BRIEF REPORT

# More complex brains are not always better: rats outperform humans in implicit category-based generalization by implementing a similarity-based strategy

**Ben Vermaercke · Elsy Cop · Sam Willems · Rudi D'Hooge · Hans P. Op de Beeck**

**Abstract** Generalization from previous experiences to new situations is a hallmark of intelligent behavior and a prerequisite for category learning. It has been proposed that category learning in humans relies on multiple brain systems that compete with each other, including an explicit, rule-based system and an implicit system. Given that humans are biased to follow rule-based strategies, a counterintuitive prediction of this model is that other animals, in which this rule-based system is less developed, might generalize better to new stimuli in implicit category-learning tasks that are not rule-based. To test this prediction, rats and humans were trained in rule-based and information-integration category-learning tasks with visual stimuli. The generalization performance of rats and humans was equal in rule-based categorization, but rats outperformed humans on generalization in the information-integration task. The performance of rats was consistent with a nondimensional, similarity-based categorization strategy. These findings illustrate through a comparative approach that the bias toward rule-based strategies can impede humans' performance on generalization tasks.

**Keywords** Animal behavior · Categorization · Implicit/ explicit cognition · Visual perception

Assigning unseen objects to previously learned categories is an ability found throughout the animal kingdom (Ashby &

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Maddox, 2005; E. E. Smith & Medin, 1981; Vogels, 1999). This process is referred to as *generalization*. One necessary condition for achieving generalization involves being able to judge the similarity between the new object and internal representations (Nosofsky, 1986; Shepard, 1987). Overall, when similarity with one specific representation is higher than the similarity with other representations, the category label related to the most similar representation is associated with the novel object (Shepard, 1987).

Many brain regions are involved when new categories are learned, and novel objects are categorized accordingly. The COVIS theory (Ashby, Alfonso-Reese, Turken, & Waldron, 1998) of category learning distinguishes two competing systems, an explicit, rule-based system and a more implicit system. The explicit system is very well developed in humans (J. D. Smith, Beran, Crossley, Boomer, & Ashby, 2010; J. D. Smith, Minda, & Washburn, 2004) and allows for superior performance when the task is best solved by the application of a relatively simple rule (rule-based, or RB). The implicit system is involved when categories cannot be distinguished by a simple rule-based solution, such as when multiple dimensions have to be integrated (information-integration, or II). The performance of humans (Ashby, Ell, & Waldron, 2003) and monkeys (Smith et al., 2010) is better in RB category learning than in II category learning. One cause for the inferior performance in II category learning is the bias of human subjects to first test verbal rules before switching to the implicit learning system. This leads to the hypothesis that the explicit system will hinder performance when learning categories that are not differentiated according to an explicit rule. Filoteo, Lauritzen, and Maddox (2010) tested this hypothesis in the context of a study in which subjects were instructed to perform a dual-task paradigm designed to diminish the involvement of the explicit system during category learning, and these researchers indeed found that performance in II category learning improved under such dual-task conditions.

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Another, as yet untested and counterintuitive, prediction derived from the COVIS framework is that animals in which the explicit system is less well developed might show better generalization in II category learning than humans do. Indeed, Jitsumori (1993) already showed that pigeons, who have a differently developed brain and might be more likely to rely on the implicit learning system, generalized better in II tasks than humans did, but this study did not include both versions of the task. J. D. Smith et al. (2011) reported that pigeons learn both RB and II tasks equally quickly/slowly. However, this study did not pinpoint whether this was due to worse performance, relative to humans, in the RB task (a logical direct consequence of a less-developed explicit system) or, alternatively, to better performance in the II task (as a consequence of the removal of interference from this explicit system). Here, we aimed to directly test the latter prediction from the interference hypothesis by means of a comparative approach.

A general problem in comparative studies between humans and other animals is that humans mostly receive relatively detailed task instructions (or derive them easily), whereas animals have to invest more time in figuring out the general task procedure. Thus, task learning is confounded with learning the specific process of interest, which is category learning and generalization. Here we solved this problem by first training the subjects, both humans and rats, in the general procedure of the task with one prototypical stimulus from each category. Once the general task and the stimulus-to-category mapping were learned for these two stimuli, we tested generalization to other, previously unseen stimuli.

Humans and rats showed equal generalization ability in RB categorization, but rats significantly outperformed humans in terms of generalization in II categorization. This result confirms that lower interference from the explicit system leads to superior generalization in II category learning.

## Method

### Rat experiment

*Animals* The experiment included 16 FBN F1 rats (F1 hybrids, first-generation offspring of crossing the Fisher and Brown–Norway strains). They were obtained from Harlan animal research laboratory (HSD, Indianapolis, Indiana) at an age of 5 months. The rats lived in groups of six per cage, and the animals from each cage were equally divided over the two conditions (RB and II). For identification, we colored each rat's tail with zero to five circles, using a black marker. All of the procedures for animal housing and testing were approved by the KU Leuven Ethics Committee for animal experiments.

*Behavioral setup* For the behavioral task, we implemented our version of the visual water-maze setup (V-Maze; Figs. S1A and S1C) described previously (Prusky, West, & Douglas, 2000; Wong & Brown 2006). The animal is released into the water at the short end of a trapezoid pool. From there, it has to find a submerged platform located in front of one of two screens (Dell 17-in. LCD monitors) at the long end of the pool. The animal has to learn which of two stimuli predicts the location of the platform. A 50-cm-long divider was placed between the two screens, to force the animal to make a choice at the end of the divider. The circular stimuli measured about 23° in diameter when seen from this point. When the rat crossed this point we scored the trial as correct or incorrect, depending on the location of the platform.

*Stimuli* Following previous studies of category learning in humans (Maddox, Ashby, & Bohil, 2003), we defined a grating stimulus space using two dimensions: orientation and spatial frequency (see Fig. 1A for more details about the different experimental conditions). The orientations ranged from 0° (horizontal) to 90° (vertical), and the spatial frequencies ranged from a minimum of 0.05 cycles per visual degree (cpd) to a maximum of 0.30 cpd. This range was selected on the basis of the contrast sensitivity values of rats obtained by Silveira, Heywood, and Cowey (1987), who showed a similar sensitivity of pigmented rats for this range of frequencies (see the supplemental information, downloadable with this article, for more details on how we compensate the remaining difference in sensitivity).

### Human experiment

*Subjects* All 24 subjects participated in the behavioral study as part of the first-year bachelor of psychology in Leuven (participation for course credits). The subjects were right-handed and 18 to 24 years old at the time of testing. All subjects had normal or corrected-to-normal vision. Informed consent was obtained, and the procedures were approved by the ethics committee of the Faculty of Psychology and Educational Sciences (KU Leuven).

*Behavioral setup* For the behavioral testing, we used a Dell desktop computer running Windows XP. The stimuli were displayed using a Dell 16-in. monitor (running at 75 Hz). The viewing distance was approximately 40 cm (see Supplemental Figs. S1B and S1D), and the subjects responded using custom-made response buttons, one in each hand.

*Stimuli* The subjects viewed the stimuli on a 16-in. CRT monitor and were instructed to fixate a small fixation cross in the middle between two gray fields in which gratings would appear for 200 ms, at fixed positions. The viewing distance was approximately 40 cm, and stimuli were presented at 5° in
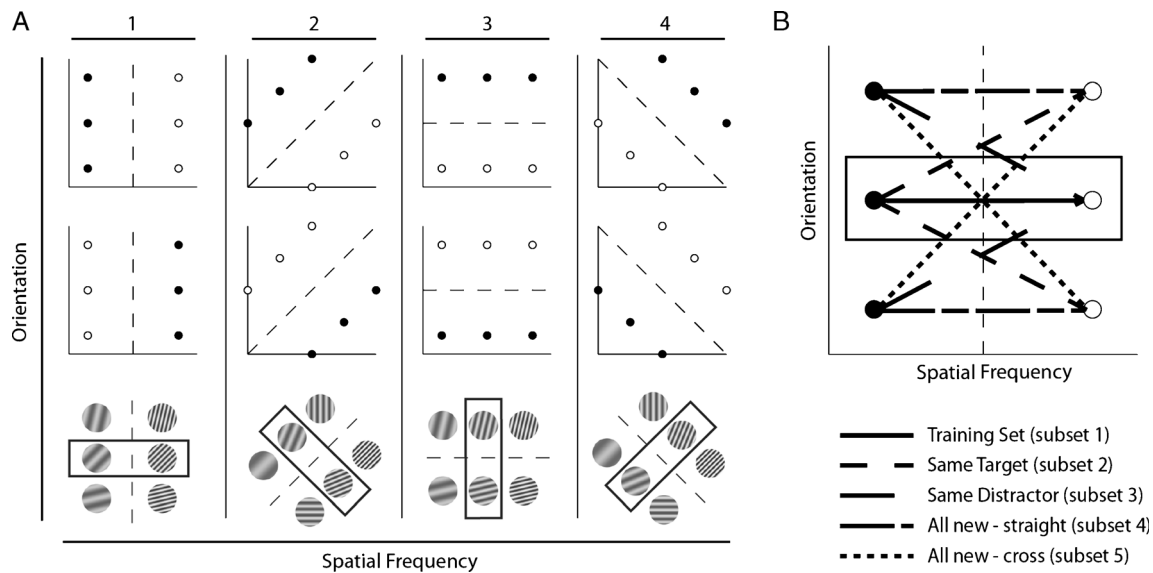
**Fig. 1** Overview of the stimuli used in all conditions. (A) The vertical axis in each plot should be read as the orientation of the grating; the horizontal axis indicates variation in the spatial frequency of the grating. Columns 1 and 3 define rule-based tasks, for which one dimension is relevant for categorization; columns 2 and 4 define information-integration tasks, for which both dimensions should be taken into account for successful categorization. We counterbalanced which stimulus category was the target (first vs. second row). This design yielded eight (4 columns × 2 rows) possible target–distractor pairs, each of which was given to two rats and two or three human subjects. The third row shows examples of the stimuli used in both training and test phases; the black rectangles indicate the training sets. (B) This plot shows the stimulus space for the test phase, illustrated with Orientation Condition 1. In total, we distinguished between five subsets of pairs: (1) the original pair (solid line), which was the pair used to train the animals in the training phase of the experiment; (2) the two pairs that contained the original target and a new distractor (short dashes); (3) the two pairs that contained the original distractor and a new target (long dashes); (4) the two pairs that consisted of new stimuli from the space that did not vary on the orthogonal dimension (irregular dashes); and (5) the two pairs that also consisted of new stimuli, but with large differences for the orthogonal dimension (dotted lines). These pairs were compared in part 3 of the analysis in order to give us an idea of how well the subjects generalized to new stimuli. The five subsets indicated in this figure correspond to different levels of generalization that were required (1 = *no generalization* . . . 5 = *maximum level of generalization*)

size and about 12º eccentricity. Their spatial frequencies were in the range of 0.2–1.2 cpd, and were chosen to result in a stimulus visibility (given the eccentricity and timing used) that was not better than what the rats could perceive. See the supplementary information for more details on how we performed this matching of frequency ranges.

Training procedure

We first trained the subjects to distinguish two grating patterns (see Fig. 1A) in a visual discrimination task. These two grating patterns were the prototypical stimuli from the two categories that each subject had to learn (see the boxed stimuli in the bottom row of Fig. 1A; see the supplemental information for more details on the training procedures). To the humans subjects, instructions were given by the experimenter that there were "good" (target) and "bad" (distractor) patterns and that both humans and rats had to detect these by trial and error. The subjects were given feedback, thus allowing them to learn which prototype constituted the target. The gratings could differ on two dimensions, orientation and spatial frequency; we counterbalanced the target and distractor categories over subjects (see Fig. 1A). For subjects in the RB

condition, only one of the two dimensions differed between the two to-be-learned categories. For subjects in the II condition, both dimensions differed. The stimuli were presented randomly on the two presentation locations, and one of these patterns consistently predicted the location to go for. Rats were clearly slower than humans in picking up the stimulus–response associations. Using the 85% crossing point of the fitted sigmoid function as a criterion, rats needed from five (fastest animal) to 17 (slowest animal) 12-trial sessions to learn the basic discrimination task (see Fig. S2). With the exception of two outlier human subjects (who never obtained performance above chance level), all of the human subjects reached this same criterion after at most the equivalent of two sessions (24 trials). The numbers of sessions needed to reach this criterion were not significantly different between the RB and II conditions (rats: $t(14) = -0.543$, $p = .596$, $d = -0.272$; humans: $t(20) = -0.076$, $p = .941$, $d = -0.032$).

Testing phase

In this phase, we first expanded the stimulus set with four new gratings that were located most distantly from the center (scheme shown in Fig. 1B; the exact stimuli are shown in

the bottom row of Fig. 1A). These six gratings were combined in nine pairs that were presented in every session. These fixed pairs were interleaved with three pairs resulting from a combination of stimuli that had a random position in stimulus space between the original central stimulus and the extremes. We included these random pairs to avoid having the animals learn simple stimulus–response mappings. Part I of the testing phase was stopped after ten sessions (total of 120 trials per rat).

## Results

Rats were trained until all of them performed above criterion (85%) for four successive trials. Their performance in the sessions after criterion was reached is summarized in Fig. 2A. This performance was the same in rats and humans, with no difference between the RB and II conditions in either of the species. These effects were tested with a 2 (species: rats vs. humans) × 2 (catType: RB vs. II) analysis of variance. We found no main effect of catType [$F_{(1, 34)} = 0.038$, $p = .846$, $\eta^2 = .001$], nor a main effect of species [$F_{(1, 34)} = 0.117$, $p = .734$, $\eta^2 = .003$]. The catType × Species interaction was also not significant [$F_{(1, 34)} = 1.158$, $p = .289$, $\eta^2 = .033$]. Thus, for the prototypical stimuli, the stimulus–category association was induced equally well for the rats and the humans, and equally well for the two category-learning tasks.

After this training phase, we tested the generalization of the animals to 120 nonprototypical exemplars from the two categories (see Fig. 1A). In the RB condition, the animals could solve the task by attending to one of the two stimulus

dimensions. In the II condition, the target stimulus could only be determined by integrating the two dimensions. We analyzed the generalization data with a 2 (species: rats vs. humans) × 2 (catType: RB vs. II) analysis of variance. The results (Fig. 2B) revealed a main effect of catType [$F_{(1, 34)} = 6.452$, $p = .016$, $\eta^2 = .095$] and a main effect of species [$F_{(1, 34)} = 5.300$, $p = .028$, $\eta^2 = .078$]. Most importantly, both effects were strongly modulated by a strongly significant interaction between catType and species [$F_{(1, 34)} = 17.037$, $p < .001$, $\eta^2 = .250$].

This interaction effect indicates that the patterns of generalization across the RB and II conditions were very different for the two species. To further investigate the direction and strength of the effects, we performed post-hoc $t$ tests. For rats, we found no difference between the two category-learning tasks [$t_{(14)} = -1.327$, $p = .206$, $d = -0.664$]. For humans, we found a strongly significant difference, with lower generalization performance in the II than in the RB condition [$t_{(20)} = 4.555$, $p < .001$, $d = 1.951$]. When comparing the performance of both species in the same conditions, no difference occurred in the RB condition [$t_{(16)} = -1.836$, $p = .085$, $d = -0.871$]. In contrast, humans performed worse than the rats in the II condition [$t_{(18)} = 3.829$, $p < .001$, $d = 1.748$]. These findings indicate that rats obtained similar performance in both versions of the task, whereas humans showed a strong deficit in the II task.

To obtain more detailed information about the pattern of generalization, we classified all of the stimulus pairs from the testing phase according to their averaged similarity to the stimuli presented in the training phase (Fig. 1B). This resulted in three types of pairs: the original pair, pairs in which an original was paired with an unseen stimulus, and pairs in which both were new stimuli. We could further distinguish
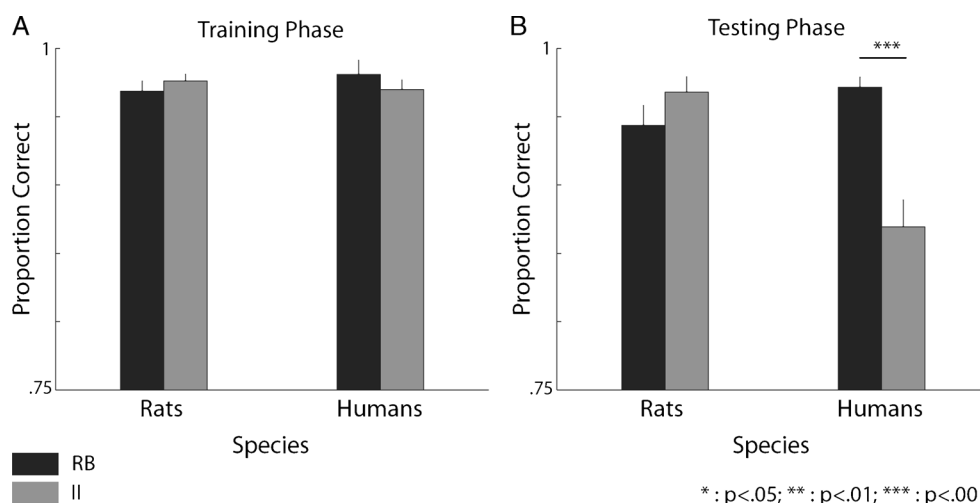


**Fig. 2** Performance in rule-based (RB) and information-integration (II) conditions for both species. (A) Plateau performance of both species at the end of the training phase. We found similar performances for both species, and no differences between the RB and II conditions. (B) Data for the generalization test phase. Rats reached performance comparable to the training levels, whereas humans clearly showed difficulties solving the II tasks

the second type, depending on whether the target or the distractor was original. Also, the third type could be divided into straight and cross pairs, corresponding to, respectively, no and maximal variation in the orthogonal dimension (the direction of the stimulus space that was irrelevant for distinguishing the categories). Thus, we looked at the performance of both groups on each of these five subsets of pairs (pairType).

The results were analyzed in a 2 (catType: RB vs. II) × 5 (pairType: subset 1–5) split-plot design, with catType as a between-subjects variable and pairType as a within-subjects variable. We performed one analysis of variance per species (rats, humans).

For rats (see Fig. 3A), we found no main effect of catType [$F(1, 14) = 2.179$, $p = .162$, $\eta_p^2 = .135$]. However, a significant main effect of pairType [$F(4, 56) = 3.492$, $p = .013$, $\eta_p^2 = .200$] was observed: Stimuli more distant from the initially learned prototype yielded worse performance. The interaction between the two factors was not significant [$F(4, 56) = 0.184$, $p = .946$, $\eta_p^2 = .013$]. These findings support the hypothesis that these animals relied on a similarity-based strategy to solve the generalization problem in both the RB and II conditions.

For humans (see Fig. 3B), we found a significant main effect of catType [$F(1, 20) = 11.363$, $p = .003$, $\eta_p^2 = .362$]. No significant main effect of pairType [$F(4, 80) = 0.091$, $p = .985$, $\eta_p^2 = .005$], nor an interaction effect [$F(4, 80) = 0.707$, $p = .589$, $\eta_p^2 = .034$], was found. These findings support the hypothesis that generalization in humans is very different between RB and II conditions, and is not related in a simple way to the similarity of novel stimuli with respect to the originally learned prototypical stimuli.

Finally, the very good generalization performance was consistent across rats. Despite the large variation between rats

in the time taken to learn the basic discrimination in the training phase (ranging from five to 17 sessions being required to reach criterion performance), which could have led to possible overtraining effects in the fast learners, this variable was not related to the much less variable generalization performance ($r = .09$, $p = .74$).

## Discussion

In sum, we reported generalization in a rule-based category scheme to be fairly similar in rats and in humans, whereas rats outperformed humans in generalization in an information-integration category distinction. The strong difference in the generalization abilities of humans in RB and II conditions confirms the wealth of data in the literature that category learning and generalization in humans is dimension-based. Note that the performance levels were higher overall than is generally reported, but our between-class distance was larger, due to the matching to the rat experiment. In contrast, rats showed similar generalization performance for RB and II category distinctions, and generalization in rats was based on overall similarity. This is a superior strategy in the case of an II category distinction, which is why rats outperformed humans in such a situation. An important note hereby is that we ruled out that the animals were using some trivial strategy or confound unrelated to the stimuli to solve the task, because their performance fell back down to chance level in a subsequent experiment using unrelated shapes (but with the same average luminance and contrast; see the supplemental information).

In order to directly compare generalization in rats and humans, we changed the category-learning protocol that is
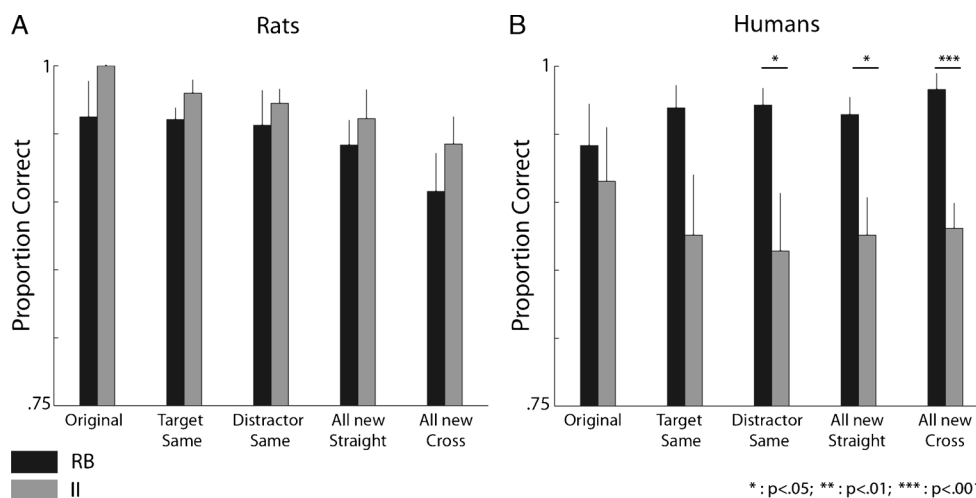


Fig. 3 Comparison of generalization to new stimuli for the two species. (A) Rats performed slightly worse for stimuli that were less similar to the original pair, but no difference emerged between the rule-based (RB) and information-integration (II) conditions. This is also indicated by the

$p$ values of the $t$ tests for each pair of bars. (B) Humans showed different patterns for both conditions. Subjects in the RB condition performed similarly for each of the subsets of pairs (no effect of generalization level), whereas subjects in the II condition performed consistently worse

typically used for comparisons of RB and II category learning. First, in previous studies, the category distinction was learned gradually by being presented with a distribution of stimuli (one stimulus at a time, and different stimuli in different trials). However, this procedure mixes up learning of the general task procedure and of the general category distinction with generalization to novel stimuli. To isolate the latter process, we used a multiphase paradigm, and first trained subjects on associating the correct response with a prototypical stimulus from each category, before generalization was tested in a later phase of the experiment. A second difference was that we used a two-alternative forced choice (2AFC) design, involving two stimuli per trial instead of one, because 2AFC is a very robust paradigm, with superior qualities from a signal detection point of view, as compared to one-interval identification paradigms (see the supplementary information).

Thus, any prediction of a difference between RB and II category distinctions would be related to the generalization phase. This prediction was based on the assumption that the switch to a multiphase 2AFC paradigm would not have consequences for finding such a difference between RB and II category learning. This seemed to be a reasonable assumption. If a subject, whether human or rat, were biased to apply a one-dimensional rule in the typical paradigm, we would expect this bias to also occur in our multiphase 2AFC paradigm. Nevertheless, it was important to test this explicitly by including human subjects in the present study. The findings confirmed that, also in our multiphase 2AFC paradigm, humans show superior generalization performance in the context of an RB rather than an II category distinction, exactly as has been found in the numerous previous studies comparing RB and II category learning (Ashby et al., 2003; Hélie, Waldschmidt, & Ashby, 2010).

In contrast, rats showed equal performance in the two conditions, and our multiphase paradigm allowed for the conclusion that they even outperformed humans in generalization in the case of an II category distinction. The rats' performance was best explained by a similarity-based generalization strategy, instead of a dimension-based strategy like the one used by humans. Why do rats employ a different strategy? This is not a trivial outcome, because the representation of stimuli in the rat visual system is in fact very similar to the representation in primates. Our stimulus space manipulated the orientation and spatial frequency of grating patterns, dimensions that are represented in the primary visual cortex (V1) of rats in a way very similar to that in monkeys (Girman, Sauvé, & Lund, 1999). Particularly intriguing is the finding that rat V1 neurons seem to show separable codings of orientation and spatial frequency (Burne, Parnavelas, & Lin, 1984; Niell & Stryker, 2008; Ohki, Chung, Ch'ng, Kara, & Reid, 2005), which is a prerequisite of dimensional processing of the stimuli that might not be there in the case of pigeons, which is also a species in which no difference has been found between RB and II category learning (J. D. Smith et al., 2011).

Thus, the choice of a similarity-based generalization strategy is most likely not directly related to the way that stimuli are represented in visual cortex, but rather to the absence of a bias to employ simple, dimension-based rules. It should be noted that rats have regions in the prefrontal cortex that are seen as homologues of primate prefrontal cortex (Uylings, Groenewegen, & Kolb, 2003) but that are obviously less developed. Interestingly, young children, whose brains are not fully developed, as compared to adults (relating mostly to the explicit system; the implicit system does not undergo many changes throughout development), still show this bias toward dimension-based rules. However, these are not applied as efficiently in children as in adults (Visser & Raijmakers, 2012). Thus, a qualitative difference most likely distinguishes rats and humans, and not so much a quantitative difference. This might explain rats' relative inability to use a rule- and dimension-based strategy, despite the fact that the dimensions that would feature in such a rule are represented in visual cortex. Our findings, in combination with the neurophysiological data in the literature, suggest that a dimension-based visual representation does not necessarily lead to a dimension-based generalization strategy. Furthermore, they suggest that the bias toward using explicit rules might not be a universal feature of mammalian neurocognition, as has been proposed (J. D. Smith et al., 2010). Up to now, researchers have found positive evidence for this in primates, and negative evidence in pigeons, but our present findings indicate that not all mammals exhibit this bias. It would seem even less likely to occur in some of the other mammalian species used in vision research, which are phylogenetically farther removed from primates than rodents (e.g., cats, dogs, or sheep; see Miller et al., 2007; Nishihara, Hasegawa, & Okada, 2006).

Most importantly, we have shown here that rats display superior generalization performance in a generalization context in which correct stimulus–response associations do not follow a dimension-based rule. This finding is in line with the hypothesized competition in the human brain between an explicit, rule-based system and an implicit category-learning system (Filoteo et al., 2010). From this hypothesis, we predicted that animals with a less elaborate rule-based system would experience less competition from this system in situations in which adequate learning cannot be based on rules, and as such, these animals would outperform humans in such situations. This prediction is counterintuitive, given that we predicted that the animal species with the less well-developed category-learning system would perform best, but nevertheless, the findings clearly support it.

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