



# Modality-invariant audio-visual association coding in crow endbrain neurons



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## ABSTRACT

Single neuron activity in the corvid nidopallium caudolaterale (NCL), the supposed avian functional analogue of the prefrontal cortex, represents associations of auditory with visual stimuli. This is of high adaptive value for songbirds that need to rely on audio-visual associations to communicate, find a mate or escape predators. However, it remains unclear whether NCL neurons can represent cross-modal associations in a modality invariant, abstract fashion. To dissociate between modality-dependent and modality-invariant NCL activity, we trained two crows to match auditory sample cues with visual test stimuli, and vice versa, across a temporal memory delay. During sample presentation, NCL activity selectively encoded associations in a modality invariant fashion. During the delay, we observed subject specific, population-level coding biases in NCL activity. Despite of these biases, task relevant information could be decoded equally well from either subject's neuronal delay activity. Decoding success was facilitated by many mixed selectivity neurons, which mediated high dimensional representations of task variables on the NCL population level. These results parallel findings from the mammalian PFC, suggesting common mechanisms responsible for the adaptability of multimodal association areas across taxa.

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## 1. Introduction

The behavioral repertoire of corvid songbirds is remarkably rich in terms of associations of auditory with visual cues. Jungle crows, for instance, do cross-modally recognize their group members (Kondo, Izawa, & Watanabe, 2012), Siberian jays signal predator categories via mobbing calls (Griesser, 2009) and Eurasian jays use auditory information to pilfer food caches (Shaw & Clayton, 2014). American crows (Richards & Thompson, 1978) and other songbirds (Suzuki, Wheatcroft, & Griesser, 2016) can even employ compositional syntax to convey and interpret meaningful vocalization sequences. In either case, auditory cues inform the animal about its visual environment.

Previously, we found that neurons in the carrion crow (*Corvus corone corone*) endbrain selectively encode such audio-visual associations (Moll & Nieder, 2015). These neurons were found in the nidopallium caudolaterale (NCL), a multimodal higher association area which integrates sensory information (Wagener & Nieder, 2016) to support executive function (Ditz & Nieder, 2015, 2016b; Veit, Hartmann, & Nieder, 2014, 2015; Veit & Nieder, 2013). Therefore, NCL is considered to be the avian functional analogue of the

mammalian prefrontal cortex (PFC) (Güntürkün, 2005; Kröner & Güntürkün, 1999; Mogensen & Divac, 1982; Nieder, 2016).

In our previous study we tested crows with auditory sample stimuli that were associated with visual test cues across a short temporal delay (Moll & Nieder, 2015). Neuronal responses recorded from awake behaving crows selectively correlated with the tested associations during the sample and delay period and were predictive of the crows' behavioral responses. However, it remains unclear whether the observed association selective neuronal activity was dependent on the exact task sequence. That is, neurons might strictly respond to an audio-visual succession but would be unresponsive if the presentation sequence was switched to visual sample and auditory test stimuli. Alternatively, NCL neurons might generalize across sensory succession and respond to any temporal order of associates, be it auditory to visual or visual to auditory. Such modality invariant neurons would represent the abstract concept of an audio-visual association. Additionally, there is a third alternative: Different NCL neurons could have very different coding properties and would therefore convey information about both task factors, association and presentation sequence (i.e. modality). Such mixed selectivity neurons are a common finding in the PFC (Rigotti et al., 2013). Notably, a population made up of mixed selectivity neurons can still be biased towards one task factor (e.g. association) (Mante, Sussillo, Shenoy, & Newsome, 2013). Alternatively, the population average of neuronal activity

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can be equally influenced by all task factors and therefore be ‘category free’ (Raposo, Kaufman, & Churchland, 2014).

In the crow, rule encoding NCL neurons have been shown to be unaffected by the rule cue modality (Veit & Nieder, 2013). In mammals, modality invariance is known from monkey PFC neurons recorded during multimodal task performance (Hwang & Romanski, 2015; Nieder, 2012). However, evidence for modality invariant representations of associates from different sensory modalities is missing from the mammalian (Fuster, Bodner, & Kroger, 2000; Gibson & Maunsell, 1997) as well as from the avian literature. In one attempt, Gibson and Maunsell (1997) trained two macaque monkeys to associate auditory sample stimuli with visual test cues and vice versa, across a temporal delay. This task was well suited to test for modality invariant, association selective neuronal responses. However, in the recorded population of inferotemporal cortex (IT) neurons, the authors did not find more selective responses during the sample period of audio-visual trials than expected by chance. During the delay, many selective neurons in one monkey responded to the visual associate of the one, but to the auditory associate of the other of the two trained associations. These representations seemed to link nonassociated stimuli (Gibson & Maunsell, 1997) and did therefore not show modality invariant association selectivity. In the other monkey, the authors found too few selective delay responses to draw any conclusion.

To test for modality invariant association neurons in carrion crows, we analyzed single neuron activity from the crow NCL during the sample and delay period of a cross-modal delayed paired associate (DPA) task (Gibson & Maunsell, 1997). Crows were trained to match auditory sample cues with visual test stimuli, and vice versa. Therefore, our task design allowed to dissociate between modality invariant neuronal responses and responses that were constrained to one association cue modality.

## 2. Methods

### 2.1. Subjects

Two tame male carrion crows (*Corvus corone corone*; bird T and bird M) weighting 540 g and 450 g were used. They were housed in a large indoor aviary in a social group (for details see Hoffmann, Ruttler, & Nieder, 2011). The crows were taken from the Institute’s breeding stock (Animal Physiology, University of Tübingen) at three weeks of age in June 2011 (bird T) and June 2012 (bird M) and raised by hand. The crows’ age was 40 (bird T) and 24 (bird M) months at the start of recording sessions. These birds were previously used in one behavioral (Moll & Nieder, 2014) and one electrophysiological study (Moll & Nieder, 2015) and were therefore well adapted to the set-up and the training procedures. During training and recording sessions, they were maintained on a controlled feeding protocol and earned food during and after daily tests. All procedures were carried out according to the guidelines for animal experimentation and approved by the national authorities, the Regierungspräsidium Tübingen, Germany.

### 2.2. Apparatus

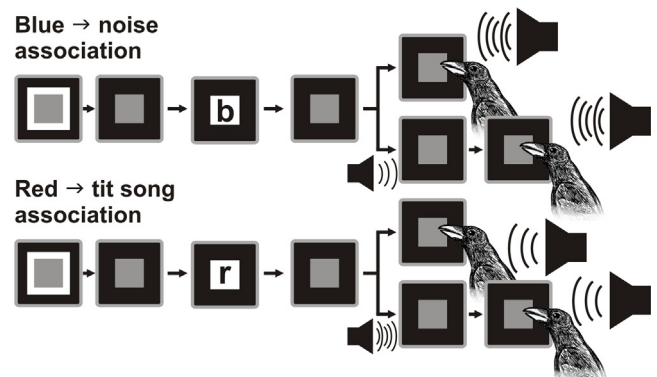
The set-up was composed of a fully controlled opaque operant conditioning chamber containing a 15 in. touch-screen (3 M Micro-touch, 60 Hz refresh rate), a custom-made feeder, one night vision infrared video camera (iSimim321R Genius), one speaker (Visaton, WB 10–100 V/8 ohm, frequency range: 100–20,000 Hz) and a wooden perch for the crows to stand on. The speaker was located 0.5 m directly in front of the bird, above and behind the screen. Leather jesses secured the crows loosely to their perch. Apart from that, crows were able to move freely and could easily reach the touch-

screen with their beak. An infrared light barrier in combination with a reflector attached to the bird’s head ensured that the bird’s head position was centered and that the bird was steadily facing the screen during stimulus presentation. Correct pecks on the screen were rewarded automatically with birdseed pellets and mealworms (*Tenebrio molitor* larvae). During reward phases, a small light integrated in the feeder lit up as additional positive feedback. For stimulus presentation and behavioral monitoring, personal computers running the CORTEX program (NIH) were used.

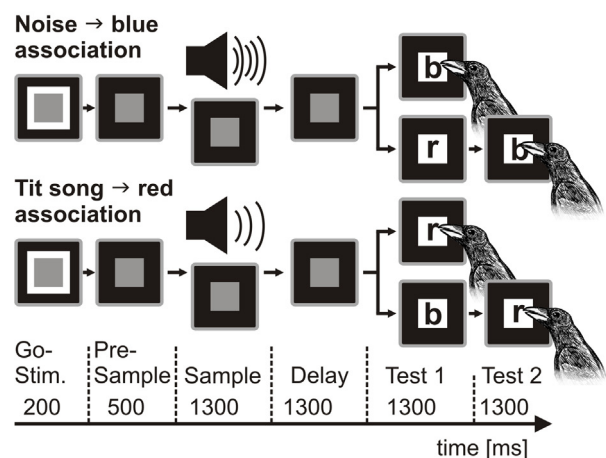
### 2.3. Behavioral protocol and stimuli

Crows were trained to match visual sample cues with their associated auditory match stimuli (“visual-auditory task”, Fig. 1A) and vice versa (“audio-visual task”, Fig. 1B). The birds were placed in front of a touch-screen monitor on which a 9 × 9 mm gray square stimulus was presented at the center of the screen throughout the whole session that switched to color (blue or red) during the sample or test period, depending on the task. A bird could initiate a trial by moving its head in the range of the infrared

#### A Protocol sequence 1: Visual-auditory



#### B Protocol sequence 2: Audio-visual



**Fig. 1.** Delayed paired associate (DPA) task protocol. 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. (A) During trials following the protocol sequence 1 (visual-auditory task), a visual sample (b: blue square, r: red square) was shown, followed by the delay after which crows had to choose the correct associated auditory test stimulus. A peck on the gray square on the touch screen during the correct playback was required to gain a food reward. Test stimuli were presented successively and their identity was randomized and balanced. (B) During trials following the protocol sequence 2 (audio-visual task), auditory stimuli were used as samples followed by visual test stimuli. Within a session, the two tasks (A and B) were presented in alternating blocks of 12 trials.

light barrier. This triggered the flashing of a white square “go stimulus” framing the always present 9 mm gray square for 200 ms. After a succeeding 500 ms pre-sample phase, the sample stimulus was presented for 1300 ms (the gray square turned to blue or red in visual-auditory trials, or an auditory playback in audio-visual trials). During the previous trial phases and the following 1300 ms delay period the bird was not allowed to move its head (significant motions were detected by the light barrier), otherwise the trial was aborted. As soon as the test phase started, as indicated by the onset of a test stimulus, the bird was allowed to move its head and to peck on the touch-screen to indicate the correct test stimulus, followed by a food reward. In non-match trials, non-match and match test stimuli (visual or auditory, depending on the task) were presented successively, with durations of 1300 ms each. In match trials only the match stimulus was presented. A match stimulus miss or an incorrect response to the non-match stimulus resulted in omission of food reward and a 3 s time out, indicated by a gray screen during which the computer remained dormant. The two tasks, visual-auditory and audio-visual, were presented in alternating blocks, where each block ended after 12 correct responses. Associations were presented in a pseudo-randomized fashion. All relevant task parameters were balanced.

Two auditory stimuli were used, white noise (bandpass filtered, 500 Hz–8 kHz) and a tit song segment (for spectrograms see Moll & Nieder, 2015). Both stimuli were 1300 ms in duration and had 20 ms linear ramps at the beginning and the end. They were recorded at 16-bit resolution, at a sampling rate of 44,100 kHz and presented at 65 dB/SPL sound pressure level. Stimuli were equalized in root mean square (rms) amplitude (Adobe Audition CS6) to ensure equal loudness.

#### 2.4. Surgery and recordings

All surgeries were performed while the animals were under general anaesthesia. Crows were anaesthetized with a ketamine/rompium mixture (50 mg ketamine, 5 mg xylazine/kg initially and supplemented on demand (approximately hourly) by 17 mg ketamine, 1.7 mg xylazine/kg i.m.). After the surgery, the crows received analgesics (Butorphanol (Morphasol®), 1 mg/kg i.m.). The head was placed in the stereotaxic holder that was customized for crows with the anterior fixation point (that is, beak bar position) 45° below the horizontal axis of the instrument (Karten & Hodos, 1967). Using stereotaxic coordinates (center of craniotomy: AP 5 mm; ML 13 mm), we chronically implanted two microdrives with four electrodes each, a connector for the headstage and a small headpost to hold the reflector for the light barrier. We recorded from eight chronically implanted glass-coated tungsten microelectrodes (2 MΩ impedance, Alpha Omega LTD, Israel) on two custom-built microdrives in the left hemisphere of bird T. The electrodes targeted the NCL of the telencephalon. In bird M we implanted with the same stereotaxic coordinates, but in the right hemisphere; the location of the electrodes was histologically verified to lie in the NCL (Veit & Nieder, 2013). At the start of each session, the electrodes were advanced manually to obtain high-quality recordings. Each microdrive had a lift of 6 mm, which was exploited to record from the NCL across different depths over a period of several weeks (38 recording sessions for bird T, 29 recording sessions for bird M). Neurons were not preselected for any involvement in the task. Signal amplification, filtering and digitizing of spike waveforms were accomplished using the Plexon system (Dallas, TX, USA). For each recording session, the birds were placed in the recording setup, a headstage containing an amplifier was plugged into the connector implanted on the bird's head and connected to a second amplifier/filter and the Plexon MAP box outside the setup by a cable above and behind the bird's head (all

components by Plexon). Single-cell waveform separation was performed off-line (Plexon Systems).

#### 2.5. Data analysis

All neurons with a minimum average firing activity of 1 Hz ( $n = 210$ ) were included in our analysis. Neuronal activity (single-unit discharge rates) was analyzed in two different temporal analysis windows corresponding to the sample and delay period (Fig. 1). Sample period activity was analyzed starting from 100 ms after sample onset (to account for the large sensory latency of the recorded population) to sample offset, resulting in a window duration of 1200 ms. Delay period activity was analyzed in a 1200 ms window starting 200 ms after sample offset and lasting until 100 ms after test onset, i.e. firing activity during the first 200 ms of the delay phase was clipped to exclude potential sensory offset activity. The first 100 ms of the test period were included in the delay phase analysis, to account for the sensory latency of most neurons.

A two-factor ANOVA was used to determine whether the discharge rates of a neuron varied significantly for the two different associations or task protocols ( $p < 0.01$ ). Neurons that exhibited ANOVA significant responses for any of the two main factors “association” (i.e., blue-noise and noise-blue trials vs. red-tit song and tit song-red trials) and “sequence” (i.e., visual-auditory vs. audio-visual trials) or their interaction, during the sample or delay period, were included for further population analyses (bird T: 85% (81/95), bird M: 78% (90/115)). Per definition, the preferred association of a selective neuron was the one that elicited highest discharges during the considered task period, determined separately for the visual-auditory and audio-visual task.

For illustration of single unit activity, peristimulus time histograms (PSTHs) were smoothed with a 150 ms boxcar window (step size, 1 ms). The same was done for the presentation of population activity. Population activity was calculated by averaging normalized single unit responses. These responses were normalized by subtracting the mean neuronal baseline activity from the neuronal responses and dividing the outcome by the standard deviation (SD) of the baseline activity. Baseline activity was defined as the discharge rates within the last 400 ms of the pre-sample period.

To calculate a measure of how much of a neuron's firing rate can be explained by the two task variables and their interaction across trial periods, we performed a sliding explained variance ( $\omega^2$ ) analysis. For each neuron,  $\omega^2$  was calculated separately for the two factors association, sequence and their interaction, using the equation:

$$\omega^2 = (SS_{\text{effect}} - DF * MS_{\text{error}}) / (SS_{\text{total}} + MS_{\text{error}}),$$

where  $SS_{\text{effect}}$  is the sum of squares between groups,  $SS_{\text{total}}$  is the overall sum of squares,  $DF$  is the degrees of freedom, and  $MS_{\text{error}}$  is the mean squared error within groups (Hentschke & Stüttgen, 2011). The analysis was performed in a 200 ms sliding window in steps of 20 ms.

The quality of association selective coding was quantified by using the ROC analysis derived from signal detection theory (Green & Swets, 1966). 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. For each neuron, four spike count distributions were derived, two (i.e. preferred vs. non-preferred) from visual-auditory and two from audio-visual task trials. The degree of separation between two distributions within one task was measured by the area under the ROC curve (AUROC). An AUROC value of 0.5 indicates a complete distribution overlap (no discrimina-

tion), whereas values of 0 and 1 indicate perfect separation. By convention, we used the spike counts of blue-noise (or noise-blue) association trials as the reference (baseline) distribution. Thus, in the analysis of visual-auditory trials, neurons preferring the blue-noise association had AUROC values  $< 0.5$ , whereas neurons preferring the red-tit song association had values  $> 0.5$ . For audio-visual trials, AUROC values were calculated correspondingly: Noise-blue preferring  $< 0.5$ ; tit song-red preferring  $> 0.5$ .

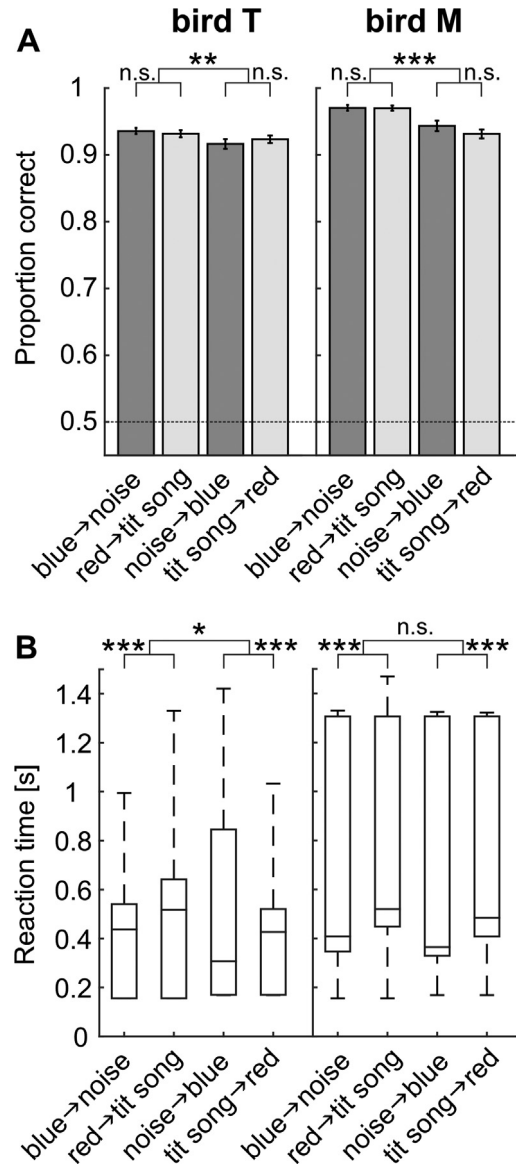
A k-Nearest-Neighbor classifier (Cover & Hart, 1967) was used to investigate how well the two associations and the four task conditions (Fig. 1) could be decoded from NCL single trial, pseudo-simultaneous population activity. For this, we used the MATLAB statistics toolbox with fivefold cross-validation and  $k = 12$  neighbors; the relative decoder performance did not depend on the exact number of neighbors. All ANOVA selective neurons (either for association, sequence or interaction, during the sample or delay period) with at least 20 trials per condition (i.e.,  $\geq 80$  trials total) were included in this analysis (bird T:  $N = 71$ ; bird M:  $N = 89$ ). The relative decoder performance did not change when all recorded neurons were included. To generate populations of similar size, we used all criteria complying neurons from bird T ( $N = 71$ ) and a random subset of 71 criteria complying neurons from bird M. From all available trials of a neuron, we randomly selected 40 trials per association (20 blue-noise and 20 noise-blue trials pooled into class 1, and 20 red-tit song and 20 tit song-red trials pooled into class 2) for the association decoding. For condition decoding, we randomly selected 20 trials per condition, resulting in four classes with 20 trials each. Trial timing was assigned randomly to create a population of pseudo simultaneously recorded neurons. These data sets were then used to perform association or condition decoding across trial periods, with a 200 ms sliding window advanced in steps of 20 ms. The entire procedure of selecting cells, selecting trials, assigning simultaneity, training and testing the model was repeated 100 times to account for differences in selecting the data. For more details on the k-Nearest-Neighbor classifier see Veit and Nieder (2013).

### 3. Results

#### 3.1. Behavioral performance was similar in the visual-auditory and audio-visual task

Two crows were trained to perform a delayed paired associate (DPA) task, in which they had to match a visual color stimulus with its associated auditory stimulus (“visual-auditory task”, Fig. 1A) and vice versa (“audio-visual task”, Fig. 1B). During a session, the two tasks (Fig. 1A and B) were presented in alternating blocks of twelve trials. In each trial of the visual auditory task, one of two visual sample stimuli (a blue or red square) was presented and had to be matched to its auditory associate (“noise” or “tit song”, respectively) across a temporal gap (delay). This presentation sequence was reversed in trials of the audio-visual task.

Both crows mastered both tasks well above chance in every recording session ( $p < 0.001$ , each session, binomial test). We found an overall correct performance of 92.7% ( $\pm 2.4\%$  SD) for bird T and 95.4% ( $\pm 1.7\%$  SD) for bird M (Fig. 2A). Performance was similar in both crows with mild differences between tasks resulting in better performances in the visual-auditory task (Fig. 2A; paired Wilcoxon, two-tailed; bird T:  $Z = 2.68$ ,  $p < 0.01$ ,  $n = 38$ ; bird M:  $Z = 4.21$ ,  $p < 0.0001$ ,  $n = 29$ ). No significant performance differences were found between associations within tasks (Fig. 2A; paired Wilcoxon, two-tailed, each comparison in both crows:  $p > 0.05$ ). This shows that both crows performed highly proficient in all four task conditions.



**Fig. 2.** Behavioral performance. (A) Average behavioral performance for each crow and each task condition across all recording sessions (bird T:  $n = 38$ ; bird M:  $n = 29$ ). Error bars indicate the SEM over sessions. (B) Boxplots of RTs for each task condition and crow. Plots display the median value and 25% and 75% quartiles over sessions.

Reaction times (RTs) for the “tit song red” association were larger than for the “noise blue” association in both crows and tasks (Fig. 2B; Wilcoxon test, two tailed, each comparison in both crows:  $p < 0.0001$ ). In addition, we found a difference in RTs between tasks for bird T, which responded faster to visual than to auditory match stimuli, (Fig. 2B; Wilcoxon test, two tailed,  $Z = 2.51$ ,  $p < 0.05$ ) but no such difference for bird M (Fig. 2B; Wilcoxon test, two tailed,  $Z = 0.77$ ,  $p = 0.44$ ). This was the only apparent difference between otherwise very similar behaving subjects.

#### 3.2. Single NCL neurons responded similarly to both associates of audio-visual associations

We analyzed single-cell activity of 210 NCL neurons (bird T: 95, bird M: 115). Most of these cells varied their firing rate selectively during the sample and/or delay period according to the learned audio-visual associations, sequence of stimulus presentation (i.e. task) or an interaction of these two factors (Table 1; bird T: 85%

**Table 1**  
Selectivity within trial periods, separately for bird T and bird M.

Percentage of cells selective for	Bird T (sample period, N = 95)	Bird M (sample period, N = 115)	Bird T (delay period, N = 95)	Bird M (delay period, N = 115)
Association	41% (39/95)	41% (47/115)	65% (62/95)	38% (44/115)
Sequence	27% (26/95)	21% (24/115)	37% (35/95)	30% (34/115)
Interaction between association and sequence	14% (13/95)	16% (18/115)	31% (29/95)	50% (57/115)
Association, no interaction	32% (30/95)	32% (37/115)	42% (40/95)	14% (16/115)
Sequence, no interaction	19% (18/95)	15% (17/115)	14% (13/95)	9% (10/115)

(81/95), bird M: 78% (90/115); two factor ANOVA,  $p < 0.01$ ). Importantly, we found in both crows 32% of cells (bird T: 30/95, bird M: 37/115) that selectively encoded learned associations during the sample period without interaction (Table 1). This means that these neurons responded selectively to both associates of one association, irrespective of which associate (visual or auditory) was presented. Examples of such association neurons are shown in Fig. 3A (bird T) and D (bird M). Both neurons significantly increased their firing rate during the sample period of both tasks (visual-auditory and audio-visual) whenever one of the preferred associates (blue square or noise) of the noise-blue association was presented. Consequently, these neurons showed a significant sample period main effect of association but no significant main effect of presentation sequence, and no interaction (two factor ANOVA, Fig. 3A:  $p < 0.0001$ ,  $p = 0.09$  and  $p = 0.55$ , respectively; Fig. 3D:  $p < 0.0001$ ,  $p = 0.16$  and  $p = 0.60$ , respectively). Examples of neurons that preferred stimuli from the other association (tit song-red) during the sample period are shown in Fig. 3B (bird T) and Fig. 3E (bird M) (two factor ANOVA,  $p < 0.0001$ , for the main factor association in both birds). These neurons (Fig. 3B and E), unlike the examples in Fig. 3A and D, were additionally influenced by the main factor sequence (two factor ANOVA,  $p < 0.0001$ ) and showed interaction (two factor ANOVA, Fig. 3B,  $p < 0.05$ , Fig. 3E,  $p < 0.0001$ ). Thus, we found both – modality-invariant neurons that were tuned to learned associations only, and neurons that were tuned to these associations but were additionally influenced by modality.

Interestingly, most association neurons from bird T maintained their association-selective firing during the sample period also throughout the delay period (e.g. Fig. 3A and B; two factor ANOVA, association:  $p < 0.0001$ , no interaction). In contrast, many of the sample period association neurons from bird M changed their selectivity in a systematic fashion (for one task only, mostly the audio-visual task) during the delay (e.g. Fig. 3D and E, note intersecting orange and green lines). Therefore, these neurons showed strong delay interaction effects of the two main factors (Fig. 3D and E; two factor ANOVA,  $p < 0.0001$ ). Notably, only few bird T neurons showed selectivity changes between the sample and delay period. We quantified these observations for both birds (Table 1) and found that delay association neurons without interactions were abundant in bird T (42%, 40/95) but rather scarce in bird M (14%, 16/115). At the same time, we found many neurons with delay interaction effects in bird M (50%, 57/115), but few in bird T (31%, 29/95). The interaction effects in bird T mainly resulted from neurons that increased their delay activity for one single condition (e.g. Fig. 3C), whereas most delay selective interaction neurons from bird M linked nonassociated stimuli (Fig. 3D–F). These neurons, for example, equally increased their delay activity after the presentation of the *not* associated red square and noise stimulus (Fig. 3F) and therefore neither represented the association nor the presentation sequence. Taken together, we found association selective neurons with and without interaction in both crows and in both analyzed task periods (Table 1). In addition, we found more complex, subject specific

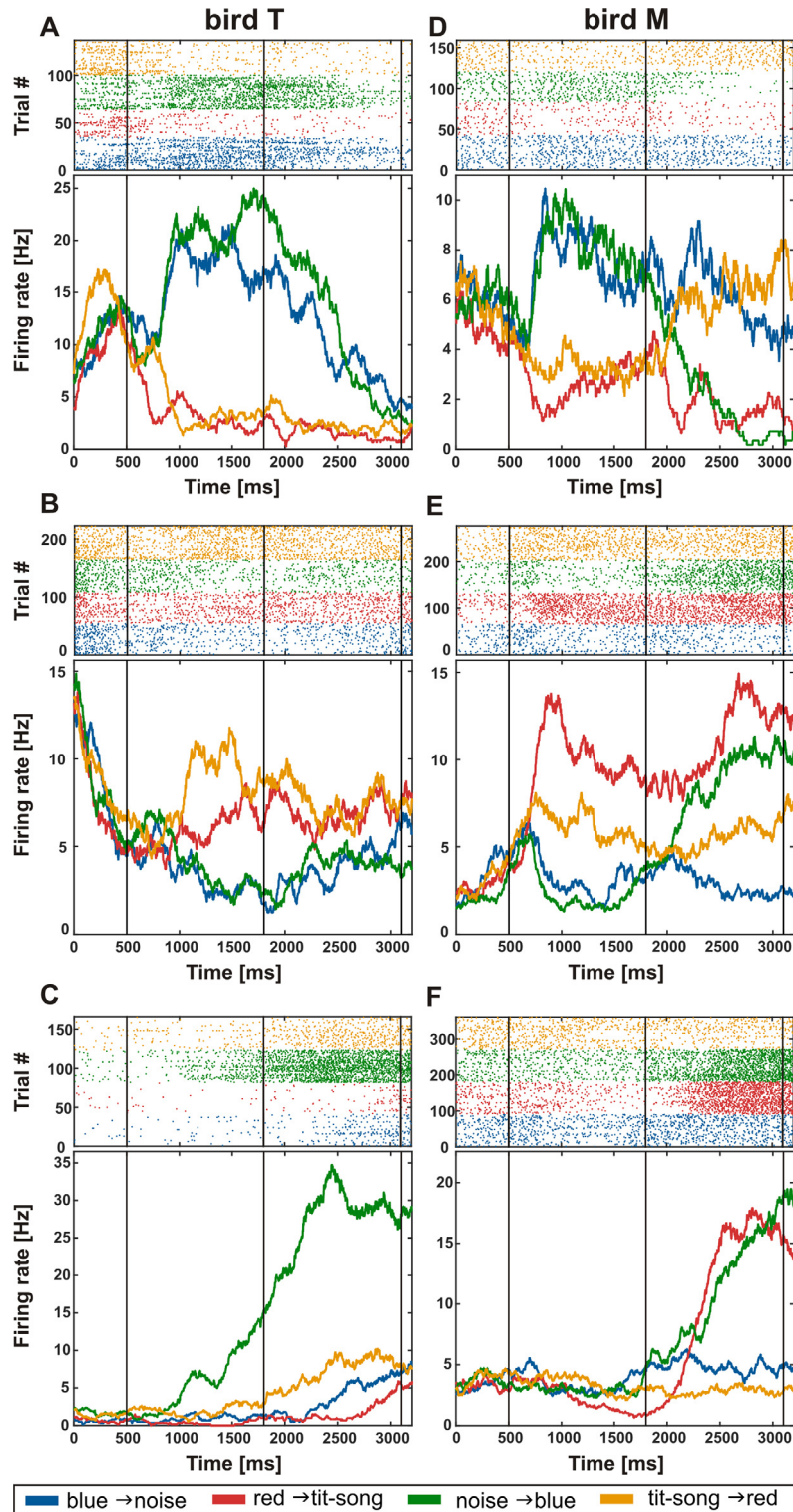
selectivity patterns during the delay period which are further analyzed below.

### 3.3. NCL population activity was biased towards modality invariant association coding

For neuronal population analysis, we first looked at the normalized, average population activity from all ANOVA selective cells (two way ANOVA, sample or delay period,  $p < 0.01$ ) for both crows separately (Fig. 4A–D; bird T:  $n = 81$ ; bird M:  $n = 90$ ). Normalized single-cell activity was grouped into preferred and non-preferred stimulus traces. The preferred stimulus was defined as the stimulus that elicited more activity either during the sample (Fig. 4A and B) or the delay period (Fig. 4C and D). To better capture the average population activity in different conditions, we plotted the activity to preferred and non-preferred stimuli separately for visual-auditory and audio-visual task trials. Therefore, population activity in Fig. 4A–D is represented by four different functions (i.e., activity functions to the preferred and non-preferred stimulus determined in visual-auditory trials, plus activity to the preferred and non-preferred stimulus determined in audio-visual trials). In bird T, activity was similar for preferred stimuli determined during the sample (Fig. 4A) or the delay period (Fig. 4C). In both cases, population activity was similar with significant differences between preferred and non-preferred stimulus trials in either trial period (Fig. 4A and C; paired Wilcoxon, two-tailed,  $p < 0.01$ ). This shows that most neurons preferred the same stimulus during the sample and delay period within a task. Mild differences between the two ways of grouping (i.e. preference determined during the sample (Fig. 4A) or delay period (Fig. 4C)) resulted mainly from the portion of neurons that exhibited selective delay but no selective sample activity and vice versa.

In bird M, however, trajectories of population activity were strongly influenced by the choice of the reference window (sample or delay period) and population activity always peaked within the applied window (Fig. 4B and D). In the trial period that was not used for preferred stimulus determination (the delay phase in Fig. 4B; the sample period in Fig. 4D) population selectivity was significant for visual-auditory task trials (paired Wilcoxon, two-tailed,  $p < 0.01$ ) but disappeared for audio-visual trials (paired Wilcoxon, two-tailed,  $p > 0.05$ ). Even a switch of selectivity between sample and delay period was observed in the population average of audio-visual trials (Fig. 4B), as expected from single neuron activity (Fig. 3D and E). This indicates a considerable amount of neurons in bird M that switched selectivity between the sample and delay period of audio-visual trials.

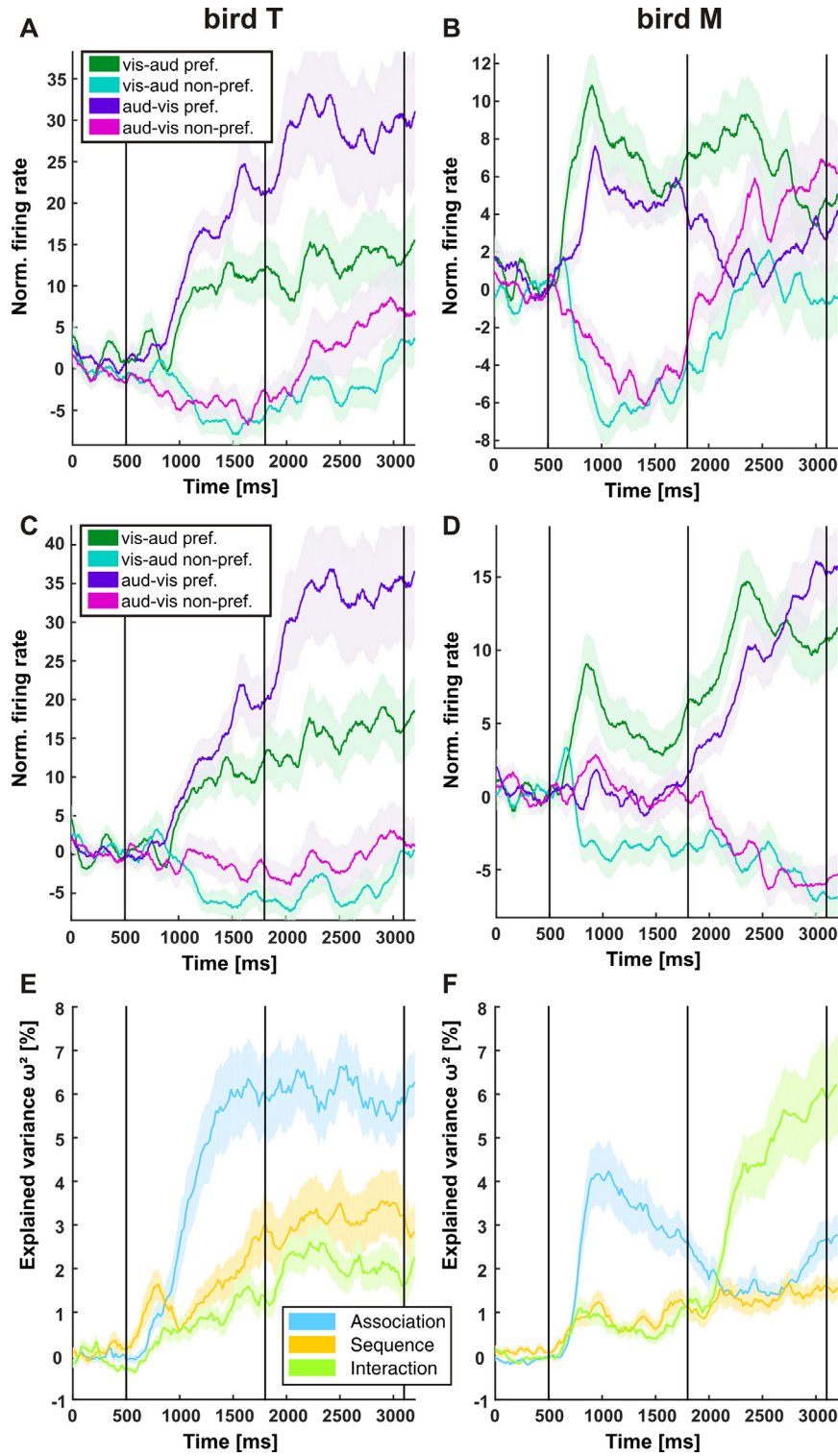
To examine which kind of information was extracted in NCL population activity across trial periods, we performed a sliding analysis of explained variance ( $\omega^2$ ) by the two main factors ‘association’ and ‘presentation sequence’ and their interaction. During the sample period, most of the variance in population activity was influenced by the main factor association in both crows (Fig. 4E and F). In bird T, the amount of information about association reached its maximum during the sample period and stayed at



**Fig. 3.** Selective activity of individual NCL neurons. Left column: bird T; right column: bird M. (A) *Upper panel:* Dot raster showing one neuron's response in individual trials, ordered by the task condition. Each dot signifies one action potential. Vertical lines mark transitions between pre-sample, sample, delay, and test period. *Lower panel:* Peristimulus time histogram (PSTH), obtained by averaging the dot rasters and smoothing with a 150 ms boxcar window. This neuron preferred the noise-blue association in a modality invariant fashion during the sample and delay period. (B) Neuron preferring the tit song-red association. This neuron showed main factor interaction during the sample period and modality invariance during the delay period. (C) A mixed selectivity neuron that strongly responded during noise blue trials but much less during blue noise trials and all other conditions. (D) Modality invariant association coding during the sample, but switch of selectivity during the delay period. (E) Neuron that shows a similar sample-delay selectivity switch as the neuron in D. Note that this neuron also switches selectivity in audio-visual trials but, unlike D, prefers the tit song-red association during the sample period. (F) Strong selectivity to nonassociated stimuli during the delay period. Notably, a strong encoding of nonassociated stimuli was never observed during the sample period. This is a rare example in which the sample-delay selectivity switch occurred in visual-auditory trials.

a high level throughout the entire subsequent delay period (Fig. 4E). In bird M, however, information about association peaked

in the first half of the sample period and afterwards dropped continuously to maintain a low level throughout the delay phase. In



**Fig. 4.** NCL population activity separately for bird T (left column) and bird M (right column). In each panel, vertical lines mark transitions between pre-sample, sample, delay, and test period. Shaded areas represent the SEM across neurons. (A) Average normalized spiking activity from all analyzed neurons of bird T ( $n = 81$ ). Visual-auditory and audio-visual trials were analyzed separately. Therefore, the stimulus preference of a neuron was determined two times, once for visual-auditory and once for audio-visual trials. Here, stimulus preferences during the *sample* period were taken as a reference for grouping. (B) As in A for bird M ( $n = 90$ ). Note the preference switch in audio-visual trials at the sample-delay transition. (C) For this averaged and normalized discharge rate from bird T, stimulus preferences during the *delay* period were taken as a reference for grouping. (D) As in C for bird M. Note that stimulus preferences during the delay of audio-visual trials do not correspond to sample preferences (also compare to B). (E) Percent explained variance ( $\omega^2$ ) derived from a two-factor ANOVA by association, presentation sequence and their interaction for bird T ( $n = 90$ ). (F) As in E for bird M ( $n = 90$ ). Note the sharp switch from explained variance by association to explained variance by interaction at the sample-delay transition.

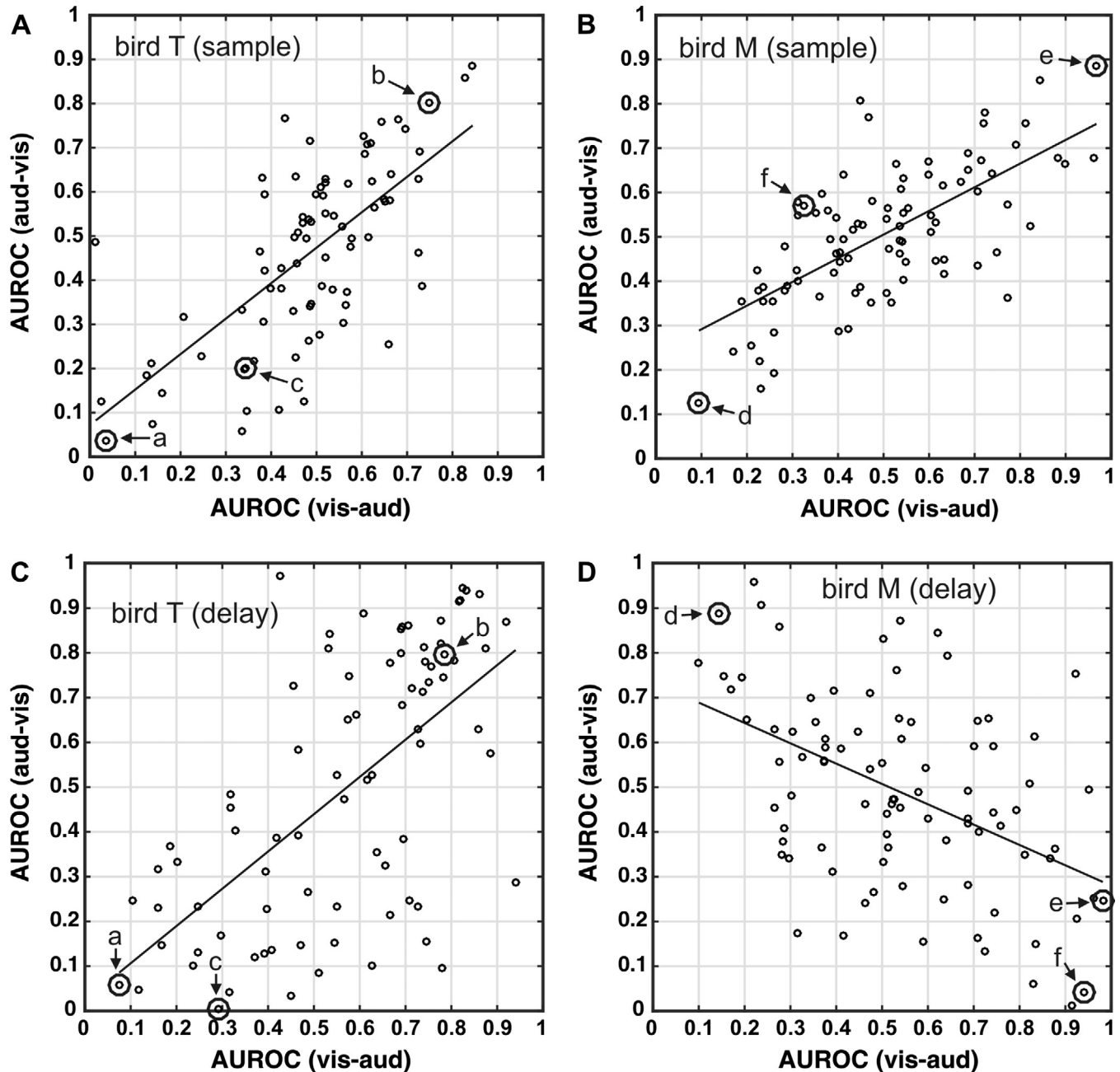
contrast, explained variance by interaction rose steeply after delay onset (Fig. 4F). In addition, we found lower (compared to the information about association) but elevated levels of sequence informa-

tion in both crows and both task periods (Fig. 4E and F). These findings complement the previous analyses of single neuron and normalized population activity. They show that both investigated

NCL populations from the two birds exhibited similar patterns of modality invariant association coding during the sample but different coding patterns during the delay period.

We now asked whether the observed proportions of association coding neurons could have been expected from category free populations (Raposo et al., 2014) with mixed selectivity (Rigotti et al., 2013). Alternatively, NCL populations could have been biased towards stable (modality-invariant) association coding or some other coding scheme (e.g. association-invariant encoding of the presentation sequence) and these coding schemes could have differed between subjects. To test this, we first applied a receiver operating characteristic (ROC) analysis for each ANOVA selective

neuron. 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. For each neuron, four spike count distributions were derived: two from visual-auditory task trials (blue-noise and red-tit song trials) and two from audio-visual task trials (noise-blue and tit song-red trials). The degree of separation between two distributions within one task 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 blue-noise (or noise-blue) association trials as the refer-



**Fig. 5.** Comparison of stimulus selectivity in visual-auditory trials with selectivity in audio-visual trials. (A) Each dot represents one neuron. AUROC values derived from visual-auditory trials (values < 0.5 indicate a blue-noise preferring neuron, > 0.5 a red-tit song preference) are plotted against AUROC values from audio-visual trials (values < 0.5 indicate a noise-blue preferring neuron, > 0.5 a tit song-red preference). Positive correlation indicates that the population is biased towards modality invariant association coding. Here neurons from bird T ( $n = 81$ ) are shown and AUROC values were calculated from *sample* period spike count distributions. (B) As A for bird M ( $n = 91$ ). (C and D) As A and B, but for the *delay* period. Note labeled data points in A–D that correspond to the sample or delay period of example neurons in Fig. 3. There was a strong bias towards modality invariant association coding during the sample period (A and B) but subject specific mnemonic delay activity during the delay (C and D).



ence (baseline) distribution. Thus, in the analysis of visual-auditory trials, neurons preferring the blue-noise association had AUROC values  $< 0.5$ , whereas neurons preferring the red-tit song association had values  $> 0.5$ . For audio-visual trials, AUROC values were calculated correspondingly: Noise-blue preferring  $< 0.5$ ; tit song-red preferring  $> 0.5$ . In a second step, we plotted the AUROC values during the visual-auditory task against the same neurons' AUROC values that were derived from audio-visual task trials, separately for both crows and trial periods (Fig. 5A–D). This allowed to analyze the selectivity strengths and preferences of a neuron in one data point. Note that the labeled data points in Fig. 5A–D correspond to the sample or delay period of the example neurons shown in Fig. 3. In category free neuronal populations with mixed selectivity, AUROC values of visual-auditory and audio-visual trials are expected to be uncorrelated. In the observed populations, however, we found the opposite result (Fig. 5A–D). During the sample period, AUROC values in both birds were highly and positively correlated (Fig. 5A and B; Spearman correlation; bird T:  $r = 0.66$ ,  $p < 0.0001$ ; bird M:  $r = 0.64$ ,  $p < 0.0001$ ). During the delay, bird T showed the same positive correlation (Fig. 5C; Spearman correlation,  $r = 0.62$ ,  $p < 0.0001$ ), while we found negative correlation in bird M (Fig. 5D; Spearman correlation,  $r = -0.43$ ,  $p < 0.0001$ ). Therefore, we found in both crows a robust population bias towards stable and modality-invariant association coding during the sample period. This bias remained equally high during the delay period in bird T but was inverted towards nonassociated stimuli in bird M.

### 3.4. Task relevant information could be decoded from two different types of population activity

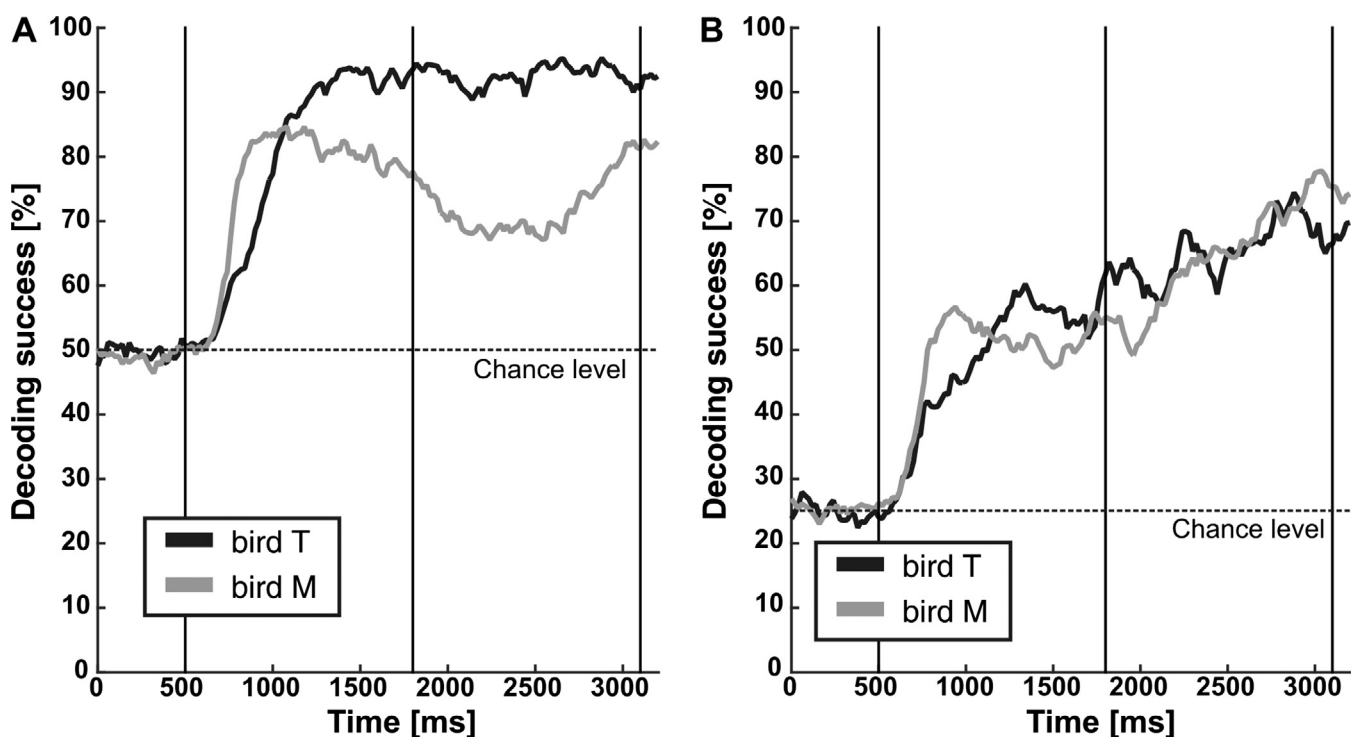
For successful task completion, our crows were not only required to know and remember the current association but, in addition, needed to represent the presentation sequence to prepare in an optimal way for the upcoming test period. This is consistent

with the finding of sequence information in the NCL populations (Fig. 4E and F) and single neurons with mixed selectivity (e.g. Fig. 3C and F). However, striking differences in the population activity between the two birds emerged during the delay period (Fig. 5C and D; association bias in bird T, nonassociated stimuli bias in bird M), even though the crows showed similar behavioral performances (Fig. 2).

To find out whether population activity in the two crows can account for behavioral success, we applied a decoding algorithm. Using a k-Nearest-Neighbor classifier (Cover & Hart, 1967), we performed a sliding decoding analysis to predict associations (Fig. 6A) and conditions (Fig. 6B) from populations' discharge rates. Only correct trials were used due to a lack of error trials. During the sample period, decoding success for associations was high in both birds (Fig. 6A; above 90% correct for bird T and well above 80% for bird M). As expected, we found association decoding differences between the two crows during the delay (Fig. 6A). However, these differences shrank towards the end of the delay so that the decoder performance mirrored performance during the sample towards the end of the delay in both birds (Fig. 6A). Moreover, when we decoded conditions (i.e., blue-noise, red-tit song, noise-blue, tit song-red) - a less abstract operation that relates directly to the task requirements - we found a full overlap of decoding success curves during the delay (Fig. 6B). In both crows, decoding success peaked shortly before test onset, at a time in the trial when the information was needed for trial completion (Fig. 6A and B).

## 4. Discussion

We report neuronal correlates of cross-modal associations in the crow NCL, an avian multimodal association area. Crows successfully matched visual sample cues across a temporal delay to their auditory associates and vice versa. During task performance, NCL single neurons as well as populations represented the cross-modal associations in a modality invariant fashion that has not



**Fig. 6.** Population decoding. (A) Performance of a k-Nearest-Neighbor classifier predicting the association in individual trials from pseudo-simultaneous NCL population activity. Dotted line indicates chance level. Vertical lines mark transitions between pre-sample, sample, delay, and test period. (B) Performance of a k-Nearest-Neighbor classifier predicting the task condition (i.e., blue-noise, noise-blue, red-tit song or tit song-red). Note the chance level at 25% (dotted line).

been shown before in non-human animals. Striking differences in the NCL population activity between the two birds were observed during the delay period. However, we found clear evidence that task relevant information could be decoded equally well from both crows' NCL delay activity. Successful decoding was facilitated by an abundance of mixed selectivity neurons which caused high dimensional representations of task variables on the population level.

#### 4.1. Behavior

The ability of crows to abstract (Ditz & Nieder, 2016a), to switch effortlessly between behavioral rules (Moll & Nieder, 2014), and to detect such rules cued by the sequence of stimulus presentation (Richards & Thompson, 1978; Suzuki et al., 2016), were prerequisites to master our block-wise presented visual-auditory and audio-visual DPA tasks. With this rarely used behavioral protocol (Gibson & Maunsell, 1997), we demonstrate the ability of crows to choose auditory stimuli based on visual cues, and vice versa. The behavioral proficiency of our crows was similar between subjects and fully comparable to the monkey study by Gibson and Maunsell (1997). Therefore, our protocol allowed for the comparative study of the neuronal basis of cross-modal associations in the absence of a six-layered neocortex.

#### 4.2. Modality invariant association coding

The design of our study allowed us to dissociate between neuronal NCL responses that were constrained to one association cue modality and neuronal responses that were driven by both visual as well as auditory associates. In both crows, one third of all recorded NCL neurons showed association-selective, modality-invariant sample-cue related activity. Additional neurons were biased towards association coding but showed interactions between the main factors association and presentation sequence (i.e. modality). Association coding was therefore the most prevalent coding bias during the sample period. Consistent with our results, visual and auditory cues can elicit modality invariant, mnemonic rule coding responses in corvid NCL neurons, when such cues are mapped onto the same behavioral rule (Veit & Nieder, 2013). However, cross-modal association studies directly comparable to our results do not exist in birds.

Two studies have investigated cross-modal associations in non-human primates (Fuster et al., 2000; Gibson & Maunsell, 1997). Fuster et al. (2000) tested one stimulus succession (audio-visual) in a study on the PFC, a protocol that did not allow to test for modality invariance. The protocol of Gibson and Maunsell (1997), on the other hand, was well suited to test for modality invariant neuronal responses. Gibson and Maunsell (1997) tested the visual-auditory and audio-visual succession and recorded neuronal activity from the monkey IT. However, they did not find more selective activity during the sample period of audio-visual trials than expected by chance. Therefore, no modality invariance was shown during the sample period (Gibson & Maunsell, 1997). During the delay, IT neurons selectively responded during both visual-auditory and audio-visual trials. Surprisingly, the mnemonic delay activity in one monkey seemed to link nonassociated stimuli. In the other monkey, very few delay selective neurons did not allow to draw any conclusion about a coding bias. We, too, observed mnemonic delay activity selective to nonassociated stimuli in one crow. This observation is further discussed below. In summary, Gibson and Maunsell (1997) did not find evidence for modality invariant cross-modal association coding in the monkey IT.

Our association-selective activity in response to both associates of a particular association is reminiscent of the activity of "pair-coding neurons". Pair-coding neurons were found in the monkey

temporal cortex while monkeys performed in an unimodal (visual) DPA task (Hirabayashi & Miyashita, 2014; Sakai & Miyashita, 1991). These pair-coding neurons responded similarly to either associate of their preferred association when used as sample stimulus (Sakai & Miyashita, 1991). As in our study, additional neurons exhibited a pair-coding bias (i.e. association bias) but showed interactions between the main factors 'association' and 'presentation sequence' (Sakai & Miyashita, 1991). These representations of visual associations can be rapidly established through learning, as shown in the crow NCL (Veit, Pidpruzhnykova, & Nieder, 2015) as well as in the monkey inferotemporal and perirhinal cortex (Messinger, Squire, Zola, & Albright, 2001). Therefore, unimodal as well as cross-modal pair-coding NCL neurons likely play a role in corvid behaviors such as communication (Griesser, 2009; Richards & Thompson, 1978), recognition of conspecifics (Kondo et al., 2012) and episodic like memory (Clayton & Emery, 2005; Clayton & Dickinson, 1998).

#### 4.3. Mnemonic NCL activity

Mnemonic DPA delay activity is thought to be a preparatory, prospective signal that leads a behavioral response (Hirabayashi & Miyashita, 2014). Unimodal and bimodal DPA studies report the predictive and prospective nature of mnemonic association signals (Asaad, Rainer, & Miller, 1998; Fuster et al., 2000; Gibson & Maunsell, 1997; Moll & Nieder, 2015; Naya, Yoshida, & Miyashita, 2001; Rainer, Rao, & Miller, 1999; Tomita, Ohbayashi, Nakahara, Hasegawa, & Miyashita, 1999; Veit, Pidpruzhnykova, et al., 2015). Across these studies, the exact onset of the prospective signal ranges considerably within a trial. Rather dependent on the study than on the brain area, the prospective signal emerges at different time points during the delay (IT: Gibson & Maunsell, 1997; PFC: Rainer et al., 1999; NCL: Veit, Pidpruzhnykova, et al., 2015), within the sample cue period (PFC: Asaad et al., 1998; IT: Tomita et al., 1999; Area TE & 36: Naya et al., 2001) or, in error trials, even shortly before sample onset (NCL: Moll & Nieder, 2015). This shows that, in some DPA studies, mnemonic information interacts with external sensory information during stimulus presentation. In other studies, however, the representation of mnemonic information emerges not before the delay period and can therefore be dissociated from sensory bottom-up responses.

It has been shown in crows (Veit, Pidpruzhnykova, et al., 2015) and primates (Hirabayashi, Takeuchi, Tamura, & Miyashita, 2013; Naya et al., 2001; Takeuchi, Hirabayashi, Tamura, & Miyashita, 2011) that single neurons can be differentially recruited to represent mnemonic (potentially prospective) content in one, and sensory (sample cue related) content in another DPA trial period. Thus, it is conceivable that we have observed a clear cut switch from sensory to mnemonic network activity in bird M at the sample-delay period transition. This switch might have become visible in bird M, but not in bird T, because of subject specific mnemonic coding strategies in combination with a similar sensory coding strategy. We therefore speculate that the observed single neuron and population activity differences between crows could reflect relatively simple coding strategy differences: While bird T's mnemonic delay activity in audio-visual trials would have encoded the upcoming visual choice targets, bird M might have prospectively encoded the nonassociated visual targets, that then had to be avoided during the test period. In visual-auditory trials, however, both birds would have employed a similar mnemonic coding strategy. Notably, the resulting negative correlation in association preference between visual-auditory and audio-visual trials during the delay in bird M has been observed previously in one macaque monkey (Gibson & Maunsell, 1997). Our interpretation is also consistent with two earlier studies on the crow NCL. In one study, neurons switched their selectivity to encode different task parameters

in different trial periods (Veit, Hartmann et al., 2015). In the other study, a transition from sensory to mnemonic representations within a trial has been shown (Veit, Pidpruzhnykova et al., 2015). Moreover, in a protocol including only two associations, it is not necessary to assume that the two described coding biases would result in different behavioral or decoder performances. Here, unlike in a protocol with more stimuli, it is irrelevant for performance whether the correct or the (only) incorrect test stimulus is used as a reference for the behavioral response.

Of course, other potential explanations might also account for the observed mnemonic coding differences between the two crows. For instance, we cannot exclude that there was a small jitter in the exact anatomical position of our NCL implants between crows. However, the potential effect of this should be small, since we recorded with eight electrodes at a time (Veit & Nieder, 2013) along different depths in both crows' NCL (from 0.3 to >5 mm in depth), just as in our previous cross-modal association study (Moll & Nieder, 2015). We did not observe any anatomical clustering of association selective neurons. Another limitation of our study is that we recorded in different hemispheres (bird T: left, bird M: right). Further investigations, with more challenging simultaneous bilateral recordings, could help to clarify potential lateralization effects (Rogers, Vallortigara, & Andrew, 2013) on mnemonic association coding.

#### 4.4. Category bias and mixed selectivity

Whatever the causes of the inter-subject, population level differences in mnemonic delay activity might have been, they did neither pose a problem for decoding nor did they have an apparent influence on behavior. These results are consistent with a recent monkey study, in which subject specific neuronal coding biases in PFC were observed along with similar behavioral and decoder performances (Mante et al., 2013). In this study, as in our results, neuronal populations were indeed differently biased between subjects (towards color in one, but not in the other monkey) but contained a considerable amount of neurons with mixed selectivity (Mante et al., 2013). This mixed selectivity in neuronal responses can result in high dimensional representations of task variables on the population level, which in turn can be exploited by classifiers (such as the k-nearest-neighbor classifier) and machine learning techniques (Raposo et al., 2014; Rigotti et al., 2013). The brain might exploits this multidimensionality as well (Rigotti et al., 2013). This is possible irrespective of whether a neuronal population is category free (Raposo et al., 2014) or, as in our study, biased towards the one or the other category (Mante et al., 2013). The observation of high dimensional representations in the avian NCL as well as in the mammalian PFC could therefore hint towards a common mechanism responsible for the remarkable adaptability of multimodal association areas across taxa.

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