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Title: Same or different? Ducks imprint on a relational concept.

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Abstract:

The ability to identify and retain logical relations between stimuli and apply them to novel stimuli is known as relational concept learning. This has been demonstrated in a few animal species after extensive reinforcement training, and it reveals the brain's ability to deal with abstract properties. Here we show relational concept learning in newborn ducklings without reinforced training. Newly hatched domesticated mallards briefly exposed to a pair of objects that were either the same or different in shape or colour later preferred to follow pairs of new objects exhibiting the imprinted relation. Thus, even in a seemingly rigid and very rapid form of learning like filial imprinting, the brain operates with abstract, conceptual reasoning, a faculty often assumed to be reserved to highly intelligent organisms.

One Sentence Summary:

Ducklings use the relational concepts "same" and "different" as targets for imprinting.

Main Text:

Relational concepts, such as “same” and “different”, have been demonstrated in a few animal species, typically following extensive training (*1, 2*). Relational concepts differ from other forms of categorical generalization. For instance, pigeons and bees can be trained to discriminate whether novel images contain humans or not (*3*), or whether novel paintings are by Monet or Picasso (*4*) relying on the similarity between features of the training and novel stimuli. In relational concept learning, however, relative properties between training stimuli generate the relationship that has to be generalized to sets of novel stimuli (*5*).

The relations of “same” and “different” have been used to study relational concept learning in a few primates and birds (*6*), using a variety of protocols. For instance, in the Identity Matching to Sample (IMTS) protocol, an animal sees a sample stimulus and subsequently chooses between two test stimuli, one of which is identical to the sample. Reinforcement can be contingent on responding to the identical one (“same”) or to the alternative (“different”). Honeybees can learn this discrimination and even transfer correct response to novel stimuli across sensory modalities (olfaction and visual texture) (*7*). The IMTS task requires learning the appropriate comparison between the working memory representation of the sample and the currently perceived test stimuli, but it does not require interpreting an abstract relationship between perceived items and then reapplying the same relation to discriminate between sets of novel objects.

A different procedure, that isolates relational learning, involves presenting more than one stimulus as a sample, and then selecting, from between various sets of stimuli, the set that has the same internal relation as the sample set, a procedure called relational matching to sample (RMTS) (*1, 8*). In RMTS what has to be retained is a relation between stimuli, rather than a representation of a perceived stimulus. Primates (*9*), pigeons (*5*), parrots (*10*), and corvids (*1*), have succeeded in such problems, and it has been cogently argued that this may indicate their possession of the ability to reason by analogy (*8*).

Demonstrating capacity for both identity and relational matching to sample has so far used reinforcement, and often-extensive training, to allow subjects to infer the target relation. This contrasts with avian filial imprinting, a specialized form of unrewarded learning by which hatchlings acquire the ability to identify and then follow a parent or substitute parental object (*11*-*13*). As could be expected from its biological adaptive significance, imprinting is one of the fastest and most reliable forms of learning (*14*). In chickens and ducklings, high fidelity imprinting responses can be acquired in a few minutes of unrewarded exposure to a stimulus (*15*).

Filial and sibling imprinting cannot be mediated just by snapshot representations of two-dimensional retinal images. Wood (2015) summarised the problem sharply: "Building an invariant object representation requires transforming patterns of retinal activity (view-specific information) into an abstract representation that is tolerant to retinal image changes and selective for a particular object (identity information)" (*16*). This is particularly relevant when considering that ducklings may benefit by recognizing not just their mother but also their group of siblings (*17*), because broods may have different degrees of heterogeneity. Evidence showing that young birds are sensitive to abstract qualities of stimuli, both spontaneously and through imprinting, supports this view and shows that imprinting is far richer, as a learning phenomenon, than had originally been envisaged (*18*-*21*) It is thus tempting to ask whether their abstraction abilities may extend to the more demanding phenomenon of relational concept representation, which has so far only been demonstrated through extensive reinforcement in species with advanced intelligence. To this effect we modified the RMTS protocol to combine it with imprinting, as follows.

Following Bateson's (*22*) and Lickliter's (*23*) procedures for effective imprinting, we hatched domesticated mallard ducklings in the dark and kept them for 1 hour in a social group, with light, food, and water. They were then exposed for 25 minutes to a moving pair of sample objects, kept for a 30min retention interval in the dark, and presented for 10min with two novel pairs of moving objects (Figure 1). Sample stimuli within the pair shown in the imprinting phase were either equal to each other in both colour and shape, or different in one of these characteristics. Test stimuli in the preference test consisted of two stimuli pairs, composed of objects novel to the birds. In one test pair the objects were equal in colour and shape, and in the other they differed in either shape or colour (Figure 2). Detailed methods may be found in Supplementary Materials.

In Experiment 1, the imprinting phase stimulus pair consisted of two red solids, which were equal to each other in shape for group 'same' and different for group 'different' (n=36 for each group). The stimuli forming the two test pairs were also red, but one pair consisted of two novel, identical shapes and the other two novel, different shapes. In Experiment 2, the imprinting stimulus pair comprised two spheres, either of same or different colour (n=40 for each group) and test stimuli were also spherical but with novel colours, equal in one pair and different in the other.

To measure preference, the number of approaches undertaken by each duckling toward each test pair was scored twice, once by an independent scorer blind to each duckling's imprinting condition and to the study's hypothesis. Ducklings that were inactive during testing (fewer than five approaches) were excluded from analysis. Preferences were assessed via sign test, with sample size being the number of individual ducklings. Ducklings making more than half of their approaches toward a given stimulus were scored as having preferred it (See Methods in Supplementary Materials). Video of sample trials (Movie S1) is available in Supplementary Materials.

Figure 3 shows the preference results. In Experiment 1, out of a total of 47 active ducklings, 32 preferred the pair bearing their imprinted shape relation (two-tailed binomial test, $p = 0.02$). In Experiment 2, out of 66 active ducklings, 45 preferred the stimulus pairs bearing their imprinted colour relation (two-tailed binomial test, $p = 0.004$). Combining both results, out of 113 active ducklings, 77 preferred the relational concept, same or different, upon which they had imprinted (two-tailed binomial test, $p < 0.0001$).

The accuracy of our ducklings was comparable to, or better than, reinforced relational concept discrimination in primates (*24*) and crows (*1*). This finding supports a richer emerging view of the representation of information in the animal brain than is presently prevalent, in which even relatively simple learning systems do not process information just through the content of sensory signals but also by encoding higher-level, abstract aspects of stimulus analyses, already the target of neural network models designed to simulate such cognitive function (*25*). The ducklings' performance indicates that their brains may be prepared, not just to respond differentially to certain visual inputs, such as scrambled objects containing species-specific elements like legs or heads or virtual points that move in a biologically plausible coordination (*20*), but also to pick up abstract relational properties between elements of their sensory input and their characteristics.

For young precocious birds, having this competence makes biological sense. For a duckling critically dependent on proximity to its mother and siblings, defining the attachment stimulus configuration as a library of sensory inputs and logical rules increases the likelihood that the mother and sibling group will be identified with high fidelity in spite of considerable variations in how they are perceived. The rules that may define the imprinted attachment target are likely to extend beyond properties of a single object such as colour, shape, or symmetry, to include properties of object assemblies such as their informational entropy (*26*).

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Materials and Methods and a video of sample trials may be found in Supplementary Materials. Video recordings of training and testing can be made available on request. Data obtained from video coding is available on Dryad (reference to be inserted here after definite acceptance).

The experiment was devised jointly by AM and AK. Experimentation, data collection, and analysis were performed by AM with the advice and support of AK. The manuscript was written jointly by AM and AK and figures were prepared by AM and edited by AK.

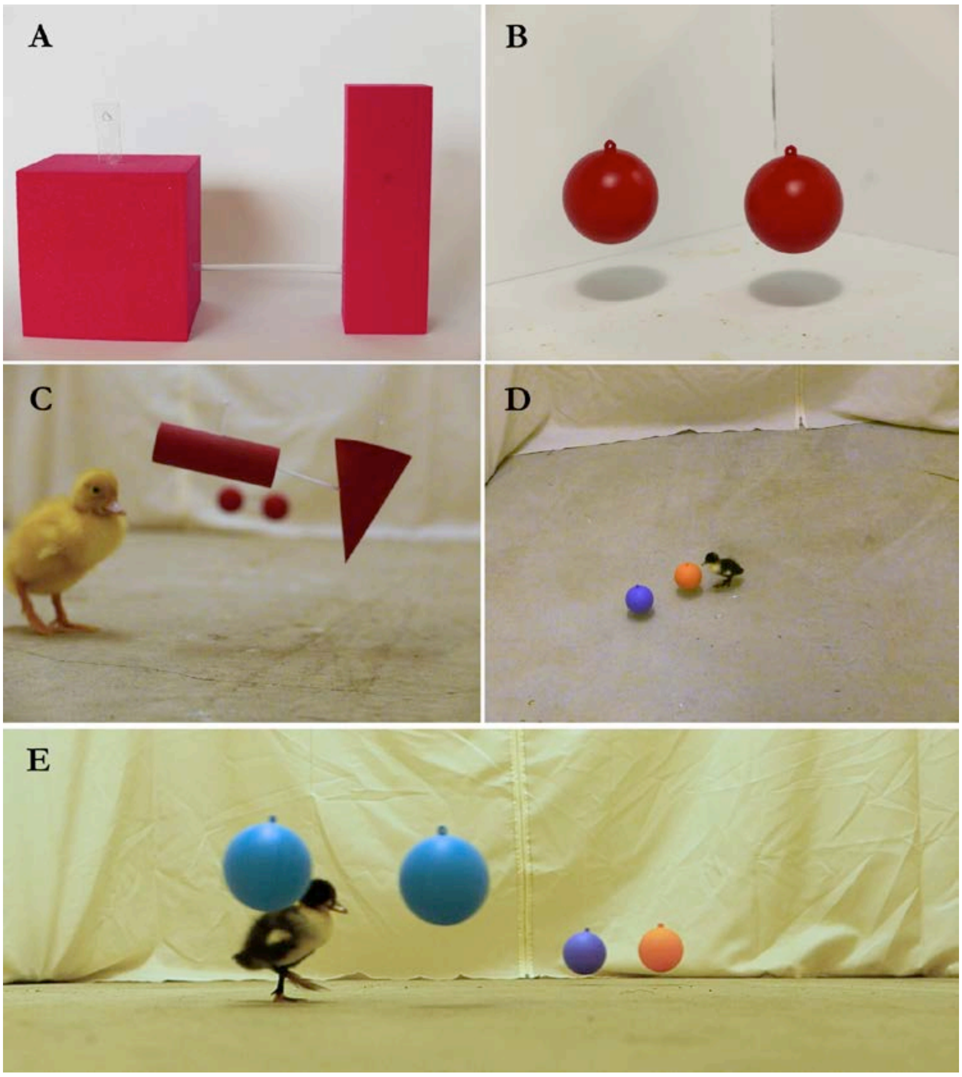

Fig. 1. Imprinting and testing stimuli .

Newborn ducklings were first exposed to a pair of objects revolving about the centre of a training arena, then tested with two novel pairs of objects. (**A**) Example of a 'different shape' training stimulus pair. (**B**) Example of a 'same colour' training stimulus pair. Following this, the ducklings were tested for preference between two novel stimulus pairs revolving in apposition. (**C**) A duckling trained with the set shown in (**A**) demonstrates its preference for a novel 'different shape' stimulus over an also novel 'same shape' stimulus. (**D**) A duckling trained with the stimulus pair shown in (**B**) approaches a novel "different colour" stimulus pair – an "incorrect" response. (**E**) The same duckling later in the same trial correctly approaches and closely follows the novel 'same colour' stimulus.

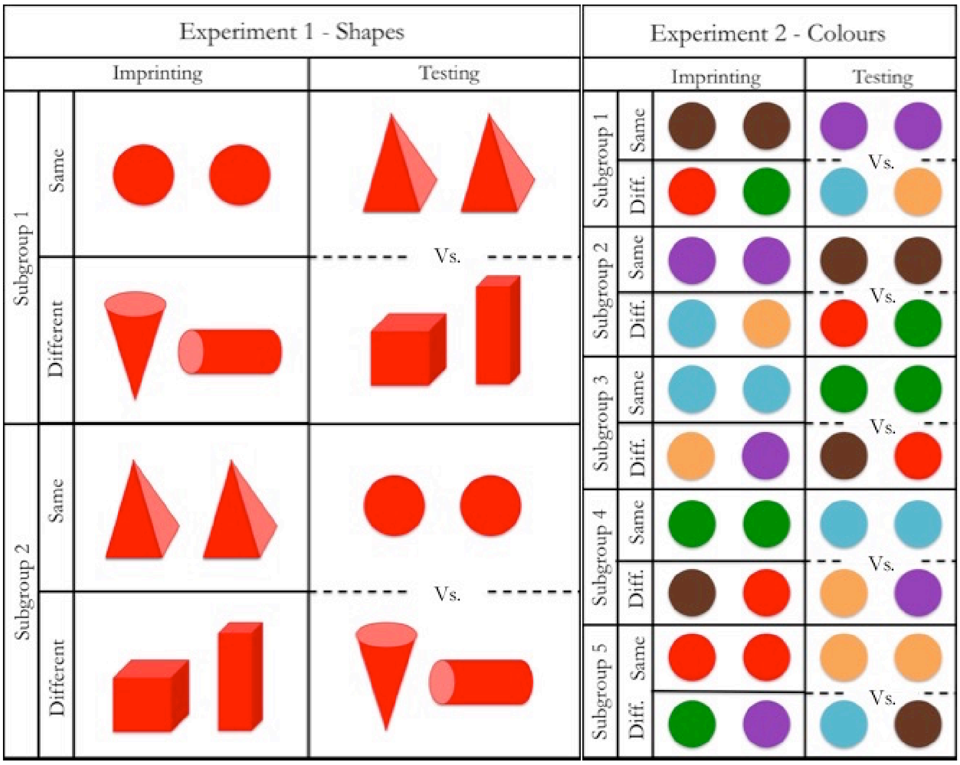

Fig. 2. Experimental Stimulus Pairs

Experiment 1 tested for responses between red objects that could differ in shape and Experiment 2 for responses between spherical objects that could differ in colour, using the pairs illustrated here. In Experiment 1 members of Subgroup 1 were initially exposed to either two spheres or a pair of a cone and a cylinder, and then tested for preference between a pair of two pyramids and a pair formed by a prism and a cube, while members of Subgroup 2 were imprinted on pairs of either two pyramids or a prism and a cube and tested on preference between a pair of spheres and a pair formed by a cone and a cylinder. In Experiment 2 members of each subgroup were trained on either two identical spheres or a pair formed by two spheres of different colours, and all participants were tested for preference between two novel identical spheres and a pair formed by two novel, differing spheres.

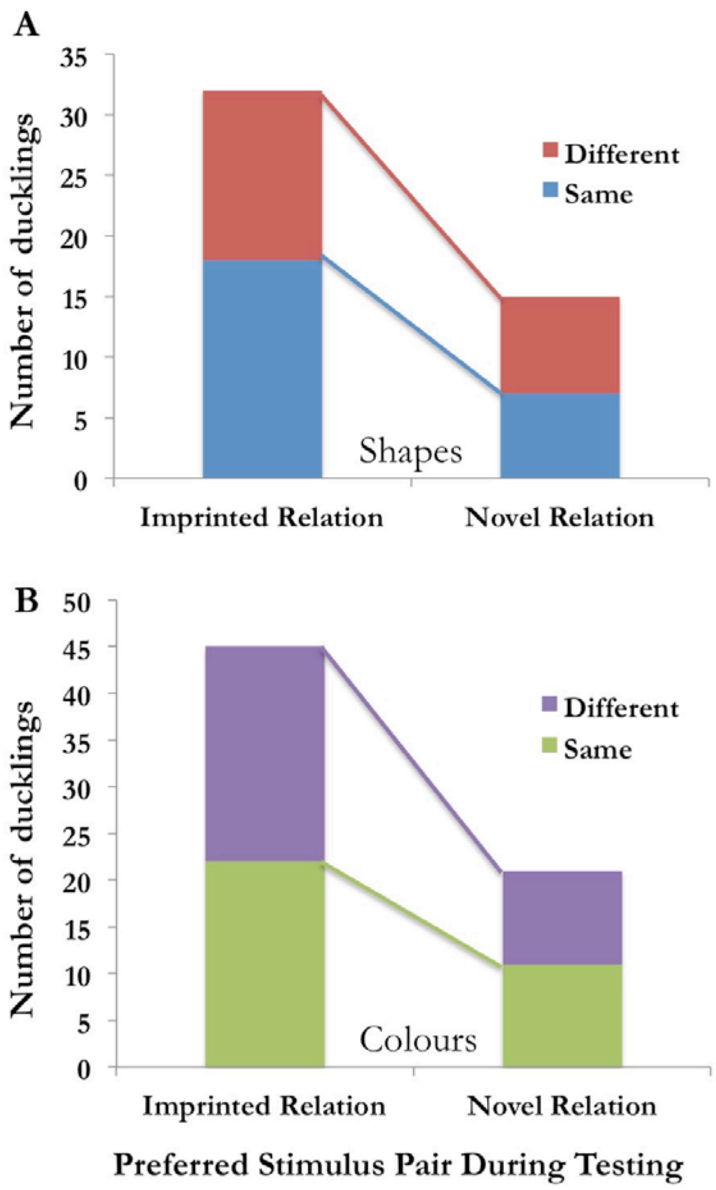

Figure 3. Ducklings' preferences for an imprinted relational concept

The number of subjects showing preference for the imprinted (left column) or alternative (right column) relation is shown for shape relations in Experiment 1 (A) and the same for colour relations in Experiment 2 (B). Ducklings preferred the imprinted relation in both shape and colour, regardless of whether the imprinted relation was 'same' or a 'different'.

Supplementary Materials:

Materials and Methods

Movie S1

References (*13,14,21,22 in main text and SM, 27 only in SM*)