZ and USA procedures, yet nearly identical results were obtained.

7.4. Model-based results

The accuracy-based results support one inference about the decision strategies pigeons use. That is, one knows from the equivalent RB and II performance levels and learning speeds that pigeons do not bring a unitary rule-based system to these tasks. If they did, they would perform well on the RB task that fits the rule-based system but poorly on the II task that does not fit that system. This is not what Smith et al. (2011a) observed.

Formal modeling underscores this conclusion. Berg and Grace (2011) compared two- and one-dimensional models to individual pigeons' II data from the New Zealand project described in Smith et al. (2011a). The best-fitting decision bounds were diagonal in 11 of 12 cases when 900-trial II data sets were modeled. These diagonal bounds accounted for 88% of the pigeons' categorization responses, showing that the pigeons used their decision bounds efficiently. This diagonality also characterized the decision bounds of the pigeons tested in the USA (Tufts) project described in Smith et al. These diagonal bounds allowed pigeons to effectively partition the Category A and B stimulus distributions and reach terminal performance levels of about 90% correct (Figures 5A,B). Pigeons do not default to vertical or horizontal decision bounds in performing II tasks. They perform adaptively according to diagonal decision bounds that imply information integration across dimensions.

These modeling results suggest a parsimonious alternative hypothesis: that pigeons bring a unitary nonanalytic category-learning system to II and RB tasks that is indifferent to the orientation or polarization of the category task within the stimulus space. The diagonal decision bounds confirm that pigeons have a well-developed nonanalytic system for category learning. However, this system would serve equally well the learning of II and RB tasks. The mechanics of conditioning and association—by which whole stimuli come to elicit adaptive behaviors—would not be different in the two tasks at all. Accordingly, this hypothesis also explains the equality in the terminal levels of performance for II and RB tasks and the equal speeds of learning. It also explains what primates and humans have added to categorization to show the different II-RB data patterns they do show.

An alternative hypothesis might be that pigeons have a strongly developed nonanalytic categorization utility that serves the II task, and an underdeveloped analytic categorization utility that serves the RB task. Then, the equal speeds and levels of learning would arise because the analytic system was underdeveloped by just the right amount to produce the precise performance equalities that we observe. This hypothesis is unparsimonious because it uses multiple systems unnecessarily to explain identical performance levels. It is

implausible because the precise match between nonanalytic robustness and dimensional weakness would be coincidental. Notice, too, that this hypothesis shares with the parsimonious hypothesis the crucial insight that pigeons are strikingly less dimensionally analytic in category-learning than are the nonhuman primates and humans.

8. General Discussion

8.1. Summary

The results reviewed here show the broad applicability of the RB-II task-dissociation framework. One can ask whether the cognitive system of any species is dimensionally polarized by rotating the dimensional axis of category tasks. If a cognitive system is not dimensionally polarized, II and RB tasks will be learned to the same level, at the same speed, and in the same nonanalytic manner. If dimensional polarization is present, a robust RB performance advantage will emerge, for then the RB task can receive the psychological privilege of dimensional analysis and rule-based decisional strategies. This framework may let comparative psychologists trace the evolutionary emergence of dimensional attention and rule-based cognition.

Here, exploring the potential of this framework across several species, humans, rhesus macaques, and capuchin monkeys participated in II and RB category tasks. All three species experienced more difficulty learning II tasks that required perceptual integration over two dimensions. Their learning in these tasks was slower and they reached lower terminal performance levels. In contrast, all three species appeared to dimensionalize the stimulus space, attended well to single dimensions, and learned RB category tasks faster and to higher terminal performance levels. Their cognitive systems were dimensionally polarized.

Remarkably, pigeon minds appeared not to preferentially appreciate one-dimensional task solutions or to use what one might call proto-rules. Pigeons showed no tendency to learn rules or to apply dimensional analysis in learning RB and II category tasks that served as mutual controls for one another. In sharp contrast to humans and broadly diverse primate species, pigeons showed complete indifference to the task's rotation in stimulus space, learning RB and II tasks equally quickly to the same level. Their cognitive systems were not dimensionally polarized.

8.2. Characterizing nonanalytic systems for categorization

Pigeons' indifference to the task's rotation in stimulus space is like humans' indifference to task rotations within non-separable stimulus spaces that defeat the analytic processes of selective attention (Foard and Kemler Nelson, 1984; L. B. Smith and Kemler Nelson, 1978). For example, with the color dimensions of saturation and brightness, humans can detect stimulus differences and make stimulus comparisons, but they do not do so using dimensional frameworks and attributions (Garner, 1974).

Pigeons' data pattern is also similar to humans' nonanalytic category learning that is probably supported by humans' implicit-striatal procedural-learning system (Ashby et al., 1998; Ashby and Ell, 2001, Maddox and Ashby, 2004). That system would not be affected by whether the category task is dimensionally aligned or not, and learning would proceed equivalently either way, because the gradual association of cortical inputs to behavioral outputs (i.e., categorization responses) would occur through the same mechanism and at the same rate in either case.

Pigeons' performance is also consistent with a cognitive organization by which they gradually associate behavioral responses to regions of perceptual space or to unanalyzed stimulus wholes, while withholding (or lacking the capacity for) stimulus analysis, selective

attention, and rule formation. This interpretation recalls Pearce's (1994) theory that some animals treat multi-dimensional stimuli as unitary, configural wholes. The nature of receptive fields in the perceptual system suggests that Pearce's suggestion about nonanalytic stimulus processing could be realized in the brain. Higher-order receptors could receive two-dimensional (spatial frequency-orientation) inputs, and could be adapted to maximally respond to some optimal combination of values along the two dimensions. Activation would degrade for less optimal stimulation, but the second-order unit would not need to have any appreciation of which dimensional input was non-optimal and by how much. It would only respond less actively to the non-optimal input. Pearce et al. (2008) demonstrated a striking failure of selective attention to dimensions by pigeons, leading them to question whether pigeons possess central attention-allocation processes. Their findings and interpretation converge strongly with the findings and interpretation in Smith et al. (2011a).

There might be inherent advantages to having a unitary category-learning system based in the nonanalytic integration of multiple dimensions. There could be a neural economy to a unitary system that would suit nervous systems that are constrained in size by the requirements for flight. Organisms could reduce strategy competition during category learning that arises from multiple systems engaging the same task, and avoid the adventitious rules that humans sometimes pursue during category learning (Jitsumori, 1993). A unitary, nonanalytic system might also be especially adept at learning complex or non-linear category-decision boundaries that would defeat a dimensionally aligned, rule-based system. And, if natural kinds and categories are often multidimensionally organized, with instances presenting category-relevant information along diverse and changing dimensions, then broad or configural attention would be adaptive for leaving the organism open in parallel to information from many potential channels, and adaptive for reducing the chance that attention would be misdirected away from crucial information. Finally, we point out that for many behavioral purposes, the dimensional provenance of signaling information does not matter. What matters is the resultant behavior, and whether it is elicited by one-dimensional or two-dimensional informational signals is beside the point of adaptation and survival.

All in all, one sees that there could be simplicity, parsimony, breadth, and power in a categorization system that only ever did one thing—associate behavioral responses to whole stimuli, without analyzing them featurally, aligning them dimensionally, or forming rules about them and their category membership. We therefore suggest that pigeons' category learning could illuminate a phylogenetically ancient associative categorization system that is widely distributed across the vertebrates and that pigeons, nonhuman primates, and humans share.

8.3. The emergence of analytic systems for categorization

In contrast to pigeons, the three primate species accorded substantial psychological privilege to dimensional rules. Therefore, to some extent, both capuchins and macaques demonstrated the use of rule-based categorization processes that are deemed in humans to be explicit, conscious, declarative, and reasoning/language-based. The results from these two species represent an important new continuity between primate and human cognition.

It is important to see that these results were not predetermined. RB and II tasks are carefully matched to one another in every aspect relating to the inherent perceptual difficulty of the categorization problem and the maximum proportion correct achievable by an ideal observer. The default expectation would be for equivalent performance between RB and II tasks.

Remember also that category learning is sometimes managed in humans (and probably in monkeys, too) by an implicit-striatal system that uses a form of procedural learning. It is an important point that this system could learn both RB and II tasks equally well. In this case, one would also predict equal RB and II performance. The implicit categorization system would not even know what rotation of a task in stimulus space it was encountering at any point, or whether that rotation was dimensionally aligned or not. Either way, it would simply associate responses to regions of perceptual space, no matter how those category regions bisected the stimulus space. We already have—in pigeons—a concrete example of a vertebrate species that appears to have only a unitary system for category learning that treats RB and II tasks equivalently. Pigeons actually demonstrate clearly that RB and II tasks are equally difficult intrinsically.

Another possibility is that macaques and capuchins might perceive multidimensional stimuli less separably and more integrally than humans (Foard and Kemler Nelson, 1984; Garner, 1974; Garner and Felfoldy, 1970; Handel and Imai, 1972; Lockhead, 1972). This would also leave the processes of categorization indifferent to the rotation of the task in perceptual space and to the dimensional alignment of the task's axes. There is also a concrete model for this—young human children sometimes perceive multidimensional stimulus combinations more integrally than adult humans do (Shepp and Swartz, 1976; Shepp et al., 1980; L. Smith and Kemler 1977, 1978; Smith and Kemler Nelson, 1984; Ward, 1983). Pearce's configural theory (Pearce, 1987, 1994) would also allow one to predict equivalent RB and II performance. That theory supposes that multi-dimensional stimulus compounds in their entirety—that is, not dimensionally analyzed—enter into associations with outcomes and responses.

We have also pointed out the potential advantages that might favor a unitary, nonanalytic categorization system. That system would grant the organism a cognitive economy, reduced strategy competition, freedom from maladaptive rules and misplaced attentional foci, a facility with non-linear category boundaries, and a facility with complexly varying aspects of family-resemblance-based natural categories.

For all the foregoing reasons, rhesus macaques and capuchin monkeys—even humans—might have been found to possess a unitary category-learning system that simply associated responses to stimuli, without overlaying axes, dimensions, and rules. But that is not what they show. They clearly have the overlay of axes, dimensions, and rules. Why?

This question brings us to the precipice of a just-so story. Therefore, we simply point out that the emergence of an explicit, analytic categorization utility would also potentially offer distinct advantages. It would allow for economical, quickly learned, easy to maintain, and easy-to-generalize category representations (i.e., rules). It would bring cognitive flexibility and attentional agility arising from dimensional analysis and selective attention. Perhaps most important, it would open up the possibilities for cognitive analysis, rules and inferences from that analysis, symbolic representations of dimensional hypotheses, and eventually even language.

The early emergence of this dimensionally analytic capability could have occurred—in fact, clearly did occur—in the absence of the verbal coding for analyzed dimensions and rules. This is an important theoretical point because there is an ongoing tendency in cognitive neuroscience to conflate the dimensional-rule pole of cognition with the verbal-declarative response modality. Nonetheless, it is possible that there are important interactions between explicit category rules and verbal coding. Verbal coding could augment the privilege of explicit rules in cognition, by facilitating their formulation or evaluation, or by facilitating their maintenance across trials. Conversely, and this could be an important point about

cognitive evolution, the pre-existing privilege of unidimensional attention and category rules could have generally promoted the development of the verbal coding and language communication of those rules. Therefore, the processing preference and privilege that developed for dimensional analysis and category rules may have been a premier adaptation that fostered cognitive evolution in the primate-hominid lineage.

8.4. Further directions

To date, the research on pigeons in this area is all there is on the class Aves. Pigeons do demonstrate that the psychological privilege accorded dimensional analysis and one-dimensional category rules is not a vertebrate-wide cognitive adaptation. However, we cannot claim that this privilege would be absent in all birds or in all non-primate vertebrates. There are bird families such as *Corvidae* (crows, jays, etc.) that are more cognitively sophisticated than pigeons (Emery, 2006; Emery and Clayton, 2004; Mackintosh et al., 1985; Wilson et al., 1985; Wimpenny et al., 2009). There are marine-mammal species (dolphins, sea lions, etc.) that may be cognitively sophisticated though they lie outside the order *Primates* (Reiss and Marino, 2001; Smith et al., 1995). So, it remains possible that explicit, rule-based cognition could arise generally as the last frost of intelligence that settles on the highest peaks of cognitive sophistication, including primates, marine mammals, and corvids. Research with these latter species would constructively augment the base of knowledge in this area, providing critical tests of the evolutionary breadth of explicit category learning.

If rule-based categorization is a primate invention, that would have one set of implications for considering the cognitive evolution of the primates. If rule-based categorization is a widely distributed, ultimate achievement of intelligent mind or reflective cognition, that would be interesting in a different way. Of course species outside the primates would face potential constraints on building systems for explicit, rule-based categorization because they would not be able to use the same brain systems that primates do for that building, and so the system might have to be organized in the brain in some other way.

The existing research, though we have sampled primate species fairly broadly, also cannot support the inference that dimensional polarization of categorization systems extends to all the primates, so that it might be judged to be an original primate invention. This would have to be concluded based on a fuller mapping of primate species, especially including the prosimians. It would be equally interesting no matter whether the prosimians showed the data pattern of dimensional polarization or not. It would either tend to cast back earlier our sense of the phylogenetic emergence of this capacity, or else it would restrict that capacity to the higher primates, just as other research has found important cognitive differences separating the prosimians and the anthropoid primate suborder (monkeys, apes, and humans —e.g., Rumbaugh & Pate, 1984).

Now, finally, we come to nonhuman primates in relation to humans. It is interesting to consider the elements of humans' rule-based categorization system that macaques and capuchins do or do not share. The human system is analytic, dimensionalizing, verbal, explicit, and conscious. The results show that macaques and monkeys share with humans the analytic and dimensional framework within which they grasped RB tasks with substantial privilege. So far, so good. However, monkeys are not verbal as humans are. They are using some form of dimensionally-analytic categorization that is not verbally grounded. Beyond that, though, our results certainly do not force the conclusion that monkeys hold their rules declaratively, fully explicitly, or in conscious awareness. Clearly, more research should be forthcoming to explore these possibilities and ground them empirically, by further dissociating explicit from implicit category learning in nonhuman primates.

For example, because the explicit system represents category information in working memory, it should be robust to delays in the feedback signal. In fact, several studies have shown that II category learning in humans is impaired if the feedback signal is delayed for even a few seconds, whereas RB learning is unaffected with delays as long as 10 seconds (Maddox et al., 2003; Maddox and Ing, 2005). Showing this dissociation in macaques or capuchins would provide further evidence that explicit and implicit category-learning systems in humans and monkeys are similar.

For another example, because rules need time and cognitive resources to be evaluated and adjusted based on feedback, RB learning but not II learning should be impaired if the amount of time to process the feedback signal is limited. This dissociation was confirmed in humans by Maddox et al., (2004). Showing this dissociation in nonhuman primates would suggest that they also process deliberately and cognitively the feedback given on training trials. It might indicate that they, like humans, are engaged in the hypothesis-testing and hypothesis-replacing processes that are the crucial components of explicit, rule-based categorization. In our view, the RB-II framework lays the groundwork for important future lines of research on animals' reflective minds and their capacities for declarative cognition.

8.5. Conclusion

The application of the RB-II dissociative framework across species is an example of the synergy that can arise among cognitive psychology, neuroscience, and comparative psychology. It is remarkable that this theoretical framework, born within human cognitive psychology and cognitive neuroscience, appears suddenly poised to open new empirical windows on the minds of many species. In return, those windows seem likely to illuminate the evolutionary roots and shoots of the stem categorization system from which that of humans and the primates emerged.

Acknowledgments

The preparation of this article was supported by Grant HD-060563, Grant 3P01HD038051-10S1 (ARRA administrative supplement), Grant P01 NS044393 from NINDS, and by support from the U.S. Army Research Office through the Institute for Collaborative Biotechnologies under grant W911NF-07-1-0072.

Appendix

This appendix summarizes the models referred to in the text and also describes the model-fitting procedures. For more details, see Maddox and Ashby (1993).

Rule-based model

The *rule-based model* assumes that the participant sets a decision criterion on one stimulus dimension (either bar frequency or orientation). The outcome of modeling is to specify the vertical or horizontal line drawn through the stimulus space that would best partition the participant's Category A responses from his or her Category B responses. This model has two parameters: a criterion value on the relevant dimension and a perceptual noise variance.

Information-integration model

The *information-integration model* assumes that the participant sets a linear decision bound that can have any slope and intercept. The outcome of modeling is to specify the line drawn through the stimulus space, of any slope and intercept, that would best partition the participant's Category A responses and Category B responses. This model had 3 parameters: the slope and intercept of the linear decision bound and a perceptual noise variance.

Model selection

The procedures for selecting the best-fitting model were as follows. Parameters were estimated using the method of maximum likelihood. That is, modeling evaluated which model would, with maximum likelihood, have created the distribution within the stimulus space of Category A and Category B responses that the participant actually produced. Then the *Bayesian Information Criterion* (Schwarz, 1978) determined model selection: *Bayesian Information Criterion* = $r \ln N - 2 \ln L$, where r is the number of free parameters, N is the sample size, and L is the likelihood of the model given the data.

References

- Ahn W, Medin DL. A two-stage model of category construction. *Cognitive Sci.* 1992; 16:81–121.
- Ashby FG, Alfonso-Reese LA, Turken AU, Waldron EM. A neuropsychological theory of multiple systems in category learning. *Psychol Rev.* 1998; 105:442–481. [PubMed: 9697427]
- Ashby FG, Ell SW. The neurobiology of human category learning. *Trends Cognitive Sci.* 2001; 5:204–210.
- Ashby FG, Ennis JM, Spiering BJ. A neurobiological theory of automaticity in perceptual categorization. *Psychol Rev.* 2007; 114:632–656. [PubMed: 17638499]
- Ashby FG, Gott RE. Decision rules in the perception and categorization of multidimensional stimuli. *J Exp Psychol Learn Mem Cogn.* 1988; 14:33–53. [PubMed: 2963894]
- Ashby FG, Maddox WT. Human category learning. *Annu Rev Psychol.* 2005; 56:149–178. [PubMed: 15709932]
- Ashby FG, Maddox WT. Human category learning 2.0. *Ann N Y Acad Sci.* 2011; 1224:147–161. [PubMed: 21182535]
- Ashby FG, Noble S, Filoteo JV, Waldron EM, Ell SW. Category learning deficits in Parkinson's disease. *Neuropsychology.* 2003; 17:115–124. [PubMed: 12597080]
- Ashby, FG.; Valentin, VV. Multiple systems of perceptual category learning: Theory and cognitive tests. In: Cohen, H.; Lefebvre, C., editors. *Handbook of Categorization in Cognitive Science.* Elsevier; New York USA: 2005. p. 547-572.
- Ashby FG, Waldron EM. The nature of implicit categorization. *Psychon Bull Rev.* 1999; 6:363–378. [PubMed: 12198775]
- Aydin A, Pearce JM. Prototype effects in categorization by pigeons. *J Exp Psychol: Anim Behav Process.* 1994; 20:264–277.
- Basile BM, Hampton RR, Suomi SJ, Murray EA. An assessment of memory awareness in tufted capuchin monkeys (*Cebus apella*). *Anim Cogn.* 2008; 12:169–180. [PubMed: 18712532]
- Beran MJ, Smith JD. Information seeking by rhesus monkeys (*Macaca mulatta*) and capuchin monkeys (*Cebus apella*). *Cognition.* 2011; 120:90–105. [PubMed: 21459372]
- Beran MJ, Smith JD, Coutinho MVC, Couchman JC, Boomer J. The psychological organization of “uncertainty” responses and “middle” responses: A dissociation in capuchin monkeys (*Cebus apella*). *J of Exp Psychol Anim Behav Process.* 2009; 35:371–381. [PubMed: 19594282]
- Berg ME, Grace RC. Categorization of multidimensional stimuli by pigeons. *J of Exp Anal Behav.* 2011; 95:305–332. [PubMed: 21547069]
- Blair M, Homa D. As easy to memorize as they are to classify: The 5-4 categories and the category advantage. *Mem Cogn.* 2003; 31:1293–1301.
- Brooks, LR. Nonanalytic concept formation and memory for instances. In: Rosch, E.; Lloyd, BB., editors. *Cognition and Categorization.* Erlbaum; Hillsdale, NJ USA: 1978. p. 169-211.
- Cook RG, Smith JD. Stages of abstraction and exemplar memorization in pigeons' category learning. *Psychol Sci.* 2006; 17:1059–1067. [PubMed: 17201788]
- D'Amato MR, Colombo M. Serial learning with wild card items by monkeys (*Cebus apella*): Implications for knowledge of ordinal position. *J Comp Psychol.* 1989; 103:252–161. [PubMed: 2776421]

- Emery N. Cognitive ornithology: the evolution of avian intelligence. *Phil Trans R Soc B*. 2006; 361:23–43. [PubMed: 16553307]
- Emery NJ, Clayton NS. The mentality of crows: Convergent evolution of intelligence in corvids and apes. *Science*. 2004; 306:1903–1907. [PubMed: 15591194]
- Erickson MA, Kruschke JK. Rules and exemplars in category learning. *J Exp Psychol Gen*. 1998; 127:107–140. [PubMed: 9622910]
- Evans TA, Beran MJ, Chan B, Klein ED, Menzel CR. An efficient computerized testing method for the capuchin monkey (*Cebus apella*): Adaptation of the LRC-CTS to a socially housed nonhuman primate species. *Behav Res Meth*. 2008; 40:590–596.
- Evans TA, Westergaard GC. Self-control and tool use in tufted capuchin monkeys (*Cebus apella*). *J Comp Psychol*. 2006; 120:163–166. [PubMed: 16719595]
- Feldman J. Minimization of Boolean complexity in human concept learning. *Nature*. 2000; 407:630–633. [PubMed: 11034211]
- Flemming TM. Conceptual thresholds for same and different in old- (*Macaca mulatta*) and new-world (*Cebus apella*) monkeys. *Behav Process*. 2011; 86:316–322.
- Foard CF, Kemler Nelson DG. Holistic and analytic modes of processing: The multiple determinants of perceptual analysis. *J Exp Psychol Gen*. 1984; 113:94–111. [PubMed: 6242409]
- Garner, WR. *The Processing of Information and Structure*. Erlbaum; Potomac, MD USA: 1974.
- Garner WR, Felfoldy FL. Integrality of stimulus dimensions in various types of information processing. *Cognitive Psychol*. 1970; 1:225–241.
- Handel S, Imai S. The free classification of analyzable and unanalyzable stimuli. *Percept Psychophys*. 1972; 12:108–116.
- Herrnstein RJ, Loveland DH, Cable C. Natural concepts in pigeons. *J Exp Psychol Anim Behav Process*. 1976; 2:285–301. [PubMed: 978139]
- Homa D, Sterling S, Trepel L. Limitations of exemplar-based generalization and the abstraction of categorical information. *J Exp Psychol Hum Learn*. 1981; 7:418–439.
- Jitsumori M. Category discrimination of artificial polymorphous stimuli based on feature learning. *J Exp Psychol, Anim Behav Process*. 1993; 19:244–254.
- Jitsumori, M. Discrimination of artificial polymorphous categories in humans and nonhumans. In: Hayes, SC.; Hayes, LJ.; Sato, M.; Ono, K., editors. *Behavior Analysis of Language and Cognition*. APA; Washington, DC USA: 1994. p. 91-106.
- Jitsumori M. Prototype effect and categorization of artificial polymorphous stimuli in pigeons. *J Exp Psychol Anim Behav Process*. 1996; 22:405–418. [PubMed: 8865609]
- Judge PG, Evans TA, Vyas DK. Ordinal representation of numeric quantities by brown capuchin monkeys (*Cebus apella*). *J Exp Psychol Anim Behav Process*. 2005; 31:79–94. [PubMed: 15656729]
- Katz JS, Wright AA, Bachevalier J. Mechanisms of same/different abstract-concept learning by rhesus monkeys (*Macaca mulatta*). *J Exp Psychol Anim Behav Process*. 2002; 28:358–368. [PubMed: 12395493]
- Kemler DG. Classification in young and retarded children's discriminative learning: The primacy of overall similarity relations. *Child Dev*. 1982a; 53:768–779. [PubMed: 7094679]
- Kemler DG. The ability for dimensional analysis in preschool and retarded children: Evidence from comparison, conservation, and prediction tasks. *J Exp Child Psychol*. 1982b; 34:469–489. [PubMed: 6218214]
- Kemler Nelson DG. The effect of intention on what concepts are acquired. *J Verb Learn Verb Behav*. 1984; 23:734–759.
- Kennedy EH, Frigaszy DH. Analogical reasoning in a capuchin monkey (*Cebus apella*). *J Comp Psychol*. 2008; 122:167–175. [PubMed: 18489232]
- Knowlton BJ, Squire LR. The learning of categories: Parallel brain systems for item memory and category knowledge. *Science*. 1993; 262:1747–1749. [PubMed: 8259522]
- Lazareva, OF.; Wasserman, EA. Category learning and concept learning in birds. In: Mareschal, D.; Quinn, PC.; Lea, SEG., editors. *The Making of Human Concepts*. Oxford University Press; Oxford; 2010. p. 151-172.

- Lea SEG, Wills AJ. Use of multiple dimensions in learned discriminations. *Compar Cogn Behav Rev.* 2008; 3:115–133.
- Lockhead GR. Processing dimensional stimuli: A note. *Psychol Rev.* 1972; 79:410–419. [PubMed: 5076869]
- Love BC. Comparing supervised and unsupervised category learning. *Psychon Bull Rev.* 2002; 9:829–835. [PubMed: 12613690]
- Mackintosh NJ, Wilson B, Boakes A, Barlow HB. Differences in mechanisms of intelligence among vertebrates. *Phil Trans R Soc Lond B.* 1985; 308:53–65.
- Maddox WT, Ashby FG. Comparing decision bound and exemplar models of categorization. *Percept Psychophys.* 1993; 53:49–70. [PubMed: 8433906]
- Maddox WT, Ashby FG. Dissociating explicit and procedural-learning based systems of perceptual category learning. *Behav Process.* 2004; 66:309–332.
- Maddox WT, Ashby FG, Bohil CJ. Delayed feedback effects on rule-based and information-integration category learning. *J Exp Psychol Learn Mem Cogn.* 2003; 29:650–662. [PubMed: 12924865]
- Maddox WT, Ashby FG, Ing AD, Pickering AD. Disrupting feedback processing interferes with rule-based but not information-integration category learning. *Mem Cogn.* 2004; 32:582–591.
- Maddox WT, Ing AD. Delayed feedback disrupts information-integration but not rule-based category learning. *J Exp Psychol Learn Mem Cogn.* 2005; 31:100–107. [PubMed: 15641908]
- McGonigle B, Chalmers M, Dickinson A. Concurrent disjoint and reciprocal classification by *Cebus apella* in seriation tasks: Evidence for hierarchical organization. *Anim Cogn.* 2003; 6:185–197. [PubMed: 12761655]
- Medin DL, Schaffer MM. Context theory of classification learning. *Psychol Rev.* 1978; 85:207–238.
- Medin DL, Schwanenflugel PJ. Linear separability in classification learning. *J Exp Psychol Hum Learn.* 1981; 7:355–368.
- Medin DL, Wattenmaker WD, Hampson SE. Family resemblance, conceptual cohesiveness, and category construction. *Cognitive Psychol.* 1987; 19:242–279.
- Minda JP, Smith JD. Prototypes in category learning: The effects of category size, category structure, and stimulus complexity. *J Exp Psychol Learn Mem Cogn.* 2001; 27:775–799. [PubMed: 11394680]
- Murphy, GL. *The big book of concepts.* Cambridge, MA USA: MIT Press; 2003.
- Nosofsky RM. Attention and learning processes in the identification and categorization of integral stimuli. *J Exp Psychol Learn Mem Cogn.* 1987; 13:87–108. [PubMed: 2949055]
- Nosofsky RM, Palmeri TJ, McKinley SK. Rule-plus exception model of classification learning. *Psychol Rev.* 1994; 101:53–79. [PubMed: 8121960]
- Paukner A, Anderson JR, Fujita K. Redundant food searches by capuchin monkeys (*Cebus apella*): A failure of metacognition? *Anim Cogn.* 2006; 9:110–117. [PubMed: 16184375]
- Pearce JM. A model of stimulus generalization for Pavlovian conditioning. *Psychol Rev.* 1987; 94:61–73. [PubMed: 3823305]
- Pearce JM. Similarity and discrimination: A selective review and a connectionist model. *Psychol Rev.* 1994; 101:587–607. [PubMed: 7984708]
- Pearce JM, Esber GR, George DN, Haselgrove M. The nature of discrimination learning in pigeons. *Learn Behav.* 2008; 36:18–199.
- Reber AS. Implicit learning of artificial grammars. *J Verb Learn Verb Behav.* 1967; 6:855–863.
- Reber PJ, Stark CEL, Squire LR. Cortical areas supporting category learning identified using functional MRI. *Proc Natl Acad Sci U S A.* 1998; 95:747–750. [PubMed: 9435264]
- Reed SK. Pattern recognition and categorization. *Cognitive Psychol.* 1972; 3:382–407.
- Reed SK. Category vs. item learning: implications for categorization models. *Mem Cogn.* 1978; 6:612–621.
- Regehr G, Brooks LR. Category organization in free classification: The organizing effect of an array of stimuli. *J Exp Psychol Learn Mem Cogn.* 1995; 21:347–363.
- Reiss DR, Marino L. Mirror self-recognition in the bottlenose dolphin: A case of cognitive convergence. *Proc Natl Acad Sci U S A.* 2001; 98:5937–5942. [PubMed: 11331768]

- Roberts AC. Comparison of cognitive function in human and nonhuman primates. *Cognitive Brain Res.* 1996; 3:319–327.
- Rosseel Y. Mixture models of categorization. *J Math Psychol.* 2002; 46:178–210.
- Rossi AF, Pessoa L, Desimone R, Ungerleider LG. The prefrontal cortex and the executive control of attention. *Exp Brain Res.* 2009; 192:489–497. [PubMed: 19030851]
- Rumbaugh, DM.; Pate, JL. The evolution of cognition in primates: A comparative perspective. In: Roitblat, HL.; Bever, TG.; Terrace, HS., editors. *Animal cognition*. Erlbaum; Hillsdale, NJ USA: 1984. p. 569-589.
- Schnyer DM, Maddox WT, Ell S, Davis S, Pacheco J, Verfaellie M. Prefrontal contributions to rule-based and information-integration category learning. *Neuropsychologia.* 2009; 47:2995–3006. [PubMed: 19643119]
- Schwarz G. Estimating the dimension of a model. *Ann Stat.* 1978; 6:461–464.
- Semendeferi K, Lu A, Schenker N. Humans and great apes share a large frontal cortex. *Nature Neurosci.* 2002; 5:272–276. [PubMed: 11850633]
- Shepard RN, Hovland CI, Jenkins HM. Learning and memorization of classifications. *J Exp Psychol.* 1961; 65:94–102. [PubMed: 13988437]
- Shepp BE, Swartz K. Selective attention and the processing of integral and nonintegral dimensions. A developmental study. *J Exp Child Psychol.* 1976; 22:73–85. [PubMed: 1003096]
- Shepp, BE.; Burns, B.; McDonough, D. The relation of stimulus structure to perceptual and cognitive development: Further tests of a separability hypothesis. In: Becker, J.; Wilkening, F., editors. *The integration of information by children*. Erlbaum; Hillsdale, NJ USA: 1980. p. 113-145.
- Smith JD, Ashby FG, Berg ME, Murphy MS, Spiering B, Cook RG, Grace RC. Pigeons' categorization may be exclusively nonanalytic. *Psychon Bull Rev.* 2011a; 18:422–428. [PubMed: 21327381]
- Smith JD, Beran MJ, Crossley MJ, Boomer J, Ashby FG. Implicit and explicit category learning by macaques (*Macaca mulatta*) and humans (*Homo sapiens*). *J Exp Psychol Anim Behav Process.* 2010a; 36:54–65. [PubMed: 20141317]
- Smith JD, Chapman WP, Redford JS. Stages of category learning in monkeys (*Macaca mulatta*) and humans (*Homo sapiens*). *J Exp Psychol Anim Behav Process.* 2010b; 36:39–53. [PubMed: 20141316]
- Smith JD, Coutinho MVC, Couchman JJ. The learning of exclusive-or categories by monkeys (*Macaca mulatta*) and humans (*Homo sapiens*). *J Exp Psychol Anim Behav Process.* 2011b; 37:20–29. [PubMed: 20718556]
- Smith JD, Crossley MJ, Boomer J, Church BA, Beran MJ, Ashby FG. Implicit and explicit category learning by capuchin monkeys (*Cebus apella*). *J Comp Psychol.* 2012 In press.
- Smith JD, Kemler Nelson DG. Overall similarity in adults' classification: The child in all of us. *J Exp Psychol Gen.* 1984; 113:137–159.
- Smith JD, Kemler Nelson DG. Is the more impulsive child a more holistic processor? A reconsideration. *Child Dev.* 1988; 50:719–727.
- Smith JD, Minda JP. Prototypes in the mist: the early epochs of category learning. *J Exp Psychol Learn Mem Cogn.* 1998; 24:1411–1436.
- Smith JD, Minda JP, Washburn DA. Category learning in rhesus monkeys: A study of the Shepard, Hovland, and Jenkins tasks. *J Exp Psychol Gen.* 2004; 133:398–414. [PubMed: 15355146]
- Smith JD, Murray MJ, Minda JP. Straight talk about linear separability. *J Exp Psychol Learn Mem Cogn.* 1997; 23:659–680.
- Smith JD, Redford JS, Haas SM. Prototype abstraction by monkeys (*Macaca mulatta*). *J Exp Psychol Gen.* 2008; 137:390–401. [PubMed: 18473665]
- Smith JD, Schull J, Strote J, McGee K, Egnor R, Erb L. The uncertain response in the bottlenosed dolphin (*Tursiops truncatus*). *J Exp Psychol Gen.* 1995; 124:391–408. [PubMed: 8530911]
- Smith JD, Tracy J, Murray MJ. Depression and categorization. *J Exp Psychol Gen.* 1993; 122:331–346. [PubMed: 8371088]
- Smith LB, Kemler DG. Developmental trends in free classification: Evidence for a new conceptualization. *J Exp Child Psychol.* 1977; 24:279–298.

- Smith LB, Kemler DG. Levels of experienced dimensionality in children and adults. *Cognitive Psychol.* 1978; 10:502–532.
- Thompson RKR, Oden DL. Categorical perception and conceptual judgments by nonhuman primates: The paleological monkey and the analogical ape. *Cognitive Sci.* 2000; 24:363–396.
- Vauclair, J. Categorization and conceptual behavior in nonhuman primates. In: Bekoff, M.; Allen, C., editors. *The cognitive animal: Empirical and theoretical perspectives on animal cognition.* MIT Press; Cambridge, MA: 2002. p. 239-245.
- von Fersen L, Lea SEG. Category discrimination by pigeons using five polymorphous features. *J Exp Anal Behav.* 1990; 54:69–84. [PubMed: 16812617]
- Waldron EM, Ashby FG. The effects of concurrent task interference on category learning: Evidence for multiple category learning systems. *Psychon Bull Rev.* 2001; 8:168–176. [PubMed: 11340863]
- Ward TB. Response tempo and separable-integral responding: Evidence for an integral-to-separable processing sequence in visual perception. *J Exp Psychol Hum Percept Perform.* 1983:103–112. [PubMed: 6220116]
- Washburn DA. Stroop-like effects for monkeys and humans: Processing speed or strength of association? *Psychol Sci.* 1994; 5:375–379. [PubMed: 11539143]
- Wasserman EA, Kiedinger RE, Bhatt RS. Conceptual behavior in pigeons: categories, subcategories, and pseudocategories. *J Exp Psychol Anim Behav Process.* 1988; 14:235–246.
- White KG, Alsop B, Williams L. Prototype identification and categorization of incomplete figures by pigeons. *Behav Process.* 1993; 30:253–258.
- Wilson B, Mackintosh NJ, Boakes RA. Transfer of relational rules in matching and oddity learning by pigeons and corvids. *Q J Exp Psychol B.* 1985; 37:313–332.
- Wimpenny JH, Weir AS, Clayton L, Rutz C, Kacelnik A. Cognitive processes associated with sequential tool use in New Caledonian Crows. *PLoS ONE.* 2009; 4:1–16.
- Wright AA, Katz JS. Mechanisms of same/different concept learning in primates and avians. *Behav Process.* 2006; 72:234–254.

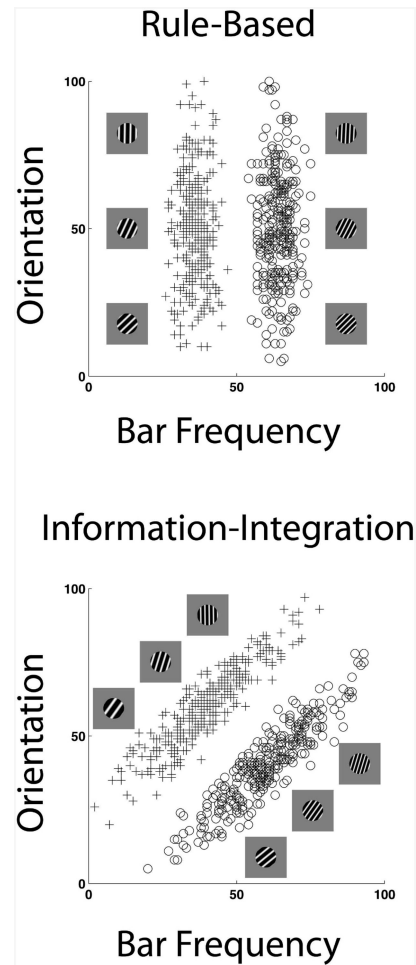


Figure 1.

Illustrating rule-based and information-integration category structures. The stimuli are sine-wave disks varying in bar spatial frequency and orientation. For each task, three illustrative Category A and Category B stimuli are provided. In addition, the plus signs and open circles illustrate the distribution of an experiment's stimuli as represented in an abstract space. The text specifies how these abstract values can be converted into physically realized stimuli. The pluses and circles, respectively, are Category A and Category B exemplars. In the top panel, only variation in bar frequency carries diagnostic category information, so optimal performance would be governed by a one-dimensional, bar-frequency rule (widely vs. narrowly spaced bars). In the lower panel, both bar frequency and orientation carry useful but insufficient category information—information from both dimensions would have to be integrated into category decisions.

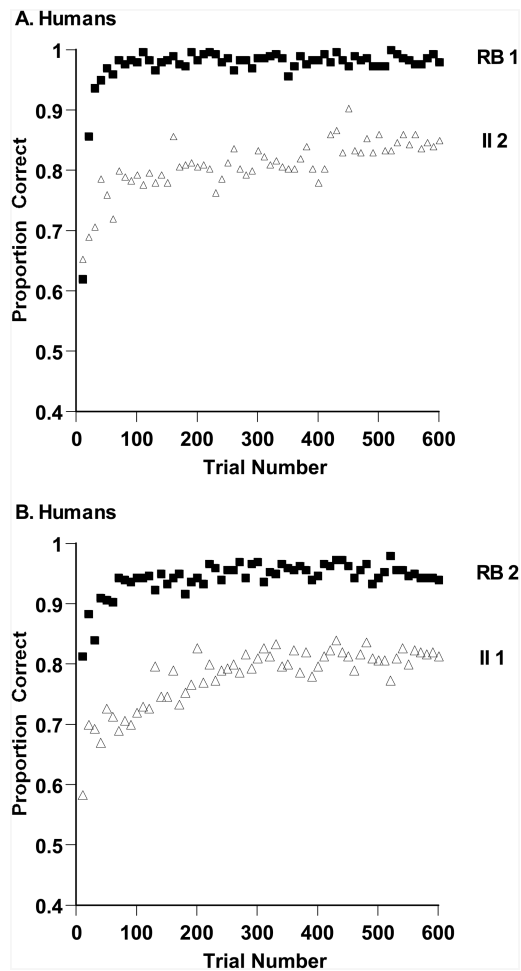


Figure 2. Humans performing rule-based (RB) and information-integration (II) tasks. *A.* Proportion of correct responses in each 10-trial block for 30 humans who performed 600 trials of an RB and II category task in that order. *B.* Proportion of correct responses in each 10-trial block for 30 humans who performed 600 trials of an II and RB category task in that order.

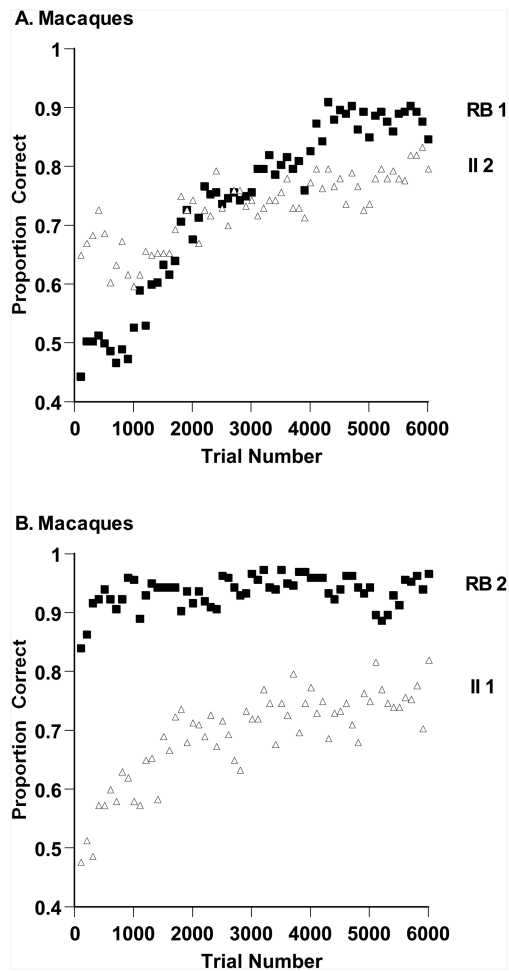


Figure 3. Macaques performing rule-based (RB) and information-integration (II) tasks *A.* Proportion of correct responses in each 100-trial block for three macaques who performed 6,000 trials of an RB and II category task in that order. *B.* Proportion of correct responses in each 100-trial block for three macaques who performed 6,000 trials of an II and RB category task in that order.

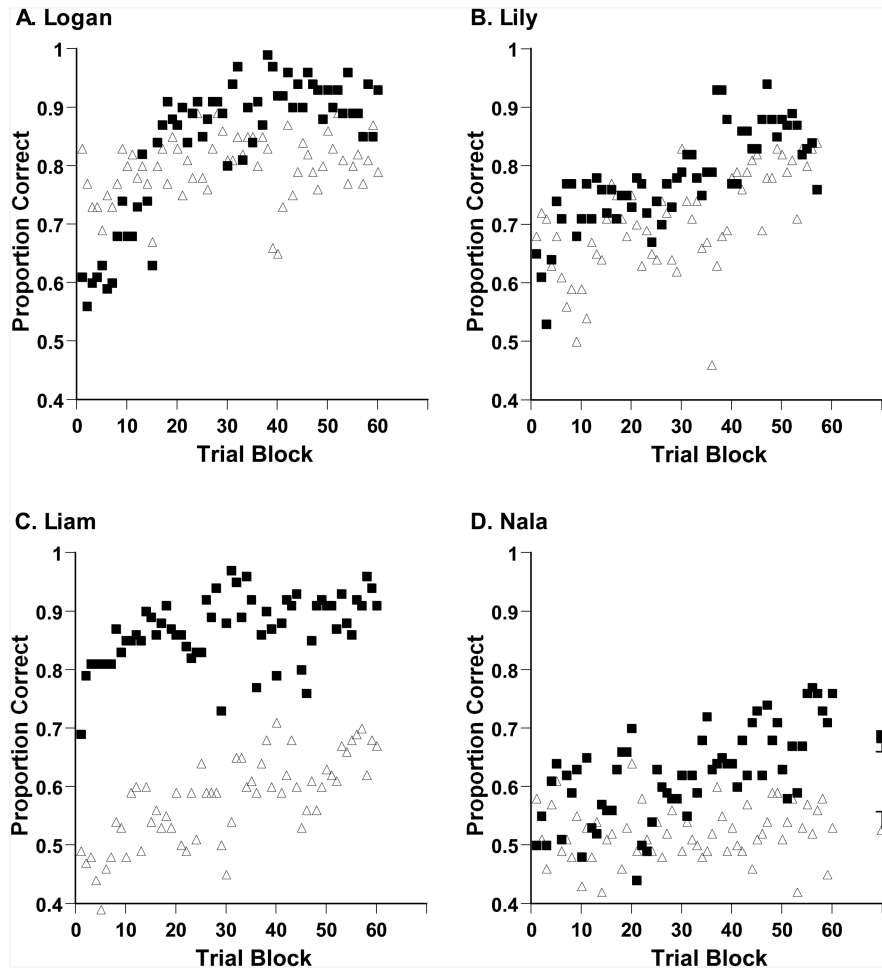


Figure 4. Capuchin monkeys performing rule-based (RB) and information-integration (II) tasks *A-D*. Proportion of correct responses in each trial block for four capuchin monkeys. Filled-square symbols and open-triangle symbols, respectively, denote performance in RB and II tasks.

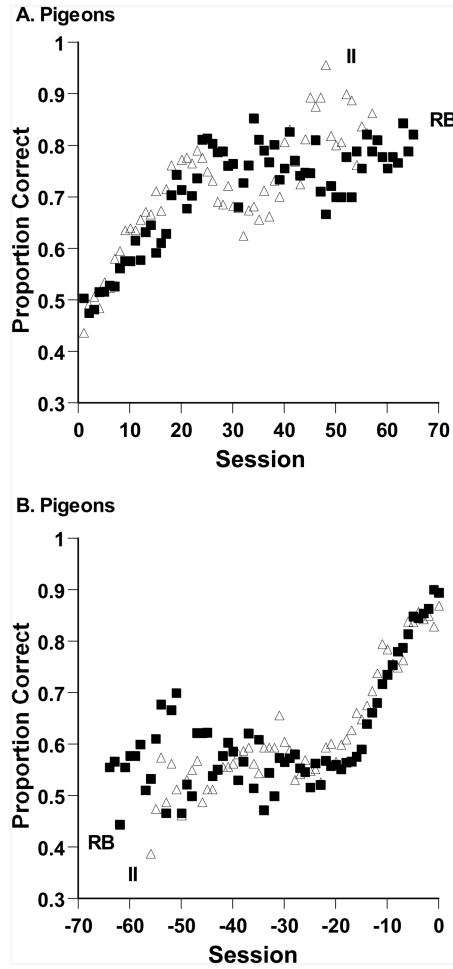


Figure 5. Pigeons performing rule-based (RB) and information-integration (II) tasks *A.* Proportion of correct responses in each session from the onset of learning forward for 8 RB-learning pigeons (filled-square symbols) and 8 II-learning pigeons (open-triangle symbols). *B.* Proportion of correct responses in each session from the criterial block backward for 8 RB-learning pigeons and 8 II-learning pigeons.