# Conscious Experience of Stimulus Presence and Absence Is Actively Encoded by Neurons in the Crow Brain

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## Abstract

■ The emergence of consciousness from brain activity constitutes one of the great riddles in biology. It is commonly assumed that only the conscious perception of the presence of a stimulus elicits neuronal activation to signify a "neural correlate of consciousness," whereas the subjective experience of the absence of a stimulus is associated with a neuronal resting state. Here, we demonstrate that the two subjective states "stimulus present" and "stimulus absent" are represented by two specialized neuron populations in crows, corvid birds. We recorded single-neuron activity from the nidopallium caudolaterale of crows trained to report the presence or absence of images presented near the visual threshold. Because of the task design, neuronal activity tracking the conscious "present" versus "absent" percept was dissociated from that involved in planning a motor response. Distinct neuron populations signaled the subjective percepts of "present" and "absent" by increases in activation. The response selectivity of these two neuron populations was similar in strength and time course. This suggests a balanced code for subjective "presence" versus "absence" experiences, which might be beneficial when both conscious states need to be maintained active in the service of goal-directed behavior. ■

## INTRODUCTION

How perceptual consciousness, the subjective experience associated with a reportable sensory event, emerges from the workings of the brain is a fundamental question in biology (Ehret & Romand, 2022; Vallortigara, 2021; Laureys, 2005; Nagel, 1974). The main method to study how neurons give rise to perceptual consciousness relies on identifying neuronal activity that specifically occurs during subjective reports of the subject under study. Such "neural correlates of consciousness (NCCs)," defined as the minimal set of neuronal events and mechanisms sufficient for a specific conscious percept (Koch, Massimini, Boly, & Tononi, 2016), have been explored in humans (Pereira et al., 2021; Gelbard-Sagiv, Mudrik, Hill, Koch, & Fried, 2018; Reber et al., 2017; Quiroga, Mukamel, Isham, Malach, & Fried, 2008; Kreiman, Fried, & Koch, 2002), in nonhuman primates (Kapoor et al., 2022; van Vugt et al., 2018; Panagiotaropoulos, Deco, Kapoor, & Logothetis, 2012; de Lafuente & Romo, 2005; Leopold & Logothetis, 1996; Logothetis & Schall, 1989), and recently also in the crow, a corvid songbird (Nieder, Wagener, & Rinnert, 2020). Common to all these experimental approaches is that physically identical stimuli spontaneously elicit one of two contrasting, endogenously generated percepts. The general finding is that a proportion of neurons in higher-order brain areas becomes active in relation to the subject's alternating conscious percept for physically identical stimuli. This holds even when reports are initially

undefined to the subject or not required, arguing that the activity of such neurons represents the subjective experience and not factors related to the impending report (Kapoor et al., 2022; Hesse & Tsao, 2020; Nieder et al., 2020).

One of the most radical contrasts in subjective experience can be witnessed when stimuli are presented near perceptual threshold of the subject (Nieder et al., 2020; van Vugt et al., 2018; de Lafuente & Romo, 2005). Despite the constant intensity of the target stimulus across trials, the perceptually ambiguous stimulus is sometimes perceived, whereas other times, the stimulus is not perceived. In other words, conscious perception switches between conscious "stimulus-present" and "stimulus-absent" states, irrespective of the constant intensity of the stimulus. As an NCC, neurons respond in relation to the changing perceptual states. Thus, the readout of neuronal activity can predict whether the subject was consciously aware or unaware of the stimulus (Nieder et al., 2020; van Vugt et al., 2018; Quiroga et al., 2008; de Lafuente & Romo, 2005).

The tacit assumption from these studies is that the NCC is only based on percept-related neurons that show elevated firing rates for perceived stimuli but remains silent when stimulus absence is experienced (van Vugt et al., 2018; Quiroga et al., 2008; de Lafuente & Romo, 2005). Within this framework, only conscious perception is encoded, whereas the absence of a percept correlates with neurons' resting activity (Pereira, Perrin, & Faivre, 2022). However, it is conceivable that not only subjective experience of the presence of a stimulus is encoded by neuronal

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activity but also the experience about the absence of a stimulus (Pereira et al., 2022). After all, both stimulus presence and stimulus absence experiences constitute explicit categorical states.

Evidence supporting the intriguing possibility that also the conscious experience of stimulus absence can be encoded actively comes from single-neuron recordings in the associative cerebral cortex of monkeys and humans (Pereira et al., 2021; Merten & Nieder, 2012). Given that evidence for neurons actively signaling the experienced absence of stimuli stem exclusively from primates, one hypothesis is that this way of implementing conscious percepts might have emerged with the advent of a mammal-specific and computationally powerful layered neocortex. Alternatively, this way of representing two subjective states by two specialized neuron populations may constitute a computational advantage that therefore might be implemented in other vertebrate classes, such as birds, with distinctly evolved endbrains (telencephala) lacking a cerebral cortex (Jarvis et al., 2005) and neuronal circuits of distinct developmental origin (Colquitt, Merullo, Konopka, Roberts, & Brainard, 2021). Recently, we reported a neuronal correlate of perceptual consciousness in the associative endbrain area *nidopallium caudolaterale* (NCL) of carrion crows (Nieder et al., 2020). In the current study, we reanalyzed this data set to explore the hypothesis that—similar to the primate neocortex—the two subjective states "stimulus present" and "stimulus absent" are represented by two specialized neuron populations in the independently evolved telencephalon of birds (Nieder, 2021).

## METHODS

### Subjects

Two 1-year-old hand-raised male carrion crows (*Corvus corone*) from the institute's breeding facility were used. They were housed in a social group of four crows in an indoor aviary. During the experiment, the crows were on a controlled feeding protocol and received their daily amount of food as reward during training and recording or, if necessary, after the sessions. The body weight was measured daily. Water was available ad libitum during the experiments and in the aviary. All procedures were carried out according to the guidelines for animal experimentation and approved by the responsible national authorities, the Regierungspräsidium Tübingen, Germany.

### Behavioral Protocol

We trained the crows to report the presence or absence of a gray visual stimulus (4.5° of visual angle) presented at six different intensity levels in the center of a black computer screen.

The experiment was conducted in a darkened operant conditioning chamber. The crow was placed on a perch in front of a touchscreen monitor (ART Development MT1599-BS), which was used only for stimulus presentation. The behavior and response of the crow were controlled by an infrared light barrier, which was located above the crow and registered the position of a reflector foil attached to the bird's head. Reward (either birdseed pellets or mealworms [*Tenebrio molitor* larvae]) was given by an automated feeder below the touchscreen. Auditory feedback was provided by speakers (Lasmex S-03) located behind the touchscreen. We used the CORTEX system (National Institute of Mental Health) to run the experiment and collect behavioral data.

The crow initiated a trial by positioning its head facing the screen whenever the go stimulus (small white cross, 2 × 2° of visual angle) was shown. Auditory feedback indicated that the light barrier had been entered and the go stimulus turned briefly into a circle (60 msec) before it vanished. This stable head position had to be maintained throughout the trial until the response phase. Premature head movements aborted the ongoing trial, which was then discarded.

After a 600-msec waiting period in which the screen was completely black, the stimulus period followed. In 50% of the trials, the visual stimulus was shown for 300 msec, whereas in the other 50%, the screen remained black. The intensity of the stimulus was close to the perceptual threshold and individually adjusted so that the two faintest stimulus values were at threshold (around 50% "yes" responses) and the two highest values were salient and always detectable. Whether a stimulus was shown or not, and the intensity of the stimulus, was shuffled pseudorandomly on a trial-by-trial basis.

Then, the screen was black for a delay of 2500 msec, after which a rule cue (colored square) informed the crow how to respond. For a correct response, the crow needed to associate its conscious experience about the stimulus with the conditional instruction signified by the rule cue. If a stimulus was present, a red square required the crow to respond (i.e., to nod and thus move the head out of the light barrier within 800 msec) to earn a reward, whereas a blue square demanded withholding from responding and maintaining a stable head position for 800 msec to receive a reward. The orthogonal rule–response relationships were applied for the absence of a stimulus. If a stimulus was absent, a red square required the crow to withhold from responding, whereas a blue square demanded a response. The rule cues were pseudorandomized, fully balanced and unbeknownst to the crow at the beginning of each trial. This prevented the bird from learning stimulus–response associations and from preparing a motor response already during the stimulus and delay periods.

### Surgery and Neurophysiological Recordings

The surgery was performed while the animal was under general anesthesia with a mixture of ketamine (50 mg/kg)

and xylazine (5 mg/kg). The animal was placed in a stereotaxic holder. We targeted the medial part of the NCL by performing a craniotomy at 5 mm anterior–posterior and 13 mm mediolateral on the left hemisphere of both birds (Kersten, Friedrich-Müller, & Nieder, 2022). Two manual micro drives containing four electrodes each (2 MΩ, Alpha Omega Co.) were implanted at the craniotomy. In addition, a miniature connector for the headstage and a small holder for attaching the reflector were implanted. After the surgery, the crows received analgesics. Each recording session started with adjusting the electrodes until a proper neuronal signal was detected on at least one channel. The neurons were never preselected for any involvement in the task. Neuronal data were recorded using the Plexon system (Plexon Inc.). Single-cell separation was done offline (Plexon Offline Sorter, Version 2.6.2).

## Data Analysis

### Behavior

Data analysis was performed using MATLAB (The Math-Works). We recorded behavioral and neuronal data during 37 sessions for Crow 1 and 41 sessions for Crow 2. During these sessions, the birds performed 22,447 (Crow 1) and 18,548 (Crow 2) single trials, respectively. The proportion of "yes" responses was plotted as a function of stimulus intensity to give rise to a sigmoidal psychometric function. For that purpose, trials with both response types (requiring head movements or no head movements according to the rule cue) were pooled.

### Neuronal Analysis

We analyzed the data set that constituted the basis of a previous publication (Nieder et al., 2020). For neuronal analyses, the trials were grouped into three different trial categories according to the crows' psychophysical performance correlating with stimulus intensity:

*Suprathreshold trials.* Salient stimuli presented at Intensities 4 and 5 were suprathreshold conditions in which the crows detected the stimulus in almost 100% of the trials. The crows produced almost exclusively "yes" responses (i.e., "hits") for such suprathreshold stimuli.

*Near-threshold trials.* Stimulus Intensities 1 and 2 represent faint intensities near the perceptual detection threshold (~50% "yes" responses) of the crows. In such trials, the subjective perception of the crows resulted in either "yes" ("hits") or "no" ("misses") responses.

*No-stimulus trials.* Stimulus Intensity 0 corresponds to the 50% of the trials in which no stimulus was presented. "No" responses correspond to "correct rejections," and "yes" responses signify "false alarms."

All neurons that were used for the following analyses had an average firing rate of at least 0.5 Hz and were recorded for at least four trials of each trial category and responses mentioned above ("hits" in suprathreshold trials, "hits" and "misses" in near-threshold trials, and "correct rejections" and "false alarms" in no-stimulus trials). In addition, all neurons were task selective; that is, they had a time interval with a significant difference in their activity to the most unambiguous conditions, namely, "correct rejections" in the no-stimulus trials and "hits" in the suprathreshold trials. To identify this task-selective time window, we used a sliding Mann–Whitney $U$ test (200-msec window duration, 10-msec step size, $p < .01$) beginning at sample onset and ending 100 msec after delay offset. A neuron was termed "task selective" if its neuronal activity differed over at least 11 consecutive windows (i.e., 300 msec in total). Task-selective intervals occurring between stimulus onset until 300 msec after stimulus onset were classified as stimulus related; all later occurring selective intervals were classified as delay related. If a neuron had more than one selective time interval during the sample and delay period, respectively, only the one with the greater difference in firing rate to suprathreshold "hit" trials versus no-stimulus "correct rejections" trials (interval with the smallest $p$ value of the Mann–Whitney $U$ test) was used.

We identified percept-related neurons, that is, task-selective neurons that showed a difference in firing rates to the crows' "yes'" versus "no" responses in near-threshold trials during their selective time windows, using receiver operating characteristics (ROCs). For that purpose, we calculated the area under the ROC curve (AUROC) as a measure of how well a neuron based on its firing rates discriminates between two conditions. A value of 0.5 indicates chance level, whereas a value of 1.0 denotes perfect discriminability. A percept-related neuron had to meet two criteria in unison: First, firing rates in suprathreshold "hit" compared to no-stimulus "correct rejection" trials had to be significantly different (i.e., task selectivity; Mann–Whitney $U$ test, $p < .01$; see paragraph above). Second, AUROC values comparing near-threshold "hits" versus near-threshold "misses" had to be significantly different (permutation test, 1000 shuffled distributions, $p < .05$). If neuronal activity was smaller in "hits" compared to "correct rejections," the AUROC values were smaller than 0.5. In this case, the AUROC value was rectified (mirrored at 0.5) so that both negative and positive deflections resulted in values greater than 0.5. Accordingly, the choice probabilities of such a neuron were also mirrored at 0.5. We compared the choice probabilities (i.e., AUROC value for near-threshold "hit" trials vs. near-threshold "miss" trials) to a distribution of AUROC values with permuted trial labels (1000 times). A neuron was called percept related if its rectified AUROC value for near-threshold trials was greater than the 5% upper bound of the permuted distribution.

The percept-related neurons were further classified into "yes" neurons and "no" neurons according to their

neuronal activity during the selective time interval. A neuron was termed "yes" neuron if its mean firing rate was higher for "hits" in suprathreshold trials than for "correct rejections" in no-stimulus trials and if its mean firing rate was higher in near-threshold "hit" trials than in near-threshold "miss" trials. The converse relations were applied to identify "no" neurons. One neuron could not be assigned to either class because it had higher firing rates in suprathreshold "hit" than in "correct rejection" trials but lower firing rates in near-threshold "hit" than in near-threshold "miss" trials.

ROC analysis was further used to investigate whether "yes" and "no" neurons encoded the crows' later report. The choice probability index describes the AUROC value for different behavioral responses with identical stimulus properties (Britten, Newsome, Shadlen, Celebrini, & Movshon, 1996). To that aim, we used the firing rates of each neuron during its selective time interval to calculate the choice probability for "yes" versus "no" responses in near-threshold trials ("hits" vs. "misses") and in no-stimulus trials ("correct rejections" vs. "false alarms"), respectively. In addition, we calculated the AUROC value for suprathreshold "hit" versus no-stimulus "correct rejection" trials as a reference. If a neuron reflects the crow's subjective experience, it is expected to discriminate between "yes" and "no" responses, although stimulus intensities were identical, and with qualitatively similar activity as for suprathreshold "hits" versus no-stimulus "correct rejections."

To determine the onset latency and duration of significant neuronal activity for "yes" and "no" neurons, we employed a sliding window of 50-msec duration and 1-msec step size. The onset of significant neuronal activity was considered achieved when the neuronal activity differed by 3 $SD$s from the baseline over at least 26 consecutive windows. For each "yes" neuron (stimulus- and delay-related), we determined the onset and duration of significant "hit" activity in response to salient stimulus-present trials. In parallel, for each "no" neuron (stimulus- and delay-related), we determined the onset and duration of significant "correct rejection" activity in response to trials with no stimulus. A Mann–Whitney $U$ test was used to compare these time values.

Neuronal activity of single cells is depicted by dot raster histograms (every line corresponds to a trial, and every dot represents an action potential) and spike density functions. Spike density functions were averaged over trials and convolved with a Gaussian kernel (bin width = 300 msec, step size = 1 msec) for illustrative purposes only.

For averaging the spike density functions of different neurons, we first normalized the firing rates by subtracting the baseline activity (firing rate in a 300-msec interval 300 msec to 0 msec before stimulus onset) and dividing by the standard deviation. The baseline activity (mean firing rate across all trials) of each neuron and its standard deviation was measured during the last 300 msec before sample onset.

To quantify the time course of information about stimulus intensity and subjective "yes" versus "no" responses, we performed a sliding-window percent explained variance ($\omega^2$ PEV) analysis. For that purpose, we merged stimulus-related and delay-related percept-related neurons. Neurons that had sufficient trial numbers of at least 10 trials for each trial category ("hits" in suprathreshold trials, "hits" and "misses" in near-threshold trials, and "correct rejections" and "false alarms" in no-stimulus trials) entered the analysis ($n = 21$ "yes" neurons and 41 "no" neurons). We used a sliding window of 400-msec duration and 10-msec step size. In each window, a two-factorial ANOVA (including suprathreshold "hit," near-threshold "hit," near-threshold "miss," and no-stimulus "correct rejection" trials) was calculated, and the resultant sums of squares were used to estimate the percentage of variance attributable to either the stimulus intensity or the "yes"/"no" response for each neuron. The $\omega^2$ was calculated as follows:

$$\omega 2 = \frac{SS_{\text{factor}} - df \times MSE}{SS_{\text{total}} + MSE}$$

where $SS_{\text{factor}}$ is the sum of squares for the factor stimulus intensity and subjective percept ("yes"/"no" response), respectively; $SS_{\text{total}}$ is the total sum of squares; $df$ is the degrees of freedom, and $MSE$ is the mean squared error. This was repeated 1000 times and then averaged. We then took the average across the individual neurons yielding a population estimate of the average percentage of variance explained by each factor.

A support vector machine (SVM) classifier was used to investigate whether the activity of a neuronal population in near-threshold trials can be used to predict the decision in supra-threshold "hit" and no-stimulus "correct rejection" trials. This was done with the same neuronal populations that were used for the PEV analysis and had at least 10 trials for each trial category ("hits" in suprathreshold trials, "hits" and "misses" in near-threshold trials, and "correct rejections" and "false alarms" in no-stimulus trials). We trained the classifier in sliding windows (400-msec length, 10-msec step size) on the firing rates of "yes" and "no" responses in near-threshold trials to exclude the factor stimulus. For each window, we used the firing rates of the neurons in 10 randomly drawn near-threshold "hit" and "miss" trials, respectively. The trained classifier was then used to predict the labels of 10 randomly drawn suprathreshold "hit" trials and 10 no-stimulus "correct rejection" trials. We calculated the percentage of "yes" predictions as a measure for decision information in the tested trials. We repeated the classifier training and prediction 1000 times with newly drawn trials and calculated the mean proportion of "yes" predictions.

# RESULTS

Two carrion crows were trained in a rule-based delayed detection task to report the presence or absence of visual
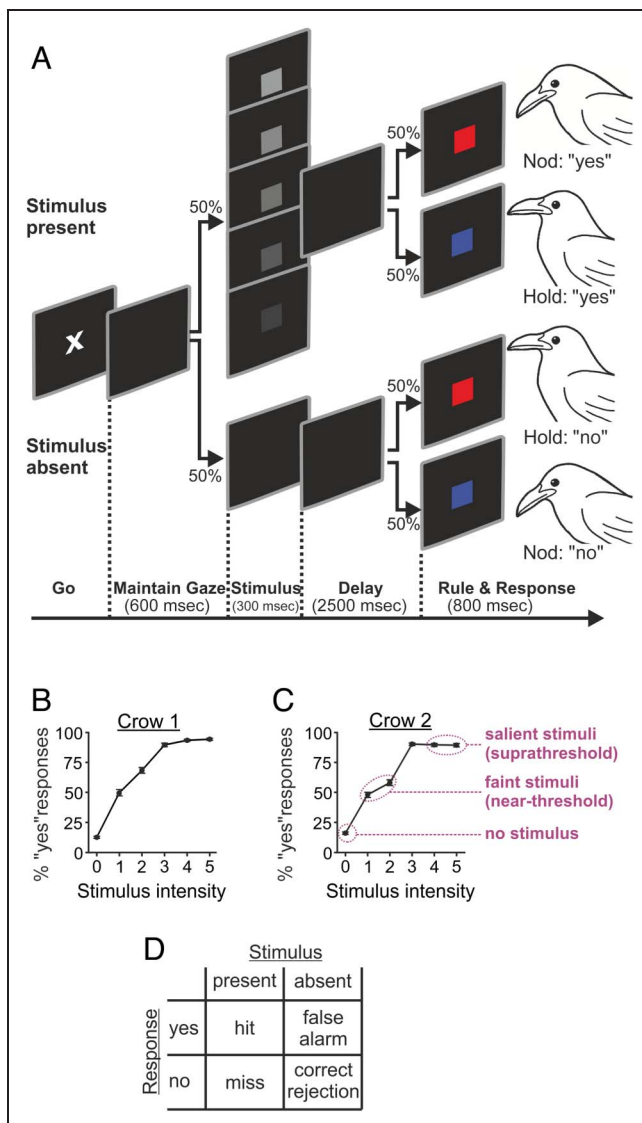
**Figure 1.** Task design and behavioral performance. (A) Visual detection task. After the crow initiated a trial in the go period, a brief visual stimulus of variable intensity appeared in 50% of the trials (stimulus present), whereas no stimulus appeared in the other half of the trials (stimulus absent). After a delay period, a rule cue informed the crow how to respond if it had seen or had not seen the stimulus. In stimulus trials (top), a red cue required a nodding response for stimulus detection ("yes"), whereas a blue cue required the crow to hold still for stimulus detection. In stimulus-absent trials (bottom), the rule–response contingencies were inverted. (B, C) Psychometric functions of Crow 1 (B) and Crow 2 (C). Error bars indicate *SEM*. Lilac ellipses illustrate the grouping of stimulus intensities into suprathreshold, near-threshold, and no-stimulus trials. (D) Signal detection theory classifies an observer's behavior at detection threshold, given two stimulus conditions (stimulus present or absent) and two possible responses ("yes, stimulus present" and "no, stimulus absent").

stimuli (Figure 1A). In half of the trials, a stimulus in five different intensity values around the crows' perceptual threshold (with intermediate stimulus intensities individually adjusted for each crow to result in a sigmoidal psychometric function) was presented, whereas a stimulus was absent in the other half of the trials. At perceptual

threshold, the crows' conscious percept was endogenously determined; a stimulus of identical intensity was sometimes seen and other times not perceived. The crows had to wait during a delay period until a rule cue informed them about how to report their percept. Therefore, the crows were unable to prepare motor responses before the rule cues, which precluded report-related processes. This allowed us to explore neuronal activity related to subjective sensory experience and its accessibility during the delay period.

## Behavior

The crows' behavioral accuracy (percent correct "yes" responses) was plotted as a function of stimulus intensity to result in a classical psychometric function (Figure 1B and C). Depending on the crows' accuracy, the trials were grouped into three categories: suprathreshold trials (presenting the two highest stimulus intensities), near-threshold trials (in which the two lowest stimulus intensities at perceptual threshold of about 50% hit rate were shown), and no-stimulus trials (without any stimulus shown; Figure 1C). The crows' responses were classified according to the framework of signal detection theory (Green & Swets, 1966): "hit" (correct "yes" response to a stimulus), "correct rejection" (correct "no" response for stimulus absence), "miss" (erroneous "no" response to stimulus presence), and "false alarm" (erroneous "yes" response for stimulus absence; Figure 1D). These response categories were later used to classify and compare neuronal activity during task performance.

## Neurophysiology

We recorded action potentials from a total of 480 neurons ($n = 174$ for Crow 1, $n = 306$ for Crow 2) in the NCL of the crows while they performed the task (Figure 1A; see Nieder et al., 2020). On the basis of a sliding-window analysis comparing firing rates for suprathreshold "hit" trials versus no-stimulus "correct rejection" trials in individual neurons (Mann–Whitney $U$ test, $p < .01$), we first isolated 262 task-selective neurons that showed selective trial intervals at some point during the stimulus and/or delay phase. According to the two most important trial phases in which report-independent subjective experiences about the stimulus situation occurred, we classified task-selective neurons into stimulus related ($n = 155$) and delay related ($n = 165$). Most neurons showed transient task-selective epochs but, as a population, spanned the entire trial period until rule cue presentation (see Figure 2A and B in Nieder et al., 2020).

Task-selective neurons may simply respond to the different intensities of the stimulus. To identify neurons that changed activity as a function of the crows' percept as reported later in the trial (later called "percept-related neurons"), we compared the discharges during the crows' "yes" versus "no" responses in near-threshold trials. If
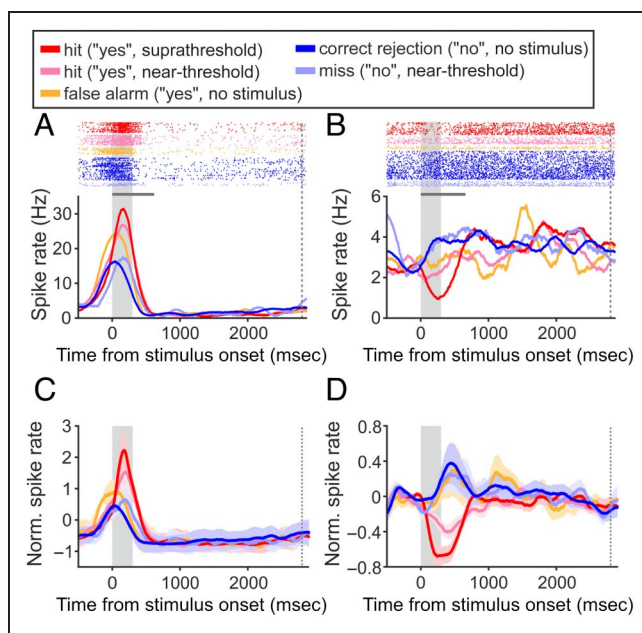
**Figure 2.** Activity of percept-related NCL neurons during stimulus presentation. (A) Activity of an example "yes" neuron. The top depicts dot raster histogram with each line corresponding to a trial and each dot corresponding to an action potential. The bottom represents the respective averaged spike density functions (smoothed by a 300-msec Gaussian kernel with a step size of 1 msec). Each curve corresponds to one of the five trial categories with warm (red, pink, and orange) colors indicating "yes" responses and cool (dark and light blue) colors indicating "no" responses. The gray-shaded area indicates stimulus presentation time; and the dashed vertical line, the end of the delay period (onset of response rule cue). The horizontal gray bar signifies the task-selective interval. (B) Activity of an example "no" neuron. Layout as in A. (C) Averaged, normalized activity of the population of all "yes" neurons ($n = 3$). Shaded regions indicate *SEM*. Color code and layout as in A. (D) Averaged, normalized activity of the population of all "no" neurons ($n = 17$). Shaded regions indicate *SEM*. Color code and layout as in A. Norm. = Normalized.

neurons are percept related and represent the crows' reported subjective experience, they are expected to change activity as a function of the crows' later report and irrespective of the identical stimulus intensity. In this case, firing rates in near-threshold trials during the crows' "yes" responses ("hits") should be similar to those during "yes" responses ("hits") in suprathreshold trials. In contrast, firing rates of percept-related neurons in near-threshold trials during the crows' "no" responses ("misses") should be similar to those during "no" responses ("correct rejections") in no-stimulus trials. Firing rates to "false alarms" were not included as additional criterion for the selection of percept-related neurons

because of activity noise caused by low trial counts. However, "false alarms" were analyzed qualitatively for the selected percept-related neurons.

### Activity of Percept-related Neurons

To objectively identify percept-related neurons, we applied the following statistical criteria in unison: First, firing rates in suprathreshold "hit" compared to no-stimulus "correct rejection" trials had to be significantly different ("task-selective neuron"; Mann–Whitney $U$ test, $p < .01$). Second, we performed an ROC analysis (i.e., a binary classifier) with firing rates taken from the selective trial intervals during "yes" versus "no" responses in near-threshold trials as well as for stimulus and delay periods separately. We derived the AUROCs as a distribution-free discriminability measure (Green & Swets, 1966). AUROC values ("choice probabilities") comparing near-threshold "hit" trials versus near-threshold "miss" trials had to be significantly different from 0.5 for percept-related neurons (permutation test, 1000 shuffled distributions, $p < .05$).

Neurons that met both criteria were classified into "yes" neurons if firing rates to "yes" responses were higher compared to "no" responses or "no" neurons if firing rates to "no" responses were higher compared to "yes" responses. Moreover, for a neuron to be classified as percept-related "yes" or "no" neuron, the firing rate changes for both comparisons had to concur for "yes" versus "no" responses; in other words, if a neuron increased its firing rate to suprathreshold "hits," it also had to increase its firing rate to near-threshold "hits" to be classified as a "yes" neuron, and vice versa for "no" neuron.

During the stimulus presentation phase, we found that 14% of the task-related neurons (21/155) were percept related (Table 1). Of those, three percept-related neurons showed higher firing rates to "yes" percepts (stimulus-present percept) compared to "no" percepts and were called "yes neurons." In contrast, 17 percept-related neurons exhibited higher firing rates to "no" percepts (stimulus-absent percept) compared to "yes" percepts and were called "no neurons." One neuron could not be assigned to either class. Two percept-related example neurons during the stimulus presentation period are shown in Figure 2A and B. Both neurons signaled the "yes" versus "no" percepts later reported by the crows and irrespective of the stimulus intensity in the different trial conditions. However, whereas the neuron in Figure 2A was a "yes" neuron and increased its firing rate for "yes" percepts, the neuron

**Table 1.** Number of "Yes" and "No" Neurons Among the Percept-related Neurons

| | Percept Related | "Yes" Neurons | "No" Neurons | Not Determinable |
|---|---|---|---|---|
| Stimulus related | 21 | 3 | 17 | 1 |
| Delay related | 47 | 19 | 28 | |

in Figure 2B qualified as a "no" neuron because it increased its firing rate to "no" percepts. This pattern of activation in example neurons was seen for the population of significant "yes" neurons (Figure 2C) and "no" neurons (Figure 2D).

During the delay phase, a significantly higher proportion of 28% (47/165) of the percept-related neurons was identified compared to the stimulus presentation period (chi-square test; $p = .001$). Here, more balanced numbers of 19 "yes" neurons and 28 "no" neurons were detected. Two percept-related example neurons during the delay period are shown in Figure 3A and B. Both neurons signaled the "yes" versus no" percepts irrespective of the stimulus intensity in the different trial conditions. The neuron in Figure 3A increased its firing rate for "yes" percepts and was classified as a "yes" neuron. In contrast, the neuron in Figure 3B increased its firing rate to "no" percepts and qualified as a "no" neuron. Activation during "false alarms" ("yes" percepts) was more similar to suprathreshold and near-threshold "hits," although no stimulus was presented. Similar patterns of overall activation as for the example neurons were seen for the population of significant "yes" neurons (Figure 3C) and "no" neurons (Figure 3D).

The negative deflection of activity for "hits" in "no" neurons (Figure 2B and D) could result from two different conditions: The deflection could reflect suppression

below the neurons' spontaneous activity; alternatively, neuronal firing could assume an increased tonic state with trial onset that is then switched off by stimulus appearance. We, therefore, compared the firing rates of individual neurons before the start of the trial with their activity after the onset of the trial but before stimulus appearance. If the neurons assume an elevated tonic state with trial onset, the firing rate is expected to be higher in the period before stimulus onset that we defined as baseline activity. We found that the firing rate in a 300-msec period before the start of a trial (400 msec to 100 msec before trial onset) was 5.68 Hz on average and indifferent from baseline activity of 5.59 Hz determined before the presentation of the stimulus (300 msec to 0 msec before stimulus onset; Wilcoxon signed-rank test, $p = .6617$, $n = 66$). This suggests that the neurons did not increase their firing rates to assume an increased tonic state in response to the absence of a stimulus. Rather, the suppression with perceived stimulus onset observed in "no" neurons (Figure 2B and D) reflects suppression below spontaneous activity in these neurons.

Next, we explored potential differences in onset latency of "yes" and "no" neurons. For each "yes" neuron (stimulus- and delay-related), we determined the onset and duration of significant "hit" activity in response to salient stimulus-present trials. Similarly, for each "no" neuron (stimulus- and delay-related), we determined the onset and duration of significant "correct rejection" activity in response to trials with no stimulus. We found that the onset latency of "yes" neurons (mean = 179 msec) was significantly shorter compared to the onset latency of "no" neurons (408 msec; Mann–Whitney $U$ test, two-tailed, $p = .0014$). No difference was detected for the duration of significant response intervals between both neuron types (Mann–Whitney $U$ test, two-tailed, $p = .1211$).

## Choice Probabilities

To quantify how well neurons discriminated the behaviorally relevant "yes" and "no" percepts irrespective of stimulus intensity, we calculated AUROC values for "yes" versus "no" responses (termed "choice probabilities"). To that aim, we compared the firing rates in near-threshold "hit" versus "miss" trials as well as "correct rejection" versus "false alarm" trials. As a reference, we also calculated the AUROC value for suprathreshold "hit" versus no-stimulus "correct rejection" trials. AUROC values of "no" neurons were, by definition, smaller than 0.5 and were rectified for further analysis. Choice probabilities were then assessed separately for percept-related neurons in the stimulus and delay periods. The choice probabilities (gray columns in Figure 4) were plotted relative to the reference AUROC values (suprathreshold "hit" vs. no-stimulus "correct rejection" trials; black columns in Figure 4).

In the stimulus presentation period, the reference AUROC values ("hits" in suprathreshold trials vs. "correct rejections") were 0.82 for "yes" neurons (Figure 4A and C)
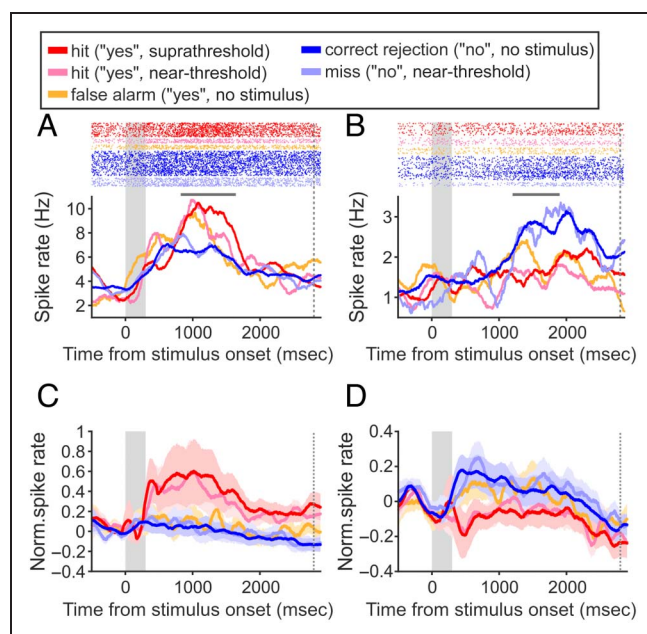


**Figure 3.** Activity of percept-related NCL neurons in the delay period. (A) Activity of an example "yes" neuron. Color code and layout as in Figure 2A. (B) Activity of an example "no" neuron. Color code and layout as in Figure 2A. (C) Averaged, normalized activity of the population of all "yes" neurons ($n = 19$). Shaded regions indicate *SEM*. Color code and layout as in A. (D) Averaged, normalized activity of the population of all "no" neurons ($n = 28$). Shaded regions indicate *SEM*. Color code and layout as in A. Norm. = Normalized.
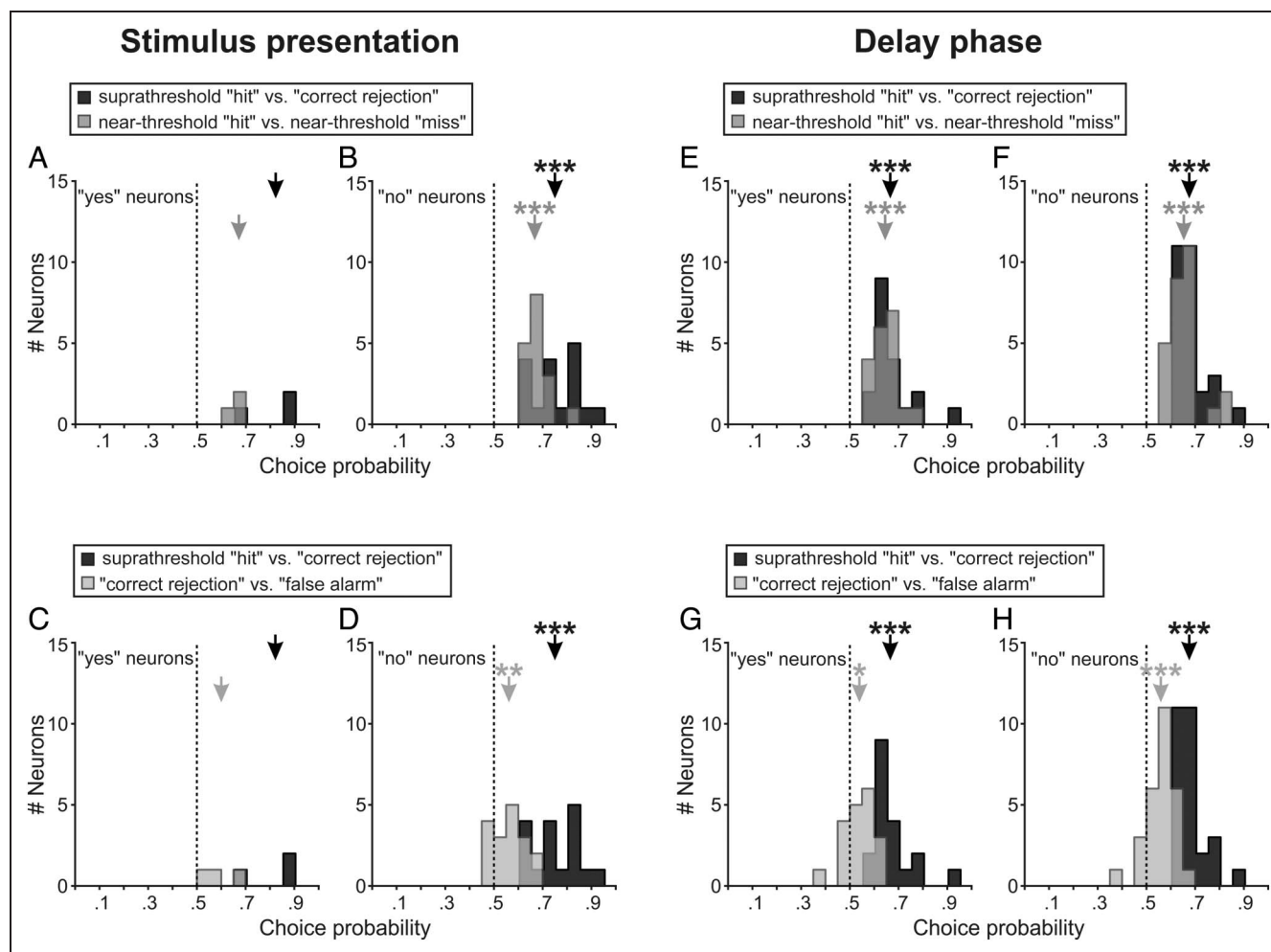
**Figure 4.** Choice probabilities of percept-related neurons. (A–D) Choice probabilities for percept-related neurons during stimulus presentation. (A) Reference AUROC values of "yes" neurons and their choice probabilities for near-threshold "hits" versus near-threshold "misses." Arrows indicate mean choice probabilities. Vertical dashed line depicts chance level at 0.5. (B) Reference AUROC values of "no" neurons and their choice probabilities for near-threshold "hits" versus near-threshold "misses." Asterisks indicate significant difference to chance level (one-sample Wilcoxon signed-rank test; \*\*\*$p < .001$, \*\*$p < .01$, \*$p < .05$). (C) Reference AUROC values of "yes" neurons and their choice probabilities for "correct rejections" versus "false alarms." (D) Reference AUROC values of "no" neurons and their choice probabilities for "correct rejections" versus "false alarms." (E–H) Choice probabilities for percept-related neurons during the delay phase. Same layout and trial conditions as in A–D.

and 0.75 for "no" neurons (Figure 4B and D), respectively, and were indifferent (Mann–Whitney $U$ test, $p = .24$). The reference ROC values of the "no" neurons were significantly higher than chance level (one-sample Wilcoxon signed-rank test, $p < .0003$, $n = 17$). The "yes" neurons could not be tested because of the low number of only three neurons. In addition, because of the low neuron numbers, the choice probabilities of the few "yes" neurons in the near-threshold "hit" versus near-threshold "miss" trials (mean = 0.67; Figure 4A) and the "correct rejection" versus "false alarm" trials (mean = 0.60; Figure 4C) were indifferent from chance level of 0.5 (one-sample Wilcoxon signed-rank test, $p = .25$, $n = 3$). However, the choice probabilities of the "no" neurons were significantly higher than the chance level of 0.5 in the near-threshold "hit" versus "miss" trials (mean = 0.67, one-sample Wilcoxon signed-rank test, $p < .0003$, $n = 17$; Figure 4B) and also for "correct rejection" versus "false alarm" trials (mean =

0.56, one-sample Wilcoxon signed-rank test, $p < .0057$, $n = 17$; Figure 4D).

In the delay period, the reference AUROC values of 0.67 for "yes" neurons (Figure 4E and G) and 0.68 for "no" neurons (Figure 4F and H), respectively, were indifferent (Mann–Whitney $U$ test, $p = .22$) but significantly above chance (one-sample Wilcoxon signed-rank test, both $ps < .0002$, $n = 28$ "yes" neurons and 19 "no" neurons). Furthermore, in the delay period, the choice probabilities of "yes" and "no" neurons in the near-threshold "hit" versus near-threshold "miss" trials were both significantly higher than chance (one-sample Wilcoxon signed-rank test, both $ps < .0002$, $n = 28$ "yes" neurons and 19 "no" neurons) and indifferent, with means of 0.64 and 0.65, respectively (Mann–Whitney $U$ test, $p = .74$; Figure 4E and F). Moreover, the choice probabilities of "yes" and "no" neurons in the "correct rejection" versus "false alarm" trials had similar means of 0.54 and 0.56, respectively

(Mann–Whitney $U$ test, $p = .23$), and were both higher than chance (one-sample Wilcoxon signed-rank test, "yes" neurons: $p < .013$, $n = 19$; "no" neurons: $p < .0002$, $n = 28$; Figure 4G and H). Taken together, both "yes" and "no" neurons in the delay period encoded the crows' subjective percept irrespective of stimulus intensity in ambiguous trials. A higher proportion of neurons turned out to be percept related during the delay period compared to the stimulus presentation period, and "yes" and "no" neurons were more balanced during the delay period than during the stimulus presentation period.

### Neuron Population Analyses

Next, we quantified how much information about the subjective report as opposed to stimulus intensity was carried by the separate populations of "yes" and "no" neurons throughout the trial. To that aim, we merged the percept-related neurons with sufficient trial numbers in the stimulus and delay periods and calculated the $\omega^2$ PEV in sliding windows throughout the trial. For the population of "yes" neurons ($n = 21$), the information about stimulus intensity and subjective experience oscillated until the end of the delay. Briefly before the onset of the response rule, information about stimulus intensity had vanished, whereas subjective experience information increased notably shortly before the crows reported their percept (Figure 5A). For "no" neurons ($n = 41$), the presentation of the stimulus elicited a sharp increase of information about the stimulus intensity, followed by a slightly delayed increase of information about the subjective report (Figure 5B). After a decay during the first half of the delay, information about the subjective report

increased again toward the end of the delay, whereas stimulus information had vanished.

Finally, we tested with a decoding analysis whether the subjective report in suprathreshold "hit" and no-stimulus "correct rejection" trials can be predicted separately by "yes" and "no" neurons in near-threshold trials. Assuming that a percept-related neuron encodes the subjective report, its firing rates should be similar according to the subjective experience and thus predictive of the report irrespective of the stimulus intensity. To investigate this, we trained an SVM classifier using the same separate neuronal populations as before ($n = 21$ "yes" neurons and 41 "no" neurons). We trained the classifier on firing rates of "yes" and "no" responses in near-threshold trials and then tested it on the firing rates in suprathreshold "hit" and no-stimulus "correct rejection" trials of the same neuronal population.

On the basis of the population of "yes" neurons, the classifier labeled "yes" and "no" responses with highest accuracy shortly after stimulus presentation and at the end of the delay (Figure 6A). At these time points, the difference between "yes" predictions to firing rates in suprathreshold "hit" and no-stimulus "correct rejection" trials was greatest (Figure 6B). In addition, training the classifier on the activity of the population of "no" neurons in near-threshold trials yielded the highest prediction accuracy for "yes" responses in suprathreshold "hit" and no-stimulus "correct rejection" trials shortly after stimulus presentation and, after a drop-off, increasingly in the second half of the delay (Figure 6C). Apart from more pronounced accuracy after stimulus onset, the time course of the accuracy of "yes" predictions was comparable for "yes" neurons (Figure 6B) and "no" neurons (Figure 6D).
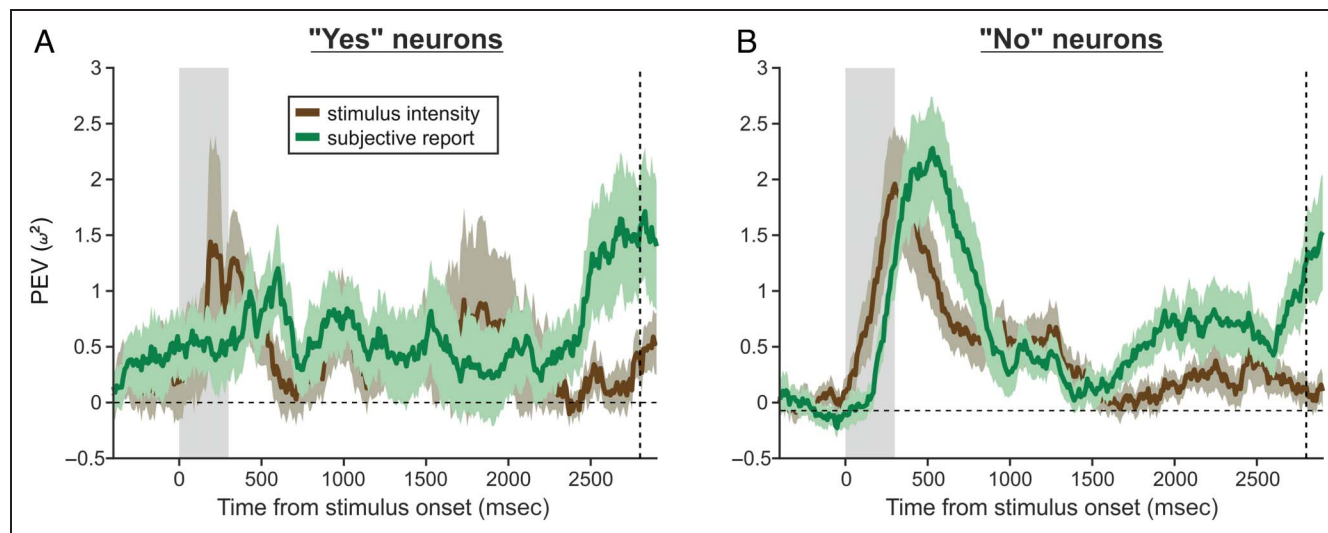


**Figure 5.** Time-resolved PEV analysis. (A) Time course of information about stimulus intensity and subjective report carried by the activity of "yes" neurons ($n = 21$) throughout a trial. Colored shadings indicate *SEM* across the neurons. Gray-shaded area depicts stimulus presentation time; and vertical dashed line, the end of the delay (onset of response rule cue). (B) Same as in A but for the population of "no" neurons ($n = 41$).
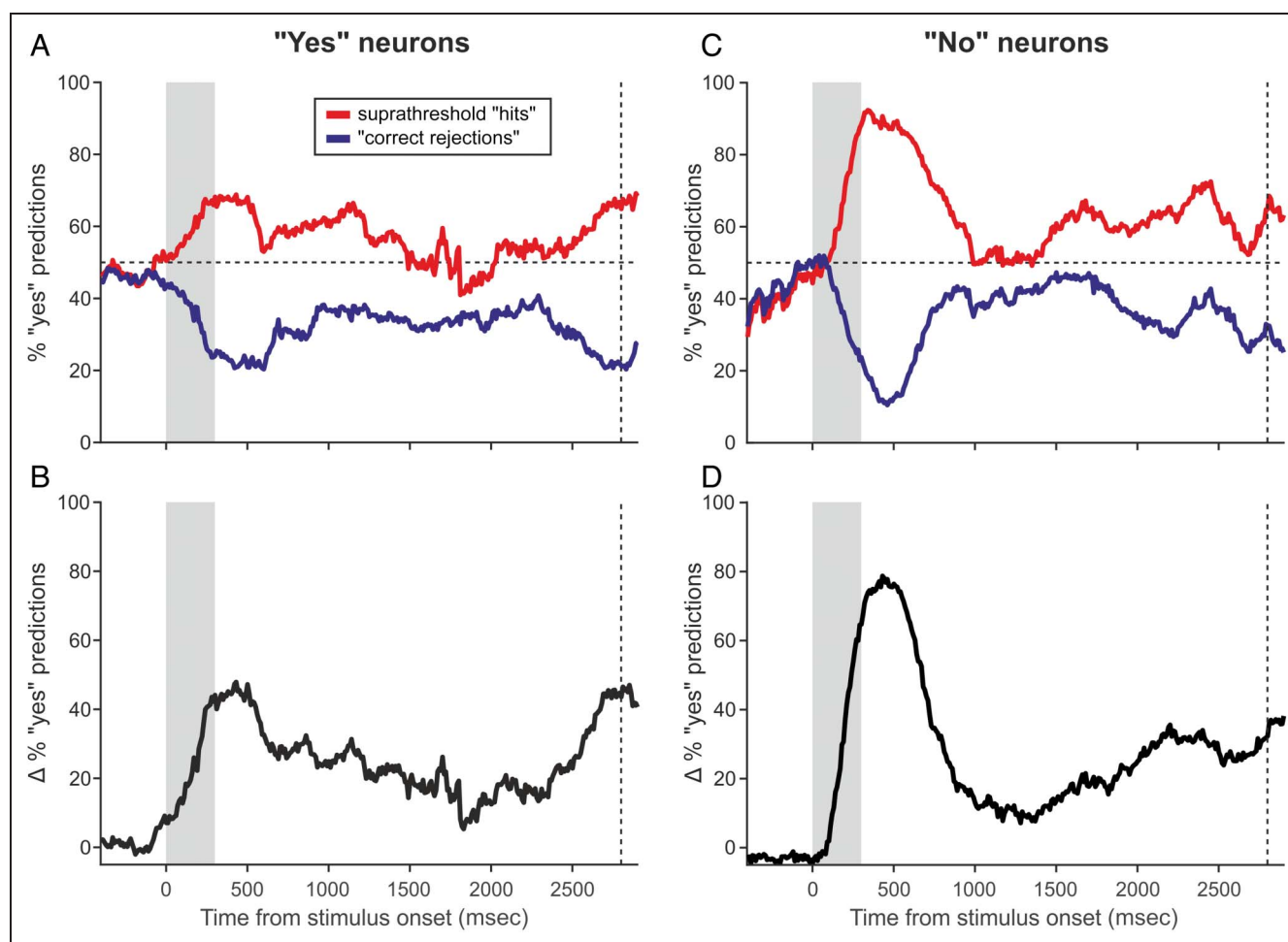
**Figure 6.** Classification accuracy of an SVM classifier. (A) Proportion of assigned "yes" labels to firing rates of "yes" neurons ($n = 21$) in suprathreshold "hit" trials and no-stimulus "correct rejection" trials of an SVM classifier, which was trained on the firing rates of "yes" and "no" responses in near-threshold trials. Horizontal dashed line indicates chance level at 50%. Gray-shaded area depicts stimulus presentation time, and vertical dashed line indicates end of the delay (onset of response rule cue). (B) Difference between the proportions of assigned "yes" labels to suprathreshold "hit" and no-stimulus "correct rejection" trials shown in A. (C) Same as in A but for the population of "no" neurons ($n = 41$). (D) Same as in B but for the population of "no" neurons ($n = 41$).

## DISCUSSION

We trained crows to report the presence or absence of low-contrast images presented near to visual threshold (note that this process only requires awareness; it does not require self-awareness or metacognition of experience). Neuronal activity tracking the conscious percept (i.e., present or absent) was dissociated from that involved in planning a motor response by use of a poststimulus response rule cue that varied from trial to trial. Distinct populations of "yes" and "no" neurons signaled the subjective percepts of "seen" versus "unseen," respectively. Importantly, the magnitude of activation of these two neuron populations was similar in timing and strength. This suggests a balanced encoding of awareness in the crow NCL by neurons actively signaling subjective stimulus presence and absence.

The shorter onset latency of "yes" neurons compared to "no" neurons suggests that the neuronal activation of "yes" neurons to the onset of a seen stimulus was temporally more precise and thus faster compared to the activation related to stimulus absence in "no" neurons. For "no" neurons, responses to the absence of a stimulus may be less precise and potentially more variable from trial to trial (Ganupuru, Goldring, Harun, & Hanks, 2019).

### Active Encoding of Percepts About Stimulus Absence in the Brain

A main finding of the current study is that a distinct population of "no" neurons in the crow NCL actively encoded the crows' perceived absence of stimuli by firing rate increases. This is a remarkable finding as it is commonly assumed that only the perceived presence of stimuli is actively encoded by increasing firing rates of neurons (de Lafuente & Romo, 2005, 2006). According to this common assumption, only the conscious presence of a stimulus is signaled by neurons that accumulate positive stimulus evidence until an upper threshold is reached that

causes a conscious stimulus-present percept; the conscious no-stimulus percept is supposed to be represented by the absence of specific neuronal activity equivalent to resting state activity (Pereira et al., 2022).

In line with our finding, previous studies reported that a behaviorally relevant lack of sensory evidence favoring perceived absence of a stimulus may also be actively encoded by neurons in cortical association areas of non-human primates, animals known to show visual awareness (Ben-Haim et al., 2021). Neurons in the dorsolateral pFC of macaque monkeys reporting the subjective presence or absence of visual stimuli actively signal the perceived absence of a stimulus (Merten & Nieder, 2012). Such stimulus-absence signals in pFC are predominantly found during the delay period after a missed stimulus (Merten & Nieder, 2012). Similar findings were reported in single-neuron recordings in posterior parietal cortex of human patients with epilepsy while they detected weak and unpredictable vibrotactile stimuli (Pereira et al., 2021). In this human study, some neurons showed a higher increase in firing rates for misses compared to hits, raising the intriguing possibility that missed/absent percepts are encoded actively also in the human brain (Pereira et al., 2021). These empirical findings agree with models of awareness states that postulate symmetric/balanced encoding of presence and absence experiences (Fleming, 2020, 2021). Together, these data call for a greater focus on examining percepts and decisions about stimulus absence. These findings also question whether absence percepts can be used as a baseline or control condition in studies of perceptual awareness, as is often done.

## Temporal Two-stage Process of Sensory Consciousness

Our results in crows suggest a temporal two-stage process in sensory consciousness. NCL "yes"- and "no"-neuron populations change from initially predominantly encoding stimulus intensity to mainly representing the crows' subjective experience later in the trial and before a behavioral report is required. Notably, the active coding of the "stimulus absence" percept primarily emerged during the delay phase when the crows' subjective percept was maintained until the response type was instructed. This suggests a postsensory, cognitive processing stage in which the categorical "no" signal arose.

This activation cascade is reminiscent to results in the primate cerebral cortex; here, the early activity is also primarily involved in unconscious vision, whereas neuronal responses associated with subjective experiences are delayed relative to stimulus onset (Quiroga et al., 2008; de Lafuente & Romo, 2006; Supèr, Spekreijse, & Lamme, 2001; Lamme & Roelfsema, 2000; Thompson & Schall, 1999). This two-stage process in conscious perception may constitute a general principle of how sensory awareness is realized in the vertebrate brain.

The two-stage process can, in principle, be explained by the "global neuronal workspace theory" (Dehaene & Changeux, 2011; Baars, 2002). This neurobiological conception of consciousness theorizes that only intensive enough sensory activity is able to access awareness by eliciting a network state called "global ignition" in higher brain centers such as the primate pFC. The NCL would be the ideal site for such an "ignition" because—like pFC in the primate brain—it operates at the apex of the telencephalic processing hierarchy in the avian brain (Nieder, 2017; Güntürkün, 2005). This "all-or-none ignition" event results in stimulus-driven activity to become persistent in recurrent and interconnected brain networks, even after the stimulus itself has vanished (Mashour, Roelfsema, Changeux, & Dehaene, 2020; van Vugt et al., 2018). This can explain why percept-related activity in NCL is seen in the delay phase after the brief stimulus has ceased.

As an elaboration and extension of the original "global neuronal workspace theory," our findings suggest that sensed stimulus energy is not the only trigger that can lead to an ignition of large-scale networks when causing "stimulus presence" percepts. Rather, the absence of stimuli can also ignite brain networks by sufficient activation of pools of "no" neurons to cause explicit "stimulus absence" experiences, as long as "nothing" is a behaviorally relevant category. As "no" neurons cannot be excited by incoming stimulus energy (which is lacking by definition for absent stimuli), brain-internal mechanisms must excite (or disinhibit) "no" neurons to signal conscious "absence" states as subjective categorical representation. The precise mechanisms of how "no" neurons become activated needs to be deciphered in the future.

## "Nothing" Represented as a Behavioral Category

In our behavioral protocol, not only the presence but also the absence of stimuli was behaviorally relevant and needed to be reported by the crows. Therefore, "nothing" became a behavioral category and as such was most likely needed to be actively encoded by neurons. This categorical active "absence" signal is reminiscent of quantitative empty-set representations (Nieder, 2016). Neurons in the crow (Kirschhock, Ditz, & Nieder, 2021) and monkey brain (Ramirez-Cardenas & Nieder, 2019; Ramirez-Cardenas, Moskaleva, & Nieder, 2016; Okuyama, Kuki, & Mushiake, 2015) are tuned to the preferred numerosity zero (i.e., the empty set). Numerosity-zero-tuned neurons respond with a maximum discharge to numerosity zero and show a progressive drop-off of activity toward higher numerosities. Neurons tuned to zero even emerge spontaneously in deep neural networks of object discrimination (Nasr & Nieder, 2021).

Both "stimulus absence" and "empty set" activity require a transformation from a sensory "no-event" to an internally generated, categorical representation, probably through trial-and-error reinforcement learning. A cortical

circuit model exemplified how category selectivity could arise from reinforcement learning (Engel, Chaisangmongkon, Freedman, & Wang, 2015). This model posits that systematic correlations between trial-to-trial fluctuations of firing rates and the accompanying reward after appropriate behavioral choices cause neurons that progressively become category selective (Engel et al., 2015). According to this model, even initially nonselective neurons developed categorical tuning, as long as they exhibit firing rate fluctuations that correlated with behavioral choices. Thus, when a crow learns to explicitly respond to "nothing" or numerosity zero to receive a reward, this mechanism might suffice to produce neurons that respond actively to "no" percepts and numerical zero categories.

## Neurobiological Principles of Sensory Consciousness Across Evolution

Our findings in crows can also inform the neurobiological principles of sensory consciousness across evolution (Nieder, 2022; Nieder et al., 2020). Birds diverged from the mammalian lineage 320 million years ago (Hedges, 2002; Kumar & Hedges, 1998). Since then, birds evolved radically different endbrain structures (Jarvis et al., 2005). Nevertheless, some birds, notably members of the corvid songbird family (crows, ravens, jays), show sophisticated cognitive behaviors such as endogenous attention (Hahner & Nieder, 2023; Quest, Rinnert, Hahner, & Nieder, 2022) and robust working memory (Wagener, Rinnert, Veit, & Nieder, 2023; Liao, Brecht, Johnston, & Nieder, 2022; Smirnova, Zorina, Obozova, & Wasserman, 2015; Veit & Nieder, 2013) indicative of conscious experiences (Nieder, 2022, 2023; Nieder et al., 2020). In contrast to mammals, the crow telencephalon—and the NCL in particular—is lacking a layered neocortex and has instead evolved a nuclear anatomical arrangement with surprisingly high associative neuron numbers (Kersten et al., 2022; Ströckens et al., 2022; Olkowicz et al., 2016). Our data suggest that the active coding of both stimulus presence and absence is a computational principle for sensory consciousness irrespective of the precise anatomical layout and across remotely related phylogenetic taxa (Nieder, 2021).

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## Data Availability Statement

Code is available from the corresponding author upon reasonable request. All behavioral and electrophysiological data are archived at the Institute of Neurobiology, University of Tübingen, Germany.

## Author Contributions

A. N. and L. W. designed and conducted the experiments, analyzed the data, and wrote the article. A. N. supervised the study.

## Diversity in Citation Practices

Retrospective analysis of the citations in every article published in this journal from 2010 to 2021 reveals a persistent pattern of gender imbalance: Although the proportions of authorship teams (categorized by estimated gender identification of first author/last author) publishing in the *Journal of Cognitive Neuroscience* (*JoCN*) during this period were M(an)/M = .407, W(oman)/M = .32, M/W = .115, and W/W = .159, the comparable proportions for the articles that these authorship teams cited were M/M = .549, W/M = .257, M/W = .109, and W/W = .085 (Postle and Fulvio, *JoCN*, 34:1, pp. 1 -3). Consequently, *JoCN* encourages all authors to consider gender balance explicitly when selecting which articles to cite and gives them the opportunity to report their article's gender citation balance.

## REFERENCES

Baars, B. J. (2002). The conscious access hypothesis: Origins and recent evidence. *Trends in Cognitive Sciences*, 6, 47–52. https://doi.org/10.1016/S1364-6613(00)01819-2, PubMed: 11849615

Ben-Haim, M. S., Dal Monte, O., Fagan, N. A., Dunham, Y., Hassin, R. R., Chang, S. W. C., et al. (2021). Disentangling perceptual awareness from nonconscious processing in rhesus monkeys (Macaca mulatta). *Proceedings of the National Academy of Sciences, U.S.A.*, 118, e2017543118. https://doi.org/10.1073/pnas.2017543118, PubMed: 33785543

Britten, K. H., Newsome, W. T., Shadlen, M. N., Celebrini, S., & Movshon, J. A. (1996). A relationship between behavioral choice and the visual responses of neurons in macaque MT. *Visual Neuroscience*, 13, 87–100. https://doi.org/10.1017/S095252380000715X, PubMed: 8730992

Colquitt, B. M., Merullo, D. P., Konopka, G., Roberts, T. F., & Brainard, M. S. (2021). Cellular transcriptomics reveals evolutionary identities of songbird vocal circuits. *Science*, 371, eabd9704. https://doi.org/10.1126/science.abd9704, PubMed: 33574185

de Lafuente, V., & Romo, R. (2005). Neuronal correlates of subjective sensory experience. *Nature Neuroscience*, 8, 1698–1703. https://doi.org/10.1038/nn1587, PubMed: 16286929

de Lafuente, V., & Romo, R. (2006). Neural correlate of subjective sensory experience gradually builds up across cortical areas. *Proceedings of the National Academy of Sciences, U.S.A.*, 103, 14266–14271. https://doi.org/10.1073/pnas.0605826103, PubMed: 16924098

Dehaene, S., & Changeux, J.-P. (2011). Experimental and theoretical approaches to conscious processing. *Neuron*, *70*, 200–227. https://doi.org/10.1016/j.neuron.2011.03.018, PubMed: 21521609

Ehret, G., & Romand, R. (2022). Awareness and consciousness in humans and animals—Neural and behavioral correlates in an evolutionary perspective. *Frontiers in Systems Neuroscience*, *16*, 941534. https://doi.org/10.3389/fnsys.2022.941534, PubMed: 35910003

Engel, T. A., Chaisangmongkon, W., Freedman, D. J., & Wang, X.-J. (2015). Choice-correlated activity fluctuations underlie learning of neuronal category representation. *Nature Communications*, *6*, 6454. https://doi.org/10.1038/ncomms7454, PubMed: 25759251

Fleming, S. M. (2020). Awareness as inference in a higher-order state space. *Neuroscience of Consciousness*, *2020*, niz020. https://doi.org/10.1093/nc/niz020, PubMed: 32190350

Fleming, S. M. (2021). Theories of consciousness are solutions in need of problems. *Cognitive Neuroscience*, *12*, 86–88. https://doi.org/10.1080/17588928.2020.1841744, PubMed: 33176555

Ganupuru, P., Goldring, A. B., Harun, R., & Hanks, T. D. (2019). Flexibility of timescales of evidence evaluation for decision making. *Current Biology*, *29*, 2091–2097. https://doi.org/10.1016/j.cub.2019.05.037, PubMed: 31178325

Gelbard-Sagiv, H., Mudrik, L., Hill, M. R., Koch, C., & Fried, I. (2018). Human single neuron activity precedes emergence of conscious perception. *Nature Communications*, *9*, 2057. https://doi.org/10.1038/s41467-018-03749-0, PubMed: 29802308

Green, D. M., & Swets, J. A. (1966). *Signal detection theory and psychophysics* (Vol. 1, pp. 1969–2012). New York: Wiley.

Güntürkün, O. (2005). The avian 'prefrontal cortex' and cognition. *Current Opinion in Neurobiology*, *15*, 686–693. https://doi.org/10.1016/j.conb.2005.10.003, PubMed: 16263260

Hahner, L., & Nieder, A. (2023). Costs and benefits of voluntary attention in crows. *Royal Society Open Science*, *10*, 230517. https://doi.org/10.1098/rsos.230517, PubMed: 37593715

Hedges, S. B. (2002). The origin and evolution of model organisms. *Nature Reviews Genetics*, *3*, 838–849. https://doi.org/10.1038/nrg929, PubMed: 12415314

Hesse, J. K., & Tsao, D. Y. (2020). A new no-report paradigm reveals that face cells encode both consciously perceived and suppressed stimuli. *eLife*, *9*, e58360. https://doi.org/10.7554/eLife.58360, PubMed: 33174836

Jarvis, E. D., Güntürkün, O., Bruce, L., Csillag, A., Karten, H., Kuenzel, W., et al. (2005). Avian brains and a new understanding of vertebrate brain evolution. *Nature Reviews Neuroscience*, *6*, 151–159. https://doi.org/10.1038/nrn1606, PubMed: 15685220

Kapoor, V., Dwarakanath, A., Safavi, S., Werner, J., Besserve, M., Panagiotaropoulos, T. I., et al. (2022). Decoding internally generated transitions of conscious contents in the prefrontal cortex without subjective reports. *Nature Communications*, *13*, 1535. https://doi.org/10.1038/s41467-022-28897-2, PubMed: 35318323

Kersten, Y., Friedrich-Müller, B., & Nieder, A. (2022). A brain atlas of the carrion crow (Corvus corone). *Journal of Comparative Neurology*, *530*, 3011–3038. https://doi.org/10.1002/cne.25392, PubMed: 35938778

Kirschhock, M. E., Ditz, H. M., & Nieder, A. (2021). Behavioral and neuronal representation of numerosity zero in the crow. *Journal of Neuroscience*, *41*, 4889–4896. https://doi.org/10.1523/JNEUROSCI.0090-21.2021, PubMed: 33875573

Koch, C., Massimini, M., Boly, M., & Tononi, G. (2016). Neural correlates of consciousness: Progress and problems. *Nature Reviews Neuroscience*, *17*, 307–321. https://doi.org/10.1038/nrn.2016.22, PubMed: 27094080

Kreiman, G., Fried, I., & Koch, C. (2002). Single-neuron correlates of subjective vision in the human medial temporal lobe. *Proceedings of the National Academy of Sciences, U.S.A.*, *99*, 8378–8383. https://doi.org/10.1073/pnas.072194099, PubMed: 12034865

Kumar, S., & Hedges, S. B. (1998). A molecular timescale for vertebrate evolution. *Nature*, *392*, 917–920. https://doi.org/10.1038/31927, PubMed: 9582070

Lamme, V. A., & Roelfsema, P. R. (2000). The distinct modes of vision offered by feedforward and recurrent processing. *Trends in Neurosciences*, *23*, 571–579. https://doi.org/10.1016/S0166-2236(00)01657-X, PubMed: 11074267

Laureys, S. (2005). The neural correlate of (un)awareness: Lessons from the vegetative state. *Trends in Cognitive Sciences*, *9*, 556–559. https://doi.org/10.1016/j.tics.2005.10.010, PubMed: 16271507

Leopold, D. A., & Logothetis, N. K. (1996). Activity changes in early visual cortex reflect monkeys' percepts during binocular rivalry. *Nature*, *379*, 549–553. https://doi.org/10.1038/379549a0, PubMed: 8596635

Liao, D. A., Brecht, K. F., Johnston, M., & Nieder, A. (2022). Recursive sequence generation in crows. *Science Advances*, *8*, eabq3356. https://doi.org/10.1126/sciadv.abq3356, PubMed: 36322648

Logothetis, N. K., & Schall, J. D. (1989). Neuronal correlates of subjective visual perception. *Science*, *245*, 761–763. https://doi.org/10.1126/science.2772635, PubMed: 2772635

Mashour, G. A., Roelfsema, P., Changeux, J.-P., & Dehaene, S. (2020). Conscious processing and the global neuronal workspace hypothesis. *Neuron*, *105*, 776–798. https://doi.org/10.1016/j.neuron.2020.01.026, PubMed: 32135090

Merten, K., & Nieder, A. (2012). Active encoding of decisions about stimulus absence in primate prefrontal cortex neurons. *Proceedings of the National Academy of Sciences, U.S.A.*, *109*, 6289–6294. https://doi.org/10.1073/pnas.1121084109, PubMed: 22460793

Nagel, T. (1974). What is it like to be a bat. *Philosophical Review*, *83*, 435–450. https://doi.org/10.2307/2183914

Nasr, K., & Nieder, A. (2021). Spontaneous representation of numerosity zero in a deep neural network for visual object recognition. *iScience*, *24*, 103301. https://doi.org/10.1016/j.isci.2021.103301, PubMed: 34765921

Nieder, A. (2016). Representing something out of nothing: The dawning of zero. *Trends in Cognitive Sciences*, *20*, 830–842. https://doi.org/10.1016/j.tics.2016.08.008, PubMed: 27666660

Nieder, A. (2017). Inside the corvid brain—Probing the physiology of cognition in crows. *Current Opinion in Behavioral Sciences*, *16*, 8–14. https://doi.org/10.1016/j.cobeha.2017.02.005

Nieder, A. (2021). Consciousness without cortex. *Current Opinion in Neurobiology*, *71*, 69–76. https://doi.org/10.1016/j.conb.2021.09.010, PubMed: 34656051

Nieder, A. (2022). In search for consciousness in animals: Using working memory and voluntary attention as behavioral indicators. *Neuroscience & Biobehavioral Reviews*, *142*, 104865. https://doi.org/10.1016/j.neubiorev.2022.104865, PubMed: 36096205

Nieder, A. (2023). Neuroscience of cognitive control in crows. *Trends in Neurosciences*, *46*, 783–785. https://doi.org/10.1016/j.tins.2023.07.002, PubMed: 37524636

Nieder, A., Wagener, L., & Rinnert, P. (2020). A neural correlate of sensory consciousness in a corvid bird. *Science*, *369*, 1626–1629. https://doi.org/10.1126/science.abb1447, PubMed: 32973028

Okuyama, S., Kuki, T., & Mushiake, H. (2015). Representation of the numerosity 'zero' in the parietal cortex of the monkey.

*Scientific Reports*, *5*, 10059. https://doi.org/10.1038/srep10059, PubMed: 25989598

Olkowicz, S., Kocourek, M., Lučan, R. K., Porteš, M., Fitch, W. T., Herculano-Houzel, S., et al. (2016). Birds have primate-like numbers of neurons in the forebrain. *Proceedings of the National Academy of Sciences, U.S.A.*, *113*, 7255–7260. https://doi.org/10.1073/pnas.1517131113, PubMed: 27298365

Panagiotaropoulos, T. I., Deco, G., Kapoor, V., & Logothetis, N. K. (2012). Neuronal discharges and gamma oscillations explicitly reflect visual consciousness in the lateral prefrontal cortex. *Neuron*, *74*, 924–935. https://doi.org/10.1016/j.neuron.2012.04.013, PubMed: 22681695

Pereira, M., Megevand, P., Tan, M. X., Chang, W., Wang, S., Rezai, A., et al. (2021). Evidence accumulation relates to perceptual consciousness and monitoring. *Nature Communications*, *12*, 3261. https://doi.org/10.1038/s41467-021-23540-y, PubMed: 34059682

Pereira, M., Perrin, D., & Faivre, N. (2022). A leaky evidence accumulation process for perceptual experience. *Trends in Cognitive Sciences*, *26*, 451–461. https://doi.org/10.1016/j.tics.2022.03.003, PubMed: 35382993

Quest, M., Rinnert, P., Hahner, L., & Nieder, A. (2022). Exogenous and endogenous spatial attention in crows. *Proceedings of the National Academy of Sciences, U.S.A.*, *119*, e2205515119. https://doi.org/10.1073/pnas.2205515119, PubMed: 36442123

Quiroga, R. Q., Mukamel, R., Isham, E. A., Malach, R., & Fried, I. (2008). Human single-neuron responses at the threshold of conscious recognition. *Proceedings of the National Academy of Sciences, U.S.A.*, *105*, 3599–3604. https://doi.org/10.1073/pnas.0707043105, PubMed: 18299568

Ramirez-Cardenas, A., Moskaleva, M., & Nieder, A. (2016). Neuronal representation of numerosity zero in the primate parieto-frontal number network. *Current Biology*, *26*, 1285–1294. https://doi.org/10.1016/j.cub.2016.03.052, PubMed: 27112297

Ramirez-Cardenas, A., & Nieder, A. (2019). Working memory representation of empty sets in the primate parietal and prefrontal cortices. *Cortex*, *114*, 102–114. https://doi.org/10.1016/j.cortex.2019.02.028, PubMed: 30975433

Reber, T. P., Faber, J., Niediek, J., Boström, J., Elger, C. E., & Mormann, F. (2017). Single-neuron correlates of conscious perception in the human medial temporal lobe. *Current Biology*, *27*, 2991–2998. https://doi.org/10.1016/j.cub.2017.08.025, PubMed: 28943091

Smirnova, A., Zorina, Z., Obozova, T., & Wasserman, E. (2015). Crows spontaneously exhibit analogical reasoning. *Current Biology*, *25*, 256–260. https://doi.org/10.1016/j.cub.2014.11.063, PubMed: 25532894

Ströckens, F., Neves, K., Kirchem, S., Schwab, C., Herculano-Houzel, S., & Güntürkün, O. (2022). High associative neuron numbers could drive cognitive performance in corvid species. *Journal of Comparative Neurology*, *530*, 1588–1605. https://doi.org/10.1002/cne.25298, PubMed: 34997767

Supèr, H., Spekreijse, H., & Lamme, V. A. (2001). Two distinct modes of sensory processing observed in monkey primary visual cortex (V1). *Nature Neuroscience*, *4*, 304–310. https://doi.org/10.1038/85170, PubMed: 11224548

Thompson, K. G., & Schall, J. D. (1999). The detection of visual signals by macaque frontal eye field during masking. *Nature Neuroscience*, *2*, 283–288. https://doi.org/10.1038/6398, PubMed: 10195223

Vallortigara, G. (2021). The efference copy signal as a key mechanism for consciousness. *Frontiers in Systems Neuroscience*, *15*, 765646. https://doi.org/10.3389/fnsys.2021.765646, PubMed: 34899201

Veit, L., & Nieder, A. (2013). Abstract rule neurons in the endbrain support intelligent behaviour in corvid songbirds. *Nature Communications*, *4*, 2878. https://doi.org/10.1038/ncomms3878, PubMed: 24285080

van Vugt, B., Dagnino, B., Vartak, D., Safaai, H., Panzeri, S., Dehaene, S., et al. (2018). The threshold for conscious report: Signal loss and response bias in visual and frontal cortex. *Science*, *360*, 537–542. https://doi.org/10.1126/science.aar7186, PubMed: 29567809

Wagener, L., Rinnert, P., Veit, L., & Nieder, A. (2023). Crows protect visual working memory against interference. *Journal of Experimental Biology*, *226*, jeb245453. https://doi.org/10.1242/jeb.245453, PubMed: 36806418