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reported in this paper are tabulated in a database in the supplementary materials. We are most grateful to the reviewers who gave recommendations for improving this paper.

SUPPLEMENTARY MATERIALS

www.sciencemag.org/content/353/6296/283/suppl/DC1
Materials and Methods

Figs. S1 and S2
Table S1
Database S1
References (33)

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EVOLUTIONARY COGNITION

Ducklings imprint on the relational concept of “same or different”

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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 describe relational concept learning in newborn ducklings without reinforced training. Newly hatched domesticated mallards that were briefly exposed to a pair of objects that were either the same or different in shape or color later preferred to follow pairs of new objects exhibiting the imprinted relation. Thus, even in a seemingly rigid and very rapid form of learning such as filial imprinting, the brain operates with abstract conceptual reasoning, a faculty often assumed to be reserved to highly intelligent organisms.

Relational concepts, such as “same” and “different,” have been demonstrated in a few animal species, typically after 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), by relying on the similarity between features of the training and of the 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”). Honey bees can learn this discrimination and even transfer a 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

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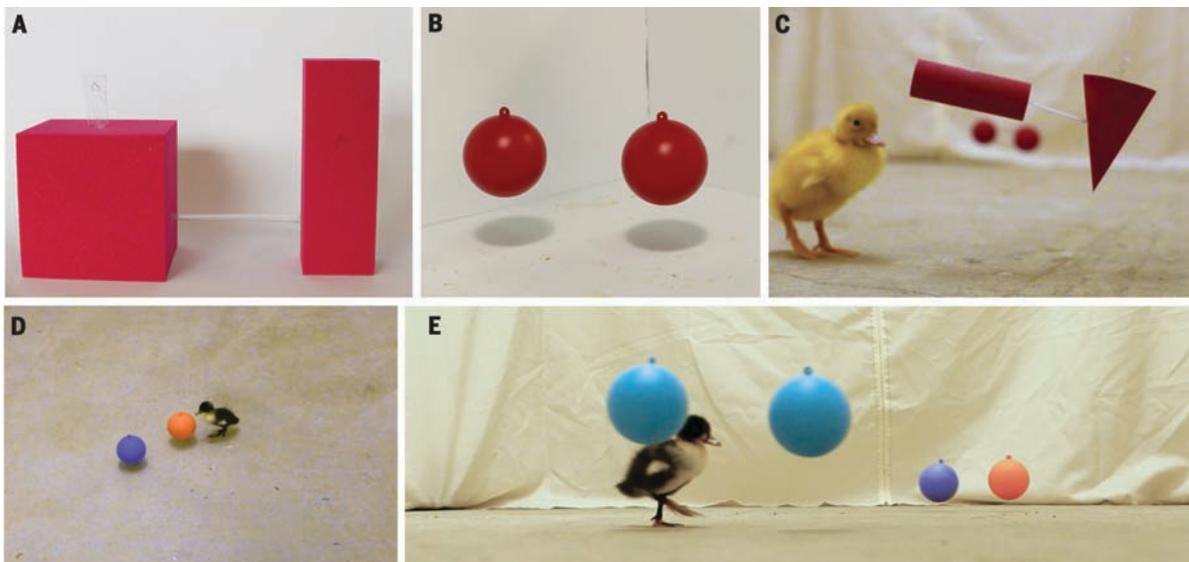


Fig. 1. Imprinting and testing stimuli. Newborn ducklings were first exposed to a pair of objects revolving about the center of a training arena, then tested with two novel pairs of objects. (A) Example of a “different shape” training stimulus pair. (B) Example of a “same color” training stimulus pair. After this exposure, the ducklings were tested for their 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 color” stimulus pair—an incorrect response. (E) The same duckling later in the same trial correctly approaches and closely follows the novel “same color” stimulus.

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 solving such problems, and it has been cogently argued that this may indicate their possession of the ability to reason by analogy (8).

Demonstrating the 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 chicks 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 summarized 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 min to a moving pair of sample objects, kept for a 30-min retention interval in the dark, and presented with two novel pairs of moving objects for 10 min (Fig. 1). Sample stimuli within the pair shown in the imprinting phase were either equal to each other in both color 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 color and shape, and in the other they differed in either shape or color (Fig. 2). Detailed methods may be found in the 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” ($n = 36$ ducklings 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 of two novel, different shapes. In exper-

iment 2, the imprinting stimulus pair was two spheres, either of the same color or different colors ($n = 40$ ducklings for each group), and test stimuli were also spherical but had novel colors, 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

Experiment 1 - Shapes				Experiment 2 - Colors			
		Imprinting	Testing			Imprinting	Testing
Subgroup 1	Same			Subgroup 1	Same		
	Different				Diff.		
Subgroup 2	Same			Subgroup 2	Same		
	Different				Diff.		
Subgroup 3	Same			Subgroup 3	Same		
	Different				Diff.		
Subgroup 4	Same			Subgroup 4	Same		
	Different				Diff.		
Subgroup 5	Same			Subgroup 5	Same		
	Different				Diff.		

Fig. 2. Experimental stimulus pairs. Experiment 1 tested for responses between red objects that could differ in shape, and experiment 2 tested for responses between spherical objects that could differ in color, using the pairs illustrated here. In experiment 1, members of subgroup 1 were initially exposed to either two spheres or a pair formed by a cone and a cylinder and were then tested for preference between a pair of two pyramids and a pair formed by a prism and a cube, whereas members of subgroup 2 were imprinted on pairs of either two pyramids or a prism and a cube and were then 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 colors, and all ducklings were tested for preference between two novel identical spheres and a pair formed by two novel differing spheres.

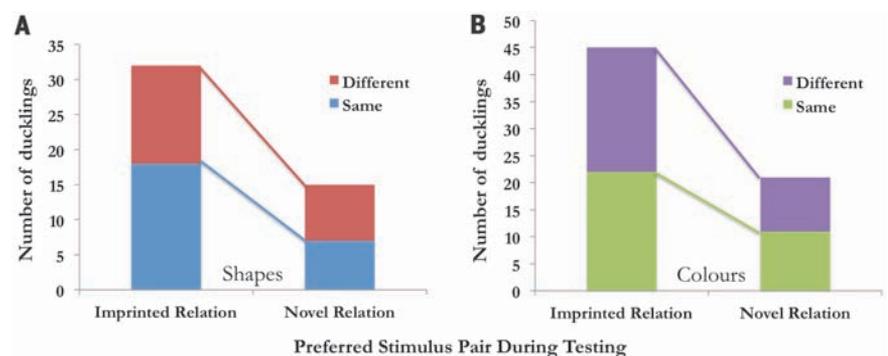


Fig. 3. Ducklings’ preferences for an imprinted relational concept. The number of ducklings showing preference for the imprinted (left column) or alternative (right column) relation is shown for shape relations in experiment 1 (A) and the same for color relations in experiment 2 (B). Ducklings preferred the imprinted relation in both shape and color, regardless of whether the imprinted relation was “same” or “different.”

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 the methods in the supplementary materials). Video of sample trials (movie S1) is available in the 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 color 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 (7). 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 those elements' 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 color, shape, or symmetry, to include properties of object assemblies such as their informational entropy (26).

REFERENCES AND NOTES

1. A. Smirnova, Z. Zorina, T. Obzova, E. Wasserman, *Curr. Biol.* **25**, 256–260 (2015).
2. E. A. Wasserman, *Psychol. Bull.* **113**, 211–228 (1993).
3. R. J. Herrnstein, D. H. Loveland, C. Cable, *J. Exp. Psychol. Anim. Behav. Process.* **2**, 285–302 (1976).
4. W. Wu, A. M. Moreno, J. M. Tangen, J. Reinhard, *J. Comp. Physiol. A Neuroethol. Sens. Neural Behav. Physiol.* **199**, 45–55 (2013).
5. T. R. Zentall, M. Galizio, T. S. Critchfield, *J. Exp. Anal. Behav.* **78**, 237–248 (2002).
6. A. A. Wright, J. S. Katz, *Behav. Processes* **72**, 234–254 (2006).
7. M. Giurfa, S. Zhang, A. Jenett, R. Menzel, M. V. Srinivasan, *Nature* **410**, 930–933 (2001).
8. R. G. Cook, E. A. Wasserman, *Psychon. Bull. Rev.* **14**, 1107–1114 (2007).
9. E. A. Wasserman, J. Fagot, M. E. Young, *J. Comp. Psychol.* **115**, 42–52 (2001).
10. I. M. Pepperberg, *Anim. Learn. Behav.* **15**, 423–432 (1987).
11. K. Lorenz, *J. Ornithol.* **83**, 289–413 (1935).
12. P. Bateson, *Anim. Behav.* **27**, 470–486 (1979).
13. P. Bateson, *Anim. Learn. Behav.* **7**, 259–262 (1979).
14. P. P. G. Bateson, *Biol. Rev. Camb. Philos. Soc.* **41**, 177–211 (1966).
15. P. Bateson, J. B. Jaekel, *Anim. Behav.* **24**, 386–390 (1976).
16. J. N. Wood, *Dev. Sci.* **18**, 194–205 (2015).
17. E. H. Hess, D. B. Hess, *Psychon. Sci.* **14**, 129–130 (1969).
18. O. Rosa-Salva, L. Regolin, G. Vallortigara, *Dev. Sci.* **13**, 565–577 (2010).
19. G. Vallortigara, L. Regolin, F. Marconato, *PLOS Biol.* **3**, e208 (2005).
20. L. Regolin, L. Tommasi, G. Vallortigara, *Anim. Cogn.* **3**, 53–60 (2000).
21. R. Rugani, L. Regolin, G. Vallortigara, *Dev. Sci.* **13**, 790–797 (2010).
22. P. P. G. Bateson, A. A. P. Wainwright, *Behaviour* **42**, 279–290 (1972).
23. R. Lickliter, G. Gottlieb, *J. Comp. Psychol.* **101**, 40–46 (1987).
24. J. S. Katz, A. A. Wright, J. Bachevalier, *J. Exp. Psychol. Anim. Behav. Process.* **28**, 358–368 (2002).
25. P. Bateson, G. Horn, *Anim. Behav.* **48**, 695–715 (1994).
26. T. R. Zentall, E. A. Wasserman, O. F. Lazareva, R. K. Thompson, M. J. Rattermann, *Comp. Cogn. Behav. Rev.* **3**, 13–45 (2008).

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Table S1

Movie S1

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BIODIVERSITY

Has land use pushed terrestrial biodiversity beyond the planetary boundary? A global assessment

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Land use and related pressures have reduced local terrestrial biodiversity, but it is unclear how the magnitude of change relates to the recently proposed planetary boundary (“safe limit”). We estimate that land use and related pressures have already reduced local biodiversity intactness—the average proportion of natural biodiversity remaining in local ecosystems—beyond its recently proposed planetary boundary across 58.1% of the world’s land surface, where 71.4% of the human population live. Biodiversity intactness within most biomes (especially grassland biomes), most biodiversity hotspots, and even some wilderness areas is inferred to be beyond the boundary. Such widespread transgression of safe limits suggests that biodiversity loss, if unchecked, will undermine efforts toward long-term sustainable development.

Land use and related pressures have been the main drivers of terrestrial biodiversity change (1) and are increasing (2). Biodiversity has already experienced widespread large net losses (3), potentially compromising its contribution to resilient provision of ecosystem functions and services, such as biomass production and pollination, that underpin human well-being (4–7). Species-

removal experiments suggest that loss of ecosystem function accelerates with ongoing species loss (5), implying that there may be thresholds beyond which human intervention is needed to ensure adequate local ecosystem function (8, 9). The loss of 20% of species—which affects ecosystem productivity as strongly as other direct drivers (5)—is one possible threshold, but it is unclear by which