






The structure of prior knowledge enhances memory in experts by reducing interference

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The influence of prior knowledge on memory is ubiquitous, making the specific mechanisms of this relationship difficult to disentangle. Here, we show that expert knowledge produces a fundamental shift in the way that interitem similarity (i.e., the perceived resemblance between items in a set) biases episodic recognition. Within a group of expert birdwatchers and matched controls, we characterized the psychological similarity space for a set of well-known local species and a set of less familiar, nonlocal species. In experts, interitem similarity was influenced most strongly by taxonomic features, whereas in controls, similarity judgments reflected bird color. In controls, perceived episodic oldness during a recognition memory task increased along with measures of global similarity between items, consistent with classic models of episodic recognition. Surprisingly, for experts, high global similarity did not drive oldness signals. Instead, for local birds memory tracked the availability of species-level name knowledge, whereas for nonlocal birds, it was mediated by the organization of generalized conceptual space. These findings demonstrate that episodic memory in experts can benefit from detailed subcategory knowledge, or, lacking that, from the overall relational structure of concepts. Expertise reshapes psychological similarity space, helping to resolve mnemonic separation challenges arising from high interitem overlap. Thus, even in the absence of knowledge about item-specific details or labels, the presence of generalized knowledge appears to support episodic recognition in domains of expertise by altering the typical relationship between psychological similarity and memory.

knowledge | memory | organization | expertise | schema

Prior knowledge profoundly influences how we perceive and remember new information. This relationship can unfold at multiple levels, varying with the resolution of prior knowledge, from details about individual items to the broad organization of knowledge structures. Increased knowledge for a domain is often associated with subcategory-level concepts, which decompose basic-level concepts (e.g., bird) into increasingly specific subdivisions (e.g., raptor vs. songbird; finch vs. sparrow) (1, 2). Subcategories encompass collections of discrete exemplars or instances that share attributes and that sometimes require appreciation of subtle distinctions to differentiate. This level of knowledge is often accompanied by unique verbal labels for members of a subcategory (e.g., chipping sparrow) that enhance abstraction and improve the detection of commonalities across different experiences (3, 4). At this end of the specificity continuum, studies have found that prior knowledge of individual items increases episodic memory for stimuli such as famous versus nonfamous faces (5, 6), familiar versus unfamiliar objects (7), and known versus unknown facts (8).

In addition to supporting detailed knowledge of individual exemplars, domain knowledge can manifest at broader levels. Here, high-level knowledge structures are developed by abstracting conceptual and perceptual information acquired across multiple episodes. For example, an appreciation of generalized attributes or features (e.g., that insectivores have narrower beaks than seed-eating birds) might help one identify novel exemplars (e.g., birds of an unfamiliar species) as belonging to one of these broader categories. Work on schemas and categorization has emphasized the importance of studying the structure of relationships within knowledge networks in addition to the attributes of items in isolation (9–13). Although memory can also benefit from high-level knowledge structures (14–16), the manner in which this takes place remains unclear. One possibility is that the successful identification of conceptual divisions that organize a network can serve to mitigate interference from otherwise overlapping items. In a network that is efficiently parcellated by prior knowledge, aspects of similarity that might otherwise hinder mnemonic separation are reduced, and superficially similar items are differentiated along meaningful conceptual dimensions.

The importance of interitem similarity (i.e., the perceived relationships between items in a set—e.g., a collection of study-list words, faces, or subcategory exemplars) features

Significance

What we remember is shaped by what we already know. For example, remembering the angelfish from a recent aquarium visit is easier for those who already know what angelfish are and know things about them. In addition to facilitating memory retrieval of specific items, prior knowledge also supports memory by providing an overarching organizational structure for new information. Here, we show how expert knowledge leads birdwatchers to organize birds based on conceptual features, in contrast to novices who organize birds based on perceptual features. In turn, experts' organizational structure supports memory by reducing interference typically caused by high overlap among items, even when to-be-remembered birds were unfamiliar species. These findings demonstrate how the organization of generalized knowledge promotes memory.

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prominently in global matching models of memory and categorization (17–21), which provide a promising framework for exploring how the organization of knowledge influences memory. In the context of episodic recognition, these models predict that memory for a probe item should depend on its aggregate similarity (or global match) to other items in a study set, with greater similarity driving oldness signals associated with both hits and false alarms (22, 23). Various dimensions of similarity (e.g., normative semantic relatedness, perceptual overlap of images) can be modeled, but past work has often considered sets of stimuli for which interitem relationships are relatively consistent across participants. In the real world, however, the strength and nature of relationships between items vary greatly with experience, which may lead to corresponding differences in the mnemonic similarity of episodic representations. For the same set of items, the predictions of matching models should depend on which features help to organize a domain of information. Similarity in the context of well-developed conceptual networks may, instead, reflect meaningful relations that prove beneficial to memory rather than hindering it. Thus, along with facilitating recognition of individual items, prior knowledge may change the relationship between interitem similarity and memory decisions.

In order to examine how prior knowledge shapes memory at different levels of abstraction, the present study focused on bird experts who had generalized knowledge about bird features and categories but had specific knowledge about only some of the subcategory exemplars (i.e., individual species, or “items”). An extensive body of work has shown memory advantages associated with expertise (14, 16), including for various domains of object processing (24–27). The level at which prior knowledge operates, however, can sometimes be difficult to disentangle. Here, we examined the impact of both species-level knowledge (explicit name test) and subjective organization for the entire stimulus set, which revealed generalized dimensions that shape perceived interitem similarity (e.g., taxonomic features, bird color). These tasks were performed using a set of birds local to the geographic region of expert participants as well as a visually similar set consisting of nonlocal species. Measures of name knowledge and subjective organization were then related to memory decisions on an episodic recognition test in which participants determined whether a new set of photos depicted previously studied or unstudied species. A group of matched nonexpert control participants completed the same tasks.

Following past work, we expected that memory performance would differ by group and would relate to the level of intragroup expertise reflected in knowledge tests. We also assumed that knowledge of individual species would positively track memory, showing the importance of subcategory concepts and verbal labels in categorization and memory (4, 28, 29). In the absence of species-level knowledge, however, broader structural dimensions of knowledge (e.g., interitem relationships) may play a larger role in guiding memory. We therefore sought to determine how the overall organization of knowledge contributed to memory, particularly when individual species were unfamiliar. Using each participant’s subjective bird organization data as input for a matching model of recognition, we explored a potential route by which structured prior knowledge may benefit memory; namely, that knowledge organized through expertise divides conceptual space, attenuating uninformative global similarity signals. Specifically, we investigated how the organizational structure of expert knowledge supports episodic memory by constraining the negative effects of high interitem similarity. We did so by mapping relationships in prior knowledge to corresponding recognition memory outcomes. This approach emphasizes the wider importance of examining the configuration

of relational structures in prior knowledge for predicting and interpreting memory function.

Materials and Methods

Participants. Participants in the expert group were recruited through contacts with community organizations such as the Toronto Ornithological Club and Toronto Field Naturalists. Information about the study was also distributed via online outreach, but only to organizations located within the province of Ontario, given the geographic range of local bird stimuli. These participants confirmed that they could identify more than 20 individual species found in the local habitat and that their bird knowledge extended beyond common backyard species. Rather than yielding a homogenous sample of experts, this approach resulted in participants with a continuum of prior knowledge, ranging from intermediate to advanced levels. In order to provide a close match with participants in the expert group, control participants were recruited from other organizations in Ontario that focused on outdoor or natural interests (e.g., gardening and horticulture, fishing, hiking). Control participants were selected to match the expert group on age, sex, and years of education (Table 1). Control participants were limited to individuals without local bird knowledge beyond common backyard species; however, variability in knowledge was also present in this sample. Although this intragroup variability may have somewhat diminished the reported group differences, it allowed us to better match motivational aspects between groups and enabled the exploration of continuous aspects of prior knowledge across participants, particularly within the expert group. The final sample consisted of 66 experts and 57 controls after 2 participants were excluded due to low memory performance (1 from each group with >2.5 SD below group mean D-Prime, averaged across lists), and 1 participant was excluded from the expert group after misinterpreting instructions in the naming task (naming accuracy >2.5 SD below group mean). All participants gave informed consent before beginning the study, which was reviewed and approved by the Research Ethics Board of Baycrest Hospital.

Stimuli.

Bird lists and illustrations. Bird stimuli were split into three lists of 36 species each. Each list contained birds from the same six taxonomic families (blackbirds, finches, flycatchers, sparrows, vireos, and warblers) with six species per family. The “Local” list was composed of birds found in southern Ontario as determined by ecological prevalence data averaged over the 2016 to 2018 time period, queried from the eBird database (<https://ebird.org>). The other two lists were composed of birds with nonoverlapping ranges, found principally in South America and the tropics. Birds in the “Nonlocal” lists encompassed the same six families and were selected to be similar to Local list birds so that differences between lists could be attributed to participant knowledge rather than to inherent bird features. Illustration images for each bird were contained in the *Handbook of the Birds of the World* (<https://birdsoftheworld.org>) (30).

Bird photographs. Eight separate photographs were collected from the internet for each bird species. Photographs depicted a side view of the bird and were intended to clearly show all notable features. Photographs were cropped to remove excess border and resized to 600 pixels along the long dimension. In a separate online normative study, nonexpert participants ($n = 70$) rated how well each photograph matched the corresponding field guide illustration for each species. These ratings were used to divide the set of photographs into two sets of four exemplars, the first of which was used in the episodic memory task here and the second of which was used for a separate study.

Table 1. Demographic information for participants

	Experts	Controls
<i>N</i>	66	57
% female	0.73	0.75
Age	48.1 (16.5)	47.9 (16.8)
Yr education	18.1 (2.6)	17.6 (2.4)

N, number of participants in each group; mean participant age and years of education for each group, with corresponding SD.

Procedure. In the experimental session, the sequence of tasks was 1) episodic recognition memory test (episodic memory task), 2) subjective similarity arrangement task (subjective arrangement task), and 3) multiple-choice bird name test (name selection task). The order in which we describe the tasks mirrors the sequence in *SI Appendix, Results*, which first establishes differences in prior knowledge and then explores how knowledge influences episodic memory. The episodic memory and subjective arrangement tasks, which used bird photographs and their corresponding illustrations, always included the Local list and one of the two Nonlocal list versions, counterbalanced across participants. The name selection task, which used the same bird illustrations as the subjective arrangement task, included all three lists. A detailed description of each task appears in *SI Appendix, Methods*, and code for experiments and analysis as well as study materials and data are accessible in an online repository at <https://osf.io/zjxtal> (31).

Knowledge measures. In the subjective arrangement task, participants arranged all 36 illustrations within each list on a single screen, with no time limit. Participants were told that more similar birds should be placed closer together, and less similar birds should be placed farther apart, but the parameters of similarity were not specified. Arrangements (group averages shown in Fig. 1A) were done on the Nonlocal list birds first so that experts were not biased in sorting unfamiliar species by having first considered the distinctions between more familiar Local list species. In the name selection task, each self-paced trial included a bird illustration, and participants selected which of six species names below (composed of the target and five distracters from the same bird family and list) they thought was the correct name.

Episodic memory. In the episodic memory task (Fig. 2A), participants intentionally studied a set of 18 bird photographs (4-s trials, 1-s inter trial interval [ITI]) during the study block and then made four-point recognition judgments (definitely "old" to definitely "new") to 36 bird photographs in a test block following a 30-s filler task. New photographs were used for test block trials (5 s each, 1-s ITI)—18 containing species repeated from the study block (targets) and 18 containing previously unseen species (foils). Participants were aware that their decisions should be based on the repetition of a bird species rather than on photograph repetition. Upon completion of the test block, the study-test cycle was repeated for the second set (either Local or Nonlocal list birds, with the order counterbalanced across participants). This format of recognition was used instead of identical picture repetition in order to eliminate instances of recognition that are dependent on the specific version of individual photographs shown, including instances in which memory judgments are based on the exact repetition of background details or other visual elements that are not directly related to the birds themselves. Instead, we used exemplar recognition to better reflect how memory in this domain operates in the real world (i.e., the same bird is not seen twice in exactly the same context, posture, or lighting), for which some degree of abstraction is necessary to recognize the repetition of a concept across variable contexts.

Analysis and Results. In the experimental session, the order of tasks was prioritized to avoid proactive interference during memory. In *SI Appendix, Results*, the tasks directly measuring prior knowledge are considered first, given the implications they have for interpretation of the episodic memory task.

Name Selection Task. The multiple-choice name task was used to determine differences in explicit prior knowledge among individuals, groups, and bird lists. Because some bird names contain descriptive elements, which can be used to strategically eliminate options based on prior knowledge not specific to the items themselves, performance for most participants was well above the numerical chance rate of 16.66%. A regression was conducted with "Group" and "List" as predictors and mean accuracy as the subjectwise dependent variable. This model revealed a Group by List interaction ($\beta = 0.27$, 95% CI = [0.20, 0.33], $t(121) = 8.14$, $P < 0.001$) and main effects of both Group ($\beta = 0.59$, 95% CI = [0.49, 0.69], $t(120) = 11.44$, $P < 0.001$) and List ($\beta = 0.37$, 95% CI = [0.30, 0.43], $t(121) = 10.51$, $P < 0.001$). These differences reflected higher naming performance in the expert group, who additionally showed a selective advantage for Local birds (Local: mean = 74.8%, SEM = 2.1%; Nonlocal: mean = 52.2%, SEM = 1.2%; difference: $t(121) = 13.70$, $P_{Holm} < 0.001$, $d = 2.39$). No corresponding List difference was present in the Controls (Local: mean = 43.5%, SEM = 1.4%; Nonlocal: mean = 40.6%, SEM = 1.4%, $t(121) = 1.62$, $P_{Holm} = 0.11$, $d = 0.30$). The pattern of name selection task performance confirmed that experts have higher overall name knowledge than controls and showed an

expected advantage for Local birds versus Nonlocal birds. Controls, by contrast, showed no difference in naming accuracy between Local and Nonlocal bird species.

A subset of expert group participants also completed a subsequent free-naming version of the multiple-choice task in which no options were given (*SI Appendix, Results – Free naming task*). For the Local condition, free-naming performance (mean accuracy = 54.0%, SD = 27.0%) was lower but highly correlated with multiple-choice name selection performance ($r = 0.94$). By contrast, Nonlocal free naming was near chance (mean accuracy = 1.9%, SD = 4.6%), confirming that experts were largely unfamiliar with Nonlocal birds at the species level.

Subjective Arrangement Task. Although there was no "correct" configural arrangement in the similarity arrangement task, examining how participants arranged birds provided insight into which features were most salient in an overall knowledge-based organizational structure. For each list, a similarity matrix was generated based on the normalized Euclidean distance between each bird and every other bird, with greater distances corresponding to lower perceived similarity. For visualization, we averaged these similarity matrices across participants within Group and List and generated corresponding multidimensional scaling (MDS) plots for the averaged matrices (Fig. 1A, Nonlocal list version A shown). Average matrices sorted by bird family appeared to show stronger and more consistent organizational structure in the expert group, particularly for Local list birds.

In an initial analysis, we measured how consistent the similarity matrices of participants in the same Group and List were to one another. We then examined the overall structure of similarity arrangements by computing modularity (Q), the extent to which arrangements contained discrete clusters or modules, before testing how well similarity matrices fit two explicit models: one based on taxonomic family membership (family model) and the other based on stimulus color similarity (color model). Real-world size is also known to play an important role in subcategory object perception independent of other conceptual and perceptual attributes (32). For the set of species used in the present study, however, size variance was relatively low (*SI Appendix, Results – Bird size model*), and lack of context in the stimuli made this dimension more difficult to interpret (unlike color, for instance); consequently, bird size was not a focus of further analyses.

Intersubject arrangement consistency. Within Group and List, each participant's similarity matrix was correlated with every other participant's similarity matrix, resulting in a second-order correlation for each pair of participants, with 1 signifying perfectly correlated distance matrices between participants. A density plot of these intersubject correlations for the Local list appears in Fig. 1B. In neither group did the mean correlations for the two Nonlocal counterbalance versions differ from one another ($ps > 0.05$); therefore, the intersubject correlations (always calculated within Nonlocal counterbalance version) were subsequently pooled (Fig. 1B, Nonlocal).

A regression with Group and List as predictors for intersubject correlation showed a significant Group by List interaction ($\beta = 0.21$, 95% CI = [0.16, 0.27], $t(121) = 8.00$, $P < 0.001$) as well as main effects of Group ($\beta = 0.63$, 95% CI = [0.53, 0.74], $t(120) = 11.57$, $P < 0.001$) and List ($\beta = 0.32$, 95% CI = [0.27, 0.38], $t(121) = 11.57$, $P < 0.001$). The main effect of Group was produced by higher intersubject similarity among experts, consistent with findings from related research (33). Experts also showed higher organizational consistency for Local versus Nonlocal birds ($t(121) = 14.38$, $P_{Holm} < 0.001$, $d = 2.50$) than was found for controls ($t(121) = 2.44$, $P_{Holm} = 0.016$, $d = 0.46$). Bird organization in expert participants was, therefore, characterized by higher between-participant convergence, particularly for the Local list, whereas there was less consistency among control participants.

Graph network properties. Each subjective arrangement matrix can also be expressed as a graph network, with individual birds as nodes and distances between them as edges. One informative graph property is modularity (Q), or the degree to which networks contain dense clusters instead of items being uniformly distributed. MDS plots on the group-averaged distance matrices appeared to show tighter clustering within experts (Fig. 1A). However, it is also possible that this pattern is a product of the greater across-participant consistency in experts' arrangements (Fig. 1B) rather than an inherent property of distance matrices at the level of individual participants. We tested this possibility with a linear mixed-effects regression with Group and List as predictors and the modularity (Q) of each subjective arrangement task distance matrix as the subjectwise dependent variable.

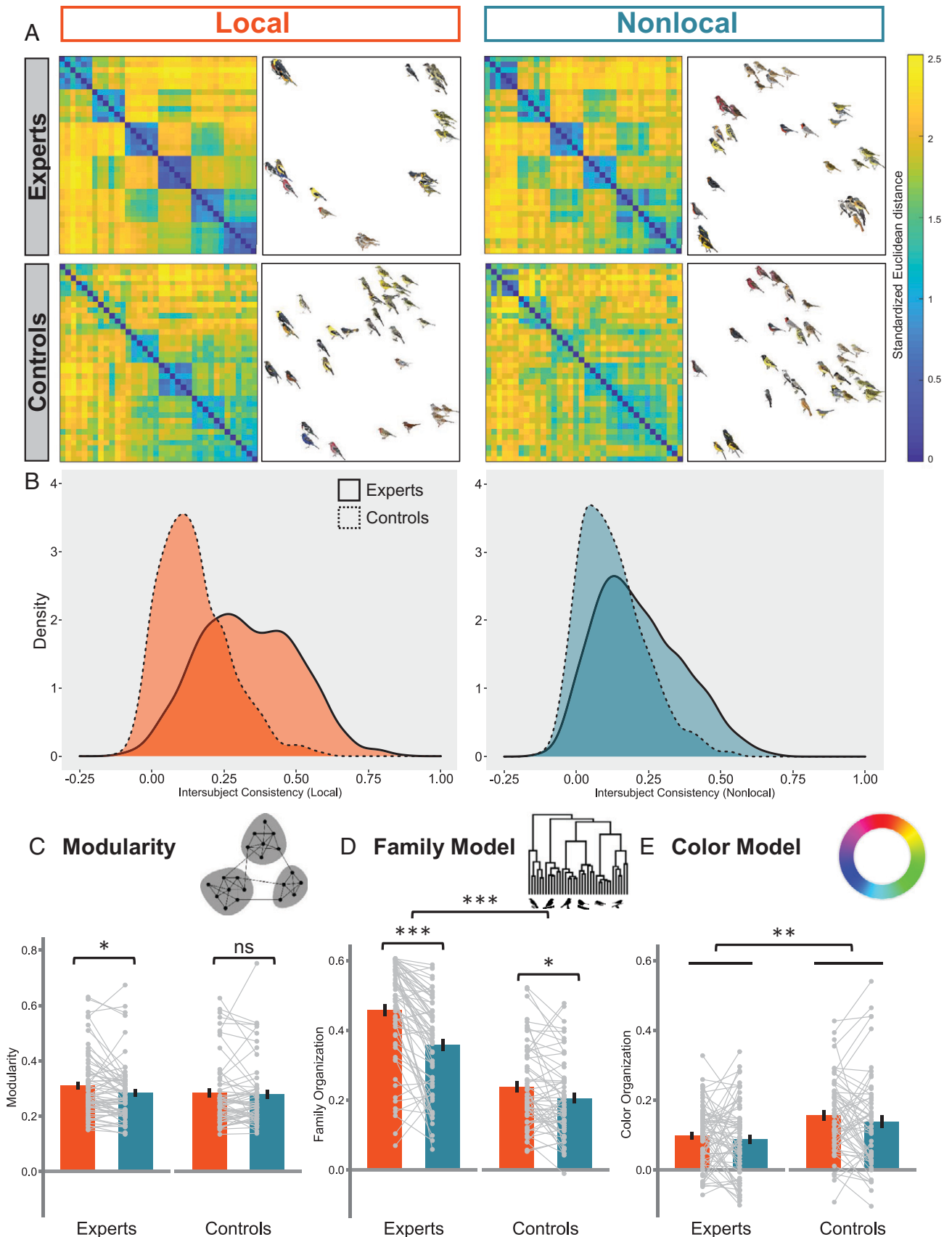
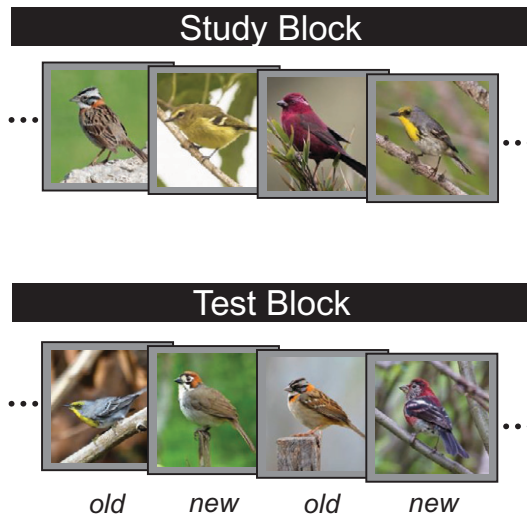
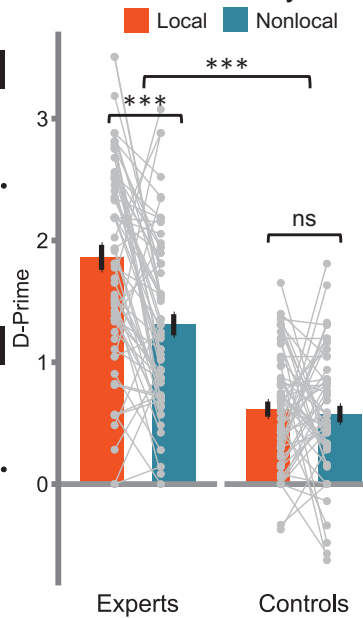


Fig. 1. Subjective arrangement task. (A) Subjective arrangement task distance matrices and corresponding MDS plots, averaged within Group and List (Non-local counterbalance version A shown). (B) Density plot of intersubject distance matrix correlations for the Local list shows higher average correspondence but wider variability between experts than between controls. (C) Group and List differences in modularity of subjective arrangement networks revealed no main effect of Group. (D) Experts showed higher correspondence between subjective arrangement matrices and taxonomic family model, which was additionally higher for Local versus Nonlocal list birds, yielding an interaction. (E) Controls showed higher correspondence between subjective arrangement task matrices and the stimulus color model. For post hoc contrasts: * $P_{\text{Holm}} < 0.05$, ** $P_{\text{Holm}} < 0.01$, *** $P_{\text{Holm}} < 0.001$. Image credit: Lynx Edicions.

A Memory task



B Overall memory



C Responses by trial type

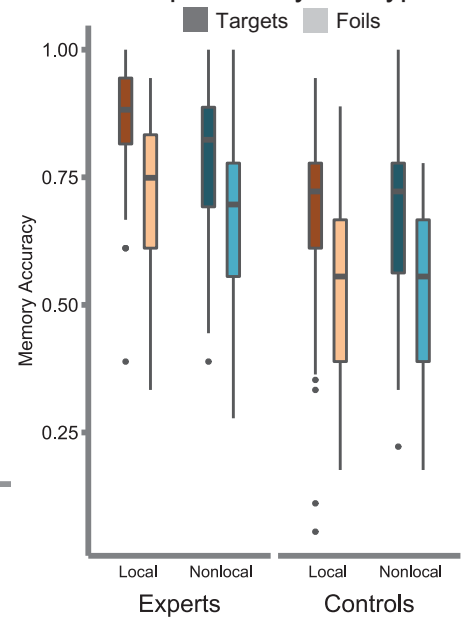


Fig. 2. Episodic memory task. (A) Schematic design. (B) Memory accuracy (D-Prime) by Group and List show greater accuracy for experts overall with additional advantage for Local condition. (C) Corresponding accuracy for targets and foils by Group and List show that improved accuracy in experts is product of both increased hit rate (targets) and correct rejection rate (foils). For post hoc contrasts: * $P_{\text{Holm}} < 0.05$, ** $P_{\text{Holm}} < 0.01$, *** $P_{\text{Holm}} < 0.001$. Image credit: Cornell Lab of Ornithology.

The Group by List interaction was not significant ($\beta = 0.04$, 95% CI = $[-0.01, 0.10]$, $t(121) = 1.60$, $P = 0.11$), nor was the main effect of Group ($\beta = 0.07$, 95% CI = $[-0.10, 0.24]$, $t(120) = 0.86$, $P = 0.39$), indicating that the architecture of individual subjective arrangement task matrices for control participants was not less modular, despite being less consistent across participants (Fig. 1C). Thus, although experts and controls may use different information in judging similarity, participants in each group did draw distinctions, grouping some subsets of birds closer to one another. The main effect of List was significant ($\beta = 0.07$, 95% CI = $[0.01, 0.12]$, $t(121) = 2.27$, $P = 0.025$), and this difference was driven by greater modularity in the Local versus Nonlocal lists within experts (Local mean $Q = 0.31$, SEM = 0.014; Nonlocal mean $Q = 0.29$, SEM = 0.013; difference: $t(121) = 2.84$, $P_{\text{Holm}} = 0.011$, $d = 0.49$). No comparable difference in modularity was found within controls (Local mean $Q = 0.28$, SEM = 0.017; Nonlocal mean $Q = 0.28$, SEM = 0.016; difference: $t(121) = 0.46$, $P_{\text{Holm}} = 0.648$, $d = 0.09$). These results show that irrespective of the dimensions used to organize bird stimuli, modular structure was somewhat higher in Local birds for experts but did not differ between groups when collapsing across list.

Subjective organization: Self-report and relationship with explicit models. Following the subjective arrangement task, participants indicated how strongly they weighted various factors in making arrangement decisions (SI Appendix, Table S1). Although the factor of "taxonomy" was the most directly related to formal knowledge, factors like "specific features" and bird "shape" captured attributes that may vary with taxonomic distinctions even when formal divisions were not known. By contrast, bird "color" was included to capture a salient bird feature that is largely independent from taxonomic distinctions. Unsurprisingly, experts rated perceived taxonomy as more important for organization than controls ($t(120) = 8.14$, $P < 0.001$, $d = 1.51$), while the reverse was true for color ($t(120) = -4.40$, $P < 0.001$, $d = -0.80$). Both groups rated specific features and bird shape highly (SI Appendix, Table S1), although in experts, these factors did not differ from ratings of taxonomy, suggesting redundancy, whereas in controls, these factors did not differ from color (all $P_s > 0.1$).

To explicitly test the influence of factors related to taxonomy and color, we next quantified how well distance matrices matched two explicit models by computing the correlation between a participant's distance matrix and the model matrix. In the first, a categorical family membership model, within-family birds were coded as identical and as orthogonal to birds of other families. This model provided an approximation of whether family membership or morphological characteristics that differ by family are important grouping factors in each participant's organizational structure. Importantly, bird families included in the study were all from the

scientific order of songbirds (Passeriformes) and were chosen specifically because they do not have easily distinguishable family attributes (in contrast to, e.g., owls or gulls). Nonetheless, because subtle characteristics are shared across birds of the same family, this model can capture attention to bird features even in the absence of explicit knowledge about taxonomic classification and may, therefore, capture variance due to self-reported reliance on anatomical features or bird shape in addition to explicit use of taxonomy (SI Appendix, Table S1).

Correspondence with this family model is shown in Fig. 1D, averaged within Group and List. A subjectwise regression with family model fit values, as the outcome measure showed a significant Group by List interaction ($\beta = 0.10$, 95% CI = $[0.05, 0.16]$, $t(121) = 3.57$, $P < 0.001$), a significant main effect of Group ($\beta = 0.57$, 95% CI = $[0.44, 0.70]$, $t(120) = 8.67$, $P < 0.001$), and a significant main effect of List ($\beta = 0.21$, 95% CI = $[0.15, 0.27]$, $t(121) = 6.98$, $P < 0.001$). The interaction was produced by a stronger difference between Local and Nonlocal birds in the expert group ($t(121) = 7.75$, $P_{\text{Holm}} < 0.001$, $d = 1.35$) than in the control group ($t(121) = 2.32$, $P_{\text{Holm}} = 0.022$, $d = 0.44$). These main effects and interactions reflect how dimensions of prior knowledge that extend beyond name knowledge, like taxonomic features, shape the similarity structure in experts. Critically, this type of knowledge is reflected in the organization of Nonlocal birds, for which family-based characteristics were identifiable even if individual bird species were unfamiliar.

Next, we tested a similarity model based on bird color. In controls, self-reported reliance on color was not statistically different from specific features or bird shape, both factors that should be better captured by bird family model. To assess color organization quantitatively, a corresponding regression was run on color model fit values (correlation between subjective arrangement and color similarity after regressing out family structure). A main effect of Group was present ($\beta = -0.24$, 95% CI = $[-0.39, -0.10]$, $t(120) = -3.24$, $P = 0.002$) with no main effect of List ($\beta = 0.06$, 95% CI = $[-0.03, 0.15]$, $t(120) = 1.41$, $P = 0.16$) or Group by List interaction ($\beta = -0.02$, 95% CI = $[-0.11, 0.07]$, $t(121) = -0.38$, $P = 0.70$). Notably, in contrast to the main effect for family structure, this analysis showed that color similarity played a greater role in the subjective arrangement of bird stimuli for controls versus experts, consistent with the notion that novices may be particularly attentive to surface-level features (Fig. 1E).

Episodic Memory Task.

Group and list differences. Memory differences were first explored by comparing D-Prime measures between Group and List, collapsing low- and high-confidence hits/misses and false alarms/correct rejections. A second regression

was conducted in the same fashion as with the name selection task data, but with subjectwise D-Prime values as the dependent variable. The regression showed a significant Group by List interaction ($\beta = 0.15$, 95% CI = [0.07, 0.23], $t(121) = 3.62$, $P < 0.001$), a significant main effect of Group ($\beta = 0.58$, 95% CI = [0.47, 0.69], $t(120) = 10.33$, $P < 0.001$), and a significant main effect of List ($\beta = 0.19$, 95% CI = [0.11, 0.27], $t(121) = 4.20$, $P < 0.001$). The main effect of Group was produced by better memory in experts, whereas the interaction resulted from better Local versus Nonlocal memory within experts (Local: mean = 1.86, SEM = 0.10; Nonlocal: mean = 1.31, SEM = 0.09; difference: $t(121) = 5.74$, $P_{\text{Holm}} < 0.001$, $d = 1.00$), with no corresponding List difference seen for controls (Local: mean = 0.62, SEM = 0.06; Nonlocal: mean = 0.57, SEM = 0.07; difference: $t(121) = 0.39$, $P_{\text{Holm}} = 0.696$, $d = 0.07$) (Fig. 2B).

An examination of separate hit and false alarm rates found that this difference in memory sensitivity was produced by both a lower hit rate and a lower correct rejection rate within the Controls (Fig. 2C). Similarly, within experts, decreased accuracy for both targets and foils led to lower memory for Nonlocal birds, as evidenced by a lack of difference in response bias (assessed by comparing values of C , criterion) between the two groups ($t(177) = -1.13$, $P = 0.26$, $d = 0.15$) and between the two lists within experts ($t(65) = -0.56$, $P = 0.58$, $d = -0.07$).

Relationship between memory performance and knowledge measures across participants. After establishing differences in mean episodic memory performance between groups, we next turned to examining variability among participants within each group. These intragroup analyses explored how the continuum of prior knowledge, particularly within experts, relates to episodic memory performance. Subjectwise linear regressions controlling for Nonlocal counterbalance version examined how D-Prime was related to both name selection task accuracy as well as tendency to organize stimuli by family and color (Fig. 3). For experts, memory discriminability (D-Prime) was predicted by name knowledge for the Local list ($\beta = 0.71$, 95% CI = [0.53, 0.89], $t = 8.05$, $P < 0.001$), and a significant but weaker association was found between name selection task performance and D-Prime for the Nonlocal list ($\beta = 0.26$, 95% CI = [0.00, 0.51], $t = 2.02$, $P = 0.047$). No significant relationships between D-Prime and name knowledge were found in controls ($ps > 0.1$), (see Fig. 3A). Thus, in addition to the substantial differences in memory and name knowledge between groups, experts' memory tracked name selection task performance, particularly for Local list birds.

We next explored relationships between recognition memory performance and the organizational structure present in each participant's subjective arrangement data, considering both family and color organization (Fig. 1). In experts, the strength of family organizational structure significantly predicted D-Prime for both Local ($\beta = 0.63$, 95% CI = [0.43, 0.82], $t = 6.41$, $P < 0.001$) and Nonlocal ($\beta = 0.40$, 95% CI = [0.17, 0.63], $t = 3.52$, $P < 0.001$) lists, whereas in Controls, trends were apparent in each list (Local: $\beta = 0.24$, 95% CI = [-0.02, 0.51], $t = 1.85$, $P = 0.070$; Nonlocal: $\beta = 0.24$, 95% CI [-0.02, 0.51], $t = 1.83$, $P = 0.073$) (Fig. 3B). In controls, name selection task accuracy was unrelated to memory; however, participants who had stronger family organization showed a trend for better recognition memory, suggesting that more generalized relational knowledge may be beneficial even for participants who lack detailed domain knowledge.

Finally, we examined the influence of color-based organization. In experts, stronger color organization for Local birds was associated with worse memory performance ($\beta = -0.28$, 95% CI = [-0.52, -0.04], $t = -2.32$, $P = 0.024$), and no significant relationship was found for Nonlocal birds ($\beta = 0.00$, 95% CI = [-0.25, 0.26], $t = 0.04$, $P = 0.97$). No significant relationships between color organization and memory were observed in controls (all $Ps > 0.1$) (Fig. 3C). Together, these relationships reveal variability within the expert group. Better name knowledge and family-based organization strongly tracked recognition memory performance, particularly within the Local list. By contrast, experts whose arrangements more strongly reflected color had lower memory, suggesting that they may perceive interitem relationships along dimensions favored by control participants (Fig. 1E).

Trialwise relationship between episodic memory and name selection task performance within participants. For both the name selection task and the episodic memory task, expert knowledge of individual species is expected to account for better performance in the Local compared to Nonlocal conditions. By contrast, more generalized knowledge may underpin memory for Nonlocal birds (SI Appendix, Results - Mediation), which was still substantially higher for experts

compared to controls. One possibility is that for Nonlocal birds, expert performance on the name selection task relies more heavily on inference based on generalized prior knowledge than on familiarity with individual Nonlocal species (SI Appendix, Results - Free naming task). In this scenario, correct name selection responses may be less predictive of memory outcomes at the level of individual items (within participants) even though a relationship appeared for the group (across participants) (Fig. 3A and SI Appendix, Results - Mediation). We tested this possibility with a trialwise regression examining the relationship between name selection task outcomes (correct or incorrect) and memory accuracy, collapsing across targets and foils.

Although experts remembered Local birds better overall, of particular interest for this analysis was whether the trialwise influence of name knowledge (correct vs. incorrect name selected) contributed to memory outcome similarly across the two lists. This analysis showed that the influence of name selection outcome on memory was much stronger for the Local versus Nonlocal lists, resulting in a significant interaction ($b = 0.18$, $z = 4.92$, $P < 0.001$), with pairwise contrasts (memory accuracy \times name selection) showing a significant difference only for Local list birds (Local: $z = 7.86$, $P_{\text{Holm}} < 0.001$; Nonlocal: $z = 1.86$, $P_{\text{Holm}} = 0.063$) (Fig. 4). This dissociation suggests that the mnemonic advantage conferred by item-specific verbal labels contributes to experts' memory advantage for Local birds but does not account for their superior memory for Nonlocal birds. Abstracted knowledge that broadly affects the way experts process information about birds influences their performance throughout but appears to be particularly relevant for memory in the absence of specific labels. These trialwise results provide convergent evidence with findings from the mediation analysis (SI Appendix, Results - Mediation), which also suggest that more abstracted knowledge may underpin the across-participant correlations between naming selection performance and memory.

Perceived similarity associated with increased oldness signals in controls but not experts. Results from across-participants analyses (Fig. 3 and SI Appendix, Fig. S1) revealed that experts and controls had comparably modular subjective bird organization, but only in experts did this track taxonomic family structure and relate to memory performance. However, another potential mnemonic impact of greater similarity between items is increased perceived oldness, which can produce memory interference as predicted by global matching models. When considering the mnemonic implications of interitem relationships, the extent to which similarity indexes beneficial organization versus confusability likely depends on the role that prior knowledge plays in shaping conceptual networks. After probing knowledge-related influences on organizational structure (i.e., overall correspondence with perceptual and conceptual dimensions), we next examined how interitem relationships operated on trial-by-trial memory outcomes within these structures.

An analysis relating subjective similarity to memory addressed this wider question by testing whether the tendency to respond "old" to memory probes at test was influenced by an item's aggregate proximity to encoding set items in subjective similarity space (Fig. 5A, Top). For each item at retrieval, the mean distance to every other study set item was calculated using each participant's subjective arrangement matrix (statistical significance of the following global similarity effects remained unchanged when an exponential transformation function was applied). These trialwise global similarity values were entered as the dependent variable in a mixed-effects regression with predictors of Group, List, and trialwise Memory response (subjective "old" or "new"). Results showed a main effect of Memory response ($b = -0.018$, $t = -5.11$, $P < 0.001$), which was produced by higher global similarity for "old" as compared to "new" responses (i.e., lower distance; Fig. 5A, Bottom), consistent with the predictions of global matching models. However, a significant Group by Memory response interaction ($b = 0.009$, $t = 2.64$, $P = 0.008$) was also present because the global similarity influence on memory response was observed only for controls (Local: z -ratio = -4.66 , $P_{\text{Holm}} < 0.001$; Nonlocal: z -ratio = -2.82 , $P_{\text{Holm}} = 0.019$; Local \times Nonlocal interaction: z -ratio = -1.29 , $P_{\text{Holm}} = 0.40$); no significant differences were found within Experts for either list ($Ps > 0.1$) (Fig. 5A, Bottom).

The previous finding showed that recognition judgments in controls reflect a memory probe's relationships to the entire encoding set in subjective similarity space, a bias that is absent in experts. To the extent that this bias operates equally on targets and foils, it should drive memory toward chance-level discrimination. Alternatively, similarity-biased judgments that operate selectively on

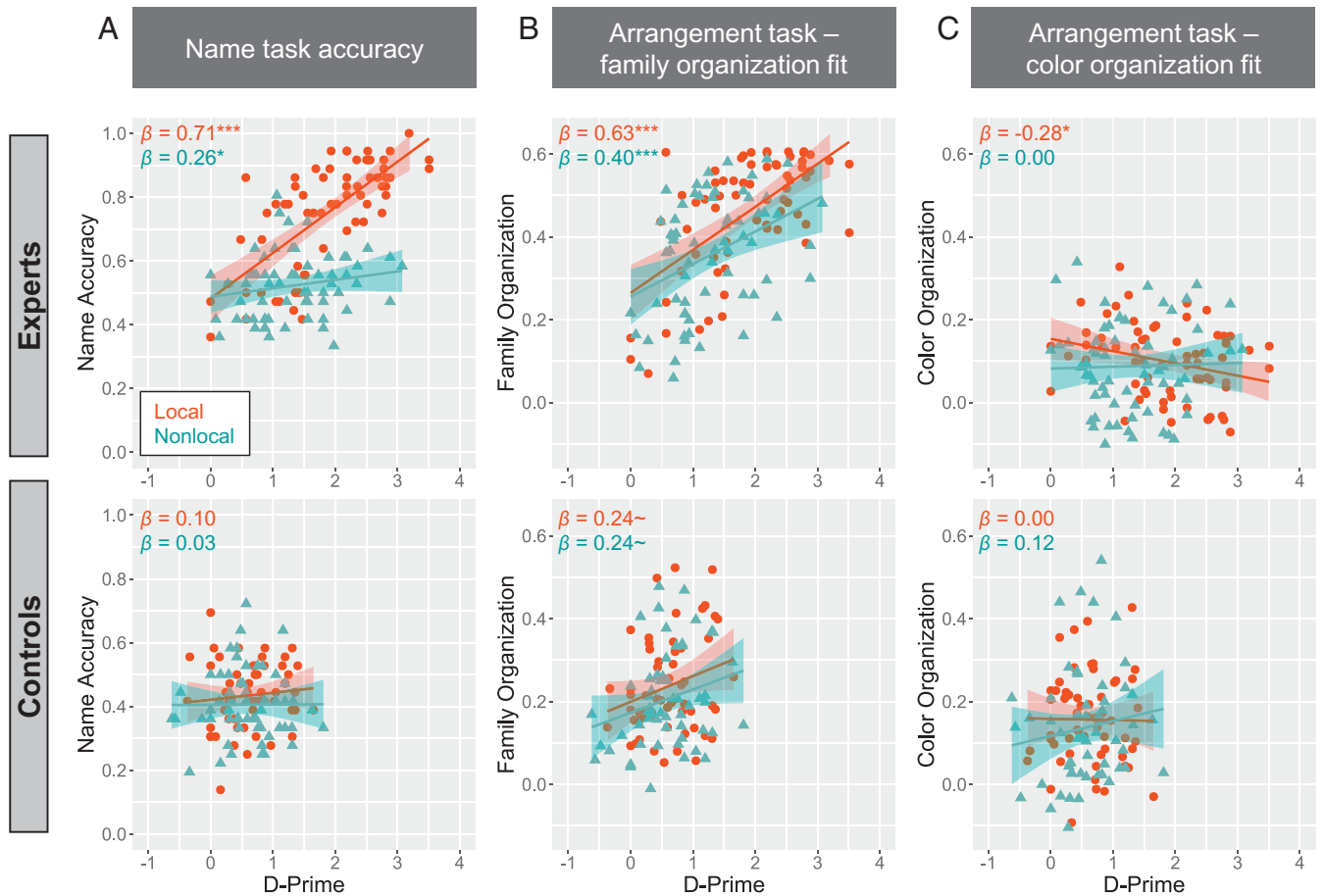


Fig. 3. Across-participants relationships with memory performance. Relationship between memory performance (D-Prime on episodic memory task) and (A) accuracy on name selection task, (B) similarity arrangement correlation with family model, or (C) similarity arrangement correlation with color model.

repeated items might still contribute to above chance discrimination. A follow-up analysis within controls was therefore conducted, which also included the factor of trial type (repeat or novel trial). No interaction between trial type and subjective response was found ($b = -0.007$, $t = -1.23$, $P = 0.22$), indicating that the observed relationship between global similarity and perceived oldness did not differ between target and foils and, thus, represented a generalized impediment to accurate mnemonic discrimination. Recognition memory in controls, therefore, reflected a fundamental assumption of global matching models of memory: perceived oldness should depend on set-level similarity. However, because this influence predominated memory responses across both targets and foils equally, overall memory discrimination was low. In experts, however, the typical relationship between set-level similarity and perceived oldness was absent.

The lack of a global relationship in experts may be related to the finding that similarity arrangements in these participants are more consistent and structured along common organizing dimensions. Rather than taking the entire set into account, expert recognition may have been disproportionately influenced by the most relevant competing exemplars, namely, members of the same bird families. As a final test of this idea, we conducted an additional analysis using intra-family similarity rather than global similarity as the dependent measure. Only experts were included in this model, given the higher variance and lack of coherent family structure in control arrangements (Fig. 5B). This analysis yielded a significant List by Memory response interaction ($b = 0.017$, $t = 2.20$; $P = 0.03$) and a significant main effect of List ($b = -0.133$, $t = -7.14$, $P < 0.001$) but not of Memory response ($P > 0.1$). As expected, the strong effect of List results from higher perceived intrafamily similarity for Local birds, converging with results from the family similarity model (Fig. 1D). The List by Memory interaction resulted from the fact that increased “old” responses were related to higher intrafamily similarity only for Nonlocal birds, although the response difference did not reach significance for the Nonlocal list alone ($z\text{-ratio} = -1.86$, $P = 0.062$) (Fig. 5B). Although more subtle than the group difference present in global

similarity, this result indicates that in the absence of item-level representations, perceived oldness in experts may be influenced by proximity along abstracted conceptual dimensions. Thus, memory errors in experts are both less frequent and driven by a smaller subset of competing items. For Local birds, species-level prior knowledge appears to generally protect from interference by even the nearest set members.

Results from these itemwise distance regressions underscore how subjective similarity differentially impacts episodic memory in the two groups. In controls, increased similarity between an item and other set members increases the likelihood of indiscriminate “old” responses, driving memory toward chance. This phenomenon is consistent with an interpretation of similarity as a proxy for confusability, along with findings that subjective organization in controls tends to capture more superficial features (Fig. 1E). Indeed, a corresponding regression analysis using image-based similarity suggests a comparable pattern of results (SI Appendix, Results – Image-based similarity and memory). By contrast, subjective similarity in experts was unrelated to subjective memory response. Instead, experts had more consistent organization along conceptual features (Fig. 1D), and this organization benefited memory (Fig. 3 and SI Appendix, Fig. S1). Interestingly, some evidence that experts were susceptible to mnemonic separation errors was evident for less familiar nonlocal birds, for which responses appeared to reflect the contours of conceptual structure (i.e., driven by family overlap). For well-known local birds, memory sensitivity was robust even to high intrafamily overlap. Therefore, as the dimensions of similarity change to reflect established organizational divisions in prior knowledge, the role similarity plays in mnemonic discrimination appears to shift qualitatively.

Discussion

The influence of prior knowledge on memory is ubiquitous and can operate at many levels. Past work has often focused on

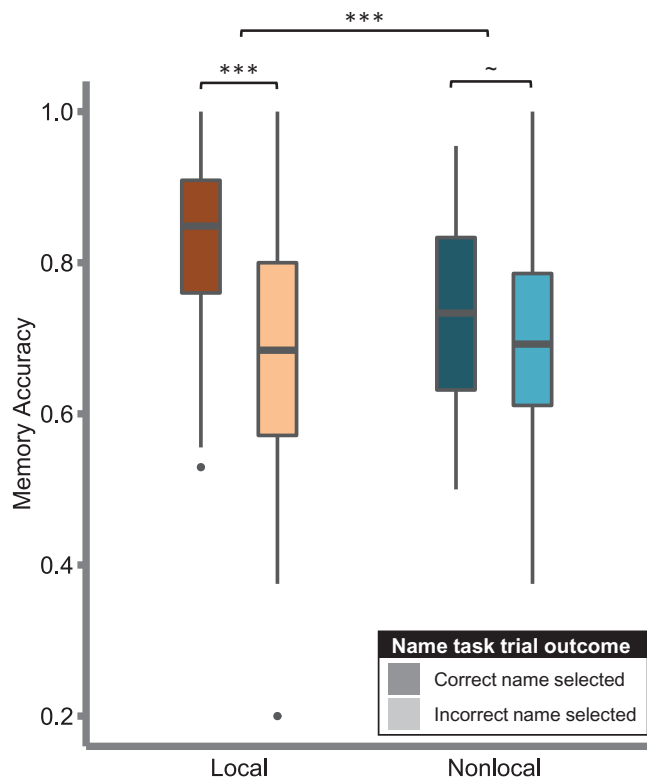


Fig. 4. Trialwise relationship between name selection and memory. Memory accuracy plotted as a function of name selection task outcome (correct vs. incorrect name selected) and List (Local and Nonlocal) within experts only. Species-level knowledge tracked memory outcome for Local but not Nonlocal birds. Post hoc contrasts: $\sim P_{\text{Holm}} < 0.10$, $*P_{\text{Holm}} < 0.05$, $**P_{\text{Holm}} < 0.01$, $***P_{\text{Holm}} < 0.001$.

relating memory to knowledge at the level of individual stimuli, or between populations who differ in overall expertise, with less attention to how the structure of knowledge influences memory. In the present study, we connected memory to the organization of items within a group of expert birdwatchers and matched controls. Unsurprisingly, experts had better memory than controls and remembered local birds that were well known at the species level better than they remembered nonlocal birds. When experts lacked species-level name knowledge, their memory performance was associated with how they perceived the relationships among these unknown birds, as reflected by the tendency to organize birds into broader taxonomic families. Conversely, in controls, the organization of knowledge was more idiosyncratic and oriented toward surface-level (color) as compared to conceptual (taxonomic features) properties. Subjective organization of stimuli also revealed a potential mechanism through which domain knowledge supports memory. Whereas high interitem similarity biased memory and reduced discrimination in controls, consistent with cognitive memory models, this relationship was absent in experts. Domain knowledge may, therefore, lead experts to mentally organize items in a way that attenuates the mnemonic interference that often arises from high superficial similarity between items.

Different tests can tap different aspects of prior knowledge. In addition to assessing species-level (item) knowledge, we measured the structure of the relationships among items based on subjective similarity. This enabled us to describe both conceptual and perceptual dimensions of these relational knowledge structures (33–36). Although both experts and controls drew distinctions between subgroups and had comparable levels of modular structure within arrangements, we found greater

organizational consistency within experts. Explicit models showed that this convergence in experts was due to the reliance on taxonomic features for grouping, whereas structure in controls was more likely to reflect bird color overlap. Although color can be important for subordinate object identification (37, 38), attention to surface-level features is also characteristic of categorization decisions by novices (33, 39) and may be associated with higher memory interference (40). Greater family-based organization in experts is consistent with attention to other features or feature conjunctions that may be less perceptually obvious but that contribute to parsing subcategory distinctions (41–46). Notably, both experts and controls reported high reliance on bird “features” in subjective arrangement judgments. One possibility is that similar sets of features may have been considered by both groups but used differently with respect to organization. For example, the same “feature” (e.g., beak) can be evaluated with respect to shape, size, or color and can be combined with other features for the purposes of classification (e.g., finches and sparrows overlap in beak shapes but generally have forked vs. flat tails, respectively). Future work will be necessary to bridge research that carefully manipulates features within experimentally created taxonomies with naturalistic object processing in real-world domains of expertise.

The type of broader conceptual knowledge reflected in arrangements may be particularly important for memory when the specificity of prior knowledge is lower, as was the case for nonlocal birds. For local birds, experts showed a tight correspondence between species-level name knowledge and memory. This is consistent with past research on memory for items of expertise (47–50) and the importance of lexicalization and verbal labels, which may promote both abstraction (51) and distinctiveness (52)—important factors for the current memory task. For nonlocal bird species, however, species-level knowledge was largely unavailable, increasing the demand on generalized knowledge. Family-based organization in experts was weaker for nonlocal compared to local birds overall. However, only in the nonlocal set did this organizational measure mediate the relationship between name knowledge and memory. This result encapsulates many aspects of past work on schema-supported memory, including the operation of schemas or categories in the absence of high unit-level detail (9, 53, 54) and increased reliance on relational properties among concepts rather than on items in isolation (11, 55). Generalized knowledge of bird families and relationships among them may have helped partition the items in the study set into subgroups, within which attention to distinctive attributes could be constrained (56–60), thereby reducing interference and enhancing memory integration (10). In controls, by contrast, the absence of stable organizing principles may have increased reliance on features that were less reliable for identification (e.g., color, which can vary across photos of the same species more than, e.g., body structure).

The role of abstracted knowledge in providing organizational structure to memory judgments encompasses longstanding questions about how perceived similarity between items influences recognition. In global matching models of memory (17, 20, 61, 62), recognition judgments are contingent on the overlap in feature space between a given memory probe and other items in the study set, with greater aggregate similarity increasing perceived oldness for both repeated and novel items (22, 23). However, for the same set of items, the information upon which perceived similarity is based may vary widely due to prior knowledge. In experts, perceived similarity reflects stable organizational relations that may promote memory by replacing attention to confusable surface features. More

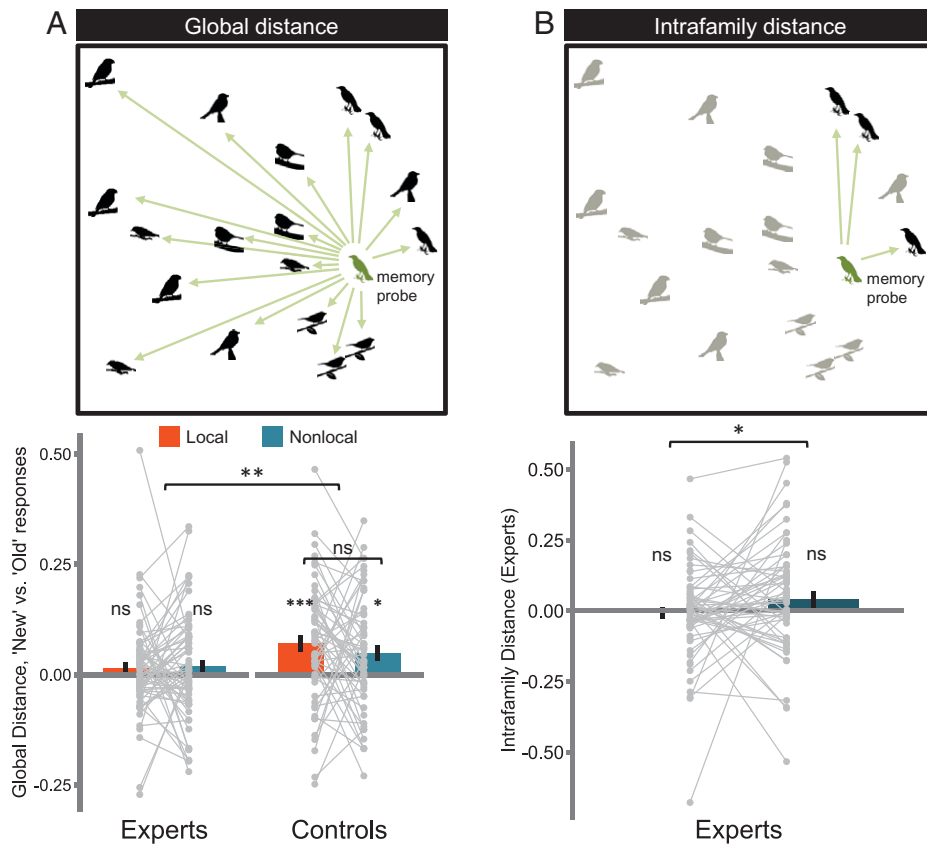


Fig. 5. Distance-memory relationships. Summary data for trialwise regression in which memory response for a given item is related to that item's similarity (plotted as distance measure) to other items in the subjective arrangement task. Bars reflect difference in average distance between items receiving "new" and "old" responses, with positive bars indicating that items endorsed as "old" during recognition have higher similarity (i.e., lower distance) to other encoding set items. (A) For global distance, controls show this expected effect for both Local and Nonlocal lists, but the relationship is absent in experts. (B) In examining distance only for birds of the same family, experts do show this distance-memory relationship for Nonlocal birds more than Local birds. For post hoc contrasts: * $P_{\text{Holm}} < 0.05$, ** $P_{\text{Holm}} < 0.01$, *** $P_{\text{Holm}} < 0.001$. Image credit: Cornell Lab of Ornithology.

broadly, the role that interitem similarity plays in influencing memory judgments may, therefore, depend on which aspects of the relationship between items are indexed by such judgments.

To test whether the relationships between perceived similarity and memory changed as a function of knowledge organization, the present matching model related each memory response to a probe item's set-level (global) similarity in subjective similarity space, expressed in the subjective arrangement task. This analysis showed that controls were more likely to respond "old" to retrieval probes with high set-level similarity, irrespective of whether the item was previously presented. This indiscriminate reliance on perceived similarity for memory decisions drove memory performance toward chance. In contrast to the strong link between perceived similarity and memory responses shown in controls, experts showed no corresponding relationship for either local or nonlocal birds. Birds with higher global similarity to other study set birds were no more likely to be endorsed as "old" than those perceived to be less similar. This finding aligns with the notion that interitem similarity in controls signifies a lack of differentiation, resulting in a greater proportion of encoding set items that contribute to recognition memory signals. By contrast, experts' ability to mentally divide similarity space along meaningful dimensions may have reduced interference from other items during the recognition decision.

The fact that experts were not completely immune from similarity-related influences on memory paradoxically serves as

further evidence that differential concept organization drives superior memory in experts. Focusing on items with the highest conceptual overlap, we found some evidence that intrafamily similarity, rather than global similarity, increased "old" responses, but only for nonlocal birds, consistent with the idea that interference occurred within bounded similarity spaces. Conversely, the well-established nature of knowledge representations for individual local birds, for which name labels were often known, appears to have allowed for mnemonic separation even among close neighbors in conceptual space. Indeed, as indicated by both across-participants and trialwise analyses, name knowledge was highly predictive of memory accuracy for local birds.

Together, our findings show that prior knowledge influences memory in multiple ways. In addition to the well-known benefits associated with subcategory knowledge and labels, generalized knowledge helped experts impose an organizational logic to support memory for unknown bird species. This generalized knowledge architecture likely attenuated interference that otherwise would have resulted from high interitem overlap.

Data Availability. Anonymized behavioral data (csv) have been deposited in Open Science Framework (<https://osf.io/zjxtal>) and will be accessible upon publication (31). Parts of data files not germane to reanalysis (IP addresses, computer hardware of users) may be redacted from raw participant data posted on repository.

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