CONSCIOUSNESS

A neural correlate of sensory consciousness in a corvid bird

Andreas Nieder*, **Lysann Wagener**, **Paul Rinnert**

Subjective experiences that can be consciously accessed and reported are associated with the cerebral cortex. Whether sensory consciousness can also arise from differently organized brains that lack a layered cerebral cortex, such as the bird brain, remains unknown. We show that single-neuron responses in the pallial endbrain of crows performing a visual detection task correlate with the birds' perception about stimulus presence or absence and argue that this is an empirical marker of avian consciousness. Neuronal activity follows a temporal two-stage process in which the first activity component mainly reflects physical stimulus intensity, whereas the later component predicts the crows' perceptual reports. These results suggest that the neural foundations that allow sensory consciousness arose either before the emergence of mammals or independently in at least the avian lineage and do not necessarily require a cerebral cortex.

Sensory consciousness, the ability to have subjective experience that can be explicitly accessed and thus reported, arises from brain processes that emerged through evolutionary history (*1*, *2*). Today, the neural correlates of consciousness are primarily associated with the workings of the primate cerebral cortex (*3*–*6*), a part of the telencephalic pallium that is laminar in organization (*7*–*9*). Birds, by contrast, have evolved a different pallium since they diverged from the mammalian lineage 320 million years ago (*10*, *11*). The bird pallium retains organizational principles reminiscent of the mammalian brain (*12*) but is distinctively nuclear and lacks a layered cerebral cortex (*13*–*15*). Despite this, birds demonstrate sophisticated perceptual and cognitive behaviors that suggest conscious experiences (*16*, *17*).

The associative endbrain area called nidopallium caudolaterale (NCL) is linked to high-level cognition in birds (*18*, *19*) and is considered a putative avian analog of the mammalian prefrontal cortex (*20*), which plays a predominant role in sensory consciousness in primates (*21*–*23*). To signify a "neural correlate of consciousness" in primates, brain activity that systematically changes with the subject's report of whether or not it had perceived identical stimuli is identified (*24*, *25*). We hypothesized that conscious experience originates from activity of the NCL in corvids and used a corresponding experimental protocol in which only the crows' internal state, not the physical stimulus properties, determined their subjective experience.

We trained two carrion crows (*Corvus corone*) to report the presence or absence of visual stimuli around perceptual threshold in a rule-based delayed detection task (Fig. 1A and supplementary materials and methods). At perceptual threshold, the internal state of the crows determined whether stimuli of identical intensity would be seen or not perceived. After a delay, a rule cue informed the crow about which motor action was required to report its percept. Thus, the crows could not prepare motor responses prior to the rule cues, which enabled the investigation of neuronal activity related to subjective sensory experience and its lasting accessibility.

The crows' proportion of "yes" responses in relation to increasing stimulus intensity gave rise to classical psychometric functions (Fig. 1,

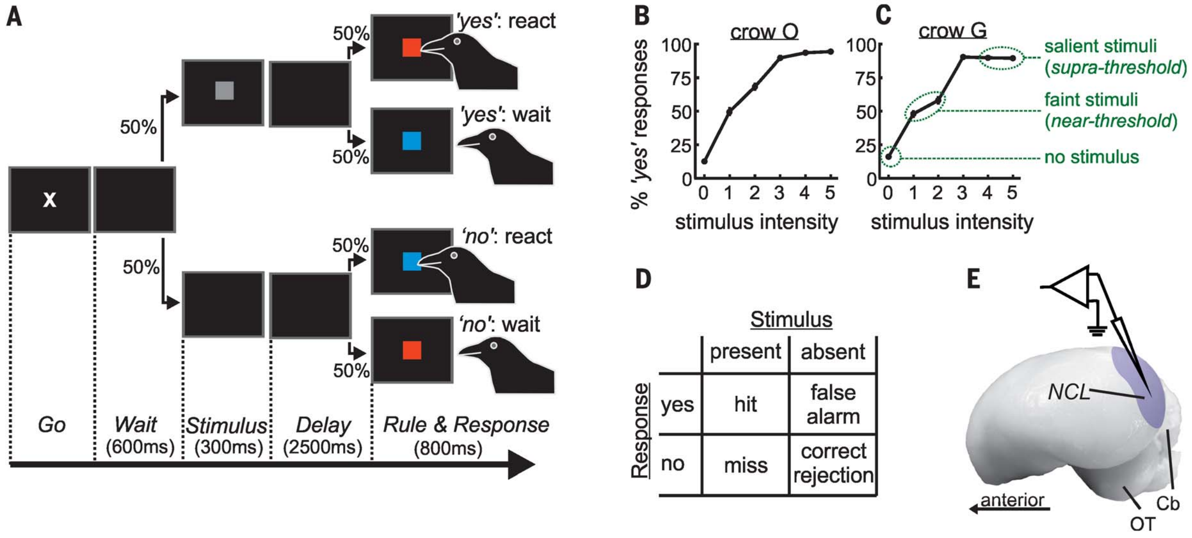

Fig. 1. Crows performed a delayed stimulus detection task. (**A**) Behavioral task. After the crow initiated a trial in the Go period, a brief visual stimulus of variable intensity appeared in 50% of the trials (stimulus trials), whereas no stimulus appeared in the other half of the trials (no stimulus trials). 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 response for stimulus detection ("yes"), whereas a blue cue prohibited a response for stimulus detection. In no-stimulus trials (bottom), rule-response contingencies were inverted. (**B** and **C**) Psychometric functions of crow O (B) and crow G (C). Grouping of trials into suprathreshold, near-threshold, and no-stimulus trials. Error bars (very small) indicate standard error of the mean. (**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"). (**E**) Lateral view of a crow brain depicting the nidopallium caudolaterale (NCL, shaded) in the telencephalon. Cb, cerebellum; OT, optic tectum.

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B and C). Trials were classified into suprathreshold (the two highest stimulus intensities), near-threshold (the two lowest stimulus intensities at perceptual threshold), and no-stimulus categories (Fig. 1C). The crows' responses were classified according to signal detection theory into "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) (Fig. 1D).

While the crows performed the task, we recorded single-cell activity of 480 neurons (n = 306 for crow G; n = 174 for crow O) from the NCL (Fig. 1E and supplementary materials and methods). We first identified 262 task-selective neurons that showed differences in firing rates for suprathreshold trials versus no-stimulus trials (Mann-Whitney U test, $p < 0.01$). The selective time intervals of these neurons that together bridged the total trial period were classified into stimulus-related (n = 155) (Fig. 2A) and delay-related (n = 165) (Fig. 2B).

Next, we compared the discharges during the crows' "yes" versus "no" responses in the different trial categories (Fig. 1C and supplementary materials and methods). If neurons signal stimulus intensity, the responses to near-threshold stimuli should be indistinguishable irrespective of the crow's response. In addition, the responses during "false alarms" are expected to be similar to "correct rejections" in the no-stimulus condition. However, if neurons represent the crows' percept, they are expected to change activity as a function of the crows' later report. In this case, firing rates to near-threshold "no" responses should resemble those during "correct rejections" in no-stimulus trials. Likewise, discharges for near-threshold "yes" responses and "false alarms" should be more similar to those of suprathreshold "yes" responses.

During stimulus presentation, neurons responded mainly to stimulus intensity and only mildly to the crow's later reported conscious percept. The example neuron in Fig. 2C discharged exclusively to the presentation of a salient stimulus, without a correlation with the crow's "yes/no" responses. The neuron in Fig. 2D showed some correlation with the crow's later report because firing rates during near-threshold "yes" responses were similar to supra-threshold "yes" responses, whereas discharges during near-threshold "no" responses resembled "correct rejections."

During the subsequent delay period, however, many neurons responded according to the crows' impending report, rather than to stimulus intensity. The neuron in Fig. 2E showed categorically higher firing rates for all "yes" responses (suprathreshold and near-threshold "hits," as well as "false alarms" in the absence of stimuli) compared to all "no" responses ("no" responses to near-threshold stimuli, "correct rejections" in the absence of stimuli) during the first half of the delay period. A similar effect can be witnessed for the neuron in Fig. 2F, which showed discharges that correlated with the report at the beginning and end of the delay period.

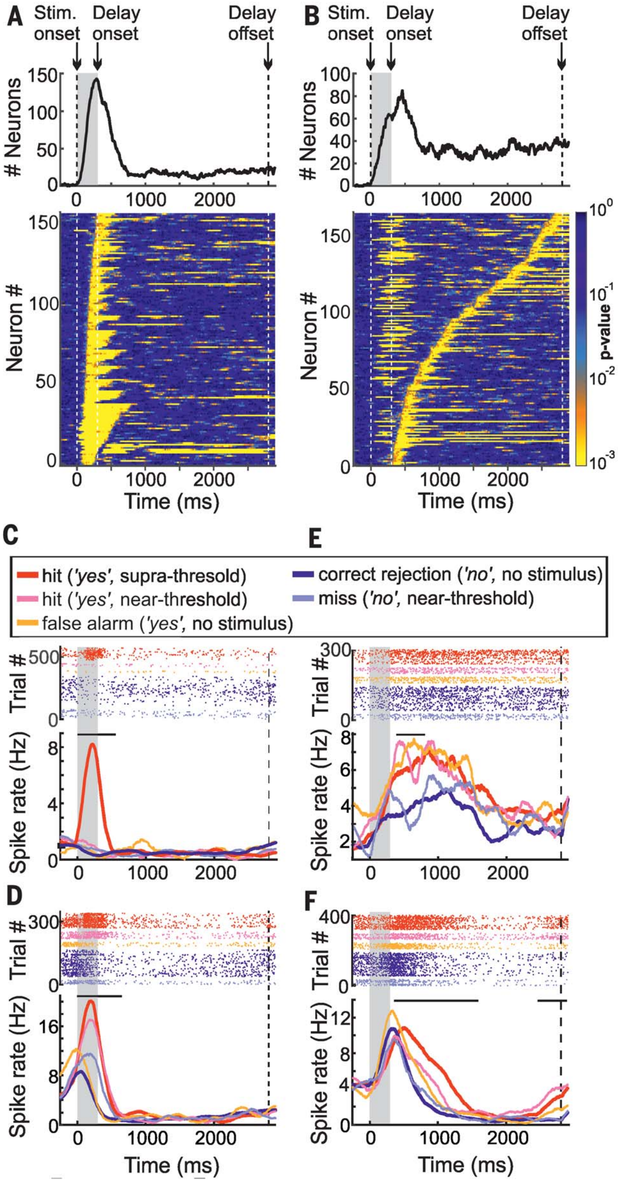


Fig. 2. Single-neuron responses in NCL. (**A** and **B**) Pattern of task selectivity for all stimulus-selective neurons during the stimulus (A) and delay period (B). Bottom: Color-coded traces of significance values (every line represents a neuron); neurons sorted according to selectivity latency. Top: Cumulative time-resolved histogram of task-selective intervals. (**C** and **D**) Activity of two stimulus-period task-selective example neurons in relation to the crow's behavioral responses. Top panels depict dot raster histograms (every line is a trial, every dot is an action potential); bottom panels represent the corresponding averaged and smoothed spike density histograms. The vertical gray shading indicates the presentation of the stimulus (onset at 0 ms), the vertical dotted line signifies the end of the delay. The color code represents the five different trial categories, with red, orange, and pink colors representing "yes" response trials, and dark and light blue colors "no" response trials. The horizontal bars in each spike-density histogram signify the task-selective interval. (**E** and **F**) Activity of two delay-period task-selective example neurons in relation to the crow's behavioral responses. Same layout as in (C) and (D).

To find out whether the activity of the 262 task-selective neurons was related to the crows' report for the same near-threshold stimuli, we compared the firing rates in the neurons' respective selectivity intervals for different trial outcomes. We used receiver operating characteristic (ROC) analysis from signal detection theory (*26*) (supplementary materials and methods). We derived the area under the ROC curve (AUC), termed choice probability, as the probability of predicting the subjective "yes/no" responses for identical stimuli for the stimulus and the delay phases separately (*27*).

We first compared the mean (rectified) activity during "hit" and "miss" trials for near-threshold stimuli in the stimulus presentation period. Choice probability was higher than the chance level of 0.5 (mean: 0.55; $p < 0.001$; one-sample Wilcoxon signed-rank test; n = 155 neurons; compared to a mean of 0.69 for suprathreshold "hits" and no-stimulus "correct rejections") (Fig. 3A). In addition, we compared the choice probability for "correct rejections" and "false alarms" during no-stimulus trials, which was comparable to chance (mean: 0.51; p = 0.08; one-sample Wilcoxon signed-rank test; n = 155 neurons) (Fig. 3B). Thus, during

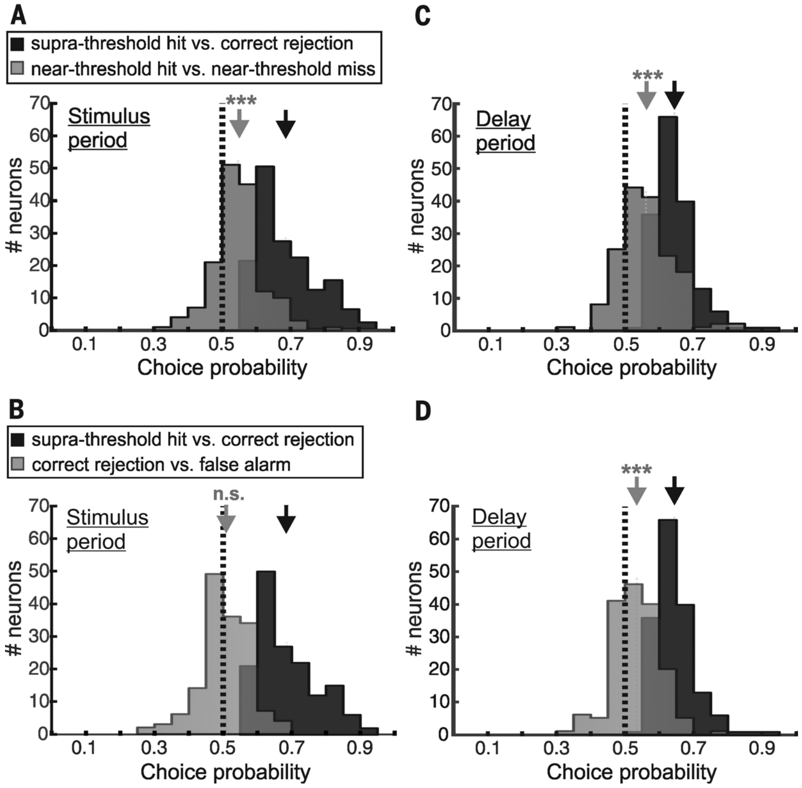


Fig. 3. Neuronal activity predicts "yes" versus "no" responses. Distribution of neuronal choice probabilities according to signal detection theory. (**A** and **B**) Choice probabilities during the stimulus period (155 neurons). (**C** and **D**) Choice probabilities during the delay period (165 neurons). Gray arrow indicates mean of choice probabilities for near-threshold hits versus near-threshold misses [(A) and (C)] and for correct rejections versus false alarms, respectively [(B) and (D)]. Choice probabilities in (A), (C), and (D) were significantly larger than chance level indicated by dotted vertical line (***$p < 0.001$; n.s., not significant). Black arrows indicate mean AUC values for suprathreshold hits versus correct rejections for comparison.

stimulus presentation, the neurons signaled the crows' subsequent report only mildly.

However, the primarily stimulus-based activity changed to a predominantly report-driven representation during the delay. Both the choice probabilities for near-threshold "hit" and "miss" trials (mean: 0.56; Fig. 3C), as well as the choice probability for no-stimulus "correct rejections" and "false alarms" (mean: 0.53; Fig. 3D), were higher than expected by chance ($p < 0.001$ for both values; one-sample Wilcoxon signed-rank test; $n = 165$ neurons). On the background of a mean AUC of 0.64 for suprathreshold "hits" and no-stimulus "correct rejections," both choice probabilities predicted the crows' perceptual report rather than the physical stimulus. Notably, this effect was found not only for the very same faint stimuli, but also on "false alarm" trials, when the crows mistakenly reported perceiving a stimulus when in fact no stimulus was present. Thus, shortly after stimulus presentation, the neurons represented the crows' later report.

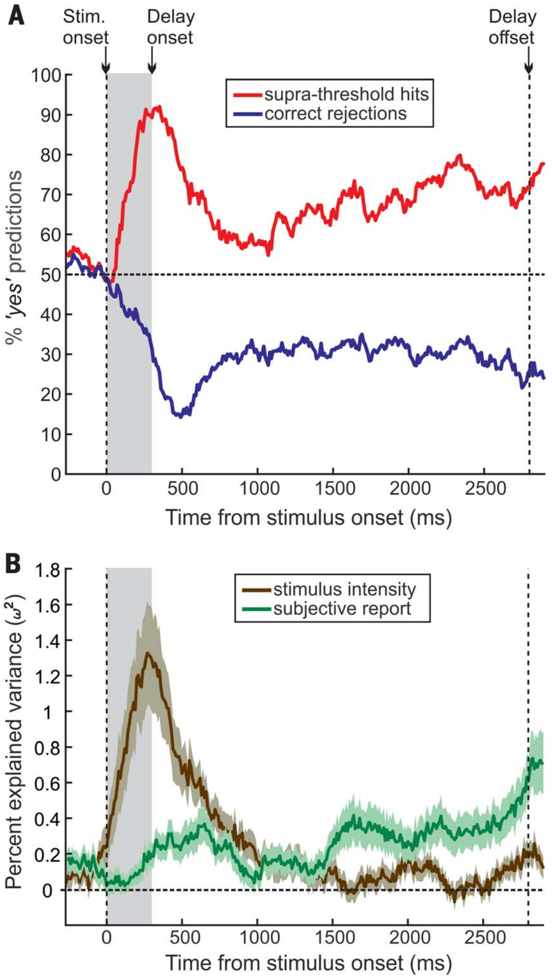
To explore the time course of choice prediction from stimulus onset to delay offset irrespective of neuronal selectivity, we applied time-resolved population analyses based on the activity of all NCL neurons with sufficient trials per trial type ($n = 152$). We first trained a support vector machine (SVM) classifier to discriminate "yes" versus "no" responses on the basis of the spiking activity (*28*) (supplementary materials and methods). Cross-validation on "hits" in suprathreshold trials and "correct rejections" in no-stimulus trials indicated reliable information differentiating the crows' alternative responses (fig. S1). To minimize the influence of stimulus intensity, we next trained the classifier with discharges exclusively from near-threshold trials in which crows subjectively made "yes" and "no" responses for identical stimulus intensities. After training, the classifier was tested with new data from the same neuronal population, but for suprathreshold "hits" versus "correct rejections" in the absence of stimuli. Indeed, the classifier was able to correctly assign the new trials into "yes" versus "no" responses, with particularly high accuracy at stimulus offset and toward the end of the delay (Fig. 4A). This indicates that a population of neurons contained information about the crows' subjective experience throughout the trial.

Finally, we quantified how much information about the physical stimulus and the later report was carried by the activity of the same population of NCL neurons across the trial. We calculated the percent explained variance (ω^2, PEV) for stimulus intensity and "yes/no" response (*29*, *30*) (supplementary materials and methods). We found that stimulus intensity information increased sharply after stimulus presentation, but then rapidly decayed and vanished during the following delay (Fig. 4B). Instead, the neurons increasingly encoded the crows' perceptual report until it reached a peak level toward the end of the delay (Fig. 4B). A similar response pattern was found for predictions on near-threshold trials of a SVM-classifier trained on population responses of "yes" responses in suprathreshold trials ("hits") and "no" responses in no-stimulus trials ("correct rejections") (fig. S2). The neuronal population results suggest that NCL neurons switch from initially mainly representing stimulus intensity to predominantly encoding the crows' subjective experience later in the trial and before a required behavioral report.

A difference between the neuronal activities of one reported perceptual state versus the other for equal visual stimuli is considered to be a "neural correlate of visual consciousness" (*3*, *5*, *21–23*). Our finding thus constitutes an empirical marker of avian sensory consciousness. As for any animal, the qualitative nature of this subjective experience—"what it is like" for a crow to be consciously aware of sensory data—remains hidden (*31*). Moreover, whether pure subjective experience itself ("phenomenal consciousness") can and should be dissociated from its report ("access consciousness") remains intensely debated (*1*, *32*).

Our report of a two-stage process in awareness in the corvid NCL is markedly similar to findings in the primate cerebral cortex, where the initial sweep of activity is also mainly involved in unconscious vision, whereas activity correlating with consciousness is delayed relative to stimulus onset activity (*21*, *33–36*). To explain these effects, the global neuronal workspace theory (*25*, *37*) posits that only sensory activity that is strong enough can access awareness by causing a state termed "global ignition" in higher brain centers such as prefrontal cortex. "Ignition" causes information about a brief stimulus to become sustained and broadcasted back through recurrent interactions between many brain areas, thereby also characterizing the transition of a sensory representation into the explicit working memory state (*1*, *23*). The NCL may very well constitute the avian brain site of an "all-or-none" ignition process that leads either to a high degree of activation causing and maintaining

Fig. 4. Time-resolved neuron population analyses. (**A**) A support vector machine (SVM) classifier trained on near-threshold trial activity predicts the crows' "yes" responses from suprathreshold "hit" trials and "no" responses from correct rejection no-stimulus trials. Chance level is 50%. (**B**) Sliding-window percent explained variance (ω^2) analysis quantifying the information about the stimulus intensity and report-associated subjective percept.



information about conscious experience across a temporal gap for a future goal, or to a vanishing response. Combining report-based behavioral protocols in crows with no-report protocols may help to disentangle the neural mechanisms involved in generating, maintaining, and reporting conscious experience (*38*, *39*). This two-stage process in awareness could prove to be a general and evolutionarily stable principle of how sensory consciousness is achieved in vertebrates in general.

Our finding also provides evidence for the phylogenetic origins of consciousness (*2*). It excludes the proposition that only primates or other mammals possessing a layered cerebral cortex are endowed with sensory consciousness. To reconcile sensory consciousness in birds and mammals, one scenario would postulate that birds and mammals inherited the trait of consciousness from their last-common ancestor. If true, this would date the evolution of consciousness back to at least 320 million years when reptiles and birds on the one hand, and mammals on the other hand, evolved from the last common stem-amniotic ancestor (*40*). Alternatively, consciousness emerged independently on the basis of convergent evolution on different branches of the vertebrate "tree of life." According to this hypothesis, consciousness was absent in the common stem-amniotic ancestor, but—comparable to homeothermy—evolved later and independently during the rise of, at least, birds and mammals. Yet another scenario would predict a gradual emergence of consciousness. Here, different degrees of conserved pallial connectivity patterns in vertebrates could give rise to aspects of sensory consciousness across phylogeny. Combining measurements of brain signals with controlled behavioral protocols will help to delineate the origins of conscious experience in the animal kingdom.

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SUPPLEMENTARY MATERIALS

science.sciencemag.org/content/369/6511/1626/suppl/DC1
Materials and Methods
Figs. S1 and S2

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Consciousness shared

Humans have tended to believe that we are the only species to possess certain traits, behaviors, or abilities, especially with regard to cognition. Occasionally, we extend such traits to primates or other mammals––species with which we share fundamental brain similarities. Over time, more and more of these supposed pillars of human exceptionalism have fallen. Nieder *et al.* now argue that the relationship between consciousness and a standard cerebral cortex is another fallen pillar (see the Perspective by Herculano-Houzel). Specifically, carrion crows show a neuronal response in the palliative end brain during the performance of a task that correlates with their perception of a stimulus. Such activity might be a broad marker for consciousness.

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