

# Generalization of Category Knowledge and Dimensional Categorization in Humans (*Homo sapiens*) and Nonhuman Primates (*Macaca mulatta*)

J. David Smith, Alexandria C. Zakrzewski,  
and Jennifer J. R. Johnston  
University at Buffalo, The State University of New York

Jessica L. Roeder  
University of California, Santa Barbara

Joseph Boomer  
University at Buffalo, The State University of New York

F. Gregory Ashby  
University of California, Santa Barbara

Barbara A. Church  
University at Buffalo, The State University of New York

A theoretical framework within neuroscience distinguishes humans' implicit and explicit systems for category learning. We used a perceptual-categorization paradigm to ask whether nonhumans share elements of these systems. Participants learned categories that foster implicit or explicit categorization in humans, because they had a multidimensional, information-integration (II) solution or a unidimensional, rule-based (RB) solution. Then humans and macaques generalized their category knowledge to new, untested regions of the stimulus space. II generalization was impaired, suggesting that II category learning is conditioned and constrained by stimulus generalization to its original, trained stimulus contexts. RB generalization was nearly seamless, suggesting that RB category knowledge in humans and monkeys has properties that grant it some independence from the original, trained stimulus contexts. These findings raise the questions of (a) how closely macaques' dimensional categorization verges on humans' explicit/declarative categorization, and (b) how far macaques' dimensional categorization has advanced beyond that in other vertebrate species.

**Keywords:** category learning, category rules, procedural learning, attention, primate cognition, humans, macaques, pigeons

Categorization is a crucial cognitive adaptation underlying many aspects of learning and behavior. It is a focus of research with humans (Ashby & Maddox, 2011; Brooks, 1978; Feldman, 2000; Knowlton &

Squire, 1993; Kruschke, 1992; Murphy, 2002; Nosofsky, 1987; Rosch & Mervis, 1975) and animals (Cerella, 1979; Herrnstein, Loveland, & Cable, 1976; Jitsumori, 1994; Lea & Ryan, 1990; Smith, Redford, & Haas, 2008; Vaucclair, 2002; Wasserman, Kiedinger, & Bhatt, 1988; Zentall, Wasserman, Lazareva, Thompson, & Rattermann, 2008).

Humans may have multiple category learning systems (Ashby & Ell, 2001; Cook & Smith, 2006; Erickson & Kruschke, 1998; Homa, Sterling, & Trepel, 1981; Nosofsky, Palmeri, & McKinley, 1994; Rosseel, 2002; Smith & Minda, 1998). For example, neuroscientists have distinguished an implicit procedural learning system from an explicit rule learning system (Ashby & Valentin, 2005; Maddox & Ashby, 2004; Smith, Berg, et al., 2012). The implicit system learns through contemporaneous reinforcement signals to associate stimuli to responses in a process akin to conditioning (Ashby & Waldron, 1999). Participants lack declarative access to implicit category knowledge. The explicit system learns by testing hypotheses and deriving rules about dimensions relevant to categorization. It relies on working memory and executive functions. Participants have declarative access to explicit category knowledge. Many have granted explicit rules an important role in human categorization (Ahn & Medin, 1992; Ashby & Ell, 2001; Erickson & Kruschke, 1998; Feldman, 2000; Medin, Wattenmaker, & Hampson, 1987; Nosofsky et al., 1994; Regehr & Brooks, 1995; Shepard, Hovland, & Jenkins, 1961).

This article was published Online First July 13, 2015.

J. David Smith, Alexandria C. Zakrzewski, and Jennifer J. R. Johnston, Department of Psychology, University at Buffalo, The State University of New York; Jessica L. Roeder, Department of Psychological & Brain Sciences, University of California, Santa Barbara; Joseph Boomer, Department of Psychology, University at Buffalo, The State University of New York; F. Gregory Ashby, Department of Psychological & Brain Sciences, University of California, Santa Barbara; and Barbara A. Church, Department of Psychology, University at Buffalo, The State University of New York.

Supported by Grant HD-060563 from National Institute of Child Health and Human Development (NICHD), Grant P01 NS044393 from National Institute of Neurological Disorders and Stroke (NINDS), and by support from the U.S. Army Research Office through the Institute for Collaborative Biotechnologies under Grant W911NF-07-1-0072. We thank our undergraduate research assistants in the University at Buffalo (UB) lab and our research associates at the Language Research Center of Georgia State University (LRC-GSU) for their help with data collection with the humans (UB) and macaques (LRC-GSU).

Correspondence concerning this article should be addressed to J. David Smith, 346 Park Hall, University at Buffalo, The State University of New York, Buffalo, NY 14260. E-mail: [psysmith@buffalo.edu](mailto:psysmith@buffalo.edu)

The implicit–explicit distinction is based on research using tasks like those in Figure 1. Each member of Category A (o) and B (+) is a conjoint stimulus presenting values along two perceptual continua. In one case (A), the diagonal of the stimulus space partitions the categories. Both dimensions present useful information for responding. Ideally, one would integrate information across dimensions to reach a category decision. Thus, this is an information-integration (II) task. Participants are not shown this category space. They must discover the II principle from within the task’s trial-by-trial framework (stimulus, response, reinforcement).

In the other case (B), a vertical boundary partitions the categories. Category A and B instances are distinguishable by their *x*-axis value. The *y*-axis values provide no category information. One approach to solving this rule-based (RB) task is to discover this dimensional rule by selective attention and hypothesis testing within the task’s trial-by-trial framework. However, by using this standard RB task label, we do not mean to imply that learning in this task must be by abstract, explicit, declarative rules. Learning in RB tasks might also be facilitated by simpler, selective-attention processes that lack important features of humans’ explicit rules.

II and RB tasks are a useful minimal-contrast pair. Their categories are matched for size, discriminability (*d'*), within-category exemplar similarity, and between-category exemplar separation. The tasks are simply different rotations within stimulus space. Their equivalence has been confirmed in independent demonstrations that pigeons (*Columba livia*) learn II and RB tasks equally quickly to the same level (Smith et al., 2011; R. G. Cook, personal communication, December 2013).

Despite their equivalence, II and RB tasks have shown many empirical dissociations—in behavioral, brain imaging, and neuropsychological patient studies (Ashby, Maddox, & Bohil, 2002; Ashby, Queller, & Berretty, 1999; Maddox & Ashby, 2004; Maddox, Ashby, & Bohil, 2003; Maddox & Ing, 2005; Smith et al., 2014). For example, Smith et al. (2014) let participants learn II and RB tasks, but with feedback delivered in summary form after each trial block. Summary feedback eliminated II learning because it disabled the conditioning processes that link stimuli to responses. Summary feedback preserved RB learning, because participants

could still explicitly evaluate their rule and its efficacy at the end of each trial block.

The multiple-systems framework predicts these dissociations a priori, strengthening its support. However, the theoretical stakes are high, just as when the possibility of multiple memory systems emerged. There remains an ongoing debate. Some still argue that many of the relevant phenomena can be explained using a unitary category learning system (e.g., Dunn, Newell, & Kalish, 2012; Newell, Dunn, & Kalish, 2010; Newell, Moore, Wills, & Milton, 2013; Nosofsky, Stanton, & Zaki, 2005; Stanton & Nosofsky, 2007). It is a political, contentious issue. This article does not prejudge the issue. We adopt the multiple-systems idea as our working hypothesis. We accept, as many others have, the importance of rules for humans as they categorize. We seek to study the evolutionary roots and gradual emergence of rules in category learning. The evidence is sufficient to justify this working hypothesis and empirical approach. Of course, we do not claim that macaques have explicit, declarative rule knowledge. They may well have taken only the initial steps toward humans’ capacity for attentional focusing, dimensional categorization, and rule use. Indeed, the *gradual emergence* of explicit categorization is the central theoretical backdrop of our article. This emergence is an important theoretical issue for both associative and cognitive theorists.

A strength of the II–RB methodology is that it lets one explore attention and dimensional categorization in animals behaviorally, with no reliance on verbal report. One need only rotate the axis of the task, from II to RB (see Figure 1) to ask whether the cognitive systems of different species are dimensionally polarized in the sense of treating one-dimensional category separations with psychological privilege. If they are, then the dimensional task orientation—the RB task—will admit strong and rapid learning, just as a polarizing filter will strongly admit light when aligned with the axis of the light’s polarization. If cognition in that species is not dimensionally polarized, II and RB tasks will be learned at the same speed to the same level. This discovery can be made for any species that can perform behavioral discriminations.

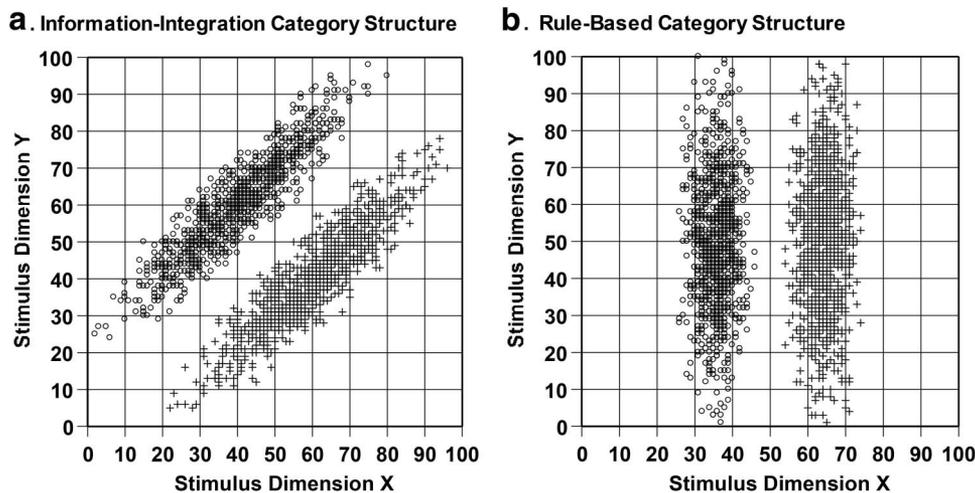


Figure 1. Information-integration (a) and rule-based (b) category structures illustrated.

Using this approach, Smith, Beran, Crossley, Boomer, and Ashby (2010) studied categorization in macaques (*Macaca mulatta*). Macaques, like humans, learned RB tasks more quickly than II tasks, suggesting that they share some aspects of humans' dimensional categorization system (but not necessarily all its explicit aspects). Smith, Crossley, et al. (2012) extended this observation to another primate lineage (capuchins [*Cebus apella*]). In contrast, pigeons are indifferent to the II–RB rotation of the category task (Smith et al., 2011). Their cognition is not dimensionally polarized in the sense of preferring dimensional categorization. The divergence among vertebrate lineages in this area raises important questions about the evolutionary emergence of selective attention, dimensional rules, and explicit categorization.

However, these cross-species observations only begin the comparative study of dimensional categorization. One also wants to know how strong the homology is between humans' and primates' RB learning. One wants to know whether primates' RB category learning processes also depend on working memory, and whether they represent dimensional hypotheses in similar ways. In this article, we took an empirical step beyond the primate demonstrations in Smith and colleagues (Smith et al., 2010; Smith, Crossley, et al., 2012). We explored in a new way the strength of human–primate homology by exploring the generalization of category knowledge when transfer to new stimuli is required. If II and RB category learning are different cognitively, and different in the same way for humans and macaques, then the ability of humans and primates to generalize their II and RB category knowledge should contrast for the reasons described now.

Adaptive responses in II tasks are believed to be entrained by reinforcement to the training stimuli. Therefore, II category learning should generalize to new stimulus contexts in a limited way constrained by stimulus distance. II learning is also believed to be implicit. Casale, Roeder, and Ashby (2012) have reported that no participant among hundreds tested was able to declare the basis for their II categorization responses. So there is no freestanding category knowledge in working memory that can bridge generalization to new stimulus contexts. For this reason, too, procedural category knowledge might have limited generalizability to novel stimuli.

In contrast, humans' adaptive responses in RB tasks seem to depend on an organizing rule held in working memory. This rule might have substantial stimulus independence. A size rule, for example, would transcend changes in perceptual features (e.g., color, shape). Moreover, the rule can reside in working memory to help the categorizer bridge over to new stimulus contexts, just as it did in Smith et al. (2014) to help the categorizer bridge over to summary feedback at the end of a trial block. Accordingly, explicit category knowledge might be more generalizable.

This II–RB difference has been demonstrated in humans. Casale et al. (2012) found that generalization to novel stimuli was seamless in RB but not II tasks. We replicated and extended this demonstration in Experiment 1. In Experiment 2, we tested macaques' generalization of II and RB category learning. Finding the same differential–generalization effects would strengthen the homology between the dimensional categorization of humans and macaques, and suggest that macaques' RB task solutions share with those in humans some cognitive features—among them some abstractness and some stimulus independence. It could suggest that

macaques have taken the first steps toward humans' capacity to learn dimensional category rules.

## General Method

### Stimuli

Stimuli were unframed rectangles containing green illuminated pixels (see Figure 2) presented top center on a black background of a computer screen. The rectangles varied in size and number of pixels lit. There were 101 size levels (Levels 0–100). A rectangle's width on the screen in pixels was given by  $100 + \text{level}$ . A rectangle's height in pixels was given by  $\text{round}(\text{width}/2)$ . Thus the stimuli varied from  $100 \times 50$  (Level 0) to  $200 \times 100$  (Level 100). Dimension size is the  $x$  axis in Figure 1's abstract stimulus spaces.

Dimension Y in Figure 1 is proportional pixel density—that is, the proportion of illuminated pixel positions. A level's proportional density was given by  $0.05 \times 1.018^{\text{Level}}$ . For Level 0, proportional density was 0.05 (5% of pixels illuminated). For Level 100, proportional density was 0.2977 (30% of pixels illuminated). Stimuli were presented on a 17-in. monitor with  $800 \times 600$  pixel resolution and viewed from about 24 in.

These stimulus dimensions complement existing RB–II research that has mainly used the perceptual dimensions of tilt and spatial frequency. The dimensions were also a strong choice here because they received an initial empirical grounding with humans in Smith et al. (2014). In Experiment 2, we extended for the first time use of these materials to another species.

### Category Structures

Figure 3 shows the II and RB category structures that allowed us to study the generalization of category knowledge to untrained regions of stimulus space. Smith et al. (2014) have shown that

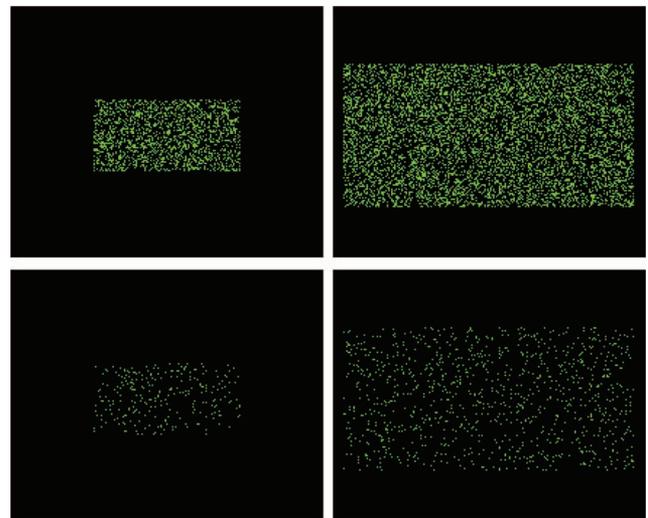


Figure 2. Four stimuli illustrating the corners of the perceptual space: stimulus 0 0 (small-sparse, lower left), stimulus 100 0 (big-sparse, lower right), stimulus 0 100 (small-dense, upper left), and stimulus 100 100 (big-dense, upper right). See the online article for the color version of this figure. See the online article for the color version of this figure.

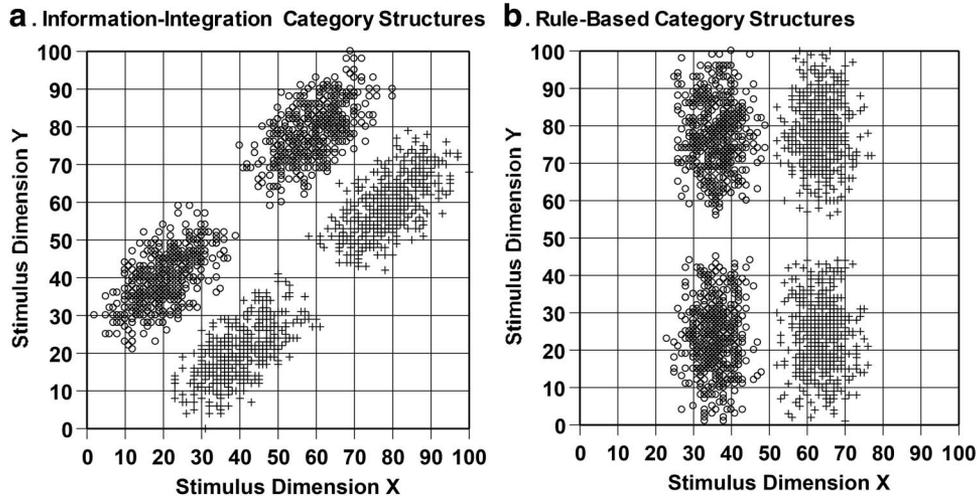


Figure 3. (a) A training–generalization information-integration category structure. Open circles and plus signs, respectively, indicate Category A and Category B stimuli. The bottom pair and top pair of stimulus ellipses, respectively, were the defined categories during training and generalization. (b) A training–generalization rule-based category structure, depicted in the same way.

these tasks produce typical II and RB performance profiles and foster different learning processes. Thus, our comparison of these RB and II tasks was empirically and theoretically grounded because they ideally instantiate multiple-systems theory. Our choice to compare one RB task to one II task fit common practice in the literature.

In essence, we broke the category structures generally used in II–RB research (see Figure 1) into separate training and generalization subtasks—respectively, the bottom pair and the top pair of ellipses in each panel of Figure 3. Following training, we asked how well humans and animals extended their category knowledge to the stimulus distributions containing novel stimuli. We measured whether II generalization would falter relative to RB generalization.

Category exemplars were chosen using established procedures (Ashby & Gott, 1988). Categories were defined by bivariate normal distributions within size-density space. As each category exemplar was selected as a coordinate pair in that space, the abstract levels were transformed into concrete stimuli with two visual features using the formulas already described.

To control for outliers, a random sample for a trial was not presented if its Mahalanobis distance (e.g., Fukunaga, 1972) exceeded 3.0. X deviations greater than 13.725 and Y deviations greater than 22.5—from the desired mean of the stimulus ellipse—were disallowed to keep dimensional values within the 0–100 scale. Additional random samples were made until these criteria were met. Table 1 shows the statistical characteristics of the Category A and B distributions. For the RB task, only dimension size carried category-relevant information. For the II task, dimensions size and density carried relevant information that needed to be integrated into a correct categorization decision.

**Formal Modeling**

We fit RB and II formal models (Maddox & Ashby, 1993) to subjects’ final training data and initial generalization data to help us understand how their decision strategies generalized to novel stimuli. The RB model assumes that participants set a criterion on one stimulus dimension (size or density). The modeling lets us specify the horizontal or vertical line drawn through stimulus

Table 1  
Distributional Characteristics for the Training and Generalization Category Tasks

Task	Condition	Category	$M_X$	$M_Y$	Var X	Var Y	Covar XY
II	Training	A	20.85	40.26	49.25	49.25	28.77
II	Training	B	40.26	20.85	49.25	49.25	28.77
II	Generalization	A	59.74	79.15	49.25	49.25	28.77
II	Generalization	B	79.15	59.74	49.25	49.25	28.77
RB	Training	A	36.28	22.5	20.48	78.02	0
RB	Training	B	63.72	22.5	20.48	78.02	0
RB	Generalization	A	36.28	77.5	20.48	78.02	0
RB	Generalization	B	63.72	77.5	20.48	78.02	0

Note. Covar = covariance; II = information integration (see Figure 3a); RB = rule based (see Figure 3b); Var = variance.

space that best partitions the subject's Category A responses from his or her Category B responses. The RB model has two free parameters: a perceptual noise variance and a criterion value on the relevant dimension. The II model assumes that participants divide the stimulus space using a diagonal decision boundary of some slope and intercept. The modeling lets us specify the line that best partitions the subject's Category A responses from his or her Category B responses. The II model assumes a general linear classifier in which subjects divided the stimulus space using a linear decision bound. The modeling lets us specify the line drawn through stimulus space, of any slope and intercept, that best partitions the subject's Category A responses from his or her Category B response. The II model has three free parameters: a perceptual noise variance and the slope and intercept of the decision bound. The model-fitting process estimated the best-fitting values for parameters and evaluated which model would have created—with maximum likelihood—the participant's observed distribution of A and B responses. Then, following our previous work, the best-fitting model was chosen as the one with the smallest Bayesian information criterion (BIC; Schwarz, 1978), which is defined as:  $BIC = r \ln N - 2 \ln L$ , where  $r$  is the number of free parameters,  $N$  is the sample size, and  $L$  is the likelihood of the model given the data.

## Hypotheses

Figure 3's II and RB generalization tasks (the upper pairs of ellipses) are equivalent structurally, as already discussed, so if a common mechanism mediates RB and II learning, then one would predict equivalent performance in both tasks. The II and RB extension of category knowledge from training to generalization tasks is identical also. That is, the decision boundary is extended across the stimulus space in the same way. One would predict equivalent II and RB generalization for this reason, too. The distance by which category knowledge is extended is identical, too, another reason to predict equivalent II and RB generalization. The levels of generalization might be poor or good, but they would be equivalent.

However, if the learning mechanisms underlying II and RB tasks are different, then one would not predict equivalent generalization. Multiple-systems theory predicts that II category knowledge would falter facing novel stimulus contexts, because it is grounded in conditioning processes yoked to training stimuli. But RB category knowledge could generalize robustly if it embodies an attentional principle or category rule, because rules exist apart and away from the training stimuli (e.g., in working memory) and could also apply to novel stimuli. For now, we will not assume any particular associative or cognitive mechanism or level behind the attentional principle or category rule, reserving that theoretical consideration for the General Discussion section.

## Experiment 1: Humans

### Method

**Participants.** Undergraduates ( $N = 68$ ; age = 19.6 years; male = 42%; female = 58%) with apparently normal or corrected-to-normal vision participated as a course requirement. Participants

were dropped from analysis—following our usual procedures—for not completing the experiment (four II participants and one RB participant), for showing reduced performance late in the session (three II participants and two RB participants), and for not exceeding chance in the last training block (two II participants and four RB participants). The final dataset included 26 II and 26 RB participants.

**Procedure.** The stimuli, category structures, and modeling were described in the General Method section. Participants were placed randomly into the II or the RB task. Each received his or her own 200 randomly selected category exemplars appropriate to the assigned task and chosen from the training stimulus distributions (lower ellipses of Figure 3). This approach—also adopted by Smith et al. (2014)—produces more generalizable results and a procedure closer to that for the monkeys. This approach may also be more ecological, because frequently category members (e.g., prey items) are sampled without replacement—because they are eaten. Following training, participants received 100 random exemplars from the generalization distributions (upper ellipses of Figure 3). These trial counts followed existing human II–RB studies (e.g., Smith et al., 2014). They were appropriate to humans learning II and RB tasks. They were feasible given the session length of one class period.

Macaques learn category tasks more slowly (e.g., Smith, Minda, & Washburn, 2004), and are generally given more trials in procedures than humans (e.g., Smith et al., 2010; Smith et al., 2008). This was the case here, too, for it is essential to produce an even learning playing field for the species. However, we point out in advance that this training difference renders the human and macaque experiments less comparable in one respect. That macaques need more trials to learn RB tasks suggests that their RB learning processes differ somewhat from those in humans, and perhaps less conscious and explicit. Throughout, our goal is not to assert identical processing by humans and macaques in RB tasks, but rather to search for similarities and differences in that processing.

**Categorization trials.** A trial consisted of a pixel box of some size and density. Below the stimulus were a letter (A and B) to the left and right of the screen, respectively, with a cursor in the middle. Participants assigned the stimulus to Category A or B by pressing the S or L keyboard key to move the cursor to one of the two response icons. These keys spatially corresponded to the screen position of the A and B. Feedback was given immediately upon response.

Following correct responses, participants received a “whoop” sound, then a CORRECT + 1 message was displayed in green text. Following incorrect responses, participants received a 2-s “buzz” sound, followed by an ERROR – 1 message displayed in red text for the duration of an 8-s timeout. For each trial, participants' cumulative points were displayed below the green/red messages. The timeout is a typical feature of our research because it motivates participants. It brought our human procedure closer to that of the monkeys. At humans' performance level in the present tasks, these timeouts would have added about 2.5 min to the session length for II participants compared with RB participants, a negligible increase in an experimental session that was already brief.

**Instructions.** Participants were told they would categorize pixel boxes, having to guess at first but learning how to respond correctly. They were told that they would gain/lose points for

correct/incorrect answers. Feedback was explained. Participants were told that cash prizes would go to the best-scoring participants. These prizes were awarded. Participants acknowledged having read the instructions and the trials began. At generalization, participants were told that they would now categorize new kinds of pixel boxes, still placing them into Category A or B.

**Results**

**Accuracy-based analyses: Learning.** Figure 4 shows humans’ average proportion correct in each 20-trial block during training and generalization of II and RB tasks. RB participants learned their task solution rapidly, progressing from 0.65 to 0.89 correct over the first 60 training trials. RB performance by humans was highly typical of performance in RB category tasks generally. On average, RB participants showed a strong improvement in performance from 0.68 to 0.96 across two consecutive blocks. Though Figure 4 shows rapid learning, these rapid changes across just two blocks are smoothed away because different participants make their transition at different points in the task. These rapid improvements, also found by Smith et al. (2014), are one reason the theoretical idea of humans’ explicit, declarative category learning is increasingly accepted, for they are most consistent with explicit, declarative category learning. But, as we discuss in Experiment 2, this interpretation need not apply to macaques’ dimensional categorization.

II participants learned their task slower and to lower terminal performance levels—up to 0.79 correct in 60 training trials and up to 0.88 correct by the end of training. These aspects of perfor-

mance, including the slightly different RB and II training-performance levels, are characteristic in human research. They are crucial observations in this area, because they support that II performance is subject to perceptual and representational error, whereas RB performance involves different processing and is protected by the application of a discrete, verbalizable rule. In short, the different baselines confirm the different processing that attends performance in RB and II tasks. The same effect was present in the results of Casale et al. (2012).

This difference in baseline might make the results to come conservative, because RB performance potentially has farther to fall at transfer. Or, perhaps RB performance was so high that scale compression would make it difficult to see the performance drop caused by the transition to transfer. But participants were not at ceiling, partially allaying this concern. Their performance had generous room to fall. If at transfer, they had changed the positioning of their dimensional criterion, or switched to a rule along the other dimension, it would have fallen. It is well documented that RB processing can be disrupted and compromised. In our view, the scale-compression idea has limited merit. RB performance has a high baseline for crucial theoretical reasons, because explicit rule processing by humans is easily replicable trial to trial, and not because of a vague and atheoretical ceiling effect. The theoretical reason for the higher RB baseline strengthens this article’s theoretical framework, and the higher baseline is grounded theoretically in many empirical demonstrations in the literature.

**Accuracy-based analyses: Transition to generalization.** RB participants had an average proportion correct of 0.90 in their first block with untrained stimuli compared to 0.94 in their last training block. So, the performance cost was only 0.04,  $t(25) = 1.76, p = .09$ , Cohen’s  $d = 0.35$ , 95% confidence interval (CI)  $[-0.05, 0.74]$ .<sup>1</sup> In fact, just two participants accounted for most of this small difference. Excluding them, participants were 0.95 at the end of training and 0.93 at the start of generalization. From either perspective, the transition to new stimuli was essentially seamless for RB participants.

II participants had an average proportion correct of 0.71 in their first block with untrained stimuli compared to 0.88 in their last block of training. Here the performance cost was substantial, 0.17,  $t(25) = 6.31, p < .001$ , Cohen’s  $d = 1.24$ , 95% CI  $[0.72, 1.74]$ .<sup>2</sup> Performance clearly faltered in the extension of II categorization performance to untrained stimuli.

To confirm the interaction effect implied by these results, we entered the proportion correct in the last block of training and the first block of generalization into a two-way analysis of variance (ANOVA) with categorization task (RB, II) as a between-participants factor and test stage (training, generalization) as a within-participant factor. The analysis found a significant main effect for task,  $F(1, 50) = 21.27, p < .001, \eta_p^2 = .30$ , with RB performance higher overall than II performance. There was also a significant main effect for stage,  $F(1, 50) = 35.21, p < .001, \eta_p^2 =$

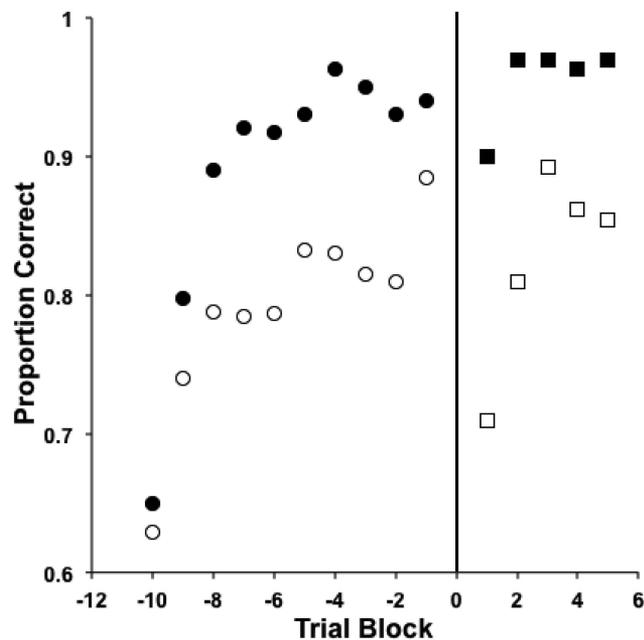


Figure 4. The proportion of correct responses in each 20-trial block for 26 humans who performed 200 training trials and 100 generalization trials of an information-integration or rule-based category task (light and dark symbols, respectively). Ten training blocks extend back from the training–generalization horizon plotted at Block 0 (vertical line) to Block –10. Five generalization blocks extend forward to Block 5.

<sup>1</sup> When the proportion correct in the last two training blocks were included, results were comparable,  $t(25) = 1.69, p = .10$ , Cohen’s  $d = 0.33$ , 95% CI  $[-0.07, 0.72]$ .

<sup>2</sup> When the proportion correct in the last two training blocks were included, results were comparable,  $t(25) = 5.10, p < .001$ , Cohen’s  $d = 1.00$ , 95% CI  $[0.52, 1.47]$ .

.41, with training performance higher overall than generalization performance. Most important, there was a significant Task  $\times$  Stage interaction,  $F(1, 50) = 13.75$ ,  $p < .001$ ,  $\eta_p^2 = .22$ , confirming that II performance selectively faltered entering generalization.

**Model-based analyses.** Humans learn rapidly in generalization, as shown by the fact that their II performance decrease was already reduced in the second 20-trial generalization block (see Figure 4). Therefore, we challenged the resolution limits of our modeling methodology to focus in on the most meaningful behavioral samples (i.e., performance just as generalization began). For this reason, the modeling results should be interpreted only qualitatively.

We fit the RB and II models to participants' last 40 RB training trials. The RB and II models fit best the performance of 23 and three participants, respectively. For the 23 RB learners, the average criterion point they chose along the X dimension was 47.0. The average BIC score for fitting the data was 16.1 (95% of responses explained by the modeling on average). These measures confirmed that the modeling provided close fits to the observed data.

We also fit the models to participants' first 40 RB generalization trials. The RB and II models fit best the performance of 23 and three participants, respectively. The average criterion point for the 23 RB learners was 49.6. The average BIC score for fitting the data was 21.0 (96% of responses explained by the modeling on average). Our qualitative conclusion is that participants flawlessly sustained their RB strategy as they entered generalization.

Regarding II performance, participants commonly choose adventitious rules even in II tasks for which a rule is nonoptimal. This tendency was stronger here because the training and generalization category distributions have less variability along the major diagonal of the stimulus space (compare Figures 1 and 3) so that dimensional rules can partition even the II categories fairly well. In fact, for the last 40 trials of II training, the RB and II models fit best the performance of 17 and nine participants, respectively, with an average BIC score of 30.6 and with 87% of responses explained by the modeling. Human rule-based learning is quite cognitively insistent, intruding where it may not be adaptive. This insistence would seem to be another confirmation of multiple-systems theory. The nine participants with diagonal decision bounds provided a test of whether such bounds survive the transition to generalization. They did not. The model fitting showed that eight of these nine participants switched to an RB strategy during the first 40 generalization trials. Only two of 26 participants produced responses that were best fit by diagonal decision bounds during generalization. Our qualitative conclusion is that there is minimal evidence for the successful extension of diagonal decision strategies to untrained regions of the stimulus space. Quantitatively, the models fit the generalization data of the II participants with an average BIC score of 43.1 (81% of responses explained by the model on average). In fact, at generalization, humans apparently immediately adopted a dimensional rule.

Experiment 1 replicated the general pattern of results when humans perform RB and II tasks. It replicated the generalization results in Casale et al. (2012). RB learners—through their performance levels and consistent decision strategies—generalized category rules faultlessly to new stimuli. II learners did not. They suffered a drop in performance levels and often seized on nonoptimal dimensional rules. These results grounded our methodology

as we evaluated whether nonhuman primates would produce the same data pattern.

## Experiment 2: Rhesus Macaques

### Method

**Subjects.** Adult male rhesus macaques (*Macaca mulatta*) Murph and Lou (21 years old) were tested. They had been trained as described elsewhere (e.g., Washburn & Rumbaugh, 1992) to respond to computer graphic stimuli by manipulating a joystick. They had participated in previous computerized experiments (e.g., Smith et al., 2010; Smith, Coutinho, Church, & Beran, 2013; Smith et al., 2008). The macaques were tested individually in their home cages at the Language Research Center (Georgia State University), with ad libitum access to the test apparatus, working when they chose during long sessions. They had continuous access to water, and worked for fruit-flavored primate pellets. They received a daily diet of fruits and vegetables independent of their efforts on the task, and thus they were not food deprived for the purposes of this experiment.

**Procedure.** The stimuli, the category structures, the category tasks, and the formal modeling were as described in the General Method section. The macaques controlled a white cursor on the screen with their joystick, moving it to make categorization responses. They also had to move this cursor (using appropriate joystick guidance) to touch the stimulus as an observing response that produced the response icons and allowed a categorization response. It is obvious, but important to note, that macaques could not be given instructions about the task. They had to discover everything about the task from the trial-by-trial progression of stimulus, response, and feedback. Therefore, the macaques faced a heavier burden than humans in the process of category learning, and especially, perhaps, in the process of learning explicit category rules.

In the first phase of category training and generalization, Lou completed 9,070 trials in training on the major-diagonal II task (see Figure 3a). During these trials, we presented only Category A and B trials from the lower stimulus distributions. Following a session that ended with Lou completing 21 consecutive 100-trial blocks with performance above 0.90, we moved him to generalization. Lou completed 12,061 trials. Now, we presented only Category A and B trials sampled from the upper stimulus distributions. We ended testing when Lou had just completed a session containing 28 consecutive 100-trial blocks with performance 0.90 or above.

In the second phase of category training and generalization, Lou completed 30,369 trials in training on the vertical RB task. In this case, we reversed the Category A and B designations from those shown in Figure 3b. This ensured that Lou would generalize poorly if he tried to extend his diagonal decision bound to the new category structure, and prompted a sharp and complete relearning by him. We also made the pixel color light red, enhancing in another way the newness of the task and the need for relearning by Lou. Following a session that ended with Lou having completed 22 consecutive 100-trial blocks with performance 0.90 or above, we moved him on to the generalization phase. Lou completed 6,298 trials. We ended testing when Lou had completed 21 consecutive 100-trial blocks with performance above 0.90.

In the first phase of category training and generalization, Murph completed 12,963 trials in training on the vertical RB task shown in Figure 3b. Following a session that ended with 19 consecutive 100-trial blocks with performance above 0.90, we moved him on to generalization. Murph completed 14,259 trials. We ended testing when Murph had just completed a session containing 31 consecutive 100-trial blocks with accuracy above 0.90.

In the second phase of category training and generalization, Murph completed 8,086 trials in training on the major-diagonal II task. Here, too, we reversed the Category A and B designations from those shown in Figure 3a and we recolored the stimulus pixels. Following a session that ended 28 consecutive 100-trial blocks with performance above 0.89, we moved him on to generalization. Murph completed 5,915 trials. We ended testing when Murph had just completed a session containing 19 consecutive 100-trial blocks with performance above 0.90.

### Results: First Training Generalization Phase

**Accuracy-based analyses: Training performance.** Figures 5a and 5b, respectively, show the proportion correct achieved by Lou and Murph in the II and RB tasks, with performance summarized over 2,000 trials in 100-trial blocks. The break between 1,000 training trials and 1,000 generalization trials is indicated by the vertical line at Block 0. We summed performance backward from that point (Trials 1–100 before generalization, 101–200 before generalization, etc.) or forward from that point (Trials 1–100 after generalization, etc.). Lou's and Murph's proportions correct over the last 1,000 training trials were 0.96 and 0.96, respectively. Thus, their performance was equated over their last training trials. We have generally found these animals to be comparable in their performance on many tasks and excellent controls for one another.

**Accuracy-based analyses: Transition to generalization.** Lou averaged 0.82 correct in his first 100 generalization trials compared with 0.96 correct in his last 100 training trials. The performance cost was substantial,  $t(198) = 3.25$ ,  $p < .002$ , Cohen's  $d = 0.23$ , 95% CI [0.09, 0.37].<sup>3</sup> Lou's performance faltered, as did humans' performance and to the same extent (0.14 vs. 0.17), in extending II category knowledge to untrained stimuli.

Murph averaged 0.93 in his first 100 generalization trials compared with 0.94 in his last 100 training trials. The performance cost was 0.01,  $t(198) = 0.29$ ,  $p = .77$ , Cohen's  $d = 0.02$ , 95% CI [-0.12, 0.16].<sup>4</sup> For Murph, as for humans, the generalization of RB category knowledge to new stimuli was seamless.

**Model-based analyses.** Formal models also let us describe the macaques' decisional strategies at different phases. Performance data from both monkeys in training and generalization stages were fit to unidimensional (RB) and multidimensional (II) models. We modeled Lou's last 100 II training trials. (Because macaques are less cognitively labile, it was safe to model a larger sample of behavior.) Lou's best-fitting diagonal decision bound had an optimal slope of 1.01 and a near-optimal placement in the space. The BIC score of 40.8, and the 96% of responses accounted for by the model, indicated that he applied this decisional strategy consistently so that the model fit his performance closely.

We also modeled Lou's first 100 II generalization trials. His best-fitting diagonal decision bound had a slope of 1.26 (steeper than optimal). Moreover, Lou was not able to apply this decision

strategy efficiently. The BIC score (104.2) for the modeling was far higher than in training. The model only explained 82% of his responses, not 96% as in training. He had not applied the decision strategy well and so the model did not fit his performance well.

We also modeled Murph's last 100 RB training trials. The modeling indicated an RB decision strategy placed optimally at 49.1 along the  $x$  axis. The BIC score of 52.1 indicated a close fit—the model explained 94% of Murph's responses. Over the first 100 generalization trials, Murph's rule boundary barely shifted to 50.8 on the  $x$  axis. The BIC score (56.7) and the percentage of responses explained (93%) were also barely changed. These analyses suggest that his use of the categorization rule survived intact its generalization to novel, untrained stimulus contexts. Lou's use of his II decision boundary did not survive intact.

### Results: Second Training Generalization Phase

**Accuracy-based analyses: Training performance.** Figures 6a and 6b show the proportion correct of Murph and Lou in the II and the RB task with performance summarized over 2,000 trials in 100-trial blocks. Block 0 is the break between training and generalization (vertical line). Trial blocks were defined backward and forward from that transition point, as already described. Murph's and Lou's proportions correct over the last 1,000 training trials were 0.95 and 0.96, respectively. Again these animals were equated in training, representing the mutual controls they often are.

**Accuracy-based analyses: Transition to generalization.** Murph averaged 0.82 correct in his first 100 generalization trials compared with 0.95 correct in his last 100 training trials. The performance loss was substantial,  $t(198) = 2.94$ ,  $p < .01$ , Cohen's  $d = 0.21$ , 95% CI [0.07, 0.35].<sup>5</sup> Murph's performance faltered, as did humans' performance, in extending II categorization performance to untrained stimuli. Lou averaged 0.95 in his first 100 generalization trials compared with 0.95 in his last 100 training trials.<sup>6</sup> There was no cost to generalization. For Lou, as for humans, the transition of RB category learning to new stimuli was seamless.

**Model-based analyses.** As before, we fit performance data from both monkeys in training and generalization stages to unidimensional (RB) and multidimensional (II) models. We modeled Murph's last 100 II training trials. His best-fitting diagonal decision bound had an optimal slope of 0.63 and a near-optimal placement in the space. The BIC score of 26.9, and the 97% of responses accounted for by the model, indicated that he applied this decisional strategy consistently so that the model fit his performance closely.

We also modeled Murph's first 100 II generalization trials. His best-fitting diagonal decision bound had a slope of 0.73 (steeper than optimal). Moreover, Murph did not apply his decision strat-

<sup>3</sup> When trials from the last two training blocks were averaged and included, results were comparable,  $t(198) = 3.14$ ,  $p < .002$ , Cohen's  $d = 0.04$ , 95% CI [-0.10, 0.18].

<sup>4</sup> When trials from the last two training blocks were averaged and included, results were comparable,  $t(198) = 1.03$ ,  $p = .30$ , Cohen's  $d = 0.07$ , 95% CI [-0.06, 0.21].

<sup>5</sup> When trials from the last two training blocks were averaged and included, results were comparable,  $t(198) = 3.42$ ,  $p < .001$ , Cohen's  $d = 0.24$ , 95% CI [0.10, 0.38].

<sup>6</sup> Lou averaged 0.93 in his last 200 training trials.

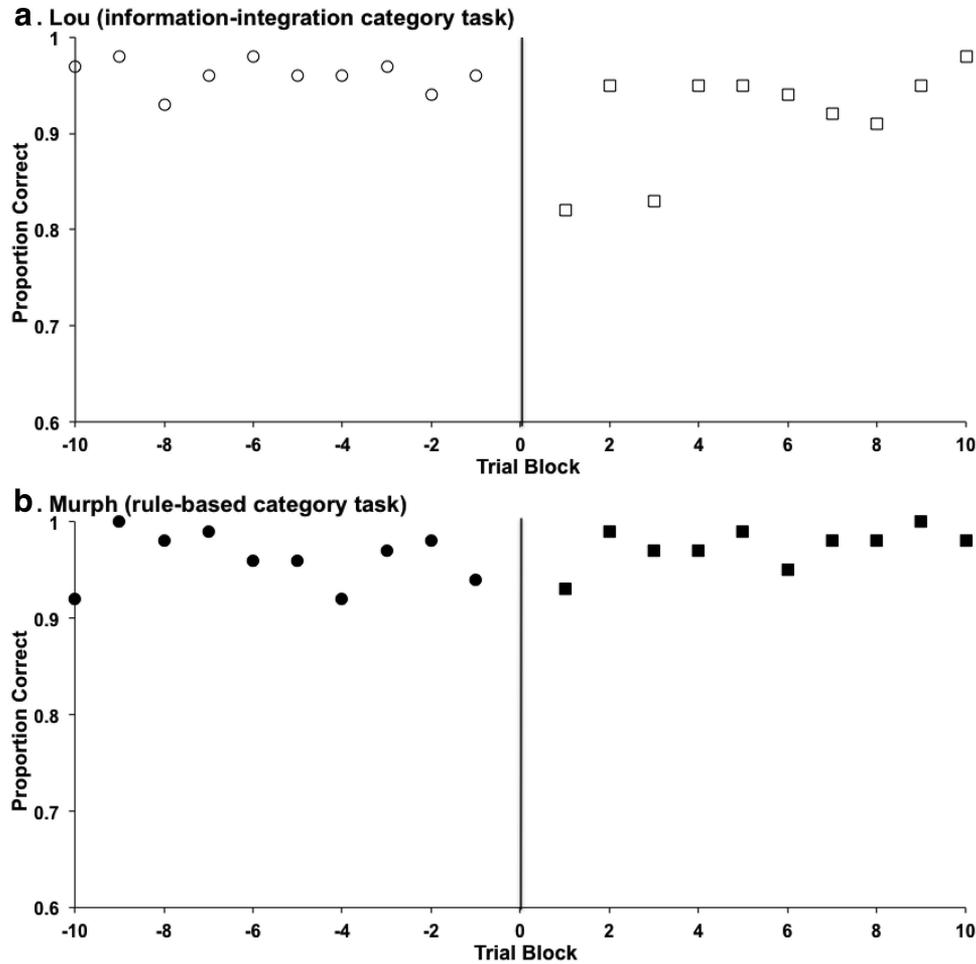


Figure 5. (a) The proportion of correct responses for the macaque Lou performing in the information-integration task. Ten 100-trial training blocks extend back from the training–generalization horizon plotted at Block 0 (vertical line) to Block –10. Ten 100-trial generalization blocks extend forward to Block 10. (b) The proportion of correct responses for the macaque Murph performing in the rule-based task, depicted in the same way.

egy efficiently. The BIC score (104.2) was now far higher than in training. And the model only explained 82% of his responses, not 97% as in training. He did not apply the decision strategy efficiently and so the model did not fit his performance well.

We also modeled Lou’s last 100 RB training trials. The modeling indicated a RB decision strategy placed optimally at 54.0 along the  $x$  axis. The BIC score of 52.9 indicated a close fit—the model explained 95% of Lou’s responses. Over the first 100 RB generalization trials, Lou’s best-fitting rule boundary barely shifted to 46.2 on the  $x$  axis. The BIC score (59.4) and the proportion of responses explained (94%) also barely changed. Lou’s use of the categorization rule survived intact its generalization to novel, untrained stimulus contexts. Murph’s use of his II decision boundary did not survive intact.

### Results: Overall Training Generalization

As with the humans, to confirm the interaction implied by the differences in generalization across the tasks, we entered the proportion correct in the last block of training and the first block

of generalization into a two-way ANOVA with categorization task (RB, II) and test stage (training, generalization) as a within-subject factors and monkey (Lou, Murph) as the between-subjects factor. There was a significant main effect of task (RB, II),  $F(1, 198) = 9.29, p < .003, \eta_p^2 = .045$ , with RB performance higher than II. There was also a significant main effect of stage (training, generalization),  $F(1, 198) = 12.50, p < .001, \eta_p^2 = .06$ , with performance at the end of training exceeding performance at the beginning of generalization. The crucial Task  $\times$  Stage interaction was also significant,  $F(1, 198) = 12.26, p < .001, \eta_p^2 = .06$ , confirming the finding that the monkeys generalized better in the RB task than in the II task. There were no significant main effects or interactions with monkey ( $F_s < 1$ ), reflecting the fact that both monkeys showed the same pattern of results.

### General Discussion

We used a generalization paradigm to ask whether humans and macaques share aspects of a dimensional categorization utility that produces category knowledge with some stimulus independence.

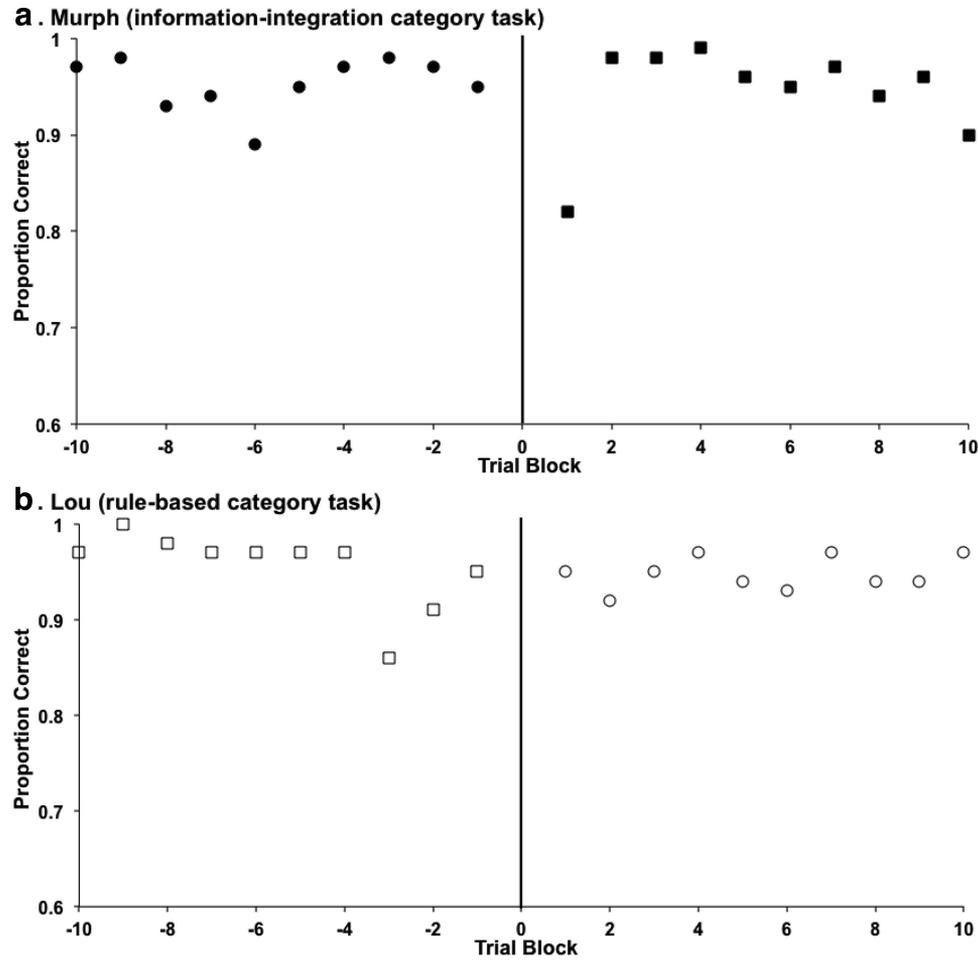


Figure 6. (a) The proportion of correct responses for macaque Murph in the information-integration task. Ten 100-trial training blocks extend back from the training–generalization horizon plotted at Block 0 (vertical line) to Block –10. Ten 100-trial generalization blocks extend forward to Block 10. (b) The proportion of correct responses for the macaque Lou in the rule-based task, depicted in the same way.

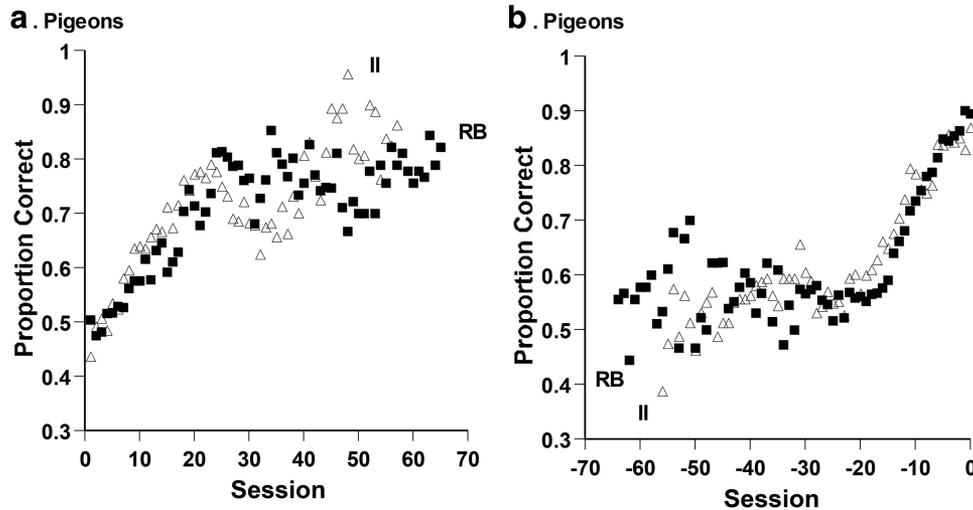
Both species learned RB and II category tasks, then performance shifted to a new area of stimulus space. II generalization was impaired, consistent with the idea that II category knowledge is yoked to the conditioning context of the training stimuli. RB generalization was seamless, consistent with the idea that RB category knowledge has independence from the training contexts. Macaques share some aspects—generalizability, independence, abstractness—of humans’ dimensional categorization. These findings join those in Smith et al. (2010) to show similarities between humans’ and macaques’ RB performance.

This does not mean that macaques’ dimensional categorization is explicit, declarative, or identical to that in humans. Apparent similarities could deserve different psychological interpretations on different cognitive levels. The nature of the dimensional rule or attentional principle underlying monkeys’ RB learning is the theoretical issue raised by the present findings.

One interpretation is that reinforcement in RB tasks can attentionally shape the animal’s psychological space. In a size-rule task (density information irrelevant), reinforcement might sharpen size discrimination thresholds, stretching that axis, separating Category

A and B ellipses, easing discrimination and classification. Reinforcement might dull density discrimination thresholds, shrinking that axis, moving generalization ellipses toward training ellipses, easing generalization. Any low-level selective-attention mechanism could accomplish this, absent an explicit or declarative dimensional rule. Thus, one need only grant macaques the basic capacity to orient attention, adjusting psychological space adaptively—elastically.

Choosing this minimal interpretation would have striking theoretical implications. Pigeons apparently do not dissociate II and RB tasks as capuchin monkeys, rhesus macaques, and humans do. Figure 7a shows performance—from the beginning of training—by eight II-learning pigeons and eight RB-learning pigeons. There is no RB advantage. The curves’ waviness arises because pigeons were removed from the task at criterion, so still-learning birds were graphed alone. Figure 7b shows performance backward from the criterial block, aligning across birds the approach to criterion. There is still no RB advantage. Rather, pigeons seem to have performed two category tasks of the same character and learnability. Smith et al. (2011) comprised two independent studies



**Figure 7.** Pigeons performing information-integration (II) and rule-based (RB) tasks. (a) The proportion of correct responses in each session from the onset of learning forward for eight II-learning pigeons (open triangles) and eight RB-learning pigeons (filled squares). (b) The proportion of correct responses in each session from the criterial block backward for eight II-learning pigeons and eight RB-learning pigeons. “Implicit and Explicit Categorization: A Tale of Four Species,” by Smith, Berg, et al., 2012, *Neuroscience and Biobehavioral Reviews*, 36, p. 2364. Adapted with permission from Elsevier.

conducted in different countries but with perfect convergence. R. G. Cook (personal communication, December 2014) has now found this result for a third time.

If we ascribe monkeys’ II–RB dissociation to the most basic selective-attention capacity, then we would conclude that pigeons do not dissociate the tasks because they lack that capacity. We would say that they lack a central attention-allocation ability, that they are global/holistic processors, that they are nonanalytic category learners. This would be a strong, interesting, and controversial conclusion. But there is a general principle at work here. Whatever is the minimum explanation that one puts in place to grant macaques their II–RB dissociation, one would provisionally deny that capacity to pigeons, and probably to many other vertebrate lineages, too. In this literature, the choice for minimalism in interpretation cuts two ways—quite sharply.

This choice could be correct. Pearce, Esber, George, and Haselgrove (2008) produced convergent findings that indicated a failure of selective attention to dimensions by pigeons. This result led them to question—as a matter of their own acute theoretical disappointment—whether pigeons possess central attention-allocation processes, which of course would be essential to any category-learning system that could find generalizable dimensional solutions to category tasks. Their findings and interpretation converge with those in Smith et al. (2011).

In addition, if pigeons have a unitary categorization system that does not distinguish II and RB tasks, then they—unlike primates—should show faltering generalization to untrained stimulus contexts for both II and RB tasks. Our pilot research has suggested that categorization by pigeons does falter in RB tasks on extension to new regions of the stimulus space.

Our goal in noting the convergence between Smith et al. (2011) and Pearce et al. (2008) is not to attack anything—certainly not pigeons. Therefore, we state clearly that there is reason to question

the denial to pigeons of a basic selective-attention mechanism. Pigeons have shown selective-attention effects in some studies (e.g., Blough, 2012; Riley & Leith, 1976; Riley & Roitblat, 1978; Sutherland & Mackintosh, 1971; Thomas, 1970; Zentall, 2005, 2012).

Yet the II–RB results stand at odds with these results: Because, if pigeons have a basic selective-attention capacity, and if that capacity powers macaques’ II–RB dissociation, then why is that system not available to power pigeons’ II–RB dissociation. There is another comparative principle at work here. We can grant pigeons their basic selective-attention capacity, as many would prefer, if we grant that macaques’ and humans’ II–RB dissociation has an origin in some different or higher level dimensional principle in categorization.

In fact, there is another level on which one could place the attentional principle or dimensional rule that macaques bring to RB tasks. Antzoulatos and Miller (2014) illustrated this theoretical perspective. They simultaneously recorded from multiple electrodes in two crucial learning centers—the dorsal striatum and lateral prefrontal cortex (PFC). Striatal activity was a strong predictor of performance governed by specific stimulus response (SR) associations, as would account for II performance across species in many studies. PFC was the strong predictor of performance governed by true classification that transcended SR association, a transcendence consistent with a higher-level dimensional principle at work in RB tasks. Antzoulatos and Miller concluded that the striatum and PFC, respectively, play greater roles in SR association and category abstraction. Their work provides a possible neuroscience perspective on the distinction we are exploring behaviorally in humans and macaques. It is consonant with ideas about the striatum’s role in learning (e.g., Arbuthnott, Ingham, & Wickens, 2000; Mishkin, Malamut, & Bachevalier, 1984; Rolls, 1994; Wickens, 1993), with the neuroscience underlying II–RB

research (e.g., Ashby, Alfonso-Reese, Turken, & Waldron, 1998; Maddox & Ashby, 2004), and with the literature on explicit executive cognition (e.g., Alexander, DeLong, & Strick, 1986; Elliott & Dolan, 1998; Goldman-Rakic, 1987; Kolb & Whishaw, 1990; Posner & Petersen, 1990; Rao et al., 1997; Robinson, Heaton, Lehman, & Stilson, 1980). It is consonant with the theoretical idea that regularities in a categorization task, as adaptive behavior establishes itself, engender cortical loops that focus attention on the perceptual feature that distinguishes the categories. This would create a category “rule” with some abstractness and stimulus independence but without language and symbolic detachment. Pigeons might naturally not have homologs of these cortical rule loops. But, on this view, they would retain a basic selective-attention capability that would express itself in some tasks, *but would not express itself in an II–RB dissociation*.

This theoretical account explains a great deal. It also has important implications for comparative psychology. It would allow for the possibility of dimensional rules in categorization even for species that are not verbal or symbolic. It would speak sharply against the frequent and harmful conflation among rules, hypotheses, and verbalization in the human literature—that is even sometimes used to question whether animals can represent rules and hypotheses. Of course, there might be nonverbal representational codes by which the brain can learn and generalize category principles and dimensional regularities in tasks.

This interpretation would also suggest something important about the emergence of humans’ explicit declarative system for rule learning. That emergence could have been gradual, in stages, from central attention mechanisms, to sustained control loops organizing dimensional behavior, to category rules in working memory, to declarative rules in reportable consciousness. Our overarching goal is to foster theoretical attention toward this progression or hierarchy of attentional–dimensional effects that could represent different processes and even different levels of cognition and awareness.

We stress that we have not shown fully abstract category rules in macaques. We continued trial-by-trial reinforcement for the humans and monkeys into generalization, so their ongoing learning was supported throughout. We did not test whether they would have available a category rule that could extend to new stimuli when direct reinforcement was never provided to the new stimuli. This would be a stronger test of abstractness and generalizability, and we do not know whether macaques could pass it. We also did not test whether macaques’ rules are held in working memory and awareness, or whether they are declarative—that is, reportable to external observers through some kind of dimensional report icon. But, on both fronts, we believe the II–RB approach is still constructive and productive, bringing one closer to answering these empirical questions by making it clear that one should ask these empirical questions.

It is an intriguing evolutionary question why the psychological privilege for dimensional rules arose in categorization systems, as happened at least in primates. There must have been advantages in attentional focusing, dimensional analysis, and guiding performance principles with stimulus independence. One can see how these independent task principles could have been a useful alternative learning system that also could have allowed the eventual use of rules, hypotheses, and finally their declarative–communicative representation. Thus, we believe that the emer-

gence of the dimensional-analytic categorization system may have been an important milestone in cognitive evolution.

We also believe that comparative research in this area has the potential to foster a useful dialog with neuroscience research, as well illustrated by the research of Antzoulatos and Miller (2014). For it will be productive to compare macaques’ and humans’ categorization competence and limits—especially for dimensional rules—and to relate these to the differential development of brain systems that serve category learning in different species. This could illuminate the structure of these capacities in human cognition, their earliest (nonverbal) expression in human development, and the special affordances of human language, all with implications for neuropsychology and cognitive development.

## References

- Ahn, W. K., & Medin, D. L. (1992). A two-stage model of category construction. *Cognitive Science*, *16*, 81–121. [http://dx.doi.org/10.1207/s15516709cog1601\\_3](http://dx.doi.org/10.1207/s15516709cog1601_3)
- Alexander, G. E., DeLong, M. R., & Strick, P. L. (1986). Parallel organization of functionally segregated circuits linking basal ganglia and cortex. *Annual Review of Neuroscience*, *9*, 357–381. <http://dx.doi.org/10.1146/annurev.ne.09.030186.002041>
- Antzoulatos, E. G., & Miller, E. K. (2014). Increases in functional connectivity between prefrontal cortex and striatum during category learning. *Neuron*, *83*, 216–225. <http://dx.doi.org/10.1016/j.neuron.2014.05.005>
- Arbuthnott, G. W., Ingham, C. A., & Wickens, J. R. (2000). Dopamine and synaptic plasticity in the neostriatum. *Journal of Anatomy*, *196*, 587–596. <http://dx.doi.org/10.1046/j.1469-7580.2000.19640587.x>
- Ashby, F. G., Alfonso-Reese, L. A., Turken, A. U., & Waldron, E. M. (1998). A neuropsychological theory of multiple systems in category learning. *Psychological Review*, *105*, 442–481. <http://dx.doi.org/10.1037/0033-295X.105.3.442>
- Ashby, F. G., & Ell, S. W. (2001). The neurobiology of human category learning. *Trends in Cognitive Sciences*, *5*, 204–210. [http://dx.doi.org/10.1016/S1364-6613\(00\)01624-7](http://dx.doi.org/10.1016/S1364-6613(00)01624-7)
- Ashby, F. G., & Gott, R. E. (1988). Decision rules in the perception and categorization of multidimensional stimuli. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *14*, 33–53. <http://dx.doi.org/10.1037/0278-7393.14.1.33>
- Ashby, F. G., & Maddox, W. T. (2011). Human category learning 2.0. *Annals of the New York Academy of Sciences*, *1224*, 147–161. <http://dx.doi.org/10.1111/j.1749-6632.2010.05874.x>
- Ashby, F. G., Maddox, W. T., & Bohil, C. J. (2002). Observational versus feedback training in rule-based and information-integration category learning. *Memory & Cognition*, *30*, 666–677. <http://dx.doi.org/10.3758/BF03196423>
- Ashby, F. G., Queller, S., & Berretty, P. M. (1999). On the dominance of unidimensional rules in unsupervised categorization. *Perception & Psychophysics*, *61*, 1178–1199. <http://dx.doi.org/10.3758/BF03207622>
- Ashby, F. G., & Valentin, V. V. (2005). Multiple systems of perceptual category learning: Theory and cognitive tests. In H. Cohen & C. Lefebvre (Eds.), *Handbook of categorization in cognitive science* (pp. 547–572). New York, NY: Elsevier. <http://dx.doi.org/10.1016/B978-008044612-7/50080-9>
- Ashby, F. G., & Waldron, E. M. (1999). On the nature of implicit categorization. *Psychonomic Bulletin & Review*, *6*, 363–378. <http://dx.doi.org/10.3758/BF03210826>
- Blough, D. S. (2012). Reaction-time explorations of visual perception, attention, and decision in pigeons. In T. R. Zentall & E. A. Wasserman (Eds.), *The Oxford handbook of comparative cognition* (pp. 674–690).

- New York, NY: Oxford University Press. <http://dx.doi.org/10.1093/oxfordhb/9780195392661.013.0006>
- Brooks, L. R. (1978). Nonanalytic concept formation and memory for instances. In E. Rosch & B. B. Lloyd (Eds.), *Cognition and categorization* (pp. 169–211). Hillsdale, NJ: Erlbaum.
- Casale, M. B., Roeder, J. L., & Ashby, F. G. (2012). Analogical transfer in perceptual categorization. *Memory & Cognition*, *40*, 434–449. <http://dx.doi.org/10.3758/s13421-011-0154-4>
- Cerella, J. (1979). Visual classes and natural categories in the pigeon. *Journal of Experimental Psychology: Human Perception and Performance*, *5*, 68–77. <http://dx.doi.org/10.1037/0096-1523.5.1.68>
- Cook, R. G., & Smith, J. D. (2006). Stages of abstraction and exemplar memorization in pigeon category learning. *Psychological Science*, *17*, 1059–1067. <http://dx.doi.org/10.1111/j.1467-9280.2006.01833.x>
- Dunn, J. C., Newell, B. R., & Kalish, M. L. (2012). The effect of feedback delay and feedback type on perceptual category learning: The limits of multiple systems. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *38*, 840–859. <http://dx.doi.org/10.1037/a0027867>
- Elliott, R., & Dolan, R. J. (1998). Activation of different anterior cingulate foci in association with hypothesis testing and response selection. *NeuroImage*, *8*, 17–29. <http://dx.doi.org/10.1006/nimg.1998.0344>
- Erickson, M. A., & Kruschke, J. K. (1998). Rules and exemplars in category learning. *Journal of Experimental Psychology: General*, *127*, 107–140. <http://dx.doi.org/10.1037/0096-3445.127.2.107>
- Feldman, J. (2000). Minimization of Boolean complexity in human concept learning. *Nature*, *407*, 630–633. <http://dx.doi.org/10.1038/35036586>
- Fukunaga, K. (1972). *Introduction to statistical pattern recognition*. New York, NY: Academic Press.
- Goldman-Rakic, P. S. (1987). Circuitry of the prefrontal cortex and the regulation of behavior by representational knowledge. In V. Mountcastle (Ed.), *Handbook of physiology* (Vol. 5, pp. 373–417). Bethesda, MD: American Physiological Society.
- Herrnstein, R. J., Loveland, D. H., & Cable, C. (1976). Natural concepts in pigeons. *Journal of Experimental Psychology: Animal Behavior Processes*, *2*, 285–302. <http://dx.doi.org/10.1037/0097-7403.2.4.285>
- Homa, D., Sterling, S., & Trepel, L. (1981). Limitations of exemplar-based generalization and the abstraction of categorical information. *Journal of Experimental Psychology: Human Learning and Memory*, *7*, 418–439. <http://dx.doi.org/10.1037/0278-7393.7.6.418>
- Jitsumori, M. (1994). Artificial polymorphous concepts in humans and nonhumans. In S. C. Hayes, L. J. Hayes, M. Sato, & K. Ono (Eds.), *Behavior analysis of language and cognition* (pp. 91–106). Oakland, CA: Context Press.
- Knowlton, B. J., & Squire, L. R. (1993). The learning of categories: Parallel brain systems for item memory and category knowledge. *Science*, *262*, 1747–1749. <http://dx.doi.org/10.1126/science.8259522>
- Kolb, B., & Whishaw, I. Q. (1990). *Fundamentals of human neuropsychology* (3rd ed.). New York, NY: Freeman.
- Kruschke, J. K. (1992). ALCOVE: An exemplar-based connectionist model of category learning. *Psychological Review*, *99*, 22–44. <http://dx.doi.org/10.1037/0033-295X.99.1.22>
- Lea, S. E. G., & Ryan, C. M. E. (1990). Unnatural concepts and the theory of concept discrimination in birds. In M. L. Commons, R. J. Herrnstein, S. M. Kosslyn, & M. B. Mumford (Eds.), *Behavioral approaches to pattern recognition and concept formation: Quantitative analyses of behavior* (Vol. 8, pp. 165–185). Hillsdale, NJ: Erlbaum.
- Maddox, W. T., & Ashby, F. G. (1993). Comparing decision bound and exemplar models of categorization. *Perception & Psychophysics*, *53*, 49–70. <http://dx.doi.org/10.3758/BF03211715>
- Maddox, W. T., & Ashby, F. G. (2004). Dissociating explicit and procedural-learning based systems of perceptual category learning. *Behavioural Processes*, *66*, 309–332. <http://dx.doi.org/10.1016/j.beproc.2004.03.011>
- Maddox, W. T., Ashby, F. G., & Bohil, C. J. (2003). Delayed feedback effects on rule-based and information-integration category learning. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *29*, 650–662. <http://dx.doi.org/10.1037/0278-7393.29.4.650>
- Maddox, W. T., & Ing, A. D. (2005). Delayed feedback disrupts the procedural-learning system but not the hypothesis-testing system in perceptual category learning. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *31*, 100–107. <http://dx.doi.org/10.1037/0278-7393.31.1.100>
- Medin, D. L., Wattenmaker, W. D., & Hampson, S. E. (1987). Family resemblance, conceptual cohesiveness, and category construction. *Cognitive Psychology*, *19*, 242–279. [http://dx.doi.org/10.1016/0010-0285\(87\)90012-0](http://dx.doi.org/10.1016/0010-0285(87)90012-0)
- Mishkin, M., Malamut, B., & Bachevalier, J. (1984). Memories and habits: Two neural systems. In G. Lynch, J. L. McGaugh, & N. M. Weinberger (Eds.), *Neurobiology of learning and memory* (pp. 65–77). New York, NY: Guilford Press.
- Murphy, G. L. (2002). *The big book of concepts*. Cambridge, MA: MIT Press.
- Newell, B. R., Dunn, J. C., & Kalish, M. (2010). The dimensionality of perceptual category learning: A state-trace analysis. *Memory & Cognition*, *38*, 563–581. <http://dx.doi.org/10.3758/MC.38.5.563>
- Newell, B. R., Moore, C. P., Wills, A. J., & Milton, F. (2013). Reinstating the frontal lobes? Having more time to think improves implicit perceptual categorization: A comment on Filoteo, Lauritzen, and Maddox (2010). *Psychological Science*, *24*, 386–389. <http://dx.doi.org/10.1177/0956797612457387>
- Nosofsky, R. M. (1987). Attention and learning processes in the identification and categorization of integral stimuli. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *13*, 87–108. <http://dx.doi.org/10.1037/0278-7393.13.1.87>
- Nosofsky, R. M., Palmeri, T. J., & McKinley, S. C. (1994). Rule-plus-exception model of classification learning. *Psychological Review*, *101*, 53–79. <http://dx.doi.org/10.1037/0033-295X.101.1.53>
- Nosofsky, R. M., Stanton, R. D., & Zaki, S. R. (2005). Procedural interference in perceptual classification: Implicit learning or cognitive complexity? *Memory & Cognition*, *33*, 1256–1271. <http://dx.doi.org/10.3758/BF03193227>
- Pearce, J. M., Esber, G. R., George, D. N., & Haselgrove, M. (2008). The nature of discrimination learning in pigeons. *Learning & Behavior*, *36*, 188–199. <http://dx.doi.org/10.3758/LB.36.3.188>
- Posner, M. I., & Petersen, S. E. (1990). The attention system of the human brain. *Annual Review of Neuroscience*, *13*, 25–42. <http://dx.doi.org/10.1146/annurev.ne.13.030190.000325>
- Rao, S. M., Bobholz, J. A., Hammelke, T. A., Rosen, A. C., Woodley, S. J., Cunningham, J. M., . . . Binder, J. R. (1997). Functional MRI evidence for subcortical participation in conceptual reasoning skills. *NeuroReport: An International Journal for the Rapid Communication of Research in Neuroscience*, *8*, 1987–1993. <http://dx.doi.org/10.1097/00001756-199705260-00038>
- Regehr, G., & Brooks, L. R. (1995). Category organization in free classification: The organizing effect of an array of stimuli. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *21*, 347–363. <http://dx.doi.org/10.1037/0278-7393.21.2.347>
- Riley, D. A., & Leith, C. R. (1976). Multidimensional psychophysics and selective attention in animals. *Psychological Bulletin*, *83*, 138–160. <http://dx.doi.org/10.1037/0033-2909.83.1.138>
- Riley, D. A., & Roitblat, H. L. (1978). Selective attention and related cognitive processes in pigeons. In S. H. Hulse, H. Fowler, & W. K. Honig (Eds.), *Cognitive processes in animal behavior* (pp. 249–276). Hillsdale, NJ: Erlbaum.
- Robinson, A. L., Heaton, R. K., Lehman, R. A. W., & Stilson, D. W. (1980). The utility of the Wisconsin Card Sorting Test in detecting and

- localizing frontal lobe lesions. *Journal of Consulting and Clinical Psychology*, 48, 605–614. <http://dx.doi.org/10.1037/0022-006X.48.5.605>
- Rolls, E. T. (1994). Neurophysiology and cognitive functions of the striatum. *Revue Neurologique*, 150, 648–660.
- Rosch, E., & Mervis, C. B. (1975). Family resemblances: Studies in the internal structure of categories. *Cognitive Psychology*, 7, 573–605. [http://dx.doi.org/10.1016/0010-0285\(75\)90024-9](http://dx.doi.org/10.1016/0010-0285(75)90024-9)
- Rosseel, Y. (2002). Mixture models of categorization. *Journal of Mathematical Psychology*, 46, 178–210. <http://dx.doi.org/10.1006/jmps.2001.1379>
- Schwarz, G. (1978). Estimating the dimension of a model. *Annals of Statistics*, 6, 461–464. <http://dx.doi.org/10.1214/aos/1176344136>
- Shepard, R. N., Hovland, C. I., & Jenkins, H. M. (1961). Learning and memorization of classifications. *Psychological Monographs: General and Applied*, 75, 1–42. <http://dx.doi.org/10.1037/h0093825>
- Smith, J. D., Ashby, F. G., Berg, M. E., Murphy, M. S., Spiering, B., Cook, R. G., & Grace, R. C. (2011). Pigeons' categorization may be exclusively nonanalytic. *Psychonomic Bulletin & Review*, 18, 414–421. <http://dx.doi.org/10.3758/s13423-010-0047-8>
- Smith, J. D., Beran, M. J., Crossley, M. J., Boomer, J., & Ashby, F. G. (2010). Implicit and explicit category learning by macaques (*Macaca mulatta*) and humans (*Homo sapiens*). *Journal of Experimental Psychology: Animal Behavior Processes*, 36, 54–65. <http://dx.doi.org/10.1037/a0015892>
- Smith, J. D., Berg, M. E., Cook, R. G., Murphy, M. S., Crossley, M. J., Boomer, J., . . . Grace, R. C. (2012). Implicit and explicit categorization: A tale of four species. *Neuroscience and Biobehavioral Reviews*, 36, 2355–2369. <http://dx.doi.org/10.1016/j.neubiorev.2012.09.003>
- Smith, J. D., Boomer, J., Zakrzewski, A. C., Roeder, J. L., Church, B. A., & Ashby, F. G. (2014). Deferred feedback sharply dissociates implicit and explicit category learning. *Psychological Science*, 25, 447–457. <http://dx.doi.org/10.1177/0956797613509112>
- Smith, J. D., Coutinho, M. V. C., Church, B. A., & Beran, M. J. (2013). Executive-attentional uncertainty responses by rhesus macaques (*Macaca mulatta*). *Journal of Experimental Psychology: General*, 142, 458–475. <http://dx.doi.org/10.1037/a0029601>
- Smith, J. D., Crossley, M. J., Boomer, J., Church, B. A., Beran, M. J., & Ashby, F. G. (2012). Implicit and explicit category learning by capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology*, 126, 294–304. <http://dx.doi.org/10.1037/a0026031>
- Smith, J. D., & Minda, J. P. (1998). Prototypes in the mist: The early epochs of category learning. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 24, 1411–1436. <http://dx.doi.org/10.1037/0278-7393.24.6.1411>
- Smith, J. D., Minda, J. P., & Washburn, D. A. (2004). Category learning in rhesus monkeys: A study of the Shepard, Hovland, and Jenkins (1961) tasks. *Journal of Experimental Psychology: General*, 133, 398–414.
- Smith, J. D., Redford, J. S., & Haas, S. M. (2008). Prototype abstraction by monkeys (*Macaca mulatta*). *Journal of Experimental Psychology: General*, 137, 390–401. <http://dx.doi.org/10.1037/0096-3445.137.2.390>
- Stanton, R. D., & Nosofsky, R. M. (2007). Feedback interference and dissociations of classification: Evidence against the multiple-learning-systems hypothesis. *Memory & Cognition*, 35, 1747–1758. <http://dx.doi.org/10.3758/BF03193507>
- Sutherland, N. S., & Mackintosh, N. J. (1971). *Mechanisms of animal discrimination learning*. New York, NY: Academic Press.
- Thomas, D. R. (1970). Stimulus selection, attention, and related matters. In J. H. Reynierse (Ed.), *Current issues in animal learning* (pp. 311–356). Lincoln, NE: University of Nebraska Press.
- Vauclair, J. (2002). Categorization and conceptual behavior in nonhuman primates. In M. Bekoff, C. Allen, & G. M. Burghardt (Eds.), *The cognitive animal: Empirical and theoretical perspectives on animal cognition* (pp. 239–245). Cambridge, MA: MIT Press.
- Washburn, D. A., & Rumbaugh, D. M. (1992). Testing primates with joystick-based automated apparatus: Lessons from the Language Research Center's Computerized Test System. *Behavior Research Methods, Instruments & Computers*, 24, 157–164. <http://dx.doi.org/10.3758/BF03203490>
- Wasserman, E. A., Kiedinger, R. E., & Bhatt, R. S. (1988). Conceptual behavior in pigeons: Categories, subcategories, and pseudocategories. *Journal of Experimental Psychology: Animal Behavior Processes*, 14, 235–246. <http://dx.doi.org/10.1037/0097-7403.14.3.235>
- Wickens, J. (1993). *A theory of the striatum*. New York, NY: Pergamon Press.
- Zentall, T. R. (2005). Selective and divided attention in animals. *Behavioural Processes*, 69, 1–15. <http://dx.doi.org/10.1016/j.beproc.2005.01.004>
- Zentall, T. R. (2012). Selective and divided attention in birds. In O. F. Lazareva, T. Shimizu, & E. A. Wasserman (Eds.), *How animals see the world: Comparative behavior, biology, and evolution of vision* (pp. 351–369). New York, NY: Oxford University Press. <http://dx.doi.org/10.1093/acprof:oso/9780195334654.003.0020>
- Zentall, T. R., Wasserman, E. A., Lazareva, O. F., Thompson, R. K. R., & Rattermann, M. J. (2008). Concept learning in animals. *Comparative Cognition & Behavior Reviews*, 3, 13–45. <http://dx.doi.org/10.3819/ccbr.2008.30002>

Received February 27, 2015

Revision received May 12, 2015

Accepted May 13, 2015 ■