PROCEEDINGS B

royalsocietypublishing.org/journal/rspb

Research



Cite this article: Song J, Luo F, ten Cate C, Yan C, Que P, Zhan X, Chen J. 2024 Stimulus-dependent emergence of understanding the 'same–different' concept in budgerigars. *Proc. R. Soc. B* **291**: 20241862.

https://doi.org/10.1098/rspb.2024.1862

Received: 7 March 2024 Accepted: 6 November 2024

Subject Category:

Behaviour

Subject Areas:

behaviour, cognition

Keywords:

relational concept learning, same-different, budgerigar, cognition

Author for correspondence:

Jiani Chen e-mail: chenjiani@lzu.edu.cn

[†]These authors contributed equally to the study.

Electronic supplementary material is available online at https://doi.org/10.6084/ m9.figshare.c.7563513.



Stimulus-dependent emergence of understanding the 'same—different' concept in budgerigars

Jingshu Song^{1,†}, Fangyuan Luo^{1,†}, Carel ten Cate^{2,†}, Chuan Yan¹, Pinjia Que³, Xiangjiang Zhan^{4,5,6} and Jiani Chen¹

¹College of Ecology, Lanzhou University, Lanzhou 73000, People's Republic of China ²Behavioural Biology, Institute of Biology Leiden, Leiden University, 2300 RA Leiden, The Netherlands ³Chengdu Research Base of Giant Panda Breeding, Sichuan Key Laboratory of Conservation Biology for Endangered Wildlife, Chengdu 610081, People's Republic of China

⁴Key Laboratory of Animal Ecology and Conservation Biology, Institute of Zoology, Chinese Academy of Sciences, Beijing 100101, People's Republic of China

⁵Cardiff University—Institute of Zoology Joint Laboratory for Biocomplexity Research, Chinese Academy of Sciences, Beijing 100101, People's Republic of China

⁶Center for Excellence in Animal Evolution and Genetics, Chinese Academy of Sciences, Kunming 650223, People's Republic of China

🔟 CtC, 0000-0002-4021-8915; CY, 0000-0002-6669-432X; JC, 0000-0003-0397-0013

The ability to understand relational concepts, such as 'same' and 'different', is a critical feature of human cognition. To what extent non-human animals can acquire such concepts and which factors influence their learning are still unclear. We examined the acquisition and the breadth of understanding the 'same-different' concept in budgerigars (Melopsittacus undulatus). Budgerigars trained to discriminate stimulus pairs in which two identical figures were either the same or different size (Experiment 1) successfully generalized the discrimination to novel stimuli belonging to various categories (size, colour, shape, geometric type and number of dots). The results of Experiment 1 thus demonstrate that budgerigars can perceive and generalize the same-different concept across dimensions after training with a limited set of stimuli differing along a single dimension. In contrast, while most budgerigars trained to discriminate two pairs of discs that were either the same or different in colour (Experiment 2) could generalize the discrimination to novel stimuli within the training category (colour), only few generalized the discrimination to another category suggesting a generalization based on perceptual similarity. The results thus show that whether budgerigars generalize a relationship by conceptual or perceptual similarity depends on the nature of the training stimuli.

1. Introduction

One critical feature of higher order human cognition is the ability to detect abstract relations among objects [1–3], providing the foundation for concept learning. The importance of such abilities has inspired many studies on whether they can be found in non-human animals. These demonstrated that animals can, for instance, categorize objects according to abstract features such as colour, shape and matter [4–7]. Another range of studies examined whether animals can acquire relational concepts, such as 'same' and 'different' [8–13], which is considered to be fundamental to human thinking [14,15]. In its simplest form, studies on acquiring and perceiving the 'same-different' concept use 'identity-matching-to-sample' (IMTS) tasks in which the animal is shown an example figure (e.g. a triangle), and next presented with two figures of which one is identical to the sample and the other is not (e.g. a square)

[16–18]. When choosing the matching figure, the animal receives a reward. After being trained in this way, the animal needs to be tested on whether it can detect the 'sameness' with stimuli differing in another dimension, e.g. if the training concerned matching on the basis of shape, acquisition of the same–different concept would result in transfer from matching by shape to matching by colour [19]. However, matching in IMTS tasks is not convincing evidence for relational learning because the animal can simply be perceiving a match rather than having acquired the concept 'same' [18,20].

A more challenging task to test the acquisition of the same-different concept is the same-different discrimination task [18,21]. In this task, animals are first trained to classify pairs of items as being the same (e.g. two triangles) or being different (e.g. a square and a circle) and next tested with novel pairs of items. Here also, critical for testing whether an abstract same-different concept has been acquired is generalization of the discrimination to stimulus pairs differing along other dimensions from the training stimuli. Using this or similar tasks, several mammal [13,22,23] and bird species [13] demonstrated the ability to identify sameness. However, there is still very limited evidence showing that non-human animals abstract the same-different concept across dimensions (such as training with same versus different shape and testing with same versus different colour).

The presence of the same-different concept is considered to be a precursor for the more advanced ability for analogical reasoning, which is fundamental to many cognitive functions in humans and considered a cornerstone of human intelligence [24,25]. The ability for analogical reasoning was initially demonstrated in chimpanzees [26]. Later experiments demonstrated its presence in some other primate species [27–29]. One way to test this ability is by using a 'relational-match-to-sample' (RMTS) task, in which an animal is shown a sample pair of figures that are either similar to each other or different in a particular dimension. It next has to select which of two pairs of other stimuli matches the within-pair relationship depicted in a sample pair. Using such an RMTS task, the ability for analogical reasoning was recently suggested to be present in two bird species: hooded crows [30] and Amazon parrots [31]. Both crows and parrots were capable of matching novel figure pairs BB with AA or EF with CD when the figures of the pair were identical or different in size, shape or colour. The presence of the ability of analogical reasoning implies that these birds also acquired the same-different concept. However, it has been suggested that the crow and parrot studies and even studies from primates do not rule out the possibility that the non-human animals might have used some lower order, perceptual rule [32,33], indicating the presence of many still debated theoretical issues concerning the same-different concept.

Many studies on same-different concept learning have also made clear that their outcome and interpretation can be affected by methodological factors, such as set size of training stimuli, the way stimuli are presented, the nature of the stimuli and others [11–13,34,35]. In addition, comparative studies have revealed that species may differ considerably in their performance in identical tasks [13], suggestive of qualitative and quantitative species differences in cognitive abilities. Given the importance of the same-different concept for providing the basis for analogical reasoning, and the impacts that methodology and species identity have on demonstrating the presence and broadness of the same-different concept, there is a need for further comparative studies that examine the acquisition and extent of this relational concept using different training and testing paradigms, as well as more extensive and varied sets of test stimuli.

In the current study, we examine the acquisition and breadth of the same-different concept in the budgerigar, a bird species so far not tested for relational learning. The budgerigar is a small parrot species, and previous studies have shown that this species is quite capable in problem-solving [36–38]. Budgerigars also demonstrated abstract rule learning in an auditory discrimination task in which they showed being capable of classifying short sound strings consisting of three elements according to their underlying relational structure (XYX or XXY) [39]. We trained two groups of ten budgerigars each to discriminate between 'same' and 'different' relations between items in a two-choice discrimination task. The stimulus items consisted of two geometric figures that were either the same (XX pattern) or different (XY pattern). The training dimensions were size (Experiment 1) or colour (Experiment 2, figure 1). Using different training stimuli in the two experiments allowed us to address whether the nature of these stimuli affected the generalization to novel stimuli. All birds were trained to discriminate the stimuli of 'same' relations from the stimuli of 'different' relations. After acquiring the discrimination, transfer of the discrimination was tested by presenting novel stimuli within the same dimension as the training (i.e. novel pairs of items either identical or non-identical in size (Experiment 1) or in colour (Experiment 2)), as well as to stimuli from novel categories, differing along other dimensions: shape, geometric type, number and colour (for birds in Experiment 1) or size (for birds in Experiment 2, figure 1).

Unlike previous studies, our novel category test stimuli did not have identical items indicating sameness, but only maintained a *relative* 'same' relationship between items in specific, and novel dimensions. For example, the two items of the 'same' test stimuli in the 'shape' category were of the same shape but differed in size (e.g. a big lightning symbol and a small lightning symbol) and hence were comparable with the training stimuli of the 'different' relation used in Experiment 1 (e.g. a big heart and a small heart). However, the two 'different' items in the 'shape' test set differed not only in size but also in symbol (e.g. a big lightning symbol and a small musical note; figure 1). Providing a correct response thus required the birds to ignore the physical size similarity to the earlier trained stimuli, and instead to make a decision based on the relative degree of 'same' among the two items of the two test stimuli presented. We also included sets of test stimuli belonging to very different stimulus categories, such as with different numbers of dots, to further reduce the possibility that the budgerigars could use perceptual features as a basis for their choice. The budgerigars showed capability of generalizing relational concepts. However, training on the 'size' dimension was more likely to result in acquisition of the 'same–different' concept than training on the 'colour' dimension.

| | Training | | | | | Test | | | | | | | | |
|-----------------|----------------|---------------------|-------------------|-----------|------|------------|------------|------------|------|------------|--------|--|-------------------|-----|
| | Pair 1 2 | S+ | S- | Pair 1 | Size | | Shape | | Туре | | Number | | Colour | |
| Experiment 1 | | ** ++ | | | •• | • | •• | • | • • | • 1 | | | •• | •• |
| | 3 4 | | | 2 | | | 11 | \ > | | * * | | | •• | • • |
| | 5 6 | # # | ↓ + | 3 | | |) > | ♪ ヽ | | ~ | | | \mathbf{O} | |
| | 7 8 | * * | * * ∘ ○ | 4 | | " | + + | ب د | € (| | ••• | | $\bullet \bullet$ | |
| Experiment 2 | 1 2 | •• | •• | 1 | ** | • • | •• | • | • • | • 1 | | | •• | •• |
| | 3 4 | | | 2 | ++ | + • | 11 | • | | * * | | | •• | |
| | 5 6 | $\bigcirc \bigcirc$ | | 3 | " | |) | Þ × | | ▲ ♦ | | | | |
| | 7 8 | | | 4 | | • | + + | ÷ c | € (| | • | | •• | •• |

Figure 1. Training and test stimuli of Experiments 1 and 2.

2. Materials and methods

(a) Subjects

Twenty adult budgerigars (10 males and 10 females) were used, equally distributed between the two experiments. They were experimentally naive, purchased from local breeders and kept in our laboratory with ad libitum food and water for over three months before introducing them to the experiments. Vegetables, mineral grit mixes and baths were provided regularly. Animal use and care followed the guidelines of Animal Experiments of Lanzhou University and conformed to governmental regulations concerning the ethical use of animals. Body weight was measured before and after experiments to keep track of unwanted weight loss (electronic supplementary material, table S2).

(b) Apparatus

Training and tests were conducted in a cage (60 cm long × 40 cm wide × 40 cm high) placed in a sound-attenuated chamber under a 10:14 dark–light photoperiod with illumination from a light-emitting diode ceiling-mounted luminaire (without ultraviolet spectrum). An opaque white polyvinyl chloride (PVC) sheet was inserted into the cage to create two compartments. One compartment with a perch was a 'waiting room' and the other one was an 'exam room'. The PVC sheet was tied to a nylon string that was hung on a stand to lift it (figure 2; electronic supplementary material, video S1). During the experiments, the sheet was gently lifted after the experimenters placed two Petri dishes covered with figures of stimuli into the 'exam room', allowing the birds to enter this compartment and to choose between the two discs.

(c) Stimuli

The training and test stimuli were either achromatic (grey) or coloured (budgerigars are known to have excellent colour vision [40]) and consisted of two geometric figures expressing the 'same' or 'different' relations. The two figures were the same or different in size, shape, geometric type, number of dots or colour (figure 1). All stimuli were resized to fit in a circle with a 4.5 cm radius and pixelated in Adobe Photoshop 2020 and then printed using a printer (HP Colour Laser Jet Pro MFP m281Fdw). The printed circle with the stimuli on it was cut and attached to a Petri dish inside its lid (figure 2). A white paper was attached to the remaining part of the Petri dish to ensure that the experimental subjects could not see the food inside the dish.

(d) Training phase

In the training, the birds were given a two-choice task (for more details, see the electronic supplementary material). All birds received the stimuli expressing the 'same' relation as positive stimuli (S+) and the stimuli of the 'different' relation as negative stimuli (S–). The stimuli were not counterbalanced as in most previous studies, in which 'same' stimuli were the S+ for some subjects, but the S– for others [8,9,20,39]. Learning may differ depending on whether the choice of the 'same' or 'different' pairs is reinforced [9,41], as the complexity of 'same' and 'different' may be asymmetric [42,43]. However, the aim of the current study was not to detect whether reinforcements with the 'same' relation differ from those with 'different' relations.



Figure 2. Photos of the experimental set-up (a) Apparatus for the experiments. (b) Bird discriminating achromatic stimuli. (c) Bird discriminating colour stimuli.

When the subjects made the correct choice, they were allowed to eat a small amount of seed in the dish. If an incorrect choice was made, the birds received an empty dish and a punishment of waiting for an extra 30 s between trials (the interval between trials for the correct choice was around 5 s). In Experiment 1, ten birds (five males and five females) were trained with eight pairs of stimuli that had two figures, either the same or different in size. In Experiment 2, another ten birds (five males and five females) were trained similarly but with coloured discs expressing the same or different relation (figure 1). Pseudo-random sequences of 100 trials were generated in R 4.4.1 [44] to decide which position (left or right) the two dishes would be put in the cage and which pair of stimuli (pairs 1–8) would be provided. This procedure was also used for presentation of the test stimuli. The subjects were considered to have met the training criterion when their correct rate was \geq 75% [4,13,45] for three consecutive training blocks (100 trials per block).

(e) Test phase

When the birds reached the training criteria, they proceeded to the test phase (electronic supplementary material, video S1). During this phase, the training stimuli and the test stimuli were mixed and occurred at a ratio of 60% and 40%. To exclude learning through reinforced choices during the test, a response to any test stimulus was rewarded [46], regardless of whether the choice of the birds was correct. This provided the subjects with the opportunity of learning the irrelevance of the categorization. Although this might induce a potential bias, it would be a conservative one, making correct responses more convincing of having acquired the same–different concept. Each of the five test categories contained four pairs of stimuli that the birds had never seen before. Each pair of test stimuli was presented 10 times during the test. The presence of stimuli during the test category) as the randomized factors. Test with 'size' category was first performed, subsequently with 'shape', 'type', 'number' and 'colour' categories in Experiment 1. The same was conducted in Experiment 2 except the 'colour' category was the first to test.

(f) Statistical analyses

At the group level, the results of each test were analysed using a one-sample *t*-test to determine whether the proportion of correct choices was higher than the chance value of 50%. An exact binomial test was used to analyse the probability of success at the individual level. The fitted learning curves that indicated the probabilities of successful choices in the training were constructed using the sigmoid function (logistic regression model based on the responses to the learning trials and the distributions of these responses) with binary data (choice of S+ and S–) as the dependent variable and trials as the independent variable [38,45,47]. All statistical analyses were performed in R 4.4.1 [44].

3. Results

(a) Training

All birds' discrimination started from chance (Experiment 1: 51.70% \pm 1.37 s.e. in the first three blocks, t = 1.23, p = 0.25 and n = 10; Experiment 2: 51.14% \pm 0.56 s.e. in the first three blocks, t = 2.01, p = 0.08 and n = 10, 100 trials per block; figure 3*a*,*b*), indicating they had no intrinsic bias to respond more strongly to stimuli containing identical or non-identical figures. Five



royalsocietypublishing.org/journal/rspb

Proc. R. Soc. B 291: 20241862

Figure 3. Individual learning performances during the training. (*a*) Mean percentage of correct responses to the eight stimulus pairs for the ten birds in Experiment 1. (*b*) Mean percentage of correct responses to the eight stimulus pairs for the ten birds in Experiment 2. Bars show 95% CI.

out of ten birds trained with the stimulus set of eight pairs of stimuli containing 'same' and 'different' relationships in size (Experiment 1) reached criterion (correct choice for the stimulus set >75% for three consecutive blocks) within a range of 7–46 blocks (30.20 ± 8.93 s.e., n = 5), with two of them (m27, f22, figure 3*a*) showing a steep learning curve. The other individuals stayed at chance level, even after 5000 trials of training, and we ended the training as no improvements were observed (figure 3*a* and electronic supplementary material, figure S1A). The discrimination patterns for the eight different stimulus pairs used in the training showed a similar increase within the individual birds (electronic supplementary material, figure S1A).

All 10 birds trained using stimuli with 'same' and 'different' relationships based on colour (Experiment 2) learned the discrimination. Their learning seems to proceed more incrementally than for the birds in Experiment 1 (figure 3). All birds met the training criterion within 22–87 blocks (44.10 ± 6.33 s.e., n = 10). Some stimulus pairs seemed more difficult to learn than others, but different birds exhibited different discrimination patterns for different stimulus pairs (figure 3*b* and electronic supplementary material, figure S1B). The number of training blocks required to reach the criterion for learning (for those birds reaching the criterion) was not significantly different between Experiments 1 and 2 (Welch's two sample *t*-test: t = -1.27, p = 0.24). The subjects were next tested on various transfer tasks that had novel stimuli of their training category, as well as stimuli from novel categories (figure 1; electronic supplementary material, video S1).

(b) Generalization tests

In Experiment 1, five out of ten birds that met the training criterion were next tested to investigate the generalization of the discrimination to novel stimuli in the size category as well as stimuli in the novel categories of shape, geometric type, number and colour (figures 1 and 4). The test stimuli were given interspersed between training stimuli. All birds readily generalized the trained discrimination to the novel stimuli in the trained size category. Importantly, all birds also showed more correct responses to the stimuli with a higher degree of 'sameness', irrespective of the stimulus categories (n = 5, all $p \le 0.001$; figure 4). An analysis at the individual level showed that all birds performed above chance by choosing appropriate relations when presented with novel stimuli in all five categories (all p < 0.05, except for the response to the colour category by bird m15, p = 0.08; electronic supplementary material, table S1).

For the ten birds in Experiment 2, all birds met the training criterion and were tested in five generalization tests with novel colour stimuli and the novel stimulus categories of shape, geometric type, number and size (figures 1 and 5). As in Experiment 1, here also the birds responded above chance in tests with novel exemplars of the trained category (colour; n = 10, 67.00% ± 3.05% s.e., t = 5.68, p < 0.001; figure 5). The appropriate choice for the size category was also significantly higher than 50%,



royalsocietypublishing.org/journal/rspb

Proc. R. Soc. B 291: 20241862

Figure 4. Performance in the tests during Experiment 1. (*a*) Percentage of correct choices in the five tests with novel stimuli of size, shape, geometric type and colour (mean \pm s.e., n = 5). *Correct responses are significantly higher than the chance level of 50% (p < 0.05). (*b*) Individual performances in the five tests.



Figure 5. Performance in the tests during Experiment 2. (*a*) Percentage of correct choice in the five tests with novel stimuli of size, shape, geometric type and colour (mean \pm s.e., n = 10). *Correct responses are significantly higher than the chance level of 50% (p < 0.05). (*b*) Individual performances in the five tests.

albeit slightly (n = 10, 56.25% ± 2.45% s.e., t = 2.70, p = 0.02; figure 5). No significant discrimination was present for the other test stimulus sets. Analysis of individual data showed that seven out of ten birds performed better than chance by choosing the appropriate relations in the novel colour generalization test (p < 0.05; electronic supplementary material, table S1). One of these birds (m12) chose the correct relational stimulus in all the five tests (all $p \le 0.02$; figure 5*b* and electronic supplementary material, table S1). Another bird (f24) responded significantly higher than chance in three tests (colour, type and number categories, all $p \le 0.02$) and had the tendency to respond above chance in size category (26 correct choices out of 40 trials, p = 0.08; figure 4*b* and electronic supplementary material, table S1).

4. Discussion

The results of our experiments indicate that budgerigars can generalize 'same' and 'different' relations to equivalent relationships among stimuli from novel categories that share no physical similarity to the training stimuli. However, the emergence of this ability seems to depend on the nature of the training stimuli. With the current set-up, the birds needed to detect the degree of 'sameness' in the relationships between two figures in one stimulus and compare this with the degree of 'sameness' in the relationship between two figures in another stimulus to make a correct choice. Noticeably, the test stimuli used for the novel

Α

% of correct choice

categories in our study varied in dimensions to which the budgerigars had not been exposed before. In particular, the birds from Experiment 1 showed being capable of assessing such relative sameness relationships. Below, we first briefly discuss our training method and next the interpretation of the outcomes of the two experiments.

(a) Training method

The budgerigars achieved the ability to generalize after being trained in a two-choice discrimination task with a limited set of eight training stimulus pairs, and without using preparatory progressive alignment training as is commonly used in other paradigms [30,31]. It is known that set size of training stimuli may affect conceptual learning and transfer [11]. Previous research has suggested that primates may require fewer exemplars to learn abstract concepts than non-primates [48]. However, studies on Clark's nutcrackers [48] and black-billed magpies [49] showed that these birds outperformed non-human primates in the abstract-concept learning when trained with limited exemplar set (8 and 56 pairs of 'same' and 'different' stimuli, respectively). The success of learning and transferring observed in our study is in line with the findings on nutcrackers and magpies to learn the same-different concept after limited training. It suggests that acquisition of this relational concept in budgerigars can develop quickly or is already present without a need for an extensive preceding training. Future studies are needed to examine whether this rapid acquisition is due to the training method or whether budgerigars are special in this respect.

(b) Training stimuli affect the emergence of conceptual abstraction

The noticeable difference in the performance between the birds in Experiments 1 and 2 demonstrates a clear effect of the nature of the training stimuli on the ability to generalize. Below, we first discuss the results obtained in Experiment 1, which shows the clearest evidence of conceptual learning.

In Experiment 1, the stimuli in the training contained two identical figures that were either the same or different in size. In line with the results obtained in many IMTS and RMTS studies, the response to novel test stimuli from the familiar category (size) was comparable with that to the trained items. A simple explanation for the success of this transfer might be that budgerigars have an intrinsic tendency to respond more strongly to a stimulus containing identical items. However, our training data show that all birds started the discrimination from chance level, making this explanation unlikely.

It is also unlikely that the transfer of correct choices from training to the other categories of test stimuli was based on lower order perceptual learning mechanisms, such as the presence or absence of identical items, symmetry or the same degree of between-item variability. If the training had resulted in the birds learning to respond to stimuli containing figures of identical size, they should not show any preference when tested with colour stimuli as these test stimuli were all of the same size. Also, no correct choice would be expected in the categories of shape and geometric type as these stimuli were all of different size and even different shape. Furthermore, in the 'shape' test, the two figures in stimuli of 'same' category were similar to the training stimuli of the 'different' category in Experiment 1 by being of the same shape but differing in size. However, the two figures in the 'different' test stimulus set differed not only in size but also in symbol. Therefore, a correct response required the birds to ignore the physical similarity of the 'same' test stimuli to the earlier trained 'different' stimuli, but to make a decision based on the relative degree of difference among the two items of the two test stimuli presented. Finally, if the preference for the test stimuli was based on an intrinsic preference for certain types of configurations or on using a learned lower order perceptual relatedness, one would expect that the birds of Experiment 2 would show a similar strength in preference for 'same' stimuli towards the novel stimulus categories of shape, type and number as shown by the birds in Experiment 2 reveal no tendency towards choosing more similar stimuli.

The consistent and high response to the stimulus pairs that maximized the 'sameness' in the tests (even though none corresponds to the identical pairs in the training) in most tests thus supports the interpretation that the budgerigars in Experiment 1 learned to discriminate between the stimuli by comparing the relation between the two figures within a 'same' training stimulus with the relation between the figures in the 'different' training stimulus and transferred the same-different distinction to test stimuli from the familiar category as well as to novel stimuli from different categories.

The results of Experiment 2 are, on the whole, different from those of Experiment 1. A first difference concerned the training phase. While more birds succeeded in the initial training, the learning curves of different individuals in Experiment 2 seem to progress more gradually, lacking any individuals showing the steep curves observed in two of the birds in Experiment 1. Also, almost each of the individuals in Experiment 2 had particular stimulus pairs that were learned more slowly than others (electronic supplementary material, figure S1B). Compared with Experiment 1 (electronic supplementary material, figure S1B). Compared with Experiment 1 (electronic supplementary material, figure S1A), the differences observed in the training phase may indicate that budgerigars in Experiment 2 paid more attention to each separate stimulus pair and learned them one by one, i.e. they learned by rote memory that a particular pair of same-colour dots was correct stimulus. A focus on memorizing individual stimulus pairs rather than using the more abstract underlying similarities and differences in the relations present within and between the stimuli can also explain the poor performance on the transfer to novel stimulus categories. Although for two birds (m12 and f24) the colour training may have induced relational learning comparable with the birds in Experiment 1, most birds showed no transfer of the differential responses to stimuli belonging to novel categories, and only seven out of the ten birds could transfer the relationships from the training stimuli to the novel colour test stimuli. Whether these individual differences in concept learning relate to other differences, similar to what

Birds, including the budgerigar, are known to have good colour perception [43], and colours can be important for food recognition and mate selection [52]. Colour may, therefore, be a very salient cue for budgerigars and can easily attract their attention. In an additional experiment, we found that budgerigars learned to associate a colour with food much faster than an achromatic (grey) stimulus (trials required to meet 80% correct in colour training: 43.33 ± 3.33 s.e., achromatic feature: 346.67 ± 82.12 s.e., n = 3; F. Luo & W. Zhao 2024, unpublished data). Such an inherent focus on colour might block or interfere with the attention to the abstract relational features of the stimulus set. It may have limited the learning to a more basic perceptual rule, such as that the two figures in one stimulus are always identical and in the other different. If the birds in Experiment 2 have a focus on identical pairs as correct stimuli, this may also explain that 'size' was the only novel stimulus category to get a significantly higher correct score. This is the only category in which the two figures of the 'same' stimuli are identical, as they are in the colour training stimuli. Alternatively one might argue that the birds in this experiment learned another more specific rule: choose same-colour. Such a rule might explain why the birds did not discriminate when test stimuli of both categories were all grey. However, neither interpretation would explain the results of the three birds that did not score above chance with novel coloured stimuli. So, although the colour training of Experiment 2 did result in relational learning in two birds, the results for most birds indicate learning of a perceptual rule (two figures in a stimulus need to be identical to prefer it) rather than a conceptual one or even (for three birds) of attending only to the memorized individual training pairs.

5. Conclusions

Our findings add to the growing number of studies demonstrating that non-human animals can learn to apply the relational 'same-different' concept. We demonstrate that budgerigars can acquire the same-different concept after being trained with a limited set of training stimuli differing along a single dimension and apply it across dimensions. Further investigations are required to address whether training using 'different' stimuli as S+ results in a different outcome compared with training using 'same' stimuli as S+ and whether and to what extent the two-choice discrimination training method and set-size influence concept learning.

The remarkable difference between the results of Experiments 1 and 2 in our study indicates that the nature of the training stimuli can have a strong impact on whether the responses to novel stimuli are based on their conceptual or their perceptual similarity with the training stimuli. This calls for a further exploration of the influence of the nature of training stimuli on the emergence of relational learning, and whether the differential impact observed in our study is also present in other species. Experiments using a variety of training categories may provide more information on how different categories of stimuli affect learning strategies and outcomes within and between species.

Ethics. Animal use and care followed the guidelines of Animal Experiments of Lanzhou University and conformed to governmental regulations concerning the ethical use of animals (Law of the People's Republic of China on the Protection of Wildlife; Regulations from the State Forestry and Grassland Administration on Properly Resolving Issues Related to Captive Breeding of Parrots). This study was approved by the Animal Care and Use Committee of Lanzhou University (no. EAF2022010).

Data accessibility. Data are available as electronic supplementary material [53].

Declaration of Al use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. J.S.: data curation, investigation, methodology, visualization, writing—original draft; F.L.: data curation, investigation, methodology; C.t.C.: supervision, writing—original draft, writing—review and editing; C.Y.: data curation, formal analysis, visualization, writing—review and editing; P.Q.: methodology; X.Z.: funding acquisition, methodology, supervision; J.C.: conceptualization, data curation, formal analysis, funding acquisition, methodology, supervision, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

Funding. This research was supported by funding STI2030-Marjor Project 2021ZD0204100 (2021ZD0204101), the National Natural Science Foundation of China (project no. 32070445) and the CAS Project for Young Scientists in Basic Research (YSBR-097).

Acknowledgements. Thanks to Qian Xiao and Danni Tang for discussing the results. We also thank three anonymous reviewers for their comments and suggestions.

References

- 1. Gentner D, Hoyos C. 2017 Analogy and abstraction. Top. Cogn. Sci. 9, 672–693. (doi:10.1111/tops.12278)
- 2. Gentner D, Medina J. 1998 Similarity and the development of rules. Cognition 65, 263–297. (doi:10.1016/s0010-0277(98)00002-x)
- 3. Tenenbaum JB, Griffiths TL. 2001 Generalization, similarity, and Bayesian inference. Behav. Brain Sci. 24, 629–640; (doi:10.1017/s0140525x01000061)
- 4. Pepperberg IM. 1987 Acquisition of the same/different concept by an African grey parrot (*Psittacus erithacus*): learning with respect to categories of color, shape, and material. *Anim. Learn. Behav.* **15**, 423–432. (doi:10.3758/BF03205051)
- 5. Bhatt RS, Wright AA. 1992 Concept learning by monkeys with video picture images and a touch screen. J. Exp. Anal. Behav. 57, 219–225. (doi:10.1901/jeab.1992.57-219)
- 6. Herrnstein RJ, Loveland DH. 1964 Complex visual concept in the pigeon. Science 146, 549–551. (doi:10.1126/science.146.3643.549)
- 7. Aust U, Huber L. 2002 Target-defining features in a 'people-present/people-absent' discrimination task by pigeons. Anim. Learn. Behav. 30, 165–176. (doi:10.3758/bf03192918)
- 8. Giurfa M, Zhang S, Jenett A, Menzel R, Srinivasan MV. 2001 The concepts of 'sameness' and 'difference' in an insect. Nature 410, 930–933. (doi:10.1038/35073582)
- 9. Blaisdell AP, Cook RG. 2005 Two-item same-different concept learning in pigeons. Learn. Behav. 33, 67–77. (doi:10.3758/BF03196051)

- Fuss T, John L, Schluessel V. 2021 Same or different? Abstract relational concept use in juvenile bamboo sharks and Malawi cichlids. Curr. Zool. 67, 279–292. (doi:10.1093/cz/zoy059)
- 11. Katz JS, Wright AA. 2021 Issues in the comparative cognition of same/different abstract-concept learning. Curr. Opin. Behav. Sci. 37, 29–34. (doi:10.1016/j.cobeha.2020.06.009)
- 12. Wright AA, Kelly DM, Katz JS. 2021 Same/different concept learning by primates and birds. Learn. Behav. 49, 76–84. (doi:10.3758/s13420-020-00456-z)
- 13. Leonard K, Sepehri P, Cheri B, Kelly DM. 2023 Relational complexity influences analogical reasoning ability. *iScience* 26, 106392. (doi:10.1016/j.isci.2023.106392)
- 14. James W. 1890 *The principles of psychology*. New York, NY: Holt. (doi:10.1037/10538-000)
- 15. Wasserman EA, Young ME. 2010 Same-different discrimination: the keel and backbone of thought and reasoning. J. Exp. Psychol. 36, 3–22. (doi:10.1037/a0016327)
- 16. Truppa V, Garofoli D, Castorina G, Piano Mortari E, Natale F, Visalberghi E. 2010 Identity concept learning in matching-to-sample tasks by tufted capuchin monkeys (*Cebus apella*). Anim. Cogn. **13**, 835–848. (doi:10.1007/s10071-010-0332-y)
- 17. Thompson RKR, Oden DL. 1995 A profound disparity revisited: perception and judgment of abstract identity relations by chimpanzees, human infants, and monkeys. *Behav. Processes* **35**, 149–161. (doi:10.1016/0376-6357(95)00048-8)
- Gentner D, Shao R, Simms N, Hespos S. 2021 Learning same and different relations: cross-species comparisons. *Curr. Opin. Behav. Sci.* 37, 84–89. (doi:10.1016/j.cobeha.2020.11. 013)
- 19. Premack D. 2018 On the abstractness of human concepts: why it would be difficult to talk to a pigeon. In *Cognitive processes in animal behavior*, pp. 423–451. London, UK: Routledge. (doi:10.4324/9780203710029-14)
- 20. Martinho A 3rd, Kacelnik A. 2016 Ducklings imprint on the relational concept of 'same or different'. Science 353, 286–288. (doi:10.1126/science.aaf4247)
- 21. Premack D. 1983 The codes of man and beasts. Behav. Brain Sci. 6, 125–136. (doi:10.1017/S0140525X00015077)
- 22. Herman LM, Pack AA, Wood AM. 1994 Bottlenose dolphins can generalize rules and develop abstract concepts. *Mar. Mammal Sci.* **10**, 70–80. (doi:10.1111/j.1748-7692.1994. tb00390.x)
- 23. Wasserman EA, Fagot J, Young ME. 2001 Same-different conceptualization by baboons (*Papio papio*): the role of entropy. *J. Comp. Psychol.* **115**, 42–52. (doi:10.1037/0735-7036. 115.1.42)
- 24. Sternberg RJ. 1977 Intelligence, information processing, and analogical reasoning: the componential analysis of human abilities. Hillsdale, NJ: Lawrence Erlbaum.
- 25. Gentner D. 1998 Analogy. In *A companion to cognitive science* (eds W Bechtel, G Graham), pp. 107–113, 2nd edn. Oxford, UK: Blackwell Press. (doi:10.1111/b.9780631218517.1999. 00004.x)
- 26. Gillan DJ, Premack D, Woodruff G. 1981 Reasoning in the chimpanzee: I. Analogical reasoning. J. Exp. Psychol. 7, 1–17. (doi:10.1037/0097-7403.7.1.1)
- 27. Vonk J. 2003 Gorilla (*Gorilla gorilla gorilla*) and orangutan (*Pongo abelii*) understanding of first- and second-order relations. *Anim. Cogn.* **6**, 77–86. (doi:10.1007/s10071-003-0159-x)
- 28. Truppa V, Piano Mortari E, Garofoli D, Privitera S, Visalberghi E. 2011 Same/different concept learning by capuchin monkeys in matching-to-sample tasks. *PLoS ONE* **6**, e23809. (doi: 10.1371/journal.pone.0023809)
- 29. Fagot J, Maugard A. 2013 Analogical reasoning in baboons (*Papio papio*): flexible reencoding of the source relation depending on the target relation. *Learn. Behav.* **41**, 229–237. (doi:10.3758/s13420-012-0101-7)
- 30. Smirnova A, Zorina Z, Obozova T, Wasserman E. 2015 Crows spontaneously exhibit analogical reasoning. Curr. Biol. 25, 256–260. (doi:10.1016/j.cub.2014.11.063)
- 31. Obozova T, Smirnova A, Zorina Z, Wasserman E. 2015 Analogical reasoning in amazons. Anim. Cogn. 18, 1363–1371. (doi:10.1007/s10071-015-0882-0)
- 32. Vonk J. 2015 Corvid cognition: something to crow about? Curr. Biol. 25, R69–R71. (doi:10.1016/j.cub.2014.12.001)
- Penn DC, Holyoak KJ, Povinelli DJ. 2008 Darwin's mistake: explaining the discontinuity between human and nonhuman minds. *Behav. Brain Sci.* 31, 109–130; (doi:10.1017/S0140525X08003543)
- 34. Cook RG, Qadri MA. 2021 Examining the extents of same/different processing in non-human animals. Curr. Opin. Behav. Sci. 37, 98–102. (doi:10.1016/j.cobeha.2020.10.014)
- 35. Zentall TR, Wasserman EA, Lazareva OF, Thompson RKR, Rattermann MJ. 2008 Concept learning in animals. Comp. Cogn. Behav. Rev. 3, 13–45. (doi:10.3819/ccbr.2008.30002)
- 36. Medina-García A, Wright TF. 2021 An integrative measure of cognitive performance, but not individual task performance, is linked to male reproductive output in budgerigars. *Sci. Rep.* **11**, 11775. (doi:10.1038/s41598-021-91213-3)
- 37. Cowie A. 2014 Experimental studies of social foraging in budgerigars, *Melopsittacus undulatus*. PhD thesis, University of St Andrews, UK.
- 38. Chen J, Chen L, Yan C, Yu Z, Zou Y, Sun YH. 2022 Are cognition and personality related in budgerigars? Curr. Zool. 68, 315–323. (doi:10.1093/cz/zoab069)
- Spierings MJ, ten Cate C. 2016 Budgerigars and zebra finches differ in how they generalize in an artificial grammar learning experiment. *Proc. Natl Acad. Sci. USA* 113, E3977–84. (doi:10.1073/pnas.1600483113)
- 40. Goldsmith TH, Butler BK. 2005 Color vision of the budgerigar (*Melopsittacus undulatus*): hue matches, tetrachromacy, and intensity discrimination. J. Comp. Physiol. A **191**, 933–951. (doi:10.1007/s00359-005-0024-2)
- 41. Diaz F, O'Donoghue EM, Wasserman EA. 2021 Two-item conditional same-different categorization in pigeons: finding differences. J. Exp. Psychol. Anim. Learn. Cogn. 47, 455–463. (doi:10.1037/xan0000297)
- 42. Hochmann JR. 2021 Asymmetry in the complexity of same and different representations. Curr. Opin. Behav. Sci. 37, 133–139. (doi:10.1016/j.cobeha.2020.12.003)
- 43. Zentall TR, Andrews DM, Case JP. 2018 Sameness may be a natural concept that does not require learning. Psychol. Sci. 29, 1185–1189. (doi:10.1177/0956797618758669)
- 44. R Core Team. 2020 R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. See https://www.R-project.org.
- 45. Chen J, ten Cate C. 2017 Bridging the gap: learning of acoustic nonadjacent dependencies by a songbird. J. Exp. Psychol. Anim. Learn. Cogn. 43, 295–302. (doi:10.1037/xan0000145)
- 46. Lea SEG, Pothos EM, Wills AJ, Leaver LA, Ryan CME, Meier C. 2018 Multiple feature use in pigeons' category discrimination: the influence of stimulus set structure and the salience of stimulus differences. J. Exp. Psychol. Anim. Learn. Cogn. 44, 114–127. (doi:10.1037/xan0000169)
- 47. Lim TS, Loh WY, Shih YS. 2000 A comparison of prediction accuracy, complexity, and training time of thirty-three old and new classification algorithms. *Mach. Learn.* **40**, 203–228. (doi:10.1023/A:1007608224229)
- Magnotti JF, Katz JS, Wright AA, Kelly DM. 2015 Superior abstract-concept learning by Clark's nutcrackers (*Nucifraga columbiana*). *Biol. Lett.* 11, 20150148. (doi:10.1098/rsbl.2015. 0148)
- 49. Magnotti JF, Wright AA, Leonard K, Katz JS, Kelly DM. 2017 Abstract-concept learning in black-billed magpies (*Pica hudsonia*). *Psychon. Bull. Rev.* 24, 431–435. (doi:10.3758/s13423-016-1132-4)
- 50. Branch CL, Semenov GA, Wagner DN, Sonnenberg BR, Pitera AM, Bridge ES, Taylor SA, Pravosudov VV. 2022 The genetic basis of spatial cognitive variation in a food-caching bird. *Curr. Biol.* **32**, 210–219.(doi:10.1016/j.cub.2021.10.036)
- 51. Chen J, Zou Y, Sun YH, ten Cate C. 2019 Problem-solving males become more attractive to female budgerigars. Science 363, 166–167. (doi:10.1126/science.aau8181)

- 52. Vorobyev M, Osorio D, Bennett ATD, Marshall NJ, Cuthill IC. 1998 Tetrachromacy, oil droplets and bird plumage colours. J. Comp. Physiol. A 183, 621–633. (doi:10.1007/ s003590050286)
- 53. Song J, Luo F, ten Cate CJ, Yan C, Que P, Zhan X *et al*. 2024 Supplementary material from: Stimulus dependent emergence of understanding the 'same-different' concept in budgerigars. Figshare. (doi:10.6084/m9.figshare.c.7563513)