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3 **Associative learning accounts for recursive-structure**  
4 **generation in crows**

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16 **Keywords:** Recursive structures, center-embeddings, associative learning,  
17 primates, crows

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19 **Summary:**

20 Recursive sequence generation, i.e., the ability to transfer recursive patterns to  
21 novel items, was recently reported in crows (Liao et al., 2022). Here, we argue that  
22 although the reported data are certainly compatible with the recursion hypothesis,  
23 they can also be explained by other, much simpler mechanisms of associative  
24 learning.

**25 Main Text**

26 The recursion hypothesis states that recursion, the cognitive ability to  
27 generate an infinite range of expressions from a finite set of items, is the only  
28 unique human component of the language faculty and is a distinguishing feature  
29 absent from all other animal communication systems (Hauser et al., 2002). Center-  
30 embedded structures is one type of recursive structure that has been frequently  
31 used to test the recursion hypothesis in different species (e.g., Perruchet & Rey,  
32 2005; Rey et al., 2012). One example of center-embedded (CE) structure in human  
33 language is “*The antelope [a<sub>1</sub>] the lion [a<sub>2</sub>] ate [b<sub>2</sub>] ran like a snail [b<sub>1</sub>]*” in which the  
34 sentence “*the lion [a<sub>2</sub>] ate [b<sub>2</sub>]*” is embedded within the sentence “*The antelope [a<sub>1</sub>]*  
35 *ran like a snail [b<sub>1</sub>]*”, producing the  $a_1a_2b_2b_1$  CE structure.

36 A recent study (Liao et al., 2022) claims to demonstrate that crows (*Corvus*  
37 *corone*) have recursive capabilities. Using an experimental paradigm previously  
38 tested on U.S. adults, Tsimane’ adults, U.S. children, and rhesus monkeys  
39 (*Macaca mulatta*) (Ferrigno et al., 2020), they found that crows were able to  
40 transfer center-embedded structure to never-before-seen items, suggesting that  
41 recursive capabilities are not restricted to the primate lineage.

42 In Experiment 1, two crows were trained to produce a sequence of 4 pecks  
43 on a touchscreen following two lists of 4 visual items. The first and second lists  
44 were respectively composed of the 4 following symbols: { ( ) } and { [ ] }, where  
45 two inner pairs of symbols (i.e., ( ) and [ ] ) were systematically embedded into a  
46 unique outer pair of symbols (i.e., { } ). The 4 visual symbols were presented  
47 simultaneously on the screen and crows had to learn to peck them in these specific

48 orders. Note that pairs of symbols (i.e., { }) were displayed with the same font color  
49 which provided an additional visual cue. Once they had reached a sufficient level  
50 of performance, a small proportion of transfer trials (i.e., 10%) were introduced  
51 among the training trials. Transfer trials were composed of the embedded pairs of  
52 List 1 and 2 (i.e., ( ) and [ ]) and crows were simply expected to peck these 4  
53 symbols. Irrespective of the pecking order they produced, they received positive  
54 reinforcement. Analysis of the response patterns produced by crows nicely showed  
55 that they preferentially produced more center-embedded patterns (i.e., ( [ ] ) or [ (   
56 ) ] ) than crossed (i.e., ( [ ] ) or [ ( ] ) ) or tail-embedded (i.e., ( ) [ ] or [ ] ( ) ) patterns.  
57 On average, the distribution of response patterns was similar to the one previously  
58 obtained for children from 3 to 4 years old (Ferrigno et al., 2020). The authors took  
59 this result as evidence that crows have recursive abilities.

60 A careful examination of the method section reveals however that an  
61 alternative account of this result is possible in terms of simpler associative learning  
62 mechanisms. Indeed, although not immediately visible, we can see that the last  
63 two symbols of each sequence were surrounded by a visible border (e.g., { ( [ ] [ ] )}).  
64 Crows probably used these additional visual cues by learning that they *should not*  
65 be pecked first in order to get the positive reinforcement that is given at the end of  
66 the sequence. Figure S1 (from their supplementary material) provides a clear  
67 confirmation that crows learned to avoid these bordered symbols. This figure  
68 represents the proportion of each possible sequence of responses ( $n = 24$ ) for the  
69 transfer trials (we thank the first author of the study who confirmed that the order  
70 of the 24 possible sequences has to be read from bottom to top, an important detail

71 that is not provided in the legend of the figure). From this figure, it appears that  
 72 about 94% of the produced sequences never started with bordered symbols.  
 73 Again, this result is not surprising because crows were punished during training  
 74 when they began by pecking one of the bordered stimuli.

75 Therefore, on transfer trials, when crows are presented the 4 symbols in a  
 76 random order on the screen (i.e., ( [ ] ) ), they will preferentially peck first the  
 77 two symbols without any border, i.e., ( or [. Then, since they also have learned  
 78 during the training phase that after pecking ( or [, they should respectively peck ]  
 79 or ] to get rewarded, they are more likely to produce these learned adjacent  
 80 associations. Finally, the fourth peck can be made by default, with crows selecting  
 81 the only stimulus that has not been touched before or that was systematically  
 82 associated to the reward.

83 On the basis of these two simple associative learning mechanisms (i.e., 1.  
 84 Avoid bordered symbols or select symbols not surrounded by a border and 2. Peck  
 85 the visual symbol which has been associated during training to the second pecked  
 86 symbol), we can easily explain why crows produced more patterns qualified as  
 87 “center-embedded” than other patterns. According to this two-stage associative  
 88 learning account, the apparent recursive processing would be in fact a by-product  
 89 of simple associative learning mechanisms (see also Rey et al., 2012).

90 A similar explanation holds for Experiment 2 in which crows were retrained  
 91 with two novel lists of center-embedded sequences using three novel pairs of  
 92 stimuli (i.e., List 1: < [ ] >; List 2: [ ( ) ] ; note that symbol pairs from the two  
 93 lists were displayed with different colors). Transfer trials were composed of the

94 outer pair from List 1 (i.e., < [ ] > ) and the inner pair from List 2 (i.e., ( [ ] )), and  
95 under these novel combinations, crows massively produced center-embedded  
96 responses (e.g., < ( [ ] [ ] > ). However, the two-stage associative learning account  
97 also works perfectly here by assuming that crows select borderless stimuli first and  
98 more specifically, based on their learning of List 1 and List 2, they preferentially  
99 select the first item from List 1 which is the only item they have learned to peck  
100 first (i.e., “<”). Then, after selecting the other borderless stimulus (i.e., “(“), they  
101 have learned to peck its paired item (i.e., “)“). The final peck can be done by default,  
102 as in Experiment 1.

103 In Experiment 3, the two training lists were composed of two embeddings  
104 instead of one and the last element of each pair of symbols was again surrounded  
105 by a border (i.e., List 1 : { [ ( [ ] [ ] ) ] } ; List 2 : < [ ( [ ] [ ] [ ] > ). Transfer trials were  
106 either composed of the inner pair of List 1 (i.e., ( )) and the outer and middle pairs  
107 of List 2 (i.e., < [ ] > ), leading to “swap” trials, or composed of the same outer and  
108 middle pairs from List 2 (i.e., < [ ] > ) and one middle pair of List 1 (i.e., [ ] ), leading  
109 to “joint” trials. In both cases, crows produced a majority of center-embedded  
110 patterns, although the proportion was higher for “swap” compared to “joint” trials.  
111 Here also, the two-stage associative learning account can explain these results by  
112 assuming that the three first pecks were generated by avoiding bordered stimuli  
113 and by selecting the symbols that were systematically learned as first and second  
114 responses during training (i.e., < [ ]. The third peck could be generated by default  
115 by selecting the remaining borderless stimulus (i.e., “(” for “swap” trials or “[” for  
116 “joint” trials). The reason why “swap” trials produced more center-embedded

117 patterns is because after pecking “(”, crows had learned from List 1 to peck [ ] while  
118 they did not have this possibility for the innermost pair of stimuli of the sequences  
119 used in “joint” trials.

120 To sum up, the conclusion that crows are endowed with abstract recursive  
121 capacities is a possible interpretation of the results reported by Liao et al. (2022)  
122 and Ferrigno et al. (2020). However, this is not the only one. In agreement with  
123 previous studies (e.g., Rey et al., 2012), crow performance can also be fully  
124 explained by simpler associative learning mechanisms, such as the two-stage  
125 associative learning account presented here, without any need to resort to the  
126 complex recursion hypothesis.

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