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Direct and Relational Representation During Transitive List Linking in Pinyon Jays (*Gymnorhinus cyanocephalus*)

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Abstract

The authors used the list-linking procedure (Treichler & Van Tilburg, 1996) to explore the processes by which animals assemble cognitive structures from fragmentary and often contradictory data. Pinyon jays (*Gymnorhinus cyanocephalus*) were trained to a high level of accuracy on 2 implicit transitive lists, $A > B > C > D > E$ and $1 > 2 > 3 > 4 > 5$. They were then given linkage training on $E > 1$, the single pair that linked the 2 lists into a composite, 10-item hierarchy. Following linkage training, the birds were tested on nonadjacent probe pairs drawn both from within (B–D and 2–4) and between (D–1, E–2, B–2, C–3) each original list. Linkage training resulted in a significant transitory disruption in performance, and the adjustment to the resulting implicit hierarchy was far from instantaneous. Detailed analysis of the course of the disruption and its subsequent recovery provided important insights into the roles of direct and relational encoding in implicit hierarchies.

Keywords: symbolic transitive inference, cognitive representation, implicit hierarchy, operant conditioning, corvids, social complexity

Many of the structural patterns in natural phenomena are implicit and difficult to identify on the basis of single observations. Animals solve this problem by developing representations of these implicit relationships based on multiple, fragmentary experiences of features such as territorial boundaries, foraging areas, or social networks. Understanding how these representations are acquired and updated is one of the most challenging issues in animal cognition. Our research has focused on the acquisition and use of one implicit natural relationship, the transitivity of dominance relations among highly social animals.

Transitivity can be important in social settings. Animals living in stable, long-lasting groups track the status of other members along multiple dimensions such as genetic relationship, breeding condition, and dominance ranking. This social knowledge must be derived largely from multiple experiences of individual dyadic interactions (Gallistel, 1990; Tomasello & Call, 1997), which are then combined into a representation of the overall network of social relationships among all group members. The construction of this representation is aided by inferences about missing information based on currently available data, made possible because many aspects of social networks are transitive. For example, knowing that A dominates B and B dominates C allows for the inference that A likely dominates C. The ability to make such “social infer-

ences” has been demonstrated in several animal species (Pazy-Miño, Bond, Kamil, & Balda, 2003; Grosenick, Clement, & Fernald, 2007). To understand the underlying constructive process, however, procedures that allow high levels of control over relevant stimuli and events are necessary. In the research reported here, we use one such procedure—symbolic transitive inference (TI; McGonigle & Chalmers, 1977)—to study the construction and modification of representations of transitive relationships.

During the TI procedure, subjects learn an implicit list of arbitrary stimuli through successive trials on adjacent pairs in which responses to the item that is closer to the top of the list are rewarded. In a five-item list, for example, the regimen for the four “premise pairs” would be: $A > B$, $B > C$, $C > D$, and $D > E$. Once these pairs have been learned, transitive probe tests of nonadjacent pairs (particularly B ? D) are presented, typically without differential reward.¹ Above-chance performance on transitive probes has been shown in a range of species, including rats, pigeons, monkeys, chimpanzees, crows, and fish (Vasconcelos, 2008). At minimum, these results indicate that the premise pairs are not learned solely as a set of unrelated conditional discriminations (given A and B, choose A; given B and C, choose B, etc.), suggesting there is at least a formal analogy to features of social networks (Allen, 2006; Bond, Wei, & Kamil, 2010).

1. Throughout this article, we designate differentially rewarded premise pairs with “>” and uniformly rewarded, transitive probes with “?” (Wu & Levy, 2001).

The implicit ordering that animals learn during TI experiments appears to derive from two distinguishable forms of cognitive representation (Bond, Kamil, & Balda, 2003, 2010). The first is a direct encoding of stimulus value, visualized as a scalar variable that increases progressively as one moves up the hierarchy. Direct encoding can be based on a physical attribute such as size but is most commonly interpreted in terms of the associative strength that each stimulus accumulates as a consequence of its history of reward and non-reward (Couvillon & Bitterman, 1992). Strength is assumed to build up both directly through rewarded responses to the stimuli themselves (Wynne, 1995, 1997) and in some models, indirectly, through transfer of value from other simultaneously presented and rewarded stimuli (von Fersen, Wynne, Delius, & Staddon, 1991; Zentall & Clement, 2001; Zentall & Sherburne, 1998). Direct representation is not purely a function of associative strength, however. Terrace and his colleagues have clear evidence of direct encoding of hierarchical rank in their "simultaneous chaining" procedure, where a purely associative explanation seems insufficient to explain their results (Chen, Swartz, & Terrace, 1997; Terrace, 2001). A transitive choice in a direct representation would involve choosing the alternative with the higher stimulus value (Couvillon & Bitterman, 1992).

The second form of representation in implicit hierarchies is relational rather than direct. It encodes the relative ranking of pairs of stimuli without regard to their absolute positions in the list. Relational representations have sometimes been envisioned in spatial terms (Jacobs, 2006). Each pair of stimuli is assigned to a cognitive map, and based on the frequency with which they occur together, contextually related pairs gradually shift to be closer together. A hierarchical stimulus arrangement will ultimately yield a linked list in which the representation of each pair occupies a spatial position between the pairs above and below it. On the basis of this structure and the identity of the highest-valued stimulus, the relative rankings can be inferred in any novel pairing by chaining down from the top of the hierarchy through representations of adjacent pairs (D'Amato, 1991; Terrace, 2005; Terrace & McGonigle, 1994).

However they operate at a neural level (Eichenbaum, 2006), direct and relational representations provide qualitatively different types of information that are functionally integrated to construct an implicit hierarchy. How integration is achieved may best be observed in the context of a change in hierarchy structure where the experimental design goes beyond that of a single short list of premise pairs (Allen, 2006; Bond *et al.*, 2010).

One example of such a design is the "list-linking" procedure originally developed by Treichler and Van Tilburg (1996), in which rhesus macaques showed a remarkable facility for integrating pairs of implicitly ordered arrays. The monkeys' task was to combine two separately learned five-item lists (i.e., $A > B > C > D > E$ and $1 > 2 > 3 > 4 > 5$) into a single 10-item list. Macaques achieved this result surprisingly easily even when the only cross-list pair that they initially experienced was the one that tied the two lists together ($E > 1$).

When subsequently tested with novel cross-list pairs, the monkeys responded appropriately (e.g., choosing C when presented with $C ? 3$ after being trained on $E > 1$). Treichler and his associates subsequently replicated and expanded their work with studies in which macaques combined three five-item lists into a single 15-item list with minimal cross-list

training (Treichler, 2007; Treichler, Raghanti, & Van Tilburg, 2003). Although the ability to combine individual lists into an integrated whole is of interest, list linking also has considerable potential for detecting effects of different modes of representation. Linking separate lists should have differential effects on particular stimulus pairs, depending on their relative positions in the five-item component lists and the final aggregate structure. These effects should vary predictably based on the influence of direct and relational representation.

During training, for example, responses to stimuli at the top of the list (A or 1) are always rewarded, whereas those at the bottom (E or 5) are never rewarded. No configural learning is needed to determine the appropriate response to these "end-anchor" stimuli (Bryant & Trabasso, 1971), therefore interpretation of pairs that include them should be dominated by direct representation (Lazareva & Wasserman, 2006). On the other hand, stimuli drawn from corresponding ranks toward the middle of each list (e.g., B and 2 or C and 3) would have developed similar direct representations in initial list training (Chen *et al.*, 1997; Treichler, 2007), suggesting that responses to pairs of these items should be dictated primarily by relational effects. It should, therefore, be feasible to separate the distinctive roles of relational and direct representation by following changes in responses to nondifferentially rewarded probes of novel stimulus pairs, tracking them as a function of accumulated experience solely with the $E > 1$ linkage (Treichler, 2007; Treichler *et al.*, 2003).

Treichler's monkeys learned their lists very rapidly, which made it necessary to present frequent probe tests to obtain sufficient data. This presentation, however, raised other difficulties. Probe trial choices are not usually reinforced differentially, but a high proportion of nondifferential trials risked distorting acquisition (Treichler & Van Tilburg, 1996). Some of the macaques, in addition, seemed to discover that novel probe pairs produced rewards regardless of their choice, resulting in a striking decrease in transitive responding during probe trials (Treichler & Van Tilburg, 1999). As a result, Treichler used fully differential rewards even during probe tests, thereby reducing the focus on the linking treatment and requiring complex analysis to infer effects of list combinations (Treichler & Raghanti, 2010; Treichler *et al.*, 2003). Although the results were consistent with the use of both direct and relational representation (Treichler, 2007), the experiential dynamics of the linkage-induced changes in list organization were unclear because of the rewards provided for correct transitive choices in between-list pairs.

Many of these difficulties were avoided by Gazes, Chee, and Hampton (2012). They conducted a series of experiments explicitly testing the adequacy of associative models to predict TI performance in rhesus monkeys (*Macaca mulatta*). Once the monkeys had learned a single list and demonstrated transfer to novel pairs (Experiment 1), Gazes *et al.* (2012) directly measured (Experiment 2) and experimentally manipulated (Experiment 3) the associative values of the stimuli. The results of these experiments clearly demonstrated the influence of the implied order of the transitive series above and beyond any effects of associative value. In their fourth experiment, Gazes *et al.* (2012) tested the monkeys with two seven-item lists that were linked and again found clear evidence of effects of relational representation. We will describe the results of this list-linking experiment in some detail for comparison with our results in the discussion below.

Our test subjects of choice were pinyon jays (*Gymnorhinus cyanocephalus*), which are among the most social of North American corvids. They live all their lives in stable groups of from 50 to several hundred individuals, foraging as a permanent flock and breeding colonially (Marzluff & Balda, 1992). Because the number of possible dyads increases rapidly with group size, members of such large social groups are unlikely to have observed interactions between all possible pairs of group members. They must, therefore, base at least some of their judgments of relative social status on transitive inferences (Seyfarth & Cheney, 2001, 2003). In an earlier study, we demonstrated that pinyon jays make such transitive social inferences during dominance interactions under fully controlled laboratory conditions (Paz-y-Miño *et al.*, 2003).

Pinyon jays also display considerable expertise in operant TI. With a seven-item implicit hierarchy, pinyon jays acquired the premise pairs more rapidly than other corvid species and to a higher level of accuracy, showing evidence of both direct and relational representation (Bond *et al.*, 2003, 2010). During the subsequent testing phase, they demonstrated a first-item latency effect, with faster responses to pairs that were higher in the sequence (e.g., B ? D choices were faster than C ? E choices) but did not show a similar pattern for accuracy (Bond *et al.*, 2003). Terrace (1993, 2005) has considered such latency effects to be a primary indicator of the use of relational representations. Because pinyon jays have an impressive facility for relational judgments and apparently rely on both forms of cognitive representation, we tested these birds on a version of Treichler and Van Tilburg's (1996) list-linking task, anticipating that they could provide significant insight into the roles of direct and relational representation in responding to changes in hierarchical structures.

As in Treichler and Van Tilburg's procedure, we trained the jays to criterion on two five-item, four-pair lists, List X = A > B > C > D > E and List Y = 1 > 2 > 3 > 4 > 5 (Figure 1; Treichler & Van Tilburg, 1996). They were subsequently given separate training on the single terminal pair that defined the

relationship between the lists (i.e., E > 1). This training was followed by sessions in which premise pair trials were interspersed with probe tests, with gradually increasing experience on the linking pair.

We designed our procedures to minimize the effects of probe test trials on performance on other trials because of either systematic reward or frequent probes. Systematic reward can affect choices in many ways, including the relative effects of direct and relational representation. In addition, the greater the ratio of probe to normal trials, the greater the potential influence of probe trial events on subsequent choice, including increased error variance. The three features of our probe test procedures adapted to minimize such effects of probe trials on the acquired representations were (a) the ratio of probe trials to premise pair trials was kept low; (b) all responses during probe trials were rewarded regardless of choice; and (c) instead of testing all possible probe pairs, we chose a set of six probe pairs selected to highlight the effects and possible interactions of direct and relational representation.

The six novel transitive pairs we chose included two exemplars of each of three probe types. The first type consisted of within-list probes (B ? D and 2 ? 4; Figure 1). Because within-list transitivity has been confirmed in previous studies (Bond *et al.*, 2003, 2010), we predicted that the birds would behave consistently in these probes even after the lists were implicitly joined, selecting the higher ranked item (B and 2) in both cases. The second and third types were between-list probes: a pair of "near" probes that included stimuli immediately adjacent to the linking pair (D ? 1 and E ? 2; see Figure 1), and a pair of "far" probes that were drawn from correspondingly ranked items toward the middle of each list (B ? 2 and C ? 3; see Figure 1). We anticipated that because the near probes each included an end anchor from one of the component five-item lists, they would show the strongest effects of direct representation. The far probes, on the other hand, would have had similar direct representations prior to link training, suggesting that responses to these pairs should be dictated primarily by relational effects.

Method

Subjects

Five adult pinyon jays were captured in the field in northern Arizona. They were subsequently housed in individual cages at the Center for Avian Cognition at the University of Nebraska–Lincoln under environmentally controlled conditions (22 °C; 14:10-hr light-dark cycle). Captive jays were maintained on a diet of turkey starter, sunflower seeds, parrot pellets, meal worms, and pine nuts, supplemented with vitamins. During experiments, the birds were held at 85%–90% of their free-feeding weights by controlled daily feeding, with unlimited access to grit and water. All birds were initially naïve to operant procedures.

Apparatus

Stimuli were presented on a 34-cm LCD monitor embedded in the front panel of a 48 × 48 × 48-cm operant chamber. The monitor was framed with an infrared touch screen, and a thin sheet of polycarbonate was placed between the touch bezel and the monitor to serve as a resilient pecking surface. Stimuli could be displayed in three different positions, spaced

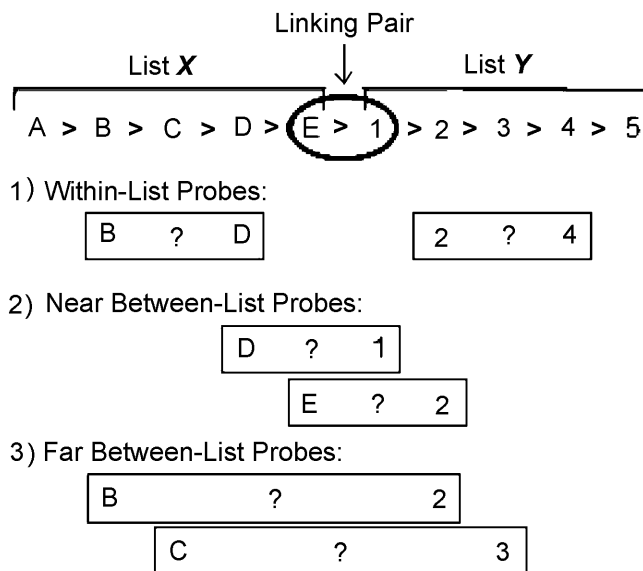


Figure 1. Schematic of experimental design. After learning Lists X and Y, birds received experience with E > 1. They were then given sessions with probe trials as indicated.

at 6.8 cm intervals across the center of the display. A perch was mounted parallel to the front panel of the chamber, positioned so that the center of the LCD was approximately at eye level. Rewards of pine nut pieces were delivered into a food well below the touch screen, signaled with a food light. The chambers were diffusely lit, and ambient white noise was provided to mask external sounds. Stimulus presentation, event timing, reward delivery, and data recording were computer controlled, using custom-coded C routines.

The stimuli comprising the two five-item lists were designed to be easily discriminated and were assigned to list positions and subjects so as to minimize possible systematic effects. Each of the 10 list stimuli was a 35-mm square of color with a black alphanumeric character superimposed in the center. The colors were red, green, blue, cyan, yellow, magenta, light blue, orange, purple, and rose, chosen to maximize their distinctiveness on a VGA monitor. The characters were J, X, L, A, Z, W, C, O, E, and U, in Arial font approximately 13-mm high. Blough (1985) reported that pigeons find these letters maximally distinctive. Characters were assigned to stimulus colors at random with the restriction that stimuli closer in color resemblance (e.g., magenta and rose) were given characters that were more distinctive in Blough's results (e.g., Z and E).

To avoid within-list pairings that might not be easily discriminated, we categorized the stimuli into the five-item groups with maximally distinctive background colors (orange, purple, light blue, green, rose; and red, blue, yellow, magenta, and cyan). We then generated eight unique two-list sequences with the restriction that four had one color grouping in List X and the other in List Y, whereas the assignment was reversed for the other four sequences. The ordering within lists was fully permuted such that no stimulus occurred more than twice in the same ordinal position. Each of the five jays was then uniquely assigned one of the eight stimulus sequences.

Pretraining

Birds were habituated to the operant chamber and autoshaped to peck a central white stimulus, a 9-mm black circle overlaid in the center of a white 35-mm square. They were then trained to peck the white stimulus in either of the two lateral positions. Each daily training session consisted of 36 trials, balanced with respect to left and right positions and randomly ordered. An initial white stimulus in the central position was then added as a start signal, and the birds were conditioned to peck it as a means of initiating the next trial. Finally, the response requirement for the lateral positions was increased to three pecks.

When a subject achieved 90% or more correct responses for three consecutive sessions, it was advanced to discriminative training on adjacent premise pairs of colored stimuli comprising two five-item lists. For consistency, we refer to these lists in terms of their eventual place in the 10-item combined structure. For each bird, the list that will ultimately be placed on top will be referred to as List X with individual stimuli designated A through E; the list that will be placed on the bottom will be List Y with stimuli 1–5. Birds were given training trials on adjacent premise pairs from each list and were rewarded for choosing the stimulus in each pair that was closer to the top of the list. Trial sequence and position of the correct response alternative were fully randomized. Each bird was trained on unique training lists that formed a unique 10-item list following linkage.

Each discrimination trial began with the display of the white start signal in the center of the display. If the signal was not pecked within 15 s, it was turned off, and the trial reinitiated after a 3-s delay. When the start signal was pecked, it was turned off, and two colored stimuli were displayed in the lateral positions. On three successive pecks to one of the stimuli, the display was darkened. Correct responses were rewarded with a food item. After 10 s, the food light was turned off and another trial was initiated 20 s later. Incorrect responses produced a 30-s delay before the next trial. If the bird failed to peck either stimulus three times within 60 s, the panel was darkened, and the trial was repeated after a 30 s delay. As in Treichler and Van Tilburg (1996), no concurrent correction procedures were applied.

In our initial protocol, the birds were presented with all eight premise pairs from both lists together in random order within each session. We found, however, that although jays can readily learn six premise pairs from a single seven-item list in this fashion (Bond *et al.*, 2003, 2010), learning two intermingled five-item lists simultaneously was a much more difficult task. After more than 1,440 trials, none of the birds was performing at better than 55%–65% correct across all premise pairs. We therefore modified the procedure, training initially on just one of the two lists in 36-trial sessions of premise pairs intermingled in random order (TRN1 in Table 1). Training for each jay continued until it achieved an accuracy level of 90% correct on each premise pair across 3 consecutive days. The subjects were then advanced to their other list and presented with the second set of four premise pairs (TRN2 in Table 1). Three of the subjects learned their List X first; the other two learned List Y first. Once criterion had been attained on the second list, the birds were given the two lists on alternating days until the same criterion was reached (TRN3 in Table 1). In the final stage of training, all eight premise pairs from both lists were presented in each session (36 trials per session; each pair presented 4–6 times per session) until a criterion of 80% on each pair across 2 consecutive days was reached (TRN4 in Table 1).

Once subjects had learned all premise pairs from both lists, they were trained on the $E > 1$ linking pair, which determined how their two lists were to be ordered into a single 10-item structure. Daily 36-trial sessions of just the linking pair were presented to the birds, using the same contingencies as for premise pair training (i.e., the birds were rewarded only for choosing E). Link training was continued until the birds attained 90% correct responses for three successive sessions (a range across birds of 5–12 sessions; LNK1 in Table 1).

Probe Testing

Following initial training with the linking pair, each jay received a block of 20 test sessions, each containing three probe trials intermingled with 33 trials of the eight premise pairs used in list training. In this first test block, there were no link trials (BLK1 in Table 1). Probe trials consisted of six novel non-adjacent stimulus combinations: two within-list pairs with a two-rank difference ($B ? D$ and $2 ? 4$), two near between-list pairs with a two-rank difference in the aggregate list ($E ? 2$ and $D ? 1$) and two far between-list pairs with a five-rank difference ($B ? 2$ and $C ? 3$; see Figure 1). Probes were randomly ordered across sessions, with the constraint that all six probes were presented across two consecutive sessions and were roughly equally spaced within sessions. All choices during probe trials were nondifferentially rewarded.

Table 1. Treatment Sequence

| Treatment condition | Pairs included | No. of trials | |
|---|--------------------------------|---------------|------|
| | | Premise | Link |
| Acquisition of first list (TRN1) | List X or List Y | 2441 | 0 |
| Acquisition of second list (TRN2) | List Y or List X | 950 | 0 |
| Alternating sessions (TRN3) | List Y, then List X | 2347 | 0 |
| Lists mingled within sessions (TRN4) | Mixture of X and Y | 194 | 0 |
| Link training (LNK1) | E > 1 | 0 | 274 |
| Probe tests without link pair (BLK1) | Mixture of X and Y | 720 | 0 |
| Link refresher (LNK2) | E > 1 | 0 | 173 |
| Probe tests on full 10-item list (BLK2) | Mixture of X and Y, plus E > 1 | 720 | 60 |
| Probe tests on full 10-item list (BLK3) | Mixture of X and Y, plus E > 1 | 720 | 60 |

The duration of training treatments was based on an accuracy criterion within subjects, therefore the indicated cumulative number of premise or link trials is a mean across subjects.

The birds then received additional experience with the linking pair, which was again presented on all trials in a series of 36-trial sessions until a criterion of 90% correct across 3 days was reached (LNK2 in Table 1). Testing then resumed for two additional blocks of 20 test sessions (BLK2 and BLK3 in Table 1). Each of these sessions consisted of 39 trials, including 33 presentations of the premise pairs, three probe trials, and three presentations of the E > 1 linking pair. During these 40 sessions, each premise pair was seen two–four times per session. Correct responses to all premise and linking pairs were reinforced; all probe trial choices were rewarded irrespective of whether they correctly reflected the stimulus relationship in the 10-item list. The only differentially reinforced stimulus pair that spanned the two component five-item lists was the E > 1 linkage, so the three successive blocks of probe tests reflected a progressive increase in the amount of prior experience with the linking pair.

Results

List Acquisition

The number of trials required to reach criterion on the first five-item list varied across subjects from 1,548 to 2,772, but the second list was generally acquired more rapidly (TRN1 and TRN2 in Table 1). Once both lists had been separately learned, the birds gradually adapted to the intermixing of premise pairs from both lists, reaching the final criterion on fully intermixed premise pairs in three to eight sessions (TRN4 in Table 1). When we analyzed performance on the five-item lists during the last three sessions preceding link training, there was no significant effect of the order of list learning and no list by pair interaction ($p > .25$ in both cases). There was a significant effect of pair position within the lists, $F(3, 12) = 3.82$, $\eta^2 = 0.35$, $p < .05$, because of higher correct responding on the end-anchor pairs.

Linkage Training

Following simultaneous training on both lists, subjects were presented with sessions during which only the linking pair (E > 1) was presented. The birds required an average of 7.6 sessions (range from 5 to 12) to attain criterion on the link-

ing pair alone (LNK1 in Table 1). After the first block of 20 test sessions (which did not include linking trials), subjects were given a second refresher round of linkage training. The birds required a mean of 4.8 sessions (range from 4–6) to achieve criterion in these retraining sessions (LNK2 in Table 1).

Probe Responses

Analysis of transitive choice — We classified responses to probe pairs as transitive or nontransitive, depending on whether they were consistent with the structure of the implicit hierarchy. The proportion of transitive probe choices was analyzed across the three 20-session test blocks, which differed in the amount of E > 1 training that had previously been received. An overall analysis of variance (ANOVA) on the proportion of transitive choices as a function of probe pair and block (6 probes \times 3 blocks, repeated across subjects) found a significant main effect of probe pairs, $F(5, 20) = 14.1$, $p < .001$, $\eta^2 = 0.42$, a significant effect of block sequence, $F(2, 8) = 26.3$, $p < .001$, $\eta^2 = 0.09$, and a significant Pair \times Block interaction, $F(10, 40) = 2.65$, $p < .02$, $\eta^2 = 0.11$. To determine the nature of the interaction, we conducted component analyses on each individual probe pair (Keppel & Wickens, 2004), testing for changes in transitive responding across blocks with one-way repeated measures ANOVA. We also tested for deviations from chance performance on each probe pair during each block with single-sample, two-tailed t tests (Figure 2a–f). This set of tests were supplemental to the overall ANOVAs, used to help understand the different patterns among probe pairs that had been shown in the overall ANOVA to exhibit significant variation across blocks.

Pinyon jays displayed strikingly different responses to the within-list probes, B ? D and 2 ? 4. All subjects made transitive choices throughout the three blocks of probe testing with pair B ? D, choosing B more than 90% of the time in all blocks with no significant block differences, $F(2, 8) < 1$ (Figure 2a). In contrast, the proportion of transitive choices on pair 2 ? 4 was not significantly different from chance in any block of probe testing, and there were again no significant differences across blocks, $F(2, 8) < 1$ (Figure 2b).

On the two near between-list probes (D ? 1 and E ? 2), the jays showed similar significant increases in transitive responding

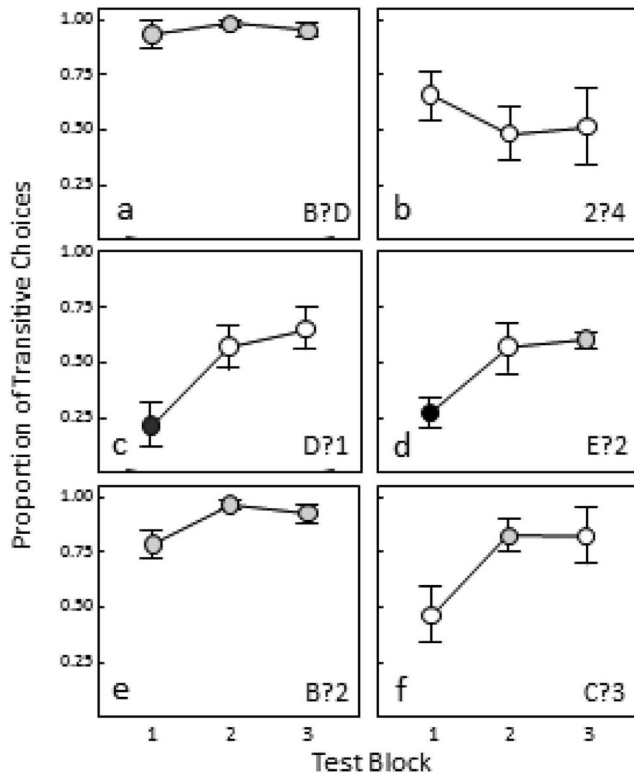


Figure 2. Mean (\pm SEM) proportion of transitive choices on each probe: **a, b**: within-list probes; **c, d**: near-between probes; **e, f**: far-between probes. Solid symbols represent proportions that are significantly different from chance (single sample, two-tailed t tests, $df = 4$, $p < .05$, in all cases). Solid circles indicate performance levels less than chance; gray circles indicate greater than chance.

across blocks: for D ? 1, $F(2, 8) = 12.58$, $p < .01$, $\eta^2 = 0.51$ (Figure 2c); for E ? 2, $F(2, 8) = 7.10$, $p < .02$, $\eta^2 = 0.49$ (Figure 2d). In both cases, transitive choices were below chance during Block 1, increased to chance levels during Block 2, and increased further during Block 3, with the proportion of transitive choices significantly exceeding chance levels for E ? 2 during the last block.

Finally, on the two far between-list probes (B ? 2 and C ? 3), the birds showed yet another pattern of transitive choices. They responded to B ? 2 with high levels of transitive responding during all three test blocks. This proportion was clearly above chance during Block 1, and it increased substantially for Blocks 2 and 3, resulting in a significant block effect, $F(2, 8) = 4.52$, $p < .05$, $\eta^2 = 0.51$ (Figure 2e). The proportion of transitive responses to pair C ? 3 also showed a significant increase across blocks, $F(2, 8) = 5.66$, $p < .03$, $\eta^2 = 0.37$ (Figure 2f). However, the proportion did not differ from chance during Block 1. It was significantly above chance during Block 2 but not during Block 3 ($p = .072$).

Analysis of choice latency — To control for the effects of nonnormality in the distribution of latencies, we analyzed the time required to make choices during probe tests using log-transformed RTs (Bond *et al.*, 2003, 2007). An overall Probe Pair \times Blocks ANOVA found significant differences in the response time to the different probe pairs, $F(5, 20) = 5.52$,

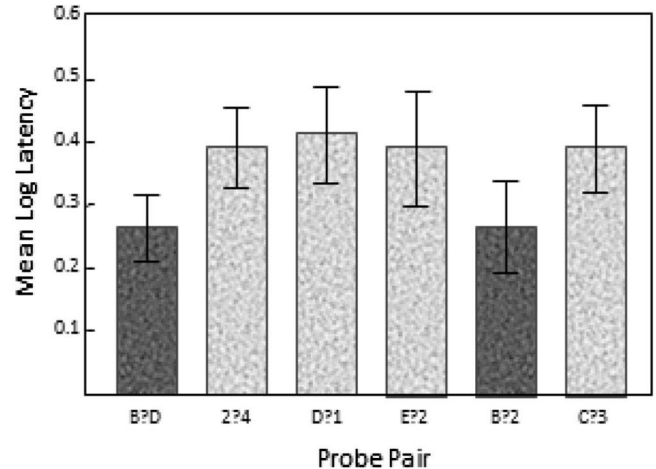


Figure 3. Mean (\pm SEM) log latency to probe pairs. Responses to B ? D and B ? 2 were significantly faster than responses to the other probes, which did not differ from each other.

$p < .01$, $\eta^2 = 0.12$, no significant effect of block, $F(2, 8) < 1$, and no Probe \times Block interaction, $F(10, 40) = 1.90$, $p = .074$. A Fisher's least square differences (LSD) test revealed that responses to probes B ? D and B ? 2 were significantly faster than responses to other probe pairs. No other differences were statistically significant (see Figure 3).

Premise Pair Performance

To assess the effects of presenting the list-linking pair (E > 1) on premise pair performance, we analyzed response accuracy by pair during the last three sessions of acquisition and the first three sessions following initial link training. We calculated a difference score—the proportion of correct responses before list linking minus after list linking—and carried out repeated measures ANOVA on the difference scores as a function of premise pair. Performance on many of the pairs was clearly disrupted by the list-linking experience, but the amount of disruption varied by position, $F(7, 28) = 3.16$, $\eta^2 = 0.46$, $p < .01$ (see Figure 4). The last pair in List X (D > E) and the first pair in List Y (1 > 2) were most affected, whereas there was only minimal impact on the penultimate pairs in each list, C > D and 3 > 4.

Response time also differed across premise pairs during the test sessions (see Figure 5). Repeated-measures ANOVA of log transformed response times revealed a significant main effect of premise pair, $F(7, 28) = 4.93$, $p = .001$, $\eta^2 = 0.09$, no significant effect of block, $F(2, 8) < 1$, and no Block \times Pair interaction, $F(14, 56) = 1.64$, $p = .096$. The differences in response times for premise pairs after linkage appeared to be because of faster responses to the pairs that were at the top of List X, (A > B and B > C) and slower responses to the last two pairs of List Y, (3 > 4 and 4 > 5; Figure 5).

Discussion

The data from both stages of the experiment clearly indicate the importance of both associative and relational processes in generating the implicit structure of the lists. During acquisition the jays were initially unable to learn two

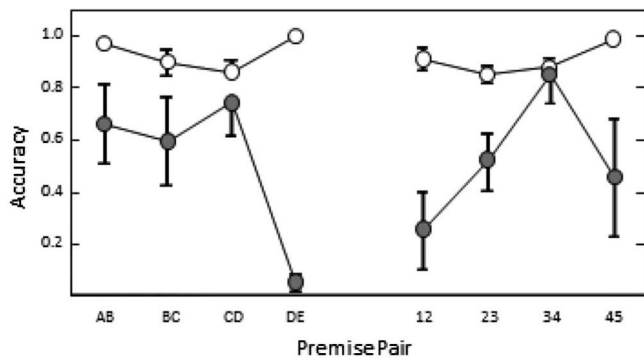


Figure 4. Mean (\pm SEM) proportion of correct choices on premise pairs before (open circles) and after (solid circles) first presentation of linking pair ($E > 1$).

five-item lists when pairs from the two lists were intermixed within training sessions, which suggests an inability to track more than one implicit transitive list at a time. After the lists had been learned separately, however, the jays choose the correct member of each pair in each list when the lists were again intermixed within sessions. Performance on each of the eight premise pairs was highly accurate, above 80% in every case. The interference effect of intermixed lists is, thus, clearly limited to acquisition. Perhaps having multiple incompatible end anchors (A and 1; E and 5) confuses a coherent ranking by associative strength, which could be an essential initial component in the formation of an implicit list structure. This implication is supported by patterns of choice following the list-linking experience.

The $E > 1$ training that linked the lists together induced the birds to respond to many of the probe trials as if the stimuli were drawn from a unified, 10-item series. Although these effects were quite striking, they were not instantaneous. Only the upper list within probe (B ? D) was initially unaffected by linkage, and all of the between-list probes underwent a gradual transformation over successive blocks, gradually approximating the expected transitory relationship. Linking also caused significant transitory disruption in performance on some of the premise pairs. The position of the disruption in the unified list and the speed with which it was resolved provide insight into the roles of direct and relational encoding in implicitly hierarchical structures. Although some evidence was supplied by changes in the accuracy and latency of responses to premise pairs, however, the most informative clues to the underlying cognitive dynamics came from the nondifferentially rewarded probe trials.

Because the stimuli in each of the far between-list probes B ? 2 and C ? 3 occupied the same ordinal position within their original lists, and the order of training on the lists was counter-balanced across jays, the initial magnitude of their direct representations should have been comparable (Chen *et al.*, 1997). This expectation is supported by the comparable accuracies and latencies for premise pairs B > C and 2 > 3 prior to training on the linking pair (see Figures 4 and 5). The far between-list probes were therefore predicted to be more sensitive to changes in relational encoding. In addition, because relational representations depend primarily on the direction of the intervening linkages, changes may occur on the basis of very limited experience. The experimental results were consistent with

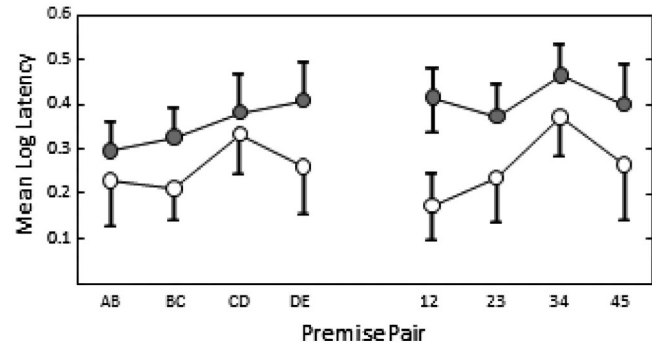


Figure 5. Mean (\pm SEM) log response latency to premise pairs before (open circles) and after (solid circles) first presentations of linking pair ($E > 1$).

this prediction. Almost as soon as the critical $E > 1$ pair was learned, the birds evidenced a preference for the item from the upper list in the aggregate structure (List X: B or C) over the item from the lower one (List Y: 2 or 3). This is particularly clear in the case of B ? 2, where the pinyon jays chose B on 75% of the trials during the first block of probe testing when the birds had had only initial training on the linking pair (Figure 2e). In the case of C ? 3, the birds showed no preference for either stimulus during Block 1 of probe testing but then rapidly developed a clear preference for C during the later blocks (Figure 2f). In their list-linking study of rhesus macaques, Gazes *et al.* (2012) also found above-chance performance on far-between pairs. Because they used longer lists, there were more far-between exemplars to analyze. But their monkeys were above chance on most far-between probes after link training, showing declining performance on pairs lower in the hierarchy. The macaques averaged 81% correct on B ? 2 and C ? 3, with lower but still above-chance scores on D ? 4, F ? 5, and G ? 6 (R. P. Gazes, personal communication, March 23, 2013).

Additional support for the rapid formation of relational representation of the combined structure can be found in the latency to respond to premise pairs as a function of their position in the 10-item list. Even in the first three sessions of the first test block (filled circles, Figure 5), the birds responded fastest to pairs that were at the top of List X (A > B and B > C) and slowest to the last two pairs of List Y (3 > 4 and 4 > 5). Terrace (2005) has suggested that this pattern of increasing latency with distance from the top of the hierarchy is diagnostic of a relational representation.

Responses to the near between-list probes D ? 1 and E ? 2 tell a somewhat different story. The stimuli in these pairs presumably contrasted strongly in their initial direct representation: Stimuli 1 and 2 were at the top while D and E were at the bottom of their respective five-item lists. This difference in associative strength would predict a preference for 1 and 2 at the outset, though ongoing training on $E > 1$ might be expected to gradually reverse the bias. This expectation is consistent with the results. In the D ? 1 probes, there was an initial bias in favor of Stimulus 1 in Block 1 of probe testing. This disappeared with further experience with the linking pair during Blocks 2 and 3, where the preference shifted significantly toward Stimulus D (Figure 2c). A nearly identical pattern was apparent in the E ? 2 probes, with an initial preference for Stimulus 2 gradually shifting toward Stimulus E with

greater linking experience (Figure 2d). The initial disparity in direct encoding in these near between-list probes appears to have slowed the adoption of fully transitive responding, relative to the rate of change seen in probes B ? 2 and C ? 3. Gazes *et al.* (2012) found a similar pattern on pair G-2 but consistently above-chance transitive performance on the other near between pair in their study, F-1.

The most unexpected effects of joining two lists were the pattern of choices to the within-list probe pairs B ? D and 2 ? 4. In the numerous TI studies that have used a five-item list, it has been traditional to test for transitive inference with probe pairs of the second versus the fourth items in the sequence. In addition, when significant results have been obtained, the preference shown has almost always been for the second item over the fourth (Allen, 2006; Vasconcelos, 2008). We had anticipated that because neither of these probes included stimuli that directly participated in the link, they would be unaffected by the restructuring, and we would see a consistent preference from the outset for B over D and for 2 over 4. There was, however, a striking asymmetry in the results. As predicted, the B ? D probe from within the upper list (List X) was minimally impacted by linkage training; the jays showed a consistent preference for B from the first block of test trials (Figure 2a). But performance on the 2 ? 4 probe from within the lower list (List Y) was seriously disrupted by training on E > 1 and did not recover to the levels shown in List X even by the end of the third block of testing (Figure 2b). During this final block, neither the 2 ? 4 within-list probe nor the C ? 3 between-list probe had fully recovered, and the median accuracy across birds was still no better than 63% for premise pairs 1 > 2, 2 > 3, and 3 > 4. It is difficult to predict how long this disruption would have lasted had training been continued.

Similar effects have been observed in primate list-linking studies. In Treichler's studies the error rates for pairs below the link were roughly double those of corresponding pairs above it (Table 2 in Treichler & Van Tilburg, 1996; Figure 12.3 in Treichler, 2007). In Gazes *et al.* (2012), multiple comparisons were analogous to B ? D versus 2 ? 4 because of their longer premise pair lists. However, in terms of mean transitive choice across probe trials, a similar pattern held for B ? D versus 2 ? 4 (73% vs. 66%), C ? E versus 3 ? 5 (69% vs. 51%) but not for the final pair D ? F versus 4 ? 6 (70% vs. 92%).

The source of differences between B ? D and 2 ? 4 may be because of effects of reward patterns for items at the top and bottom of serial lists. Because of the consistency with which end anchors are rewarded during operant TI, they appear to serve as reference points for the rest of the premise pairs. In simple associative models in which reward of a chosen stimulus increases but nonreward of that stimulus decreases its value (e.g., Couvillon & Bitterman, 1992), the high associative value associated with the end anchor and the effects of nonreward produces an oscillatory pattern of associative strength that propagates down the length of the list, an effect that is quite conspicuous in both pigeons (von Fersen *et al.*, 1991) and most species of corvids (Bond *et al.*, 2010). However, this pattern of direct representation must be disrupted by training on the linking pair. In LNK1 (see Table 1) choice of E was reinforced for the first time while choice of 1 was unreinforced also for the first time. Thus, E > 1 training should impact the associative strength of the end anchors, producing an increase for E and a decrease for 1. The decrease in the associative value of stimulus 1 may have distorted the direct repre-

sentations of stimuli further down in List Y to compensate for the change, interfering with transitive choices to the 2 ? 4 pair. Transitive choices were high to the within-list probe (B ? D) from List X but not to the equivalent probe from List Y (2 ? 4), suggesting that the anchoring effects of the top item in a list may be more influential than those of the lowest item (Bond *et al.*, 2010). This is consistent with the importance of the highest-ranked item in Terrace's simultaneous chains, where lower ranked stimuli are accessed by chaining down from the top of the list (Terrace, 2005; Terrace & McGonigle, 1994).

This interpretation of the probe contrasts is supported by the pattern of responses to the premise pairs following list linking, which had greater effects on List Y than List X premise pairs. Link training, with its novel pattern of reward for choices of the end anchors, produced a kind of associative chaos among the premise pairs above and below the link. These effects were asymmetrical, generating different overall patterns of incorrect responding in the adjacent premise pairs. Performance on the last premise pair in List X was at chance levels following link training, but at least the first two pairs in List Y were also affected (see Figure 4). Gazes *et al.* (2012; see their Figure 8) similarly found a decline in performance on the premise pair immediately preceding the linking pair but an even greater decrement in the one that followed.

Whether this persistent residual influence of the highest-ranked stimulus is a general characteristic of disturbance in implicit hierarchies is an open question, however. It may be an artifact of the use of food reward as a proxy for an intrinsically orderable stimulus array (Lazareva & Wasserman, 2006; Markovits & Dumas, 1992). We have demonstrated that pinyon jays acquire a representation of relative dominance status purely on the basis of observing the interactions of other birds (Paz-y-Miño *et al.*, 2003), and they receive no immediate reward, either social or nutritional, during these observations. Nonetheless, they make rationally legitimate transitive inferences. Similar effects of intrinsic ordering have been shown in other avian species (Emmerton *et al.*, 1997; Lazareva *et al.*, 2004) as well as fish (Grosenick *et al.*, 2007). A test of list linking in intrinsically ordered arrays could be exceedingly informative with respect to the formative role of the highest-ranked stimulus.

Differences in TI performance among corvids appear to be related to aspects of their natural history, particularly social complexity and dependence on cached food (Bond *et al.*, 2003, 2010). Comparisons between more distant taxa can be problematic for several reasons including differences in contextual variables (Bitterman, 1965) and the lack of an evolutionary common ground (Kamil, 1988). It is, nonetheless, noteworthy that pinyon jays and rhesus macaques show a striking correspondence in their patterns of response to both premise pairs and probe tests during list linking. Because of the similarity in their methodology the results of Gazes *et al.* (2012) are particularly comparable to our findings.

Relational representation in mammals has been closely tied to the hippocampal formation (reviewed in Eichenbaum, 2006; Jacobs, 2006). The hippocampus is broadly homologous in structure in birds and mammals (Colombo & Broadbent, 2000; Jarvis *et al.*, 2005), and it appears to serve similar functions with respect to spatial memory (Bingman, Erichsen, Anderson, Good, & Pearce, 2006; Bingman, Hough, Kahn, & Siegel, 2003; Bingman & Sharp, 2006). Little is known about the role of the avian hippocampus in nonspatial relational repre-

sentation, though a recent study of operant TI in pigeons (Acerbo *et al.*, 2013) revealed that hippocampal lesions disrupted established nonspatial relational memories. However, the detailed correspondence in the list-linking mechanism between Gazes's macaques and corvids suggests a broad functional homology in neurological mechanism, a finding that is clearly deserving of additional exploration.

The primary conclusion from this study is that combining two implicit hierarchies into a novel compound structure is not a unitary event. It is a process during which direct and relational representations gradually converge on a new configuration, interacting with one another and operating under varying kinetic constraints. At any given moment, the two lists may be combined into one from some perspectives and yet be virtually independent from others. Such incomplete and contradictory outcomes are frustrating to analyze, but they may be a direct result of the multiple processes that underlie the cognitive reconstruction of the natural world.

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