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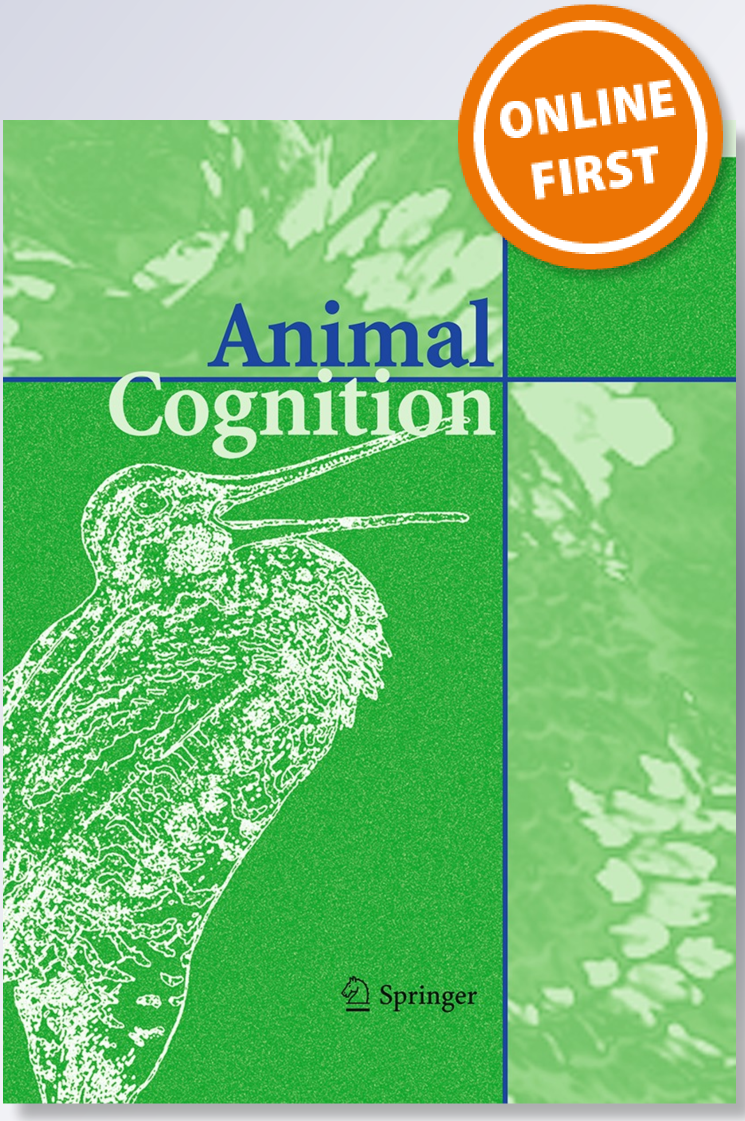

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SHORT COMMUNICATION

Analogical reasoning in amazons

Tanya Obozova[1] · Anna Smirnova[1] · Zoya Zorina[1] · Edward Wasserman[2]

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Abstract Two juvenile orange-winged amazons (*Amazona amazonica*) were initially trained to match visual stimuli by color, shape, and number of items, but not by size. After learning these three identity matching-to-sample tasks, the parrots transferred discriminative responding to new stimuli from the same categories that had been used in training (other colors, shapes, and numbers of items) as well as to stimuli from a different category (stimuli varying in size). In the critical testing phase, both parrots exhibited reliable relational matching-to-sample (RMTS) behavior, suggesting that they perceived and compared the relationship between objects in the sample stimulus pair to the relationship between objects in the comparison stimulus pairs, even though no physical matches were possible between items in the sample and comparison pairs. The parrots *spontaneously* exhibited this higher-order relational responding without having ever before been trained on RMTS tasks, therefore joining apes and crows in displaying this abstract cognitive behavior.

Keywords Analogical reasoning · Relational matching-to-sample · Identity matching-to-sample · Orange-winged amazons (*Amazona amazonica*)

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Introduction

Analogical reasoning is believed to represent a singular achievement of human cognition and intelligence (Gentner 1999; Holyoak and Thagard 1989) and to stand as the foundation for abstract conceptual thinking, including logical interference (Halford 1992). Analogical judgment may also be central to the development of social- and self-knowledge as well as to the expression of so-called theory of mind, which is said to be based on the analogical mapping of mental states from one individual to another (Thompson and Oden 2000).

Nevertheless, analogical reasoning may not be uniquely human. Initial evidence of analogical reasoning in animals came from studies of great apes trained on relational matching-to-sample (RMTS) and similar tasks (Gillan et al. 1981; Oden et al. 2001; Premack 1983; Thompson et al. 1997; Thompson and Oden 2000; Vonk 2003). Later work found that not only apes, but also monkeys can match relations between relations, suggesting that these primates too have the basic cognitive capacities for analogical reasoning (Bovet and Vauclair 2001; Fagot et al. 2001; Fagot and Maugard 2013; Fagot and Thompson 2011; Fagot and Parron 2010; Flemming et al. 2013; Truppa et al. 2010, 2011).

Recently, Smirnova et al. (2015) found that crows—one of the largest brained birds—also exhibit relational matching behavior. More importantly, crows *spontaneously* displayed this relational responding without ever having been explicitly trained on RMTS (also see, Vonk 2003). Specifically, two hooded crows were initially trained on identity matching-to-sample (IMTS) tasks with sample and comparison stimuli constructed from three categories: color, shape, and number of items. After learning these IMTS tasks, the crows reliably transferred discriminative matching behavior to sets of novel stimuli from the same three categories (other colors, shapes, and numbers of items) as well as to stimuli from a new category—stimuli varying in size—suggesting that the birds had acquired a general rule based on physical identity.

The critical RMTS test assessed the crows' ability to perceive the relationship between items in the sample stimulus pair and to match this relation to that in one of the two comparison stimulus pairs. On three-fourth of the trials (*identity trials*), the correct comparison pair was an exact match to the sample pair; so, physical identity as well as relational matching could guide accurate choice responding. On another one-fourth of the trials (*relational trials*), the correct comparison pair was a relational match to the sample pair within three categories (size, shape, or color); accurate performance on these trials required processing the relationship between the objects alone, as none of the items in the sample pair matched any of the items in the comparison pairs. The crows reliably and similarly performed both of these tasks without prior RMTS training, suggesting strong control by relational matching and possibly weaker control by stimulus identity.

The aim of the present study was to find out whether birds other than crows can *spontaneously* match stimuli on the basis of analogical relations. Among birds, parrots are excellent candidates after crows for possessing advanced cognitive abilities, because they are highly telencephalized (Boire and Baron 1994; Iwaniuk et al. 2005; Portmann 1947) and are able to solve several types of challenging cognitive tasks (Huber and Gajon 2006; Pepperberg 1999; Schuck-Paim et al. 2009; Werdenich and Huber 2006). Both corvids and parrots live in complex and variable environments and interact in intricate social groups. In addition, and compared to other birds, corvids and parrots traverse a long developmental period before becoming independent of their parents and have an extended life expectancy (Emery 2006). Nevertheless, crows and parrots engage in very different foraging and feeding behaviors; crows are omnivorous, whereas parrots primarily eat seeds, nuts, and fruit.

Methods

Subjects

Two juvenile orange-winged amazons (*Amazona amazonica*), 8–9 months of age, parrot 1 (Yasha, male) and parrot 2 (Lora, female), served as subjects. Both were housed in the aviary of the Biology Department of Lomonosov State University, Moscow, Russia. The parrots had never before been studied in perceptual or cognitive experiments.

Throughout the study, the birds had free access to water. Food deprivation was not imposed, but the birds' favorite foods (sunflower seeds and nuts) were excluded from the daily feeding mixture. Sunflower seeds and nuts were used as the reinforcer for task performance.

Apparatus

A wire mesh cage (70 cm × 45 cm × 70 cm) and a plastic tray (20 cm × 20 cm) with a handle (20 cm) served as the experimental apparatus. Figure 1a shows a photograph of a parrot in the experimental apparatus. Two cups (1 cm high and 5 cm in diameter) were placed on the tray; only one contained seeds and nuts as the reinforcer during training trials, whereas both cups contained seeds and nuts during critical testing trials. A sample stimulus card was placed behind the cups. The cups were each covered by a comparison stimulus card. The sample and comparison stimuli were white cardboard squares (7 cm × 7 cm) displaying geometric objects. The tray was prepared for each trial out of the field of the bird's vision.

Figure 1b shows a schematic drawing depicting the positions of the experimenter and the parrot at the moment when the bird made its choice. Because an opaque plastic screen (70 cm × 50 cm) separated the cage from the experimenter, the bird could not see the experimenter and the experimenter could not see the bird at the moment of choice, thereby precluding a "Clever Hans" error. Although the experimenter could not see the bird, she

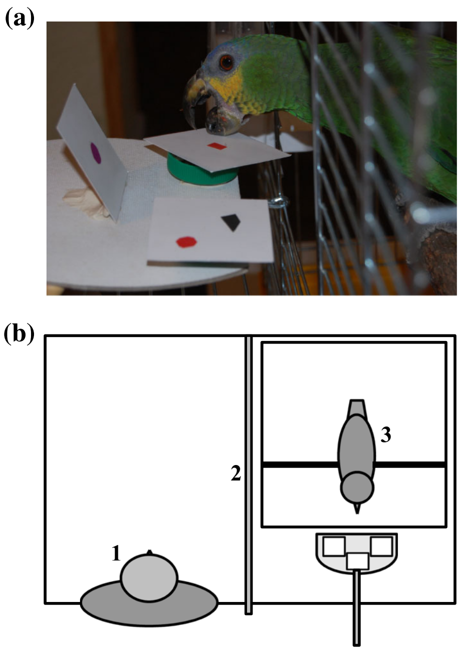

Fig. 1 **a** Parrot making its choice in IMTS training with number of items as the training category. **b** Schematic drawing of: (1) the experimenter at the moment of the parrot's choice, (2) the opaque screen separating the experimenter from the parrot, and (3) the parrot

could judge the outcome of each trial by the sounds made by the bird. When she heard the sound of a card falling from the cup, the experimenter quickly removed the tray to prevent the bird from uncovering the second cup; she later confirmed the bird's choice when the tray was fully retracted from the cage.

General procedure

The two parrots were trained and tested on two-alternative simultaneous matching-to-sample tasks. Each bird was individually placed into the experimental cage. A trial began when the tray containing the sample stimulus card and the two cups covered by the comparison stimulus cards was slid into the cage. To give the bird an opportunity to observe all of the stimuli, the tray was first placed in front of the bird for 2–3 s so that it could see all of the cards, but could not reach and uncover the cups. Then, after the tray was moved farther into the cage, the parrot was allowed to uncover one of the cups and, if the choice was correct, to receive food reinforcement. In the case of an incorrect choice, the tray was quickly removed from the cage to prevent the bird from uncovering the other cup. The sample card was always placed in the center of the tray behind the comparison cards. If the bird did not choose either comparison card after 2 min, then the tray was removed from the cage, the current session was ended, and that trial was scheduled to begin the next session on the following day. The type of sample stimulus was determined by a quasi-random schedule under the restrictions that: (a) The same sample stimulus could not be used on more than two successive trials and (b) the correct comparison stimulus could not appear in the left or right location on more than two successive trials. Otherwise, the experimental stimuli were randomized on each trial.

Experimental sessions were conducted daily and comprised from 20 to 40 trials depending on a bird's willingness to work. The methods and results of IMTS training and testing will be described in the next three sections as they were preliminary steps to the main phase of RMTS testing; only the data from RMTS testing are detailed in "Results" section.

Training on IMTS

Stimuli and procedure

The stimuli during IMTS training came from six stimulus sets that were given in the following order: cards in which the entire surface was colored black or yellow; black Arabic numerals 1 and 2 of the same size; arrays of one or two different geometric shapes (circle, square, rectangle, triangle) of different colors (red, blue, green, black), but the same size; cards in which the entire surface was colored red or blue; black Arabic numerals 3 and 4 of the same size; arrays of three or four different geometric shapes (circle, square, rectangle, triangle) of different colors (red, blue, green, black), but the same size.

Before IMTS training began, the parrots were habituated to the experimental apparatus and trained to uncover the cups. For this pretraining, the experimenter placed the seeds and nuts into a cup within the bird's field of vision and covered it with a white cardboard square. Thereafter, the bird usually uncovered the cup and ate the seeds and nuts. Later, IMTS training continued until the acquisition criterion (80 % correct choices over 96 consecutive trials; binomial test, $p < .001$) had been reached for each of the six stimulus sets.

To attain criterion for each of the six training steps, parrot 1 needed 688, 336, 128, 96, 96, and 96 training trials, respectively; parrot 2 needed 1311, 288, 277, 96, 96, and 96 training trials, respectively. The two birds needed a total of 1440 and 2164 training trials, respectively, before testing began.

IMTS testing within the training categories

Here, we explored whether juvenile orange-winged amazons could transfer their IMTS performance to novel stimuli within the training categories. On three-fourths of the trials, all of the stimuli came from the original training set (and only the correct choice was reinforced); on one-fourth of the trials, none of the stimuli came from the original training set, but they did come from the same training categories (and both correct and incorrect choices were reinforced). The novel testing stimuli came from: cards in four different shades of gray; black Arabic numerals from 5–8 of the same size; and arrays containing 5–8 geometric shapes (circle, square, rectangle, triangle, ellipse) of the same size, but different colors. A sample of 8 testing trials is presented in Table 1. Each parrot completed 288 trials. On each of the trials, the nominally correct comparison stimulus was an exact match to the sample. On 216 trials, all of the stimuli had previously been seen during training. On another 72 trials, none of the stimuli had previously been seen during training.

The overall mean percentage of correct choices for parrot 1 was 80.09 % on training trials and 79.17 % on testing trials. The overall mean percentage of correct choices for parrot 2 was 83.33 % on training trials and 75.00 % on testing trials. Binomial tests for choice accuracy on both familiar stimulus training trials and novel stimulus testing trials revealed that each parrot performed at significantly above chance levels (50 %), $p < .001$, thereby attesting to the ability of the birds to transfer a matching rule to new stimuli from the same training category.

Table 1 Examples of sample and comparison stimuli across 8 exemplary trials

Trial	Left test	Sample	Right test
1	White	White	Black
2	Array of 4 items	Array of 3 items	Array of 3 items
3	Light gray	Dark gray	Dark gray
4	Array of 5 items	Array of 5 items	Array of 6 items
5	Numeral 1	Numeral 1	Numeral 2
6	Numeral 2	Numeral 3	Numeral 3
7	Black	Black	White
8	Numeral 5	Numeral 8	Numeral 8

On three-fourths of the trials (1–3 and 5–7), only correct choices were reinforced; these were trials with the familiar training stimuli. On one-fourth of the trials (4 and 8, shaded gray), both correct and incorrect choices were reinforced; these were trials with novel testing stimuli from the training sets

IMTS testing outside the training categories

This testing phase explored whether the parrots could transfer their IMTS behavior to stimuli from a novel category—size. On three-fourths of the trials, the correct comparison stimulus was an exact match to the sample stimulus (only the correct choice was reinforced). On one-fourth of the trials, the correct comparison stimulus matched the sample in size, but depicted a different shape (both correct and incorrect choices were reinforced). The set of 12 black testing shapes included: circles, ellipses, squares, rectangles, and two types of triangles (equilateral and isosceles). Each shape appeared in one of two sizes: large and small. Each subject completed 480 trials. On 360 trials, the correct comparison stimulus was an exact match to the sample stimulus (exact match). On another 120 trials, the correct comparison stimulus matched the size of the sample (size match); here, the comparison stimuli were the same shape as one another, but they differed in size. Critically, on size match testing trials, the comparison stimuli did not match the sample stimulus in shape. A sample of 8 testing trials is shown in Fig. 2. A total of 60 stimulus combinations were used on size match trials (they were never repeated within sessions and were presented a maximum of 2 times, in different locations, across sessions), and 12 stimulus combinations were used on exact match trials (they were never repeated within sessions and were presented a maximum of 24 times across sessions).

The overall mean percentage of correct choices for parrot 1 was 73.06 % on exact match trials and 74.17 % on size match trials. The overall mean percentage of correct choices for parrot 2 was 87.22 % on exact match trials and 80.83 % on size match trials. Binomial tests for choice accuracy on both types of testing trials revealed that each parrot performed at significantly above chance levels (50 %), $p < .001$, thereby attesting to the ability of the birds to transfer a matching rule to stimuli from a novel size category even when shape identity was unavailable.

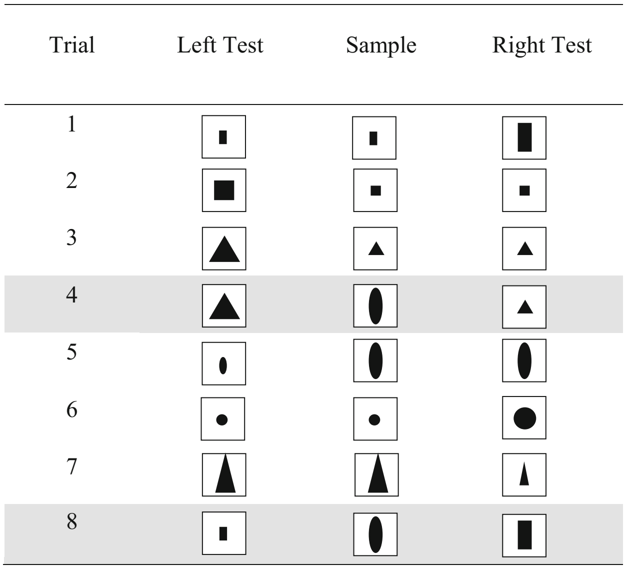

Fig. 2 Examples of sample and comparison stimuli across 8 exemplary size testing trials. On three-fourths of the trials (1–3 and 5–7), only correct choices were reinforced; these were trials in which the sample stimulus was identical to one of the comparison stimuli. On one-fourth of the trials (4 and 8, *shaded gray*), both correct and incorrect choices were reinforced; these were trials in which the sample stimulus was not identical in shape to either of the comparison stimuli, but matched the comparison stimuli on the basis of the novel category of size

RMTS testing

This most important testing phase examined the ability of the parrots to match stimuli on the basis of analogical relations. On three-fourth of the trials, the correct comparison pair was an exact match to the sample pair (*identity* trials). Here, both identity and relational matching could support accurate responding. On the other one-fourth of the trials, the parrots were tested to see whether they would choose comparison pairs that relationally matched the sample stimulus pair, even when none of the items in the sample pair physically matched any of the items in the comparison pairs (*relational* trials). Here, only relational matching could support accurate responding. On identity trials, food was given only after *correct* choices, whereas on the critical relational trials, *nondifferential* food reinforcement was given after *all* choices. These testing sessions contained 6 blocks (each block containing 6 identity trials and 2 relational trials); the trial order was randomized within each of the 6 blocks, creating 48 trials. On all trials, we scored as "correct" those choices that accorded with relational matching. Each assessment phase lasted 8 sessions. Each subject completed 384 trials: 288 *identity* trials and 96 *relational* trials, all of which involved 2-item sample and comparison stimuli in order to minimize (but not eliminate) the role of perceptual variability or *entropy* in the birds' RMTS behavior (Wasserman and Young 2010).

Size test

A set of 18 shapes (circle, ellipse, square, rectangle, equilateral triangle, and isosceles triangle; each shape appeared in one of three sizes: large, intermediate, and small) allowed us to construct the sample and comparison stimuli. Figure 3 shows that on half of the trials, the sample pair involved shapes of the same (intermediate) size, whereas on the other half of the trials, the sample pair involved shapes of different (large and small) sizes. Identity matching trials were arranged in which one comparison pair presented the same shapes in the same sizes as the sample pair; each of the sample and comparison pairs involved the same shape; and only correct choices were reinforced on these trials. Relational matching trials were arranged in which neither of the comparison pairs matched the sample pair in shape, thereby eliminating control by physical identity; on these trials, either correct or incorrect choices were reinforced. A total of 60 stimulus combinations were used on *relational* trials (they were never repeated within sessions and were presented a maximum of 2 times, in different locations, across sessions), and 12 stimulus combinations were used on *identity* trials (they were never repeated within sessions and were presented a maximum of 24 times across sessions).

Shape test

Black equal-sized circle, square, equilateral triangle, and cross-shapes were used to construct the sample and comparison stimuli. Figure 4 shows that on half of the trials, the sample pair involved identical shapes, whereas on the other half of the trials, the sample pair involved nonidentical shapes. Identity matching trials were arranged in which one comparison pair presented the same shapes as the sample pair; only correct choices were reinforced on these trials. Relational matching trials were arranged in which neither of the comparison pairs matched the sample pair in shape; on these trials, either correct or incorrect choices were reinforced. A total of 48 stimulus combinations were used on *relational* trials (they were never repeated within sessions and were presented a maximum of two times, in different locations, across sessions), and 10 stimulus combinations were used on *identity* trials (they were never repeated within sessions and were presented a maximum of 28 times across sessions).

Color test

Squares of red, green, blue, and yellow colors were used to construct the sample and comparison stimuli. Figure 5 shows that on half of the trials, the sample pair involved

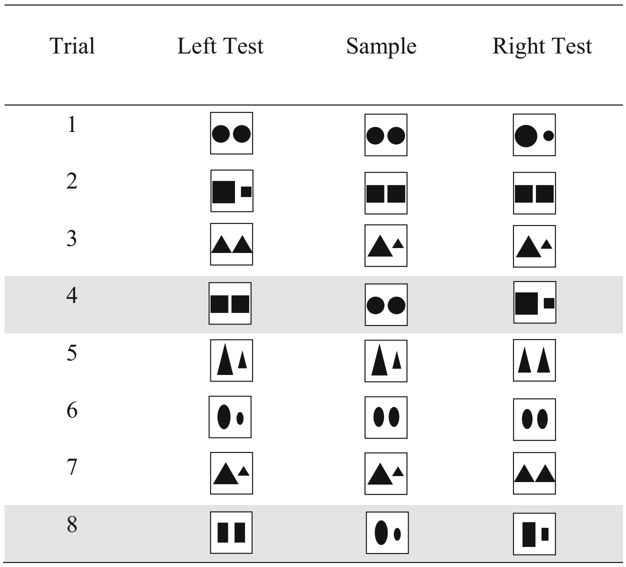

Fig. 3 Examples of identity and relational trials across 8 exemplary testing trials for size stimuli. On three-fourths of the trials (1–3 and 5–7), the correct comparison stimulus was an identity match to the sample. On one-fourth of the trials (4 and 8, *shaded gray*), the correct comparison stimulus was a relational match to the sample

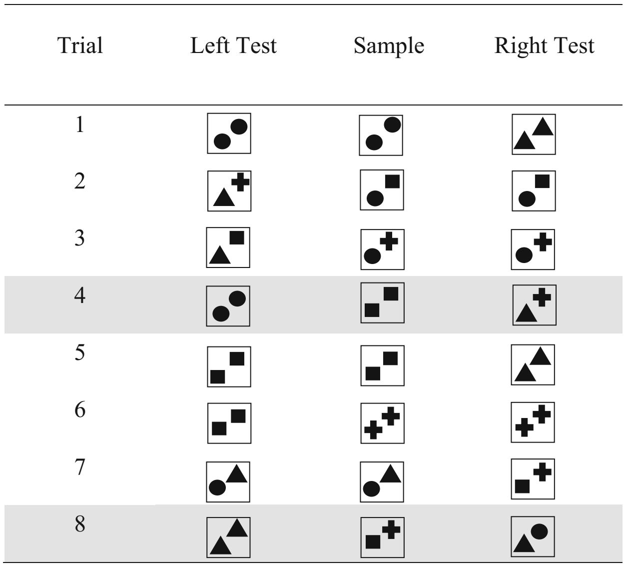

Fig. 4 Examples of identity and relational trials across 8 exemplary testing trials for shape stimuli. On three-fourths of the trials (1–3 and 5–7), the correct comparison stimulus was an identity match to the sample. On one-fourth of the trials (4 and 8, *shaded gray*), the correct comparison stimulus was a relational match to the sample

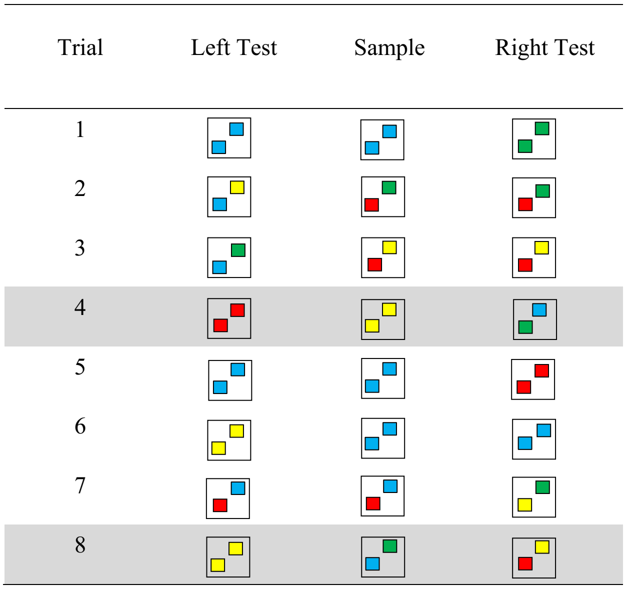

Fig. 5 Examples of identity and relational trials across 8 exemplary testing trials for color stimuli. On three-fourths of the trials (1–3 and 5–7), the correct comparison stimulus was an identity match to the sample. On one-fourth of the trials (4 and 8, *shaded gray*), the correct comparison stimulus was a relational match to the sample

identical colors, whereas on the other half of the trials, the sample pair involved nonidentical colors. Identity matching trials were arranged in which one comparison pair presented the same colors as the sample pair; only correct choices were reinforced on these trials. Relational matching trials were arranged in which neither of the comparison pairs matched the sample pair in color; on these trials, either correct or incorrect choices were reinforced. A total of 48 combinations of stimuli were used on *relational* trials (they were never repeated within sessions and were presented a maximum of 2 times, in different locations, across sessions), and 10 combinations of stimuli were used on *identity* trials (they were never repeated within sessions and were presented a maximum of 28 times across sessions).

Results

Statistical analysis details during identity and relational assessment phases

Our primary data were analyzed with logistic regressions run separately for each parrot. Each analysis examined accuracy as a function of three independent factors. Session (1–8, centered) was a time-based linear predictor. Trial type (identity vs. relational) was dummy coded (relational = 1) and then centered. Finally, because stimulus dimension had three levels (shape, size, and color), it was coded as two dummy variables: One was set to 1 for size and 0 otherwise; the other was set to 1 for color and 0 otherwise. Both were then centered.

Given that the main effect of stimulus dimension (and its various interactions) was spread across two variables, the significance of fixed effects was assessed with the χ^2 statistic for model comparison. Main effects were evaluated by comparing a model with all three main effects to one without the effect in question. Two-way interactions were evaluated by comparing a model with all two-way interactions to one without the interaction in question. Finally, comparing a model with the three-way interaction term against a model with the two two-way interaction terms evaluated the reliability of the three-way interaction. In these models, the intercept (B; in log odds) and its significance (assessed by a Wald Z statistic) tested the hypothesis that accuracy was above (when $B > 0$) or below (when $B < 0$) chance. Models were fitted using the GLM function, using a binomial error distribution (family = "binomial") in version 3.1.2 of R (http://www.cran.r-project.org/).

Choice behavior during identity and relational assessment phases

Throughout all three assessment phases of RMTS testing, both parrots exhibited highly accurate choice responding on both identity and relational trials (twelfth column in Table 2). We individually assessed each parrot's choice behavior with a logistic regression examining trial type, stimulus dimension, and session. These analyses revealed significant changes in choice accuracy over the 8 sessions in each phase for parrot 1 [$\chi^2(1) = 4.46$, $p = .0346$], but not for parrot 2: [$\chi^2(1) = 0.37$, $p = .5423$]. Analysis of parrot 1's scores revealed that its accuracy declined from 81 % in session 1 to 69 % correct in session 8. Because no interactions of session with the other variables arose for either parrot, subsequent discussion does not consider this factor (daily accuracy scores are reported in columns 4 through 11 in Table 2).

We next compared accuracy on the different kinds of trials against 50 % (random choice of comparison pairs). Averaged across all 8 sessions, parrot 1 responded at significantly above chance levels to all 6 different kinds of stimuli ($B = 1.08$, $\mathrm{SE} = 0.068$, $Z = 15.811$, $p < .0001$), with accuracy ranging from 70.83 to 78.47 % correct. A numerical (but not significant) difference was found between relational (72.92 %) and identity trials (74.88 %) [$\chi^2(1) = 0.44$, $p = .5077$]. Also, no significant trial type ×stimulus dimension interaction was found [$\chi^2(2) = 0.53$, $p = .7684$]. Overall, parrot 1 responded similarly on identity and relational trials across all dimensions, with a small, but nondifferential, reduction in accuracy over days. Averaged across all 8 sessions, parrot 2 responded at

Table 2 Mean accuracy on identity (IMTS) and relational (RMTS) trials for both parrots on all three dimensions across sessions 1–8

Bird	Dimension	Trial type	Session 1	Session 2	Session 3	Session 4	Session 5	Session 6	Session 7	Session 8	Sessions 1–8
Parrot 1	Size	Identity	83.33	91.67	66.67	41.67	50.00	83.33	83.33	66.67	70.83
		Relational	75.00	72.22	80.56	66.67	75.00	80.56	80.56	72.22	75.35
	Shape	Identity	91.66	66.67	75.00	83.33	66.67	75.00	66.67	83.33	76.04
		Relational	83.33	80.56	86.11	66.67	80.56	77.78	63.89	72.22	76.39
	Color	Identity	83.33	91.67	75.00	58.33	66.67	83.33	66.67	50.00	71.86
		Relational	80.56	75.00	75.00	69.44	69.44	63.89	69.44	66.67	71.18
Parrot 2	Size	Identity	66.67	91.67	83.33	83.33	83.33	75.00	83.33	75.00	80.21
		Relational	69.44	75.00	72.22	77.78	91.67	77.78	80.56	63.89	76.04
	Shape	Identity	75.00	83.33	75.00	91.67	75.00	66.67	66.67	66.67	75.00
		Relational	63.89	63.89	80.56	69.44	77.78	83.00	61.11	72.22	71.49
	Color	Identity	83.33	75.00	66.67	50.00	66.67	75.00	75.00	66.67	69.80
		Relational	75.00	52.78	63.89	83.33	63.89	69.44	75.00	75.00	69.79

significantly above chance levels to all 6 different kinds of stimuli ($B = 1.00$, $SE = 0.067$, $Z = 14.96$, $p < .0001$). Accuracy ranged from 69.79 to 80.21 % correct, with accuracy being numerically (but not significantly) lower on identity trials (72.22 %) than on relational trials (75.00 %). The logistic regression yielded no other significant effects.

Because of the importance of spontaneity to interpreting the parrots' RMTS behavior, we also analyzed choice accuracy in session 1 of each assessment phase (fourth column in Table 2) again using logistic regression. In session 1, parrot 1 responded at significantly above chance levels ($B = 1.50$, $SE = 0.22$, $Z = 6.80$, $p < .0001$), and there were no significant effects of trial type or stimulus dimension (all $ps > .10$); summed across all three dimensions, accuracy on identity trials averaged 79.63 % correct and accuracy on relational trials averaged 86.11 % correct. parrot 2 also responded at significantly above chance levels in session 1 ($B = 0.90$, $SE = 0.19$, $Z = 4.86$, $p < .0001$). Again, there were no significant effects of trial type or stimulus dimension (all $ps > .10$); summed across all three dimensions, accuracy on identity trials averaged 69.44 % correct and accuracy on relational trials averaged 75.00 % correct.

Discussion

Using methods very similar to those in our prior research with crows (Smirnova et al. 2015), we found that, immediately after IMTS training, our parrots not only responded discriminatively on identity matching trials, but they also did so on relational matching trials, all of these trials for the first time involving 2-item sample and comparison stimuli. These results represent evidence that parrots, like crows and apes (Vonk 2003), spontaneously perceive and respond to the relation between relations without ever having been explicitly trained to do so.

This documentation of RMTS behavior is particularly noteworthy because our parrots exhibited discriminative relational matching (averaging 80.56 % correct) that was just as robust as their identity matching (averaging 74.54 %) in session 1 across all three RMTS assessment phases. For comparative purposes, the crows in our prior project (Smirnova et al. 2015) also exhibited discriminative relational matching (averaging 77.78 % correct) that was just as robust as their identity matching (averaging 72.69 %) in session 1 across all three assessment phases. Although physical identity could have guided the parrots' and crows' choice behavior on identity trials, physical identity could not have done so on relational trials, as no physical matches were possible between the sample pairs and the correct comparison pairs. These results suggest that physical identity may have contributed very little to our birds' testing performance; relational processing seems to have been of prime importance to controlling their choice behavior.

Considering the striking phylogenetic and ecological disparities among parrots, crows, and apes, there may be good reason to expect many more species of animals to exhibit advanced conceptual abilities should experimenters put them to the test. We suspect that all of these reported successes are due to the animals' extensive previous training on a variety of IMTS tasks. Such prior training may serve as an effective scaffold on which relational responding can be built (Wasserman 2008). As Friedrich Nietzsche wrote in *Thus Spoke Zarathustra:* "He who wisheth one day to fly, must first learn standing and walking and running and climbing and dancing—one doth not fly into flying!"

In closing, we would like to consider the possibility that successful RMTS behavior may be supported by divergent perceptual and conceptual processes; different species may differently perform RMTS tasks. Fagot et al. (2001) explored this possibility in their comparative study of humans and baboons. Compared to baboons: Humans learned RMTS faster and reached higher levels of accuracy, they were more effectively transferred RMTS behavior to novel testing stimuli; they were less affected by the number of items in the sample and comparison arrays; and they were less affected by the variability or entropy of the items in the sample arrays.

Some authors (Penn et al. 2008) have deemed these behavioral disparities to reflect a *qualitative* difference between humans and baboons. Fagot et al. (2001) suggested instead that these behavioral disparities better represented a *quantitative* difference: Humans being more strongly controlled by conceptual than perceptual processes, and baboons being more strongly controlled by perceptual than conceptual processes. According to this latter view, perception and conception are not separate, but coextensive processes that jointly support cognitive behavior (Goldstone and Barsalou 1998). A key challenge for future work will be to systematically explore the role of both perceptual and conceptual mechanisms in RMTS behavior across a wide variety of species. Only then can we properly assess this central issue in comparative cognition.

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