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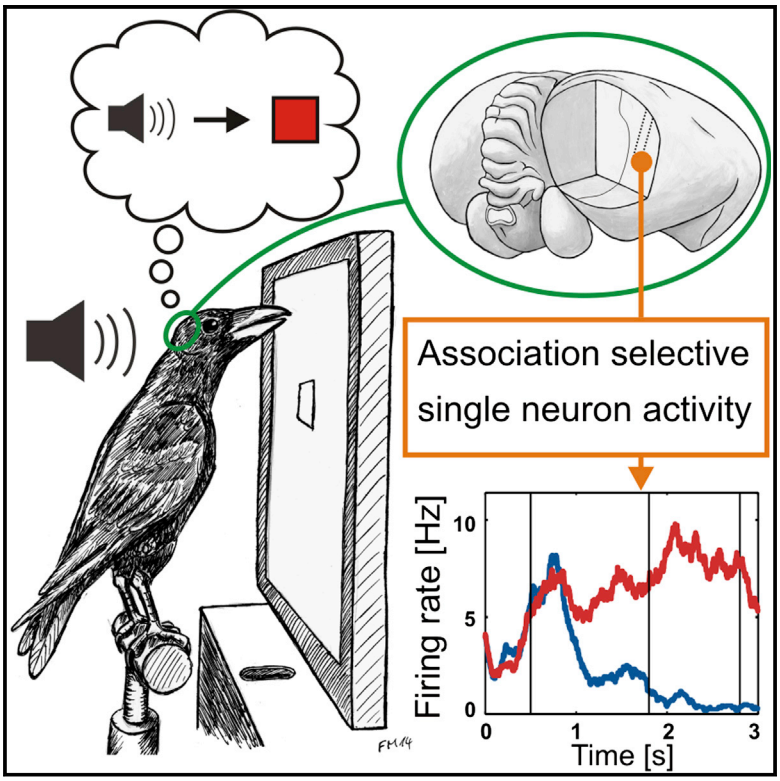
# Cross-Modal Associative Mnemonic Signals in Crow Endbrain Neurons

## Graphical Abstract

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## In Brief

Moll and Nieder report sustained single-cell activity that selectively correlated with learned audio-visual associations across time and modality in the crow endbrain association area nidopallium caudolaterale (NCL). This neuronal memory signal prospectively encoded the crows' choices and was predictive of association errors.

## Highlights

- Neuron activity was recorded in crow endbrain structure nidopallium caudolaterale (NCL)
- Sustained activity encoded audio-visual stimulus associations across time
- Association-specific NCL activity predicted the crows' behavioral performance
- Neuronal fluctuations before trial onset biased behavior in the following trial

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# Cross-Modal Associative Mnemonic Signals in Crow Endbrain Neurons

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## SUMMARY

**The ability to associate stimuli across time and sensory modalities endows animals and humans with many of the complex, learned behaviors. For successful performance, associations need to be retrieved from long-term memory and maintained active in working memory [1]. We investigated how this is accomplished in the avian brain. We trained carrion crows (*Corvus corone*) to perform a bimodal delayed paired associate task [2, 3] in which the crows had to match auditory stimuli to delayed visual items. Single-unit recordings from the association area nidopallium caudolaterale (NCL) revealed sustained memory signals that selectively correlated with the learned audio-visual associations across time and modality, and sustained activity prospectively encoded the crows' choices. NCL neurons carried an internal, stimulus-independent signal that was predictive of error and type of error. These results underscore the role of corvid NCL [4–7] in synthesizing external multisensory information and internal mnemonic data needed for executive control of behavior.**

## RESULTS

Many of the complex, learned behaviors exhibited by animals and humans depend on arbitrary associations between stimuli. The associated stimuli can belong to a single sensory modality, e.g., only visual stimuli. More challenging, however, are cross-modal associations in which the elements of a pair of associates belong to different sensory modalities. Cross-modal associations have been studied intensively in mammals, both in the wild [8] and in the laboratory [9, 10], and this behavioral capability has been related to the workings of the prefrontal cortex (PFC) [11–13]. However, despite the ubiquitous presence of such associations in the behavioral repertoire of cognitively advanced birds like corvids [14–23], the neuronal basis of cross-modal, cross-temporal associations in birds remains unexplored.

To fill in this gap, we recorded single-neuron activity in the nidopallium caudolaterale (NCL), in awake, behaving carrion crows. The NCL is an avian association area of the endbrain considered to be a functional analog of the mammalian PFC [4, 24–27]. We hypothesize to find mnemonic signals of long-term associations retrieved into working memory of the NCL to bridge the delay between sample and test stimuli and thereby to predict the crows' test stimulus choices.

### Crows Associated Sound with Color Stimuli

We trained two crows to perform an audio-visual delayed paired associate (DPA) task [2, 3] using a touchscreen monitor (Figure S1A). In each DPA task trial (Figure 1A), the crow had to match one of two sample sounds ("noise" and "tit song," Figures S3B and S3D) to its associated visual test stimulus ("blue square" and "red square") across a temporal gap (delay). Both crows performed well above chance in every recording session ($p < 0.001$ each session, bionomial test). Bird T had an average performance of 83.4% (±8% SD); bird M showed 91.7% correct responses (±5% SD) (Figure 1B). The "noise-blue" and "tit song-red" association trials were conducted with equal proficiency by crow T (Figure 1C; 83.9% and 82.9%; SD = 7.4% and 9.8%, respectively; paired Wilcoxon, two-tailed, $Z = -0.644$, $p = 0.520$, $n = 19$). Crow M showed mild performance differences (Figure 1C; 93.3% and 90.2%; SD = 4.4% and 7.4%, respectively; paired Wilcoxon, two-tailed, $Z = -2.033$, $p = 0.042$, $n = 21$).

### Single Neuron and NCL Population Activity Encoded Cross-Modal Associations

We recorded single-unit activity in the telencephalic avian brain structure NCL (Figure S1B), which was previously immunohistochemically identified in the carrion crow [6]. The spiking activity of 182 single cells from the two birds was analyzed. In both birds, the majority of single neurons varied their firing rate selectively according to the learned audio-visual associations (comparison of discharge rates between the two associations separately in the sample and delay period; $p < 0.05$, Wilcoxon test) (Table S1). The example neuron in Figures 2A–2C continuously increased its firing rate shortly after sample onset until the end of the delay period whenever the crow correctly associated the noise sound with the color blue but was suppressed for the alternative tit song-red association. The inverse response pattern can be seen for another example neuron (Figures 2D–2F); this neuron preferred the tit song-red association by increased neuronal discharges, whereas the noise-blue association correlated with a suppression of activity.

Almost one-half of the neurons (43%, or 79 out of 182) showed association-selective activity during the sample period and even more (65%, or 119 out of 182) during the memory delay. Moreover, 31% of all cells (56 out of 182) showed association selectivity during both the sample and delay period (Table S1; see also example neurons in Figures 2A–2F). This means that 47% of the delay-selective cells already exhibited their association-related activity during the sample period.

 

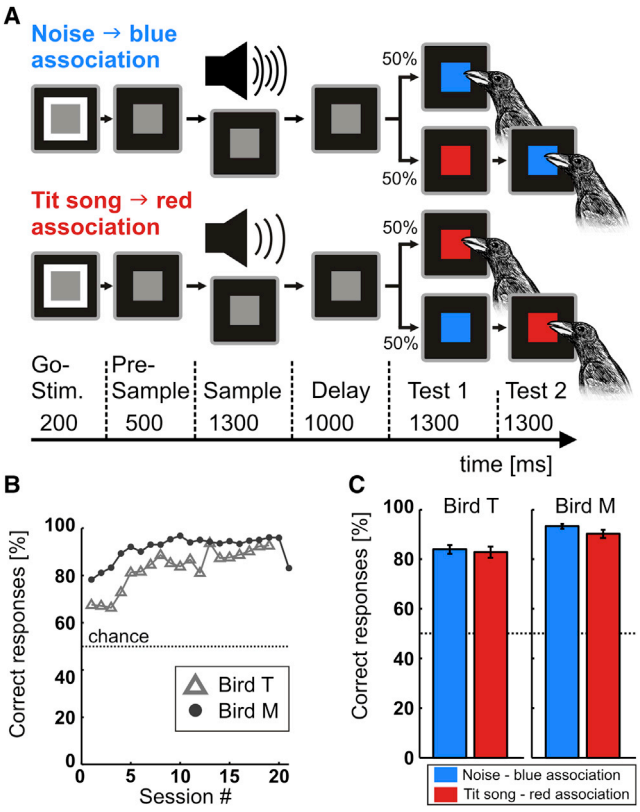


**Figure 1. Audio-Visual Association Task: Behavioral Protocol and Behavioral Performance**

(A) The crows initiated a trial by moving their heads within the range of a light barrier. This was fed back by a visual go stimulus. Then an auditory sample was played, followed by the delay after which crows had to choose the correct associated color stimulus to gain a food reward. In 50% of the trials, the first test color was a match, whereas the first test stimulus was a non-match in the other 50% of the trials.

(B) Average behavioral performance per session and bird for all recording sessions.

(C) Average behavioral performance per association and bird across all recording sessions. Error bars indicate the SEM over sessions.

The normalized population activity of all 119 delay-selective neurons is shown in Figure 2G. Neurons that were selective throughout both trial periods showed weaker activity in the sample phase than during the delay period (Figure 2G, solid lines). Noticeably, the population difference in firing rate between preferred and non-preferred association trials showed a continuous increase over time, peaking approximately at the physical onset of the visual match stimulus at the end of the delay (Figure 2G). At this point in the trial, the normalized population activity was about 10-fold higher for preferred than for non-preferred association trials.

## Neuronal Activity in NCL Predicted the Upcoming Choice Behavior

The crows' correct versus erroneous test stimulus choices could be predicted based on the activity of single neurons. The example neuron shown in Figures 2A–2C that preferred the noise-blue association during correct trials (Figures 2A and 2C) displayed the exact reversed neuronal activity in error trials (Wilcoxon test during delay period, two-tailed, $Z = 4.459$, $p < 0.001$, $n = 25$), e.g., when the crow responded to the red square following a noise presentation (Figures 2B and 2C). The same inversion of responses during errors was observed for the neuron shown in Figures 2D–2F (Wilcoxon test, two-tailed, $Z = -3.862$, $p < 0.001$, $n = 31$). This reversal of association preference during errors was already present across the entire population of delay-selective neurons shortly after sample onset (Figure 2G, dotted lines) (paired Wilcoxon, two-tailed, $Z = -5.930$, $p < 0.001$, $n = 71$). Therefore, association cells already predicted the upcoming erroneous response at a time when the sample stimulus was still played back.

## Quality of Neuronal Selectivity

We applied a sliding-window receiver operating characteristic (ROC) analysis to analyze the quality, temporal evolution, and latency of association selectivity for all individual selective neurons (Figure 2H; see also Supplemental Results and Figure S2). The ROC analysis quantified how well the two learned associations could be discriminated based on each neuron's spike count distributions in preferred versus non-preferred association trials. The degree of separation between these two distributions was measured by the area under the ROC curve (AUROC). An AUROC value of 0.5 indicates a complete distribution overlap (no discrimination), whereas values of 0 and 1 indicate perfect separation. By convention, we used the spike counts of noise-blue association trials as the reference (baseline) distribution. Thus, neurons preferring the noise-blue association had AUROC values < 0.5, whereas neurons preferring the tit song-red association had values > 0.5 (Figure 2H).

The majority of delay-selective neurons (58%, or 69 out of 119) began to exhibit their association-selective activity during the sample period, but not earlier than 190 ms after sample onset (Figure 2H, white line). Throughout the trial, more and more neurons became association selective (Figure 2H). Therefore, the average population coding strength increased continuously during sample and delay period and peaked shortly before the onset of the visual test stimulus (Figures 2H and S2C). This pattern was inverted during error trials (Figure S2D). This shows that the temporal evolution of association coding in error trials was similar to correct trials in terms of temporal dynamics but inverted in terms of association coding.

## A Stimulus-Independent, Internal Signal Predicted the Upcoming Choice Behavior

In correct trials, association-selective coding started about 190 ms after auditory sample stimulus onset (Figure 2G, solid lines in sample phase; Figure 2H, white line). Thus, as expected in a randomized DPA paradigm, we did not find association-selective neuronal activity before sample stimulus onset in correct trials. Our pre-sample phase analysis provided no evidence for association-dependent differences in firing rates (Figure 3A, correct trials; paired Wilcoxon, two-tailed, $Z = -1.358$, $p = 0.174$) or AUROC values (Figure 3B; Wilcoxon test, two-tailed, $Z = -0.564$, $p = 0.573$). However, in error trials, selective firing could be detected much earlier, notably during the pre-sample phase before sample stimulus onset (Figure 2G, dotted lines in pre-sample phase). In error trials where a crow chose the

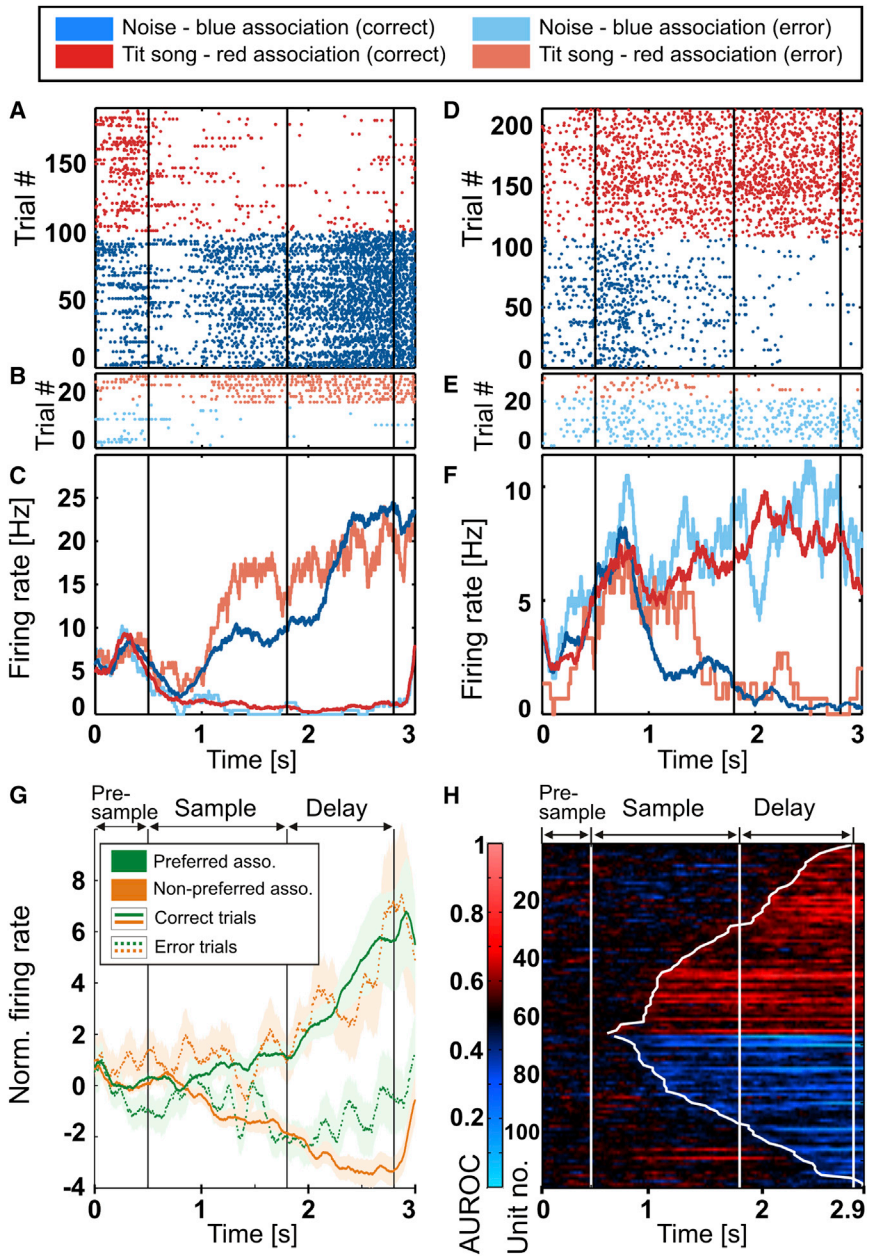


**Figure 2. Working Memory-Related Association-Selective Activity in NCL Neurons**

(A–C) Example of an individual association-selective neuron preferring the noise-blue association.

(A) Dot raster showing the neuron's response in individual trials, ordered by the presented auditory sample cue (correct trials only). Each dot signifies one action potential. Vertical lines mark transitions between pre-sample, sample, delay, and test period.

(B) Error trial dot raster in comparison to correct trial dot raster in (A).

(C) Peri-stimulus time histogram (PSTH), obtained by averaging the dot rasters and smoothing with a 150-ms boxcar window. Note that error trial curves are inverted compared to correct trial curves.

(D–F) Example neuron preferring the tit song-red association.

(D) Dot raster correct trials.

(E) Dot raster error trials.

(F) PSTH correct and error trials.

(G) Average normalized PSTH for the population of delay-selective neurons for their preferred and non-preferred association. Solid lines show the population response (n = 119) in correct trials and dotted lines (n = 71) in error trials. Shaded areas indicate SEM over neurons.

(H) Quality, temporal evolution, and latency of association selectivity for all delay-selective association neurons. Each line represents one neuron. Neurons are sorted by their association preference during delay and the latency of association selectivity. Each neuron's latency is marked by the white line that runs across sample and delay period. White vertical bars mark transitions between task periods. Noise-blue-preferring cells are, by convention, represented by delay AUROC values < 0.5 (and vice versa for tit song-red-preferring cells).

preferred stimulus, the population's pre-sample firing rate was significantly higher than in error trials where the crow picked the non-preferred stimulus (Figure 3A, error trials; paired Wilcoxon, two-tailed, $Z = -2.607$, $p < 0.01$). Accordingly, average pre-sample error trial AUROC values differed between noise-blue-preferring cells and tit song-red-preferring cells (Figures 3C and 3D, error trials; Wilcoxon test, two-tailed, $Z = 3.078$, $p < 0.01$).

The analysis above showed that incorrect choices of the preferred and non-preferred stimuli were preceded by different levels of pre-sample activity. But were these levels of activity also different from correct trial pre-sample activity and thereby predictive of the crows' errors and types of error? When we separately compared preferred and non-preferred association error trial pre-sample activity with pre-sample activity in correct trials, we found that error trial activity did in fact deviate systematically from correct trial activity (Figure 2G, compare dotted with solid lines in pre-sample phase; see also Figure 3A). Error trial behavioral responses to the preferred stimulus were, compared to correct trials, preceded by significantly increased neuronal pre-sample activity (paired Wilcoxon, two-tailed, $Z = -2.642$, $p < 0.01$), while error trial responses to the non-preferred stimulus tended to be preceded by decreased pre-sample activity (paired Wilcoxon, two-tailed, $Z = -1.708$, $p = 0.088$). Therefore, the pre-sample neuronal activity allowed to predict (to some extent) the crows' trial-by-trial choices. Remarkably, this pre-sample signal must have been generated internally since it occurred well before stimulus onset.

A global shift in firing rate during error trials did not cause the observed pre-sample activity differences between error and correct trials. The average pre-sample firing rates (across conditions) in error and correct trials did not differ (Figure 3A; paired Wilcoxon, two-tailed, $Z = -0.189$, $p = 0.850$). The same was true for average pre-sample AUROC values as well, which did

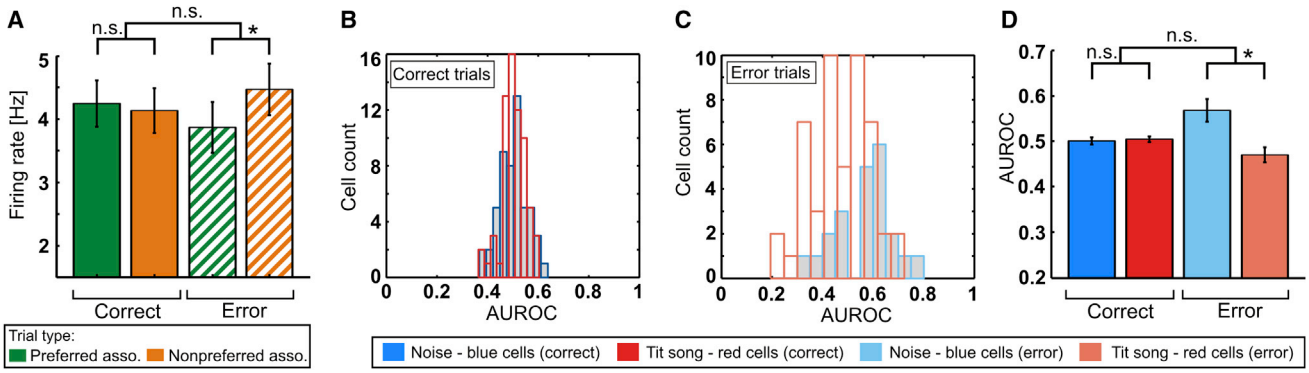


**Figure 3. Error-Predictive, Internally Generated Pre-sample Activity**

(A) Average pre-sample discharge rates of all delay-selective neurons for correct and error trials. Incorrect behavioral responses during preferred association trials were predicted by decreased pre-sample discharge rates compared to increased pre-sample discharge rates during incorrect non-preferred association trials.

(B) Histogram of pre-sample period AUROC values of all delay-selective association neurons (correct trials only).

(C) Same as (B), but for error trials. Note that this distribution approximates the distribution in Figure S2B.

(D) Average pre-sample AUROC values of all delay-selective neurons for correct and error trials. Noise-blue-preferring cells are, by convention, represented by delay AUROC values < 0.5. In the pre-sample phase of error trials these noise-blue cells had an average AUROC value > 0.5 (and vice versa for tit song-red-preferring cells), which predicted the upcoming incorrect behavioral response.

Error bars indicate the SEM over neurons.

not differ between error and correct trials (Figure 3D; Wilcoxon test, two-tailed, $Z = 0.218$, $p = 0.827$).

### Few Neurons in NCL Encoded Pure Auditory Information

To explore whether the observed delay activity reflects a retrospective memory signal of the auditory sample or indeed a prospective associative signal related to the upcoming visual associate, we also recorded from the crows while they performed a unimodal auditory match-to-sample task (Figure 4A; see Supplemental Results and Figures S3G and S3H for behavior). In the population of 109 recorded neurons, few neurons varied their firing rate significantly according to the previously played sound stimulus during the delay phase (bird T: 9%, or 8 out of 91, $p < 0.05$, Kruskal-Wallis test; bird M: 6%, or 1 out of 18, $p < 0.05$, Wilcoxon test). An example delay-selective cell is shown in Figure 4B (bird T, Kruskal-Wallis test, degrees of freedom [df] = 5, $\chi^2 = 12.06$, $p = 0.034$; see Figure S3I for the delay-selective neuron of bird M; Wilcoxon test, two-tailed, $Z = -2.787$, $p < 0.01$). We found no auditory sample-selective neurons in bird M and only a single one in bird T (1 out of 91). This lack of (mnemonic) responses to auditory stimuli in the unimodal auditory match-to-sample task stands in strong contrast to the findings in the audio-visual association task (Figure 4C) and suggests prospective associative signals carried by corvid NCL neurons.

## DISCUSSION

### Prospective Associative Signals in NCL Neurons

The audio-visual association responses we observed in the current study are conceptually different from previous reports of delay activity [28] and unimodal working memory signals [5] in the avian NCL. Diekamp et al. [28] used a delayed Go/No-Go task and found that 21% of neurons in pigeon NCL exhibited delay activity. However, as acknowledged by the authors [28], such neurons might have represented sensory, cognitive, reward, and motor components, which the task design could not disentangle. In the same vein, Rose and Colombo [4] found 67% of neurons with sustained delay activity, the majority of which responded only for a to-be-remembered stimulus, but not after the pigeon was instructed to forget the stimulus. Several follow-up studies demonstrated that this activity was based mainly on reward prediction [29–31]. Similarly, if different auditory stimuli are associated with one of two response keys, it is difficult to dissociate responses representing the associations or rather preparatory left versus right motor activity [32]. In our delayed match-to-sample task design, however, motor preparation and reward coding can be excluded, given that the crows could not predict whether they needed to respond to the first or second test stimulus to be rewarded.

In addition, our recordings during the unimodal auditory delayed match-to-sample task resulted in surprisingly few auditory-only responsive neurons, even though neural coding of acoustic signals is of crucial importance for songbirds [32–34]. This finding argues against retrospective auditory working memory representations during the audio-visual association task. The sustained activity we report can be related to a prospective cross-temporal, cross-modal association signal in NCL neurons that has not been shown before in birds. Prospective coding of visual paired associates has also been shown in monkey PFC [11, 35]. In addition, or alternatively, (some) NCL neurons could also encode the association as a whole, i.e., holistically, by responding to both items of paired associates in unimodal [2] and cross-modal [3] association tasks. Such a holistic code has been reported for infero-temporal cortex neurons in macaques [3]. To address this question in crows, cross-modal association pairs would need to be tested in both directions, i.e., in alternating audio-visual and visual-auditory blocks. The highly flexible rule-switching abilities of crows suggest that they could master such a task [6, 36].

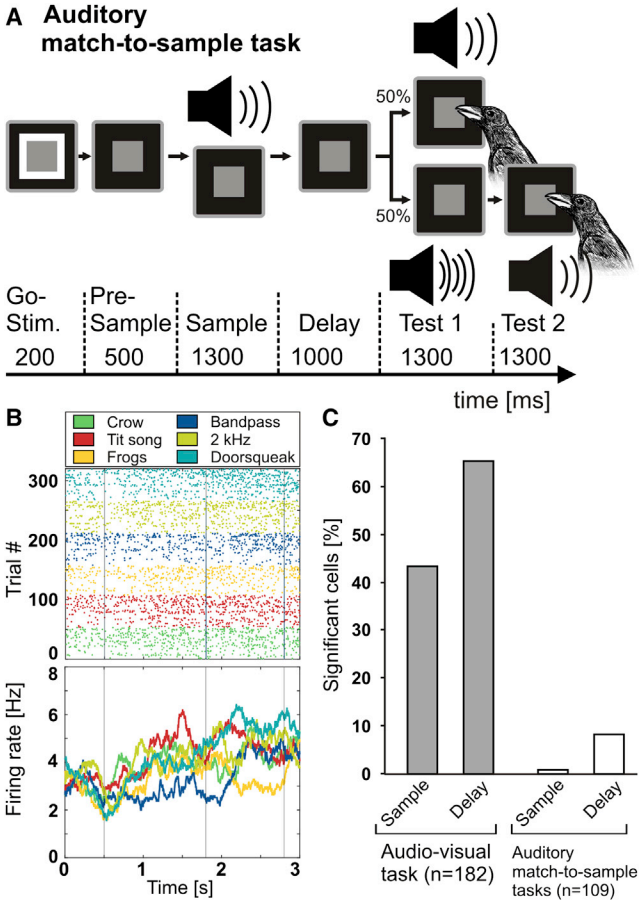


**Figure 4. Working Memory-Related, Auditory Stimulus-Selective Activity in NCL Neurons**

(A) Auditory match-to-sample task: the crows initiated a trial by moving their heads within the range of a light barrier. This was fed back by a visual go stimulus. Then an auditory sample was played, followed by the delay after which crows had to choose the correct auditory test stimulus to gain a food reward.

(B) Example of an individual neuron responding selectively to auditory stimuli during the delay phase. Top: dot raster showing the neuron's response in individual trials, ordered by the presented auditory sample cue (correct trials only). Each dot signifies one action potential. Vertical lines mark transitions between pre-sample, sample, delay, and test period. Bottom: PSTH (correct trials only), obtained by averaging the dot raster and smoothing with a 250-ms boxcar window.

(C) Percentage of stimulus-selective NCL cells during sample and delay periods for the audio-visual task (gray bars) and for the auditory match-to-sample task (white bars).

## Properties of the Cross-Modal Association Code

About half of our neurons represented the auditory sample stimulus, and even more cells bridged the delay by associating the sample with the upcoming visual test stimulus. Lower proportions of selective neurons (~20%) were found in the directly comparable study of cross-modal working memory in the monkey PFC [12], a difference that could arise from the anatomical dissimilarities between the layered mammalian cortex and the nuclear avian brain [37]. Cell proportions, neuronal latencies, and AUROC value distributions did not indicate any difference between the noise-blue-preferring and tit song-red-preferring neurons.

The delay-bridging working memory signal in the present study must originate from reactivated long-term memory representations of learned associations [1]. Such retrieved long-term memory content is of particular interest in birds, since bird association areas, unlike the mammalian neocortex, share only few connections with the hippocampus [38]. While direct connections between hippocampus and PFC play an important role in mammalian long-term memory retrieval, direct connections between the avian hippocampus and NCL are absent [38, 39]. This suggests that—besides the manifold similarities of NCL and PFC—the retrieval of long-term memory contents relies on different pathways and mechanisms in birds.

## Error Trials

NCL responses in incorrect noise-blue association trials largely mirrored the responses in correct tit song-red trials and vice versa. Such behaviorally relevant signals were previously observed in other studies of NCL [5, 6] and monkey studies of cross-modal association coding [3, 12]. However, the coding quality of NCL neurons was superior compared to monkey PFC signals. The almost binary inversion of neuronal activity during error trials and the continuously increasing population activity during the delay phase in which sensory evidence can no longer be accumulated suggest that a categorical decision is encoded in NCL, but not an accumulating decision variable value [40]. The existence of such categorical coding was shown by a recent study in which similar activity patterns in rat posterior parietal cortex (PPC) and frontal orienting fields (FOFs) were found to represent the accumulating decision variable in the one area but the categorical decision in the other area [41].

## Internal Signal

We found error-predictive pre-sample activity and investigated the origin of this stimulus-independent signal. Comparable "internal" [42] or "bias" [43] signals have been observed in mammalian neocortical areas [44] and are thought to reflect choice target values based on local reward history [42, 43, 45]. The internal signals observed in the latter studies were all potentially motor and/or value related. In contrast, in our study, the pre-sample signal that was present in incorrect trials could not represent a motor plan. In addition, there was no evidence for a value representation, since we found no influence of trial history on the crows' behavior (see Supplemental Results and Table S3). We therefore speculate that this internal signal found in NCL originates from neuronal noise fluctuations that, in some trials, cross a behavior-determining threshold before sample onset.

## EXPERIMENTAL PROCEDURES

For details, see Supplemental Experimental Procedures. All procedures complied with the European Communities Council Directive 2010/63/EC and the German Law for Protection of Animals and were approved by the national authorities, following appropriate ethics review.

## SUPPLEMENTAL INFORMATION

Supplemental Information includes Supplemental Results, Supplemental Experimental Procedures, three figures, and three tables and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2015.07.013.

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## REFERENCES

1. Fuster, J.M. (2009). Cortex and memory: emergence of a new paradigm. J. Cogn. Neurosci. *21*, 2047–2072.
2. Sakai, K., and Miyashita, Y. (1991). Neural organization for the long-term memory of paired associates. Nature *354*, 152–155.
3. Gibson, J.R., and Maunsell, J.H. (1997). Sensory modality specificity of neural activity related to memory in visual cortex. J. Neurophysiol. *78*, 1263–1275.
4. Rose, J., and Colombo, M. (2005). Neural correlates of executive control in the avian brain. PLoS Biol. *3*, e190.
5. Veit, L., Hartmann, K., and Nieder, A. (2014). Neuronal correlates of visual working memory in the corvid endbrain. J. Neurosci. *34*, 7778–7786.
6. Veit, L., and Nieder, A. (2013). Abstract rule neurons in the endbrain support intelligent behaviour in corvid songbirds. Nat. Commun. *4*, 2878.
7. Ditz, H.M., and Nieder, A. (2015). Neurons selective to the number of visual items in the corvid songbird endbrain. Proc. Natl. Acad. Sci. USA *112*, 7827–7832.
8. McComb, K., Shannon, G., Sayialel, K.N., and Moss, C. (2014). Elephants can determine ethnicity, gender, and age from acoustic cues in human voices. Proc. Natl. Acad. Sci. USA *111*, 5433–5438.
9. Sliwa, J., Duhamel, J.R., Pascalis, O., and Wirth, S. (2011). Spontaneous voice-face identity matching by rhesus monkeys for familiar conspecifics and humans. Proc. Natl. Acad. Sci. USA *108*, 1735–1740.
10. Kaminski, J., Call, J., and Fischer, J. (2004). Word learning in a domestic dog: evidence for "fast mapping". Science *304*, 1682–1683.
11. Tomita, H., Ohbayashi, M., Nakahara, K., Hasegawa, I., and Miyashita, Y. (1999). Top-down signal from prefrontal cortex in executive control of memory retrieval. Nature *401*, 699–703.
12. Fuster, J.M., Bodner, M., and Kroger, J.K. (2000). Cross-modal and cross-temporal association in neurons of frontal cortex. Nature *405*, 347–351.
13. Sierra-Paredes, G., and Fuster, J.M. (2002). Reversible impairment of auditory-visual task from cooling prefrontal cortex. In Virtual Lesions, G.L.R. Galuske, ed. (Oxford: University Press), pp. 239–245.
14. Chamberlain, D.R., and Cornwell, G.W. (1971). Selected vocalizations of the common crow. Auk *88*, 613–634.
15. Richards, D.B., and Thompson, N.S. (1978). Critical properties of the assembly call of the common American crow. Behaviour *64*, 184–203.
16. Clayton, N., and Emery, N. (2005). Corvid cognition. Curr. Biol. *15*, R80–R81.
17. Clayton, N.S., and Emery, N.J. (2007). The social life of corvids. Curr. Biol. *17*, R652–R656.
18. Shaw, R.C., and Clayton, N.S. (2014). Pilfering Eurasian jays use visual and acoustic information to locate caches. Anim. Cogn. *17*, 1281–1288.
19. Marzluff, J.M., Walls, J., Cornell, H.N., Withey, J.C., and Craig, D.P. (2010). Lasting recognition of threatening people by wild American crows. Anim. Behav. *79*, 699–707.
20. Wascher, C.A.F., Szipl, G., Boeckle, M., and Wilkinson, A. (2012). You sound familiar: carrion crows can differentiate between the calls of known and unknown heterospecifics. Anim. Cogn. *15*, 1015–1019.
21. Kondo, N., Izawa, E., and Watanabe, S. (2012). Crows cross-modally recognize group members but not non-group members. Proc. Biol. Sci. *279*, 1937–1942.
22. Griesser, M. (2009). Mobbing calls signal predator category in a kin group-living bird species. Proc. Biol. Sci. *276*, 2887–2892.
23. Hoffmann, A., Ruttler, V., and Nieder, A. (2011). Ontogeny of object permanence and object tracking in the carrion crow, Corvus corone. Anim. Behav. *82*, 359–367.
24. Divac, I., Mogensen, J., and Björklund, A. (1985). The prefrontal 'cortex' in the pigeon. Biochemical evidence. Brain Res. *332*, 365–368.
25. Kröner, S., and Güntürkün, O. (1999). Afferent and efferent connections of the caudolateral neostriatum in the pigeon (Columba livia): a retro- and anterograde pathway tracing study. J. Comp. Neurol. *407*, 228–260.
26. Güntürkün, O. (2005). The avian 'prefrontal cortex' and cognition. Curr. Opin. Neurobiol. *15*, 686–693.
27. Butler, A.B., and Cotterill, R.M. (2006). Mammalian and avian neuroanatomy and the question of consciousness in birds. Biol. Bull. *211*, 106–127.
28. Diekamp, B., Kalt, T., and Güntürkün, O. (2002). Working memory neurons in pigeons. J. Neurosci. *22*, RC210.
29. Milmine, M., Rose, J., and Colombo, M. (2008). Sustained activation and executive control in the avian prefrontal cortex. Brain Res. Bull. *76*, 317–323.
30. Milmine, M., Watanabe, A., and Colombo, M. (2008). Neural correlates of directed forgetting in the avian prefrontal cortex. Behav. Neurosci. *122*, 199–209.
31. Browning, R., Overmier, J.B., and Colombo, M. (2011). Delay activity in avian prefrontal cortex–sample code or reward code? Eur. J. Neurosci. *33*, 726–735.
32. Knudsen, D.P., and Gentner, T.Q. (2013). Active recognition enhances the representation of behaviorally relevant information in single auditory forebrain neurons. J. Neurophysiol. *109*, 1690–1703.
33. Nieder, A., and Klump, G.M. (1999). Adjustable frequency selectivity of auditory forebrain neurons recorded in a freely moving songbird via radiotelemetry. Hear. Res. *127*, 41–54.
34. Nieder, A., and Klump, G.M. (2001). Signal detection in amplitude-modulated maskers. II. Processing in the songbird's auditory forebrain. Eur. J. Neurosci. *13*, 1033–1044.
35. Rainer, G., Rao, S.C., and Miller, E.K. (1999). Prospective coding for objects in primate prefrontal cortex. J. Neurosci. *19*, 5493–5505.
36. Moll, F.W., and Nieder, A. (2014). The long and the short of it: rule-based relative length discrimination in carrion crows, Corvus corone. Behav. Processes *107*, 142–149.
37. Jarvis, E.D., Yu, J., Rivas, M.V., Horita, H., Feenders, G., Whitney, O., Jarvis, S.C., Jarvis, E.R., Kubikova, L., Puck, A.E.P., et al. (2013). Global view of the functional molecular organization of the avian cerebrum: mirror images and functional columns. J. Comp. Neurol. *521*, 3614–3665.
38. Rattenborg, N.C., and Martinez-Gonzalez, D. (2011). A bird-brain view of episodic memory. Behav. Brain Res. *222*, 236–245.
39. Allen, T.A., and Fortin, N.J. (2013). The evolution of episodic memory. Proc. Natl. Acad. Sci. USA *110* (*Suppl 2*), 10379–10386.
40. Shadlen, M.N., and Kiani, R. (2013). Decision making as a window on cognition. Neuron *80*, 791–806.
41. Hanks, T.D., Kopec, C.D., Brunton, B.W., Duan, C.A., Erlich, J.C., and Brody, C.D. (2015). Distinct relationships of parietal and prefrontal cortices to evidence accumulation. Nature *520*, 220–223.
42. Carnevale, F., de Lafuente, V., Romo, R., and Parga, N. (2012). Internal signal correlates neural populations and biases perceptual decision reports. Proc. Natl. Acad. Sci. USA *109*, 18938–18943.
43. Hanks, T.D., Mazurek, M.E., Kiani, R., Hopp, E., and Shadlen, M.N. (2011). Elapsed decision time affects the weighting of prior probability in a perceptual decision task. J. Neurosci. *31*, 6339–6352.
44. Platt, M.L., and Glimcher, P.W. (1999). Neural correlates of decision variables in parietal cortex. Nature *400*, 233–238.
45. Sugrue, L.P., Corrado, G.S., and Newsome, W.T. (2004). Matching behavior and the representation of value in the parietal cortex. Science *304*, 1782–1787.

  