The Transfer of Category Knowledge by Macaques (Macaca mulatta) and Humans (Homo sapiens)

Alexandria C. Zakrzewski University of Richmond

Barbara A. Church and J. David Smith Georgia State University

Cognitive psychologists distinguish implicit, procedural category learning (stimulus-response associations learned outside declarative cognition) from explicit-declarative category learning (conscious category rules). These systems are dissociated by category learning tasks with either a multidimensional, information-integration (II) solution or a unidimensional, rule-based (RB) solution. In the present experiments, humans and two monkeys learned II and RB category tasks fostering implicit and explicit learning, respectively. Then they received occasional transfer trials—never directly reinforced—drawn from untrained regions of the stimulus space. We hypothesized that implicit-procedural category learning—allied to associative learning—would transfer weakly because it is yoked to the training stimuli. This result was confirmed for humans and monkeys. We hypothesized that explicit category learning—allied to abstract category rules—would transfer robustly. This result was confirmed only for humans. That is, humans displayed explicit category knowledge that transferred flawlessly. Monkeys did not. This result illuminates the distinctive abstractness, stimulus independence, and representational portability of humans' explicit category rules.

Keywords: category learning, category rules, associative learning, primate cognition, macaques

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Categorization is a focus of animal and human research (e.g., Ashby & Maddox, 2011; Feldman, 2000; Herrnstein, Loveland, & Cable, 1976; Jitsumori, 1994; Murphy, 2002; Rosch & Mervis,

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Correspondence concerning this article should be addressed to Alexandria Clay Zakrzewski, Department of Psychology, University of Richmond, Richmond Hall, 28 Westhampton Way, Virginia 23173. E-mail: azakrzew@richmond.edu 1975; Smith, Redford, & Haas, 2008; Wasserman, Kiedinger, & Bhatt, 1988), naturally so because it is an essential adaptation for organizing learning and behavior. Categorization may be so essential that animals have multiple complementary category-learning systems that manage category problems of different kinds. In fact, multiple-systems theory formalizes this theoretical proposal about humans (Ashby & Ell, 2001; Cook & Smith, 2006; Erickson & Kruschke, 1998; Homa, Sterling, & Trepel, 1981; Nosofsky, Palmeri, & McKinley, 1994; Rosseel, 2002; Smith & Minda, 1998). Here, we apply this proposal across species.

One multiple-systems idea distinguishes implicit-procedural category learning from explicit-declarative category learning (Ashby & Maddox, 2011; Ashby & Waldron, 1999; Maddox & Ashby, 2004; Smith, Berg, et al., 2012). The implicit-procedural system has the following characteristics. It learns gradually by associating whole stimuli to appropriate responses. It uses processes like those of associative learning. It uses primary reinforcement systems in the brain to strengthen stimulus-response connections. This implicit-procedural category "knowledge" is held unconsciously and nondeclaratively (the implicit aspect) as a motor response skill (the procedural aspect). The explicit-declarative system has the following characteristics. It learns by testing rules about relevant features. It holds rules in working memory. These rules summarize category knowledge that is typically conscious and declarative. We note that this idea of explicit category rules is certainly not ours alone. Over decades, many researchers have granted rules an important role in human categorization (Ahn & Medin, 1992; Ashby & Ell, 2001; Bruner, Goodnow, & Austin, 1956; Erickson & Kruschke, 1998; Feldman, 2000; Medin, Wattenmaker, & Hampson, 1987; Nosofsky et al., 1994; Regehr & Brooks, 1995; Shepard, Hovland, & Jenkins, 1961). In the present article, our value added will be to consider the cognitive-

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Alexandria C. Zakrzewski, Department of Psychology, University of Richmond; Barbara A. Church, Language Research Center, Georgia State University; J. David Smith, Department of Psychology, Georgia State University.

representational character of category rules and also their species breadth.

Explicit and implicit categorization can be differentiated using rule-based (RB) and information-integration (II) category tasks (see Figure 1). Each Category A stimulus (i.e., each gray square) and each Category B stimulus (i.e., each black circle) would be formally defined as an x, y coordinate pair within the stimulus space. It would then be concretely presented to participants as a bidimensional perceptual stimulus instantiating conjointly those x and y values. The RB tasks (Figure 1a and 1c) present Category A and Category B sets of exemplars that are fully separated along one perceptual dimension so that a vertical or horizontal line through the space perfectly partitions the exemplar sets. Variation along the other perceptual dimension is irrelevant to categorization. Participants learning in RB tasks are able to verbalize the dimensional basis for their categorization responses because their category knowledge is explicit and declarative (Ashby, Alfonso-Reese, Turken, & Waldron, 1998). The II tasks (Figure 1b and 1d) present Category A and Category B sets of exemplars that are separated along the diagonals of the stimulus space. Dimensions *x* and *y* offer partial information for categorization that must be integrated into the category decision. Unidimensional rules (i.e., vertical or horizontal category boundaries) are unworkable—they would partition the stimulus space wrongly and produce many categorization errors. In this task, participants optimally need to associate appropriate category responses to particular stimuli. Participants learning II categories are not able to verbalize the basis of their categorization responses because their learning is implicit and procedural (e.g., see Casale, Roeder, & Ashby, 2012, Footnote 1). We point out that in both RB and II tasks, participants never see the whole stimulus space displayed as in Figure 1. They see single stimuli, respond, receive feedback, and learn trial by trial.

We adopt this RB–II framework in this article for several reasons. RB and II tasks are a constructive minimal-contrast pair in categorization. Their categories are matched for size, class discriminability (e.g., d'), within-category exemplar similarity,

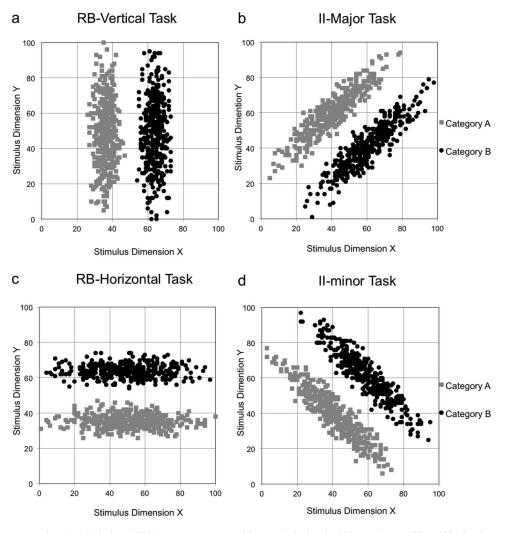


Figure 1. (a, c) Rule-based (RB) category structures illustrated, depicted within an abstract 100×100 stimulus space. The gray and black symbols, respectively, indicate Category A and Category B stimuli. (b, d) Information-integration (II) category structures, depicted in the same way. Adapted from Smith et al. (2014) by the Association for Psychological Science. Reprinted with permission.

between-category exemplar separation, and so forth. The tasks are simply angular rotations of one another through stimulus space. There is no objective a priori difficulty difference between them (Smith et al., 2014). These tasks also show many empirical dissociations—in brain imaging studies, in studies with neuropsychological patient populations, and in behavioral studies (Ashby, Maddox, & Bohil, 2002; Ashby, Queller, & Berretty, 1999; Maddox & Ashby, 2004; Maddox, Ashby, & Bohil, 2003; Maddox & Ing, 2005).

Using these tasks, we evaluate whether monkeys performing RB tasks possess a mental-representational analog of humans' explicit category rules that is abstract and generalizable. We test this by measuring spontaneous transfer to untrained stimulus contexts for which no direct reinforcement has ever been provided. We can describe now the dissociation in representational abstractness that we explored. First, responses in II tasks, conditioned by reinforcement during training, should be welded to the original trained stimuli and less transferable to new stimuli (save some transfer through similarity-based generalization). Moreover, II (implicit) learners should have only the ability to make stimulus-occasioned category responses. They would lack the conscious access to their category knowledge that might also support transfer to new stimuli. Second, in contrast, responses in RB tasks, if organized by a rule maintained in working memory, should be less tied to the original trained contexts and more transferable to new stimuli. Moreover, because category rules are not tied by conditioning to stimuli, but are rules *about* stimuli, discovered *from* stimuli, they might have stimulus independence. They might have the representational form of an abstract rule that would be generalizable.

Our exploration of the transferability of implicit and explicit category knowledge complements that in Casale et al. (2012). They used category structures like those already shown in Figure 1. However, they broke the category sets into halves so they would have a training task (e.g., an RB training task low in Figure 1a and an RB transfer task high in Figure 1a). Thus, they could determine whether category knowledge would spontaneously transfer to new and untrained stimuli. This training-transfer methodology is described below. Casale et al.'s stimuli were sine wave gratings that varied in spatial frequency and in the radial orientation of alternating dark and light bars within circular stimuli (spatial-frequency and orientation, respectively, would correspond to the x and y axes in Figure 1). In transfer, Casale et al. suddenly gave participants 100% untrained stimuli by transferring them from trained to transfer stimulus distributions. Casale et al. told participants they would be given a "new set of categories." In their strongest experiment (Experiment 3), Casale et al. gave no feedback in the transfer phase. Participants were on their own. Casale et al.'s human participants transferred RB category knowledge easily to new stimuli but not II category "knowledge." This transfer measure provides a strong test of true rule knowledge that could be applicable across species.

However, the Casale et al. paradigm itself applies poorly across species. For one thing, the unreinforced transfer phase in Casale et al.'s (2012) experiment—that works well with instructable psychology students—would force macaques to perform hundreds of unreinforced trials which in our experience they do not do. For another thing, we worried about the 100% sudden shift in the stimulus environment. We thought that this might engender, in humans and/or monkeys, a qualitative reorganization of categori-

zation performance instead of a transfer of existing category knowledge.

Our chosen paradigm addressed these issues. We presented familiar (trained) stimuli on most trials, encouraging the continuing application of existing category knowledge. We added transfer trials quietly and occasionally with no announcement, so that existing category knowledge would transfer spontaneously to those trials-if it could. We kept an ongoing presence of reinforcement to provide motivation and sustain performance. The periodic reinforcement signals gave assurance that existing category knowledge was still effective. The periodicity ensured that we never directly reinforced performance on novel transfer trials, so that new associative learning was not possible regarding these stimuli. We thought our complementary approach was worthwhile because it asked whether RB and II categorization, while ongoingly successful and familiar, would still show the strong differences in transfer that current theory predicts (Smith, Zakrzewski, et al., 2015). Our complementary approach was also ideally suited to monkeys because it sustained reinforcement (and task motivation) throughout the task.

To build our paradigm, we incorporated a comparative methodology called deferred-rearranged reinforcement (e.g., Smith, Beran, Redford, & Washburn, 2006) that has also been useful in human research (Smith et al., 2014). Participants completed trial blocks with no feedback. After each block, they received the reinforcements from all the block's correct trials together and then the timeouts from all error trials together. By this approach, we gave humans and monkeys periodic updates that their existing category knowledge was successful and worth sustaining. But, we also then had the freedom to introduce transfer trials. The sustained category knowledge would be applied to the new stimuli—maybe—and yet the participants would not know whether they had answered those trials "correctly." Thus, we could observe directly the uninstructed transferability of RB and II category knowledge.

What might we expect to observe under these conditions? One hypothesis is that RB and II learning would now generalize equally poorly. This would suggest that the two forms of learning are similar representationally (and associative in character). This would imply that it was only a jarring wholesale change of stimuli that gave RB learning special transfer properties in Casale et al. (2012). Another hypothesis is that humans might continue to show distinctive RB transfer based on true category rules, but monkeys would not. This dissociation would demonstrate the cognitive sophistication of humans' category rules and show that monkeys lack some of the abstract representational properties of true rules.

Experiment 1: Humans

Method

Participants. Ninety-five undergraduates with normal or corrected vision ($M_{age} = 19.0$ years; 48% male, 52% female) participated to fulfill a course requirement at the University at Buffalo. The experiment was approved by the University at Buffalo's Institutional Review Board. Adequate sample size for comparing RB and II performance was determined based on previous research (Smith et al., 2014), and a stopping rule of 15 usable participants per task was used. Participants were placed randomly into the RB-Vertical (RBv), RB-Horizontal (RBh), II-Major (IIM), or II-

minor (IIm) task based on their sequential participant number. These four tasks are shown in Figure 1. Due to performance criteria during Phase 1 (see Procedure), several participants did not complete the experiment in the allotted time (80 min). Following procedures in our previous studies, these participants (three RBv, six RBh, 19 IIM, seven IIm) were dropped. The final data set included 60 participants, 15 in each of the four tasks.

Stimuli. The stimuli were unframed rectangles containing green pixels presented on a black background in the computer screen's top center (see Figure 2). Rectangles varied in size as follows. A rectangle's width in pixels was given by 100 + the value of an abstract variable called *Level* that could vary from 0 to 120. The rectangle's height was equal to the width divided by 2, rounded to the nearest integer. Rectangle size is the *x*-axis in Figure 1's abstract stimulus spaces. The stimuli were shown on a 17-in. monitor with 800 × 600 pixel resolution no dashes resolution and viewed from about 24 in. Level 60 stimuli thus subtended a visual angle for participants of approximately 7.75°. There were 121 size levels (Level 0–120). Stimulus boxes varied from 100 × 50 screen pixels (Level 0) to 220 × 110 screen pixels (Level 120).

The rectangles also varied in proportional pixel density. That is, they varied in the proportion of pixels illuminated within a rectangle compared with the total possible pixels that could be illuminated within the rectangle. This variation was achieved as follows. The proportional pixel density of the rectangles was given by $0.05 \times 1.018^{\text{Level}}$. Here, too, Level was the value of an abstract variable that let us create a continuum of stimuli. Proportional density is the *y*-axis in Figure 1's stimulus spaces. For Level 0, proportional density was .05, or 5% of the total possible pixels that could be illuminated within the rectangle (e.g., 250 illuminated pixels compared to 5,000 total possible pixels in a 100 × 50 rectangle). For Level 120, proportional density was .4253 (43% of total pixels illuminated).

Category structures. We broke the category structures generally used in RB–II research (see Figure 1) into training and

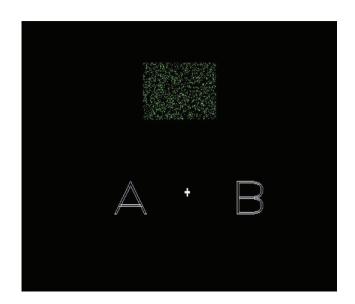


Figure 2. A category trial, with stimulus and response options shown. Stimulus rectangles varied in size and density, as described in subsection Stimuli. See the online article for the color version of this figure.

transfer distributions to study participants' transfer of category knowledge (see Figure 3). Categories were defined by bivariate normal distributions along the abstract size and density dimensions. Individual category exemplars were chosen from these distributions using established procedures (Ashby & Gott, 1988). As category exemplars were selected as x, y coordinate pairs in the stimulus space, these abstract values (i.e., a 0-120 level of size and density) were transformed into concrete stimuli with two visual features (size, proportional density). Tables S3 and S4 (in the online supplementary materials) contain details about the statistical distributions of the training and transfer distributions for each experiment. For the RBv and RBh tasks, respectively, only the dimension of size or pixel density carried information relevant to the categorization task. For the IIm and IIM tasks, the dimensions of size and density both carried category-relevant information. II learning depended on mapping correct responses to particular stimulus configurations.

In Experiment 1, as shown in Figure 3, we extended the x and y dimensions to encompass stimulus levels 0 to 120. This contrasts with the 0 to 100 stimulus ranges shown in Figure 1. The training and transfer stimulus ellipses in Experiment 1, respectively, included Levels 1 to 80 and 81 to 120 (or, in the case of Figure 3d, 120-40 and 40-1). There was an important reason for this 80-40asymmetry. The stretched-out character of the training distributions made it nearly impossible for participants to reach the training criteria in the II tasks while using a suboptimal vertical or horizontal rule. This ensured that participants emerged from II training with stronger learning and a more appropriate partitioning of the categories-so then we could ascertain more sensitively the transfer properties of that type of learning. In a preliminary experiment that had training and transfer ellipses spanning 50 stimulus levels of a 101-level stimulus space, many II participants completed training without achieving the appropriate partitioning. This made an assessment of the transfer of "II learning" difficult because true II learning had never been achieved. This preliminary study is described in the online supplementary materials.

Categorization trials. Each trial consisted of a pixel box of the chosen size and density. Below each stimulus were a central cursor and the letters A and B to the left and right on the screen (see Figure 2). In each trial, participants assigned the stimulus to Category A or B by moving the cursor to the appropriate category label. Humans used the S and L keys on the keyboard to produce cursor movements.

Procedure. There were three phases. In Phase 1, participants categorized stimuli presented from the training stimulus distributions only. Feedback was immediate. In Phase 2, participants continued to categorize training distribution stimuli only, but now with deferred-rearranged feedback given after every block of six trials. In Phase 3, participants continued to receive deferred-rearranged feedback. Now, a small percentage of trials presented stimuli from the transfer distribution (i.e., transfer stimuli). These were novel stimuli that had not been seen before. They were also stimuli that had never received immediate reinforcement.

Phase 1 included training stimuli drawn from the 80-level (long) ellipses in Figure 3. Feedback was always given immediately upon response. Following correct responses, participants received a "whoop" sound and +1 point. Following incorrect responses, participants received an 8-s timeout accompanied by a 2-s "buzz" sound and -1 point. Following feedback, participants' cumulative

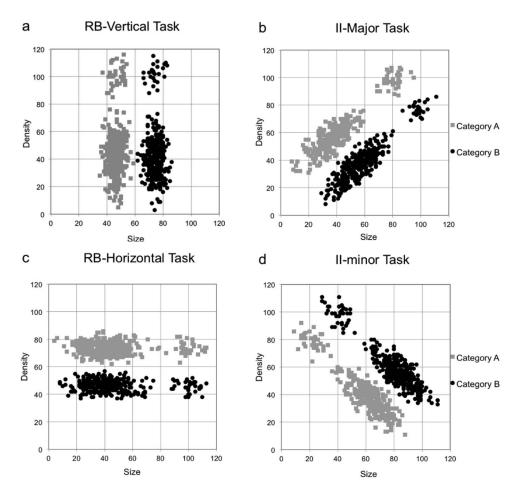


Figure 3. The category structures used in Experiment 1, depicted in the same way as Figure 1. In training, all trials presented stimuli from the (long) ellipses, which extended 80 stimulus levels, preventing participants from using suboptimal rule-based (RB) strategies during training in the information integration (II) tasks (b, d). In transfer, 25% of the trials presented stimuli from the (short) ellipses, which encompassed 40 stimulus levels.

points were displayed in white text. Participants had to complete 300 trials *and* perform above 87% correct in the most recent 60 trials. Phase 2 tested the same stimulus distributions for 96 trials. But now participants received feedback that was deferred and rearranged by trial outcome (hereafter, deferred feedback). After each response, the program simply gave the next trial. At the block's end, the participant received their positive outcomes grouped together (several whoops separated by 0.5 s for correct responses), then their negative outcomes grouped together (several buzzes paired with 4-s timeouts for incorrect responses). Their accumulated points were updated. The next trial block followed. Phase 3 contained 250 trials receiving deferred feedback, with 75% of the stimuli still drawn from the trained (long) stimulus ellipses and 25% drawn from the transfer (short) stimulus ellipses. Phase 3 began with no visible break for participants.

The session ended after 80 min or when all three phases were completed. Those who completed all three phases were included for analysis.

Instructions. Participants were told that they would categorize pixel boxes as A or B, and that at first they would have to guess but later would learn to respond correctly. They were told

that for correct and incorrect responses, respectively, they would hear a whoop and earn a point, or hear a buzz, and lose a point, and receive a timeout. Entering Phase 2, participants were told that they would now receive their positive and negative feedback outcomes clustered separately. They were told they would still gain/lose points for correct/incorrect answers, so that they should still classify accurately. Phase 3 was not delineated in any way for participants.

Formal modeling. We fit rule-learning and procedurallearning formal models (Maddox & Ashby, 1993) to the data for each phase and each participant. In Phase 3, we modeled data from the trained and transfer stimuli separately to clarify how participants' decision strategies transferred to new regions of the stimulus space. The rule-learning model assumes that participants set a criterion on one stimulus dimension, producing a vertical or horizontal category boundary. The modeling lets us specify the horizontal or vertical line that would best partition the participant's Category A and B responses. The rule-learning model has two free parameters: a perceptual noise variance and a criterion value on the relevant dimension. The procedural-learning model summarizes across the stimulus–response associations that a participant produced to estimate a category partition that the model expresses as a category boundary. The modeling lets us specify the line—a line of any slope and intercept—that best partitions the participant's Category A and B responses. However, as we discuss in more detail later, there is no presumption that the participant learned or used or mentally represented this boundary. The procedurallearning model has three free parameters: a perceptual noise variance and the slope and intercept of the decision bound.

We estimated the best-fitting values for these free parameters using the method of maximum likelihood (details in Maydeu-Olivares, 2017; Pan & Fang, 2002). The fitting process evaluated which model would have created—with maximum likelihood—the distribution of Category A and B responses that the participant produced. Following our previous work, the best-fitting model was chosen as the one with the smallest Bayesian Information Criterion (BIC, Schwarz, 1978).

Results

Accuracy-based analyses. Accuracy and modeling results are presented separately, though their combined perspective is best for interpreting the results. Table 1 shows average proportion correct achieved in the three phases of four categorization tasks (Phase 1: last 100 trials, Phase 2: all 96 trials, Phase 3: trained and transfer stimuli summarized separately from all 250 trials).

Phase 1's learning criterion ensured high accuracy. Ending Phase 1, proportion correct averaged .955 (SD = .053) and .886 (SD = .052) for RB and II participants, respectively. The RB advantage is common in this research area. It supports the theoretical distinction drawn between II and RB learning, being consistent with the idea that RB performance is protected and advantaged by the application of a rule.

Performance remained high in Phase 2 with deferred feedback. Average proportion correct was now .949 (SD = .047) and .838 (SD = .068) for RB and II, respectively, with the RB participants showing a 1% drop from Phase 1 and the II participants a 5% drop. RB learning, more than II learning, is robust to deferred feedback, probably because the category knowledge is held as an explicit-verbalizable rule in working memory. All that rule needs is the occasional signal that things are going well, and deferred feedback provides that signal (Smith et al., 2014). Phase 2 accomplished its goal to instantiate deferred feedback stably before introducing transfer trials.

Accuracy-based analyses: Generalization to transfer stimuli. Phase 3 contains the experiment's crucial results contrasting per-

Table 1

Average Proportion Correct and Standard Deviations by Phase
and Task and by Stimulus Type in Experiment 1 (Humans)

	Phase 1		Phase 3	
Task	(last 100 trials)	Phase 2	Trained	Transfer
II-major	.882 (.053)	.815 (.066)	.762 (.100)	.594 (.077)
II-minor	.890 (.054)	.862 (.064)	.786 (.061)	.608 (.110)
RB-horizontal	.937 (.069)	.940 (.055)	.950 (.038)	.910 (.082)
RB-vertical	.973 (.020)	.958 (.036)	.970 (.035)	.968 (.036)

Note. II = information-integration (Figure 3b and 3d); RB = rule-based (Figure 4a and 4c). Standard deviation values are shown in parentheses.

formance on trained and transfer stimuli. We entered the proportion correct of trained and transfer stimuli during Phase 3 into a two-factor general linear model (GLM) with categorization task (RB, II) as a between-participants factor and stimulus type (trained, transfer) as a within-participants factor. The analysis found a significant main effect for task, F(1, 58) = 327.551, p <.001, $\eta_p^2 = .850$, with RB proportion correct (M = .950, SD =.056) higher overall than II proportion correct (M = .688, SD =.123). There was also a significant main effect for stimulus type, F(1, 58) = 62.311, p < .001, $\eta_p^2 = .518$, with performance on trained stimuli (M = .867, SD = .113) higher overall than performance on transfer stimuli (M = .770, SD = .189). Most importantly, there was a significant Task × Stimulus Type interaction, F(1, 58) = 38.287, p < .001, $\eta_p^2 = .398$, confirming that II performance selectively faltered on transfer stimuli.

Two planned comparison t tests examined further the significant Task \times Stimulus Type interaction. When SDs differed by .02 or more, Welch's t test, robust to unequal variance, was used. First, RB participants on average had proportions correct of .960 (SD =.037) and .939 (SD = .069) on trained and transfer stimuli, respectively. There were no significant differences between trained and transfer performance in the RB tasks, Welch's t(44.595) =2.148, p = .150, Cohen's d = 0.357. These results confirm that the generalization of RB category knowledge to transfer stimuli was nearly perfect. Second, II participants on average had proportions correct of .774 (SD = .082) and .601 (SD = .093) on trained and transfer stimuli, respectively. There was a large and significant drop in performance on transfer stimuli compared with trained stimuli in the II tasks, t(29) = 8.025, p < .001, Cohen's d = 1.476. See the online supplementary materials for similar results from additional analyses using arcsine square root transformations.

Model-based analyses. We fit rule-learning (*x*-rule, *y*-rule), procedural-learning, and guessing models to participants' last 100 Phase 1 trials, to all 96 Phase 2 trials, and separately to all trained and transfer stimuli in Phase 3's 250 trials. Table 2 contains details of the modeling results. The modeling yields the best-fitting decision boundary that represents the partition between the categories that the subject actually achieved. To be clear, this boundary summarizes category performance. Participants may not learn this boundary, or use this boundary, or make this boundary any part of their category knowledge. For example, in the case of II learning, participants learn stimulus–response associations, the correct A–B response to many particular stimuli. This produces a category partition that the model captures as a boundary, and that we draw in the figures later, but this boundary has no necessary place in the person's category knowledge.

In Phase 1, 20 of 30 RB participants showed an appropriate (vertical or horizontal) RB boundary and 26 of 30 II participants showed an appropriate (major or minor) diagonal boundary. These strategies were sustained in Phase 2, wherein 25 of 30 RB participants were best fit by the rule-learning model and 23 of 30 II participants were best fit by the procedural-learning model. Most participants were able to keep applying their existing category knowledge despite the deferred feedback.

For trained stimuli in Phase 3, the pattern of optimal decision bounds was sustained: 28 of 30 RB participants used category rules and 20 of 30 II participants used procedural-learning strategies. The black lines in Figure 4a and 4c show the best-fitting decision bounds for trained stimulus trials in RB tasks. It is clear

Table 2

Best-Fitting Models for Experiment 1 (Humans): The Number of Participants Best Fit by Each Model by Phase and Task and by Stimulus Type in Phase 3

Best-fitting model	RBh	RBv	IIM	IIm
Phase 1 (last 100 trials)				
x-Rule		11	_	_
y-Rule	9		2	2
Integration	6	4	13	13
Guessing		_	_	
Phase 2				
<i>x</i> -Rule		12	_	
y-Rule	13	_	4	3
Integration	2	3	11	12
Guessing	_			
Phase 3 (trained)				
<i>x</i> -Rule		15	_	
y-Rule	13	_	5	4
Integration	2	_	9	11
Guessing			1	_
Phase 3 (transfer)				
x-Rule		14	3	4
y-Rule	14		6	8
Integration	1	1	1	1
Guessing	_		5	2

Note. RBh = rule-based horizontal; <math>RBv = rule-based vertical; IIM = information-integration major; IIm = information-integration minor. Numbers indicate number of participants best fit by each model.

that the performance of almost all participants reflected appropriate *y*-rule boundaries (for RBh) and *x*-rule boundaries (for RBv). The black lines in Figure 4b and 4d show the best-fitting decision bounds for trained stimulus trials in II tasks. These bounds reflected appropriate associative-learning strategies by most participants for the trained range of stimuli.

The gray lines in Figure 4 show the experiment's crucial result. The gray lines in Figure 4a and 4c show that for RBh and RBv participants, performance was consistent with an extension of appropriate *y* and *x* rules to transfer stimuli under deferred reinforcement. The extension was nearly perfect, and applied to the performance of *all but two* participants. But extension did not apply at all to II performance. Indeed, *all but two* participants reverted to suboptimal strategies, including substituting vertical and horizontal decision boundaries, guessing, and responding with extreme bias (gray lines, Figure 4b and 4d). The modeling results provide converging support to our accuracy findings.

We also analyzed participants whose best-fit model revealed a task-appropriate boundary for the trained stimuli presented in Phases 1, 2, and 3. We did this to test whether our results were somehow driven by participants who used suboptimal strategies through the experiment. In II tasks, 17 individuals had a diagonal decision boundary through the whole experiment for trained stimuli. However, there was still an enormous difference between proportions correct on trained stimuli (M = .823, SD = .052) and transfer stimuli (M = .624, SD = .090) in Phase 3, Welch's t(25.774) = 62.450, p < .001, Cohen's d = 1.930. Judging by this poor performance on transfer stimuli, even stable II participants failed to extend their decision bounds to the transfer region of the stimulus space.

In the RB task, 19 individuals sustained an appropriate best-fit rule-learning model through the whole experiment on trained stimuli. There was no significant difference in their proportions correct in Phase 3 on trained stimuli (M = .970, SD = .027) and transfer stimuli (M = .959, SD = .036), t(18) = 1.214, p = .241, Cohen's d = 0.282. Judging by their excellent performance on transfer stimuli, these participants did extend their optimal decisional bound to the transfer stimuli included in Phase 3.

Figure 5 shows decision bounds for trained and transfer stimuli during Phase 3 for those who maintained appropriate strategies for trained stimuli in all three phases, depicted in the same way as Figure 4. Of the 19 participants in the RB tasks who sustained appropriate unidimensional strategies during trained stimuli throughout the experiment, nine were in the RBv task (Figure 5a) and 10 were in the RBh task (Figure 5c). Of the 17 participants in II tasks who sustained appropriate II strategies during trained stimuli throughout the experiment, seven were in the IIM task (Figure 5b) and 10 were in the IIm task (Figure 5d).

The black lines in Figure 5 necessarily show task-appropriate boundaries because Figure 5 only includes participants whose best-fit model revealed a task-appropriate boundary for the trained stimuli presented in Phases 1, 2, and 3. The gray lines in Figure 5, on the other hand, show strategies during transfer stimuli in Phase 3 for these stable strategy users. The gray lines in Figure 5a and 5c show that all but one of these RB participants extended the appropriate x- and y-rule boundaries to transfer stimuli under deferred reinforcement. Like to the rest of the RB participants, they did so nearly perfectly. But, none of the II participants who were stable strategy users extended their diagonal decision boundaries successfully (Figure 5b and 5d). These results show that even for the most stable II learners in our experiment, II learning was welded to the original learning contexts, disallowing its extension to transfer stimuli. But for the stable RB learners, transfer was immediate, flexible, and flawless.

Experiment 2: Monkeys

Method

Experiment 2 replicated Experiment 1 with two rhesus monkeys. Some small methodological adjustments are described now.

Subjects. Male macaques (Macaca mulatta) Murph and Obi (23 and 13 years old, respectively) were tested. They had been trained, as described elsewhere (Washburn & Rumbaugh, 1992), to respond to computer-graphic stimuli by manipulating a joystick. They had participated in previous computerized experiments (Beran, Evans, Klein, & Einstein, 2012; Beran, Perdue, & Smith, 2014; Beran & Smith, 2011; Smith, Beran, Crossley, Boomer, & Ashby, 2010). Macaques were tested in their home cages at the Language Research Center (Georgia State University), with ad libitum access to the test apparatus, working when they chose to during long sessions. They had continuous access to water. They worked for fruit-flavored primate pellets. They received a daily diet of fruits and vegetables independent of task participation, and thus, they were not food deprived for the purposes of the experiment. This study complied with approved Georgia State University Institutional Animal Care and Use Committee protocols.

Murph was a subject in Smith et al.'s (2015) study, which used methods like those used here. Specifically, both tasks used unframed pixel box stimuli with identical size and pixel density levels, described later in subsection Stimuli. However, in the study

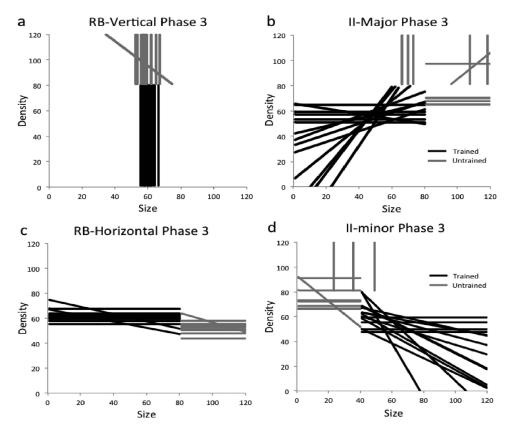


Figure 4. Decision bounds fitting Phase 3 trial responses for trained (black lines) and transfer (gray lines) stimuli in the (a) vertical rule-based (RB) task, (b) the major-diagonal information-integration (II) task, (c) the horizontal rule-based task, and (d) the minor-diagonal information-integration task. Participants with a best-fit model of guessing are not included in the figure.

by Smith et al. (2015), Murph's stimuli were green (in his RB task) and light red (in his II task). Here, Murph's stimuli were light blue (in his RB task) and yellow (in his II task). In Smith et al. (2015), Murph began with a RBv task in which the relevant dimension was size (x-axis). Category A was smaller and Category B was larger. During training, 100% of trials sampled stimuli from the bottom half of the y-dimension (density). At transfer, there was a sudden 100% shift to all transfer trials, which sampled stimuli from the top half of the y-dimension (density). Murph's second and final task in the study by Smith et al. (2015) was IIM. The A and B ellipses were switched and rotated to a 45° angle so that no transfer of knowledge from his previous RBv task could occur. During training, Murph was presented with stimuli from A and B ellipses on the lower/bottom half of both x (size) and y (density) dimensions. At transfer, 100% of all trials were sampled from the upper/top half of both x (size) and y (density) dimensions.

Four months and 16 days passed between the end of Murph's (IIM) transfer task in Smith et al. (2015) and the beginning of his (RBh) training in the present study. Here, Murph began with an RBh training task in which the relevant dimension was pixel box density (*y*-axis). Category A stimuli were denser and Category B stimuli were sparser. During training, 100% of trials sampled stimuli from the lower half of the *x*-dimension (size). At transfer, 10% of all trials sampled stimuli from the upper half of the *x*-dimension (size). Here, the transfer trials were introduced quietly

and unobtrusively within ongoing performance, instead of a sudden 100% shift to all transfer trials. Murph's second task in the present study was IIm. As before, the A and B ellipses were switched and rotated to a 45° angle. However, unlike the IIM task in Smith et al. (2015), during IIm training here, 100% of trials sampled stimuli from the upper half of the *x*-dimension (size) and lower half of the *y*-dimension (density). At transfer, 10% of all trials were sampled from the top half of the *y*-dimension (density) and bottom half of the *x*-dimension (size).

No knowledge could be carried from previous tasks into the present tasks. Murph's final task in Smith et al. (2015) was IIM (100% of stimuli from the transfer distribution) and his first task in the present study was RBh (100% of stimuli from the training distribution), again leaving no room for savings in learning. Finally, regardless of task or stimuli, Murph in Phase 1 had to prove his learning up to a 95% level, ensuring that the crucial manipulations of the experiment did not begin until he joined Obi at the same level of task mastery.

Small-sample primate research in comparative psychology. Experiment 2 typifies an experimental approach in comparative psychology that conducts an intensive investigation with a small number of animal participants. Here, the two monkeys completed 276,515 trials over two years to produce the experiment's data. Small-sample research has played a crucial role in comparative psychology's empirical success and theoretical development. It has

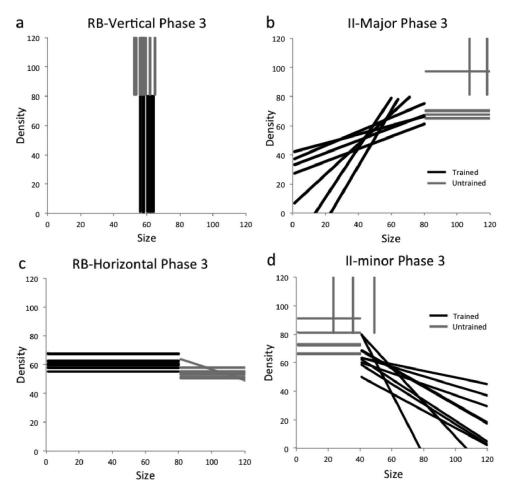


Figure 5. Decision bounds for trained (black lines) and transfer (gray lines) stimuli during Phase 3 for the 36 participants who had appropriate decision bounds for trained stimuli in all three phases, depicted in the same way as Figure 4. Participants with a best-fit model of guessing are not included in the figure. RB = rule-based; II = information-integration.

anchored the fields of ape language (Savage-Rumbaugh, 1986), parrot cognition (Pepperberg, 1983), dolphin language (Herman & Forestell, 1985), ape conceptual functioning (Boysen & Berntson, 1989), ape theory of mind (Premack & Woodruff, 1978), selfawareness (Gallup, 1982), animal metacognition (Smith et al., 1995), and other fields, too. Small-sample research serves especially well when an investigation is trial-intensive, when it has complex stages of testing, and when it involves a novel and difficult-to-train regimen of reinforcement. All of these factors are present in the current experiment. In similar situations, it is frequently adopted in human research, too (Kreutzer, Leonard, Flavell, & Hagen, 1975). It is especially prominent in studies of psychophysics. So, we believe that this research approach was well suited to the present investigation. We also believe that smallsample research will continue to play an important role in cognitive and comparative psychology-indeed, it may be a necessary way of the future. As the pressure increases to minimize the captive animals used in research, it may allow animal participants to still offer their profoundly important cognitive-science insights while encouraging researchers to design projects sensitively and

delicately. In this way, we can maximize beneficence, minimize our research "footprint," and adapt well to the present scientific environment.

Stimuli. There were 101 size levels (Levels 0–100). Stimulus boxes varied from 100×50 (Level 0) to 200×100 (Level 100). There were also 101 density levels. For Levels 0 and 100, respectively, proportional density was .05 and .2977 (5% and 30% of total pixels illuminated). Obi's II and Murph's RB tasks used light-blue stimuli. Obi's RB and Murph's II tasks used yellow stimuli. We changed stimulus color between RB and II tasks to lessen task confusion. Stimulus color remained the same through all three phases of each task. The use of 101 stimulus levels followed on previous II–RB research with animals. It also seemed appropriate for this reason. Monkeys' "category-rule" system is likely less cognitively intrusive and dominant than that of humans, so monkeys need less the extra insulation against adventitious rules that humans require.

Category structures. The training and transfer stimulus ellipses, respectively, included Levels 0 to 50 and 51 to 100 (see

Figure 6). We closely monitored Murph and Obi's performance during training to ensure that both monkeys' performance reflected the appropriate diagonal decision strategy in the II task before the next phase. This monitoring was not so easily done with humans, who completed all three phases within one experimental session. This is another reason why humans were given insulating 80-level training ellipses that discourage adventitious rules.

Categorization trials. The trials were presented just as for humans. The macaques controlled a white cursor on the screen with their joystick, moving it to make categorization responses. For each trial, 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. This was their trial start response documenting their trial readiness.

Procedure. Murph and Obi completed both RB and II tasks, with three phases in each task. We counterbalanced the order of RB and II tasks, with Murph starting with the RB task and Obi starting with the II task. If either monkey used knowledge from the previous task, they would perform poorly. Each phase began with no warning. Phase 1 included training stimuli drawn from the training ellipses in Figure 6. Feedback was always given immediately upon response. Following correct responses, monkeys received a "whoop" sound and a pellet. Following incorrect responses, participants received a 20-s timeout accompanied by a 2-s "buzz" sound. In the RB task, Murph completed 2,881 trials and Obi completed 6,417 trials. Both monkeys' performance accuracy exceeded 95% correct in their last 1,000 trials. In the II task, Murph completed 26,292 trials and Obi completed 32,201 trials. Both monkeys' performance accuracy exceeded 95% correct in their last 1,000 trials.

In Phase 2, monkeys were gradually introduced to deferredrearranged feedback, with blocks of two, three, four, five, and six trials. That is, now at the end of a block of trials, monkeys received their positive outcomes grouped together (e.g., several whoops

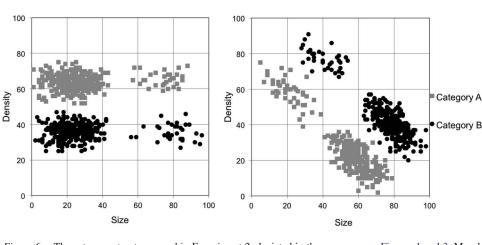
RB-Horizontal Task

а

separated by 1 s for correct responses) and then their negative outcomes grouped together (e.g., several buzzes paired with 20-s timeouts for incorrect responses). We still tested only the trained stimuli but now gradually deferred feedback as performance remained above 85% correct measured across segments of 20 trials. When Phase 2 began, there was a 100% chance that only one-trial blocks (immediate feedback) would be presented. When performance exceeded 85% correct, the chance that a two-trial block would be presented increased by 1% (out of 100%) on every trial until there was a 100% chance that two-trial blocks were presented. Then, the chance of three-trial blocks began at 1% and increased to 100%, as long as performance remained above 85% correct. This ramping continued until the animals reached six-trial blocks of deferred feedback. This allocation prevented monkeys' performance from crashing in response to an abrupt change in feedback. Obi had trouble remaining above 85% correct after reaching six-trial blocks. This may have been due to some forgetting between sessions. To help him recover, we allowed the Phase 2 program in RB and II tasks to ramp backward to smaller trial blocks (from six to one) when he performed below 85% correct. In the RB task, Murph completed 11,171 trials and Obi completed 7,603 trials. We ended RB Phase 2 when each monkey performed above 95% across 2,000 trials with six-trial block feedback only. In the II task, Murph completed 15,321 trials and Obi completed 75,496 trials. Both monkeys performed at 90% correct or better (Murph was 93% correct and Obi 90% correct) in the last 1,000 trials with six-trial block feedback only.

In Phase 3, all trials were fully deferred-rearranged, with feedback occurring only after six trials. Now, there was a 10% chance that trials would present stimuli from the transfer distributions (see Figure 6). In the RB task, Murph completed 46,993 trials and Obi completed 7,320 trials. In the II task, Murph completed 29,298 trials and Obi completed 15,522 trials. We focused our analysis on the start of Phase 3, so as to evaluate equivalently how each monkey performed on trained compared with transfer stimuli.

II-minor Task



b

Figure 6. The category structures used in Experiment 2, depicted in the same way as Figures 1 and 3. Murph and Obi completed both rule-based (RB) horizontal and information integration (II) minor tasks. In training, all trials presented stimuli from half of the stimulus space (left pair of stimulus ellipses in the RB horizontal task; bottom pair in the II minor task). In transfer, 10% of the trials presented stimuli from the other half of the stimulus space (right ellipses in the RB horizontal task; top ellipses in the II minor task).

Table 3
Proportion Correct by Phase and Task and by Stimulus Type in
Experiment 2 (Monkeys)

	Phase 1	Phase 2	Phase 3 (first 100 trials)	
Task	(last 100 trials)	(last 100 trials)	Trained	Transfer
Murph				
RB-horizontal	.93	.88	.90	.56
II-minor	.93	.95	.83	.63
Obi				
II-minor	.99	.93	.83	.63
RB-horizontal	.99	.89	.89	.64

Note. RB = rule-based (Figure 6a); II = information-integration (Figure 6b). Performance is presented in the order that each monkey received RB and II category tasks (order was counterbalanced between subjects).

Results

Accuracy-based analyses. Table 3 shows proportion correct achieved in the three phases of RB and II categorization tasks by both monkeys. To see how monkeys performed over the course of the experiment, see the online supplementary materials (Figures S4–S7) for proportion correct throughout each phase. Task order was counterbalanced, with Murph starting with the RB task and Obi starting with the II task.

Like Experiment 1, we ensured performance in Phase 1 ended with high accuracy and appropriate decision bounds. Ending Phase 1 in the RB task, Murph and Obi showed proportions correct of .93 and .99, respectively. Ending Phase 1 in the II task, performance was the same for each monkey: .93 and .99 for Murph and Obi, respectively. Each monkey ended categorization of training stimuli with immediate feedback at the same level for both II and RB tasks.

Performance at the end of Phase 2 remained high with deferred feedback. Proportion correct for the end of Phase 2 was .88 (RB) and .95 (II) for Murph and .89 (RB) and .93 (II) for Obi. Monkeys were well matched at the end of Phase 2. Murph and Obi's performance differed only by 1% in the RB task and by 2% in the II task.

Accuracy-based analyses: Generalization to transfer stimuli. Phase 3 contains the experiment's crucial results contrasting performance on trained and transfer stimuli. In the RB task, the proportion correct for the first 100 trained stimuli was .90 (Murph) and .89 (Obi), but the proportion correct for the first 100 transfer stimuli was .56 (Murph) and .64 (Obi). To statistically compare performance with trained and transfer stimuli for each monkey, we used McNemar's test, which is a nonparametric test that is used to assess the significance of the difference between two paired binomial data sets (McNemar, 1947). McNemar's test confirmed that, in contrast to humans in Experiment 1, there was a significant difference in the RB task between performance on trained and transfer stimuli for both Murph, p < .001 (two-tailed), odds ratio (OR) = .493, 95% confidence interval (CI) [.361, .666], and Obi, p < .001 (two-tailed), OR = .600, 95% CI [.444, .805]. See the online supplementary materials for similar findings with additional analyses using arcsine square root transformations. This result draws a crucial distinction between humans' and monkeys' ability to generalize RB category knowledge to transfer stimuli under deferred feedback.

It is crucial to see that the findings presented here are not in any way a null result. These collapses of performance with transfer stimuli occurred amid obviously successful training, high levels of task mastery, highly accurate ongoing performance, and so forth. The result is a striking and significant contrast between performance with trained and transfer areas of the stimulus space, a positive result concerning the difference in performance level achieved on trained and transfer stimuli.

In the II task, the proportion correct for the first 100 trained stimuli was .83 for both Murph and Obi. They were well matched in their trained stimulus performance on this task, too. The proportion correct for the first 100 transfer stimuli was .63 for both Murph and Obi. McNemar's test showed that the two proportions were significantly different, p = .006 (two-tailed), OR = .667, 95% CI [.496, .892], for both Murph and Obi. See the online supplementary materials for similar findings with additional analyses using arsine square root transformations. This failure to transfer II category knowledge under deferred reinforcement is consistent with results found in humans (Experiment 1) and in

Table 4

Best-Fitting Models for Experiment 2 (Monkeys): Best-Fitting Model, Bayesian Information Criterion (BIC) Score, and Percent Responses Accounted for Are Shown by Phase and Task and by Stimulus Type

	Phase 1	Phase 2	Phase 3 (first 100 trials)		
Task	(last 100 trials)	(last 100 trials)	Trained	Transfer	
Murph					
RB-horizontal	y-Rule (BIC = $55.5, 93\%$ fit)	y-Rule (BIC = $50.6, 90\%$ fit)	y-Rule (BIC = $59.5, 90\%$ fit)	Guessing $(BIC = 98.9)$	
II-minor	Integration $(BIC = 55.5, 94\% \text{ fit})$	Integration $(BIC = 44.6, 95\% \text{ fit})$	Integration (BIC = 102.4 , 84% fit)	x-Rule (BIC = $67.13, 89\%$ fit)	
Obi					
II-minor	Integration $(BIC = 23.8, 98\% \text{ fit})$	Integration $(BIC = 58.8, 93\% \text{ fit})$	Integration $(BIC = 74.6, 84\% \text{ fit})$	x-Rule (BIC = 71.6, 89% fit)	
RB-horizontal	y-Rule (BIC = 22.7, 99% fit)	y-Rule (BIC = 65.6, 90% fit)	y-Rule (BIC = 78.0, 87% fit)	y-Rule (BIC = 59.4, 88% fit)	

Note. RB = rule-based (Figure 6a); II = information-integration (Figure 6b). A large percent of the responses accounted for by the model indicates that the subject applied this decisional strategy consistently so that the model fit his performance closely.

humans and monkeys under immediate feedback (Smith et al., 2015).

Model-based analyses. We fit rule-learning, procedurallearning, and guessing models to each monkey's last 100 Phase 1 trials, last 100 Phase 2 trials, first 100 Phase 3 trained stimuli, and first 100 Phase 3 transfer stimuli for RB and II tasks. Table 4 shows the best-fitting model by monkey, by task, by phase of the experiment, and by stimulus type within Phase 3 of the experiment.

Murph: RB task. For the last 100 Phase 1 trials in the RB task, modeling indicated a RB decision strategy placed optimally, near the center of the *y*-axis (51.4). Murph's RB strategy continued in Phase 2 and the first 100 trained stimuli in Phase 3 (Figure 7a–c, black lines). However, for the first 100 transfer stimuli in Phase 3, the best-fit model was biased guessing. Murph called a majority of transfer stimuli "A," failing to extend his RB boundary to novel stimuli under deferred feedback (Figure 7c). In the case of best fit by the biased guessing model, because Murph may have just guessed trial by trial, no decision boundary can appropriately be drawn on Figure 7c.

Murph: II task. For the last 100 Phase 1 trials in the II task, modeling indicated a diagonal decision bound with a slope of -0.53 (Figure 7d). Murph's II strategy barely changed in Phase

2 (slope = -0.44; Figure 7e). For the first 100 trained stimuli in Phase 3, Murph's decision bound had a slope of -0.79 (Figure 7f, black line). However, for the first 100 transfer stimuli in Phase 3, the best-fit model was a unidimensional decision strategy placed at 58.8 on the *x*-axis (Figure 7f, gray line). Once again, Murph called a majority of the transfer stimuli "A." He failed to generalize his II decision boundary to new stimuli under deferred feedback. This is not surprising given that Murph was unsuccessful in generalizing II strategies to novel stimuli even under immediate feedback (Smith et al., 2015).

Obi: II task. For the last 100 Phase 1 trials in the II task, modeling indicated a diagonal decision bound with a steep slope of -2.54 (Figure 8a). Obi's II strategy was sustained in Phase 2, with a best-fitting diagonal decision bound that flattened to a slope of -0.44 (Figure 8b). For the first 100 trained stimuli in Phase 3, Obi's decision bound had a slope of -1.65 (Figure 8c, black line). However, like Murph, Obi failed to extend this diagonal decision boundary (Figure 8c, gray line). The best-fit model for the first 100 transfer stimuli in Phase 3 was unidimensional on the *x*-axis. Like Murph, Obi called a majority of the transfer stimuli "A" (Figure 8c).

Obi: RB task. For the last 100 Phase 1 trials in the RB task, modeling indicated a RB decision bound placed optimally at 49.4 on

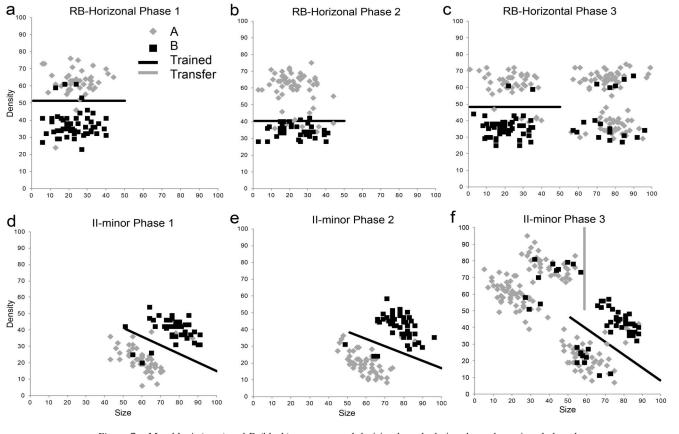


Figure 7. Murph's A (gray) and B (black) responses and decision bounds during three phases in rule-based (RB; a-c) and information-integration (II; d-f) tasks. In Phase 1, responses for the last 100 trials are shown (a, d). In Phase 2, response for the last 100 trials are shown (b, e). In Phase 3, responses for the first 100 trianed and first 100 transfer trials are shown (c, f). Decision bounds for trained (black lines) and transfer (gray lines) stimuli are depicted as they were in Figures 5 and 6 for humans.

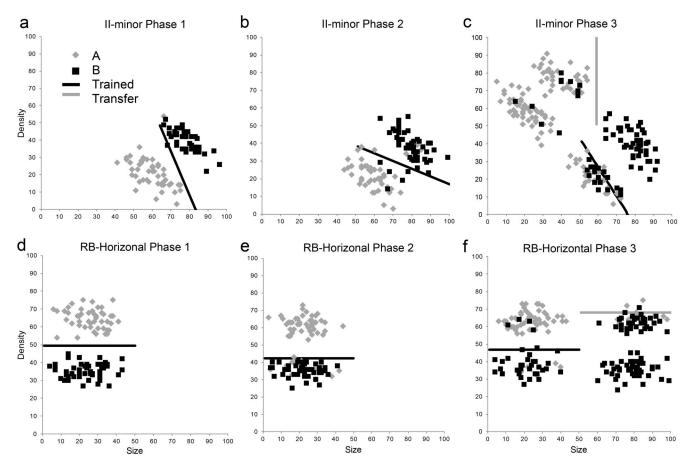


Figure 8. Obi's A (gray) and B (black) responses and decision bounds (training: black lines; transfer: gray lines) during three phases in rule-based (RB; a-c) and information-integration (II; d-f) tasks, depicted as in Figure 7.

the *y*-axis (Figure 8d). Obi's RB strategy continued and his boundary on the *y*-axis barely moved in Phase 2 (Figure 8e) and the first 100 trained stimuli in Phase 3 (Figure 8f, black line). For the first 100 transfer stimuli in Phase 3, the best-fit model remained unidimensional on the *y*-axis; however, as Figure 8f (gray line) illustrates, the decision bound was far too high on the *y*-axis, at 68.2. Obi also showed a nearly complete response bias on the transfer stimuli. Given the dominant result, it is immaterial whether the modeling algorithm produced a horizontal or a sloped decision boundary. As already shown, accuracy-based analyses confirmed a significant drop in performance on these transfer stimuli (63% correct) compared with trained stimuli (83% correct) in Phase 3.

General Discussion

We asked whether RB category knowledge has a different representational character that makes it less associative and more transferable. As expected, humans' and two macaques' II category learning did not transfer under deferred feedback, with accuracy falling 17% for the humans and 20% for each macaque. II category learning is entrained to specific stimuli and lacks a stimulusindependent aspect that bridges to new stimuli. This finding supports the current neuroscience description of II learning as the striatal binding of cortical inputs to response outputs. By that description, only trained cortical representations should strongly elicit appropriate responses.

Moreover, many participants made no pretense of transferring their II learning. Instead, they managed transfer under deferred feedback by seemingly implementing nonoptimal, adventitious rules. By this we mean only that they produced model fits showing vertical or horizontal decision bounds that were not appropriate to the II (diagonal) category structure. It is intuitive that when cortical inputs fail to activate a response, as with transfer stimuli, the cognitive system would require a secondary strategy. This might well take the form of the inappropriate rules we seemed to observe.

In contrast, RB category knowledge easily transferred—for humans. Humans' RB category knowledge has abstract and portable representational content. Probably, it is encoded as a declarative rule held in working memory. Such a rule would not be welded to trained stimuli but freely applicable to transfer stimuli. Macaques did not show this distinctive RB transfer. Their decision bounds were optimal for the training stimuli, even with deferred feedback. However, when transfer stimuli were presented, their strategies collapsed. They lacked portable "rules" to apply to transfer stimuli. The results demonstrate a distinctive species difference in the character of RB knowledge across species and a limitation on monkeys' capacity to entertain explicit category rules as humans do. This result converges with that in the study by Smith, Minda, and Washburn (2004). They surveyed broadly monkeys' and humans' categorization abilities (also Shepard et al., 1961). Humans clearly learned explicit category rules in the tasks that afforded rules. They learned RB tasks especially easily, performed them especially accurately, and learned them in an insightful moment of rule discovery. Monkeys did not.

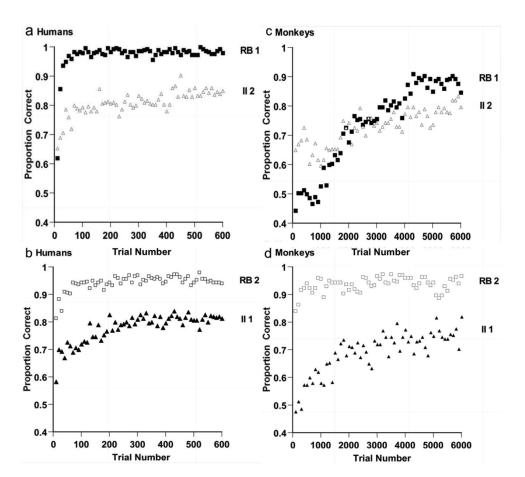
Combined, the results here and in the study by Smith et al. (2004) could suggest that monkeys lack the cognitive capacity for the explicit category rules that humans use fluently. However, complexities have emerged in other studies that recommend a more nuanced interpretation.

One complexity is that Smith et al. (2010) found that macaques do differentiate RB and II category tasks. They learn RB tasks faster and to higher accuracy levels than they do II tasks, as humans do. This cross-species result is shown in Figure 9. Smith, Crossley, et al. (2012) extended this observation to a New World primate species (capuchin monkeys, *Cebus apella*). These results might suggest that monkeys share some—but not all—aspects of humans' explicit rule learning capability, enough so that dimensional category rules are advantaged in learning (Smith et al., 2010; Smith, Crossley, et al., 2012) but not enough so that rules become portable in transfer (present results).

However, one might suggest instead that unidimensional RB tasks are inherently simpler to learn associatively so that almost any learning system would show this advantage. This inherent-simplicity argument fails, though. Smith et al. (2011) showed that pigeons are indifferent to the RB or II rotation of the category task in stimulus space. Unlike humans and monkeys, they learn both tasks equally quickly to the same level.

Or, one might suggest that the learning advantage for RB tasks only needs a low-level attentional process to focus on the relevant dimension. This attentional argument also fails. This argument would grant a selective attention mechanism to macaques but not to pigeons, discomfiting many who study birds and who observe their ability to change attentional focus (discussion in Pearce, Esber, George, & Haselgrove, 2008; Smith et al., 2011). Moreover, if selective attention powered the RB learning advantage for mon-

Figure 9. (a) Proportion of correct responses in each 10-trial block for 30 humans who performed 600 trials of a rule-based (RB) and information-integration (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. (c) Proportion of correct responses in each 100-trial block for three monkeys who performed 6,000 trials of an II and RB category task in that order. (d) Proportion of correct responses in each 100-trial block for three monkeys who performed 6,000 trials of an II and RB category task in that order. (d) Proportion of correct responses in each 100-trial block for three monkeys who performed 6,000 trials of an II and RB category task in that order. (d) Proportion of correct responses in each 100-trial block for three monkeys who performed 6,000 trials of an II and RB category task in that order. (d) Proportion of correct responses in each 100-trial block for three monkeys who performed 6,000 trials of an II and RB category task in that order. (d) Proportion of correct responses in each 100-trial block for three monkeys who performed 6,000 trials of an II and RB category task in that order. Adapted from Smith et al., (2010) by the American Psychological Association. Reprinted with permission.



keys, then they would easily have transferred that attentional focus to the transfer stimuli in the present tasks. Given selective attention to the relevant dimension, there would not even be "trained" and "transfer" stimuli. There would effectively only be, for example, sparse and dense stimuli. In this respect, our results pose a mystery about selective attention and rules in categorization. We need to explain why macaques' attentional focus that gives them an RB performance advantage (Smith et al., 2010) applies only to the edge of the training-stimulus distributions. How is it that attention is welded to the range of familiar stimuli? How is that an attentional focus? What have humans done to break that weld? And is breaking that weld the thing that grants humans the flexible use of true category rules, setting them apart from other species?

Another complexity is that Smith et al. (2015)—similar to the present study-asked macaques to transfer their RB and II category knowledge to new regions of the stimulus space. However, in the study by Smith et al., the novel stimuli arrived suddenly as 100% of stimuli and trial-by-trial reinforcement continued unabated, so that each new stimulus received immediate, veridical feedback and learning commenced immediately. Note that this use of continuous veridical reinforcement is different from other transfer studies in which transfer stimuli would be nondifferentially reinforced. In the case of continuous reinforcement, both species showed impaired II transfer, suggesting that II learning is conditioned by and yoked to its trained stimulus contexts. The II result for both species is just like that found here. RB transfer was seamless for humans, also as found here. But RB transfer was seamless for the macaques, too, a very different result from that found here. It is also a matter of theoretical interest that RB learning transfers to new stimuli almost instantaneously when supported by immediate reinforcement, but transfers poorly when unsupported by immediate reinforcement.

Thus, humans show a suite of cognitive phenomena that compose their mature and dominant capacity for explicit-declarative categorization. They learn RB tasks fast to high levels (Smith et al., 2010). They transfer category rules instantaneously to novel stimuli when immediate feedback is given every trial (Smith et al., 2015). They transfer category rules spontaneously to novel stimuli even when reinforcement is deferred so that reinforcement credit cannot be assigned to individual stimulus–response pairs (present data). They learn RB categories by insightful discovery (Shepard et al., 1961; Smith et al., 2004). They hold category rules in working memory and declare them verbally (Casale et al., 2012).

In contrast, the existing results suggest that macaques could be a transitional form. They show the first three of these RB phenomena—fast learning, highly accurate performance (Smith et al., 2010), and seamless transfer given continuous trial-by-trial reinforcement (Smith et al., 2015). Pigeons do not (Smith et al., 2011). We interpret this data pattern to suggest that macaques' cognitive systems lie near the threshold for achieving true RB categorization. They transcend low-level selective attention. They bring some more advanced dimensionally analytic information process to bear on RB tasks. But they do not bring to bear all the explicit cognitive processes that humans do. And so, our goal is to titrate this threshold, so as to understand more clearly the emergence of humans' explicit cognition and to understand more clearly primates' cognitive constraints.

One theoretical possibility is that humans' ultimate rule capability is afforded by our distinctive use of abstract symbols and by our expression of them linguistically and propositionally (e.g., the As are sparse). In this case, macaques would never produce the RB performances that humans do. This would be an important conclusion about species differences in cognition and about the fitness considerations that fostered the evolution of explicit, declarative cognition.

However, another theoretical possibility is that humans' prefrontal cognitive system is more mature, advanced, and dominant in cognition and more active in searching for RB solutions to tasks. This would explain why humans discover rules insightfully and why humans spontaneously extend RB category knowledge to transfer stimuli. It is possible that a cognitive system could exist with a dominant, active, exploratory capacity that might show human-like rule use, even if that system had no abstract symbols, or declarative rules, or verbal language. Of course, this possibility is a thought experiment that itself raises important theoretical questions. Do humans do what they do because they are linguistic and propositional or do they describe linguistically and propositionally what their prefrontal cortical system does anyway, language or no?

In the end, we believe that research titrating the threshold of explicit-declarative rules is relevant to comparative and developmental psychologists and neuroscientists because it raises productive questions at the intersection between human and animal cognition. Can some animals transcend associative learning, showing a form of explicit (RB) cognition? What are the simplest and best paradigms for exploring this transition? What aspects of explicit cognition can animals share with humans, which not, and which aspects are actually shared? When do children cross the threshold to explicit cognition, and what are the earliest steps they take in making this transition? What were the first steps the nonhuman primates took in cognitive evolution toward humans' explicit system of categorization? What are the differences in the neural systems that afford associative and explicit categorization performances? Are parallel neural differences seen in human and animal minds? We invite our colleagues in diverse areas to join us in mapping and illuminating this intriguing psychological threshold.

This invitation comes with a caution that points to some limitations in existing research-including our own research and including the present research. It is a commonplace that animals learn by reinforcement and behave because of reinforcement, and consequently, scientists traditionally follow the logic of immediate and direct reinforcement. Unfortunately, this will make associative-learning strategies "pay" for animals. They may memorize exemplars and respond to them reactively. They may not be incentivized fully to transcend associative learning. They may suffice with a comfortable and easily accessible learning approach. All of these tendencies could be amplified by macaques' transitional status as creatures with fairly dominant associative-learning systems and fairly timid explicit-declarative systems. It will need the ingenuity of our colleagues to design the paradigms that can explore the latter system more richly, revealing the true "top" of nonhuman primates in this domain. The research presented here is a step in suggesting where and how to start looking for that top, but many carefully designed studies using converging methods will be needed to complete that assessment.

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