Exogenous and endogenous spatial attention in crows

Malte Quest[a,1], Paul Rinnert[a,1], Linus Hahner[a] (iD), and Andreas Nieder[a,2]

Attention describes the ability to selectively process a particular aspect of the environment at the expense of others. Despite the significance of selective processing, the types and scopes of attentional mechanisms in nonprimate species remain underexplored. We trained four carrion crows in Posner spatial cueing tasks using two separate protocols where the attention-capturing cues are shown at different times before target onset at either the same or a different location as the impending target. To probe automatic bottom-up, or exogenous, attention, two naïve crows were tested with a cue that had no predictive value concerning the location of the subsequent target. To examine volitional top-down, or endogenous, attention, the other two crows were tested with the previously learned cues that predicted the impending target location. Comparing the performance for valid (cue and target at same location) and invalid (cue and target at opposing locations) cues in the nonpredictive cue condition showed a transient, mild reaction time advantage signifying exogenous attention. In contrast, there was a strong and long-lasting performance advantage for the valid conditions with predictive cues indicating endogenous attention. Together, these results demonstrate that crows possess two different attention mechanisms (exogenous and endogenous). These findings signify that crows possess a substantial attentional capacity and robust cognitive control over attention allocation.

attention | corvid | psychophysics | cognitive control

Attention describes the selective processing of one aspect of the environment at the expense of others. Selective attention is thought not only to organize the flood of sensory stimuli according to behavioral significance (1, 2), but also to ensure that behavior is properly oriented and committed to its goals (3, 4). Therefore, attention is an indispensable ingredient of elaborate cognition enabling adaptive and intelligent behavior in both vertebrates (5, 6) and invertebrates (7, 8).

Importantly, attention comes in two different flavors (9, 10). The first type is exogenous (reflexive) attention, which operates in a passive, fast, transient, involuntary, stimulus-driven, and bottom-up manner. Exogenous attention allows an automatic orienting response to sudden stimulation. It is thought to be a phylogenetically older capability because it works in an automatic fashion that can be implemented with reflex-like circuits to react quickly to stimuli, such as food or predators (11). Exogenous attention is certainly widespread in the animal kingdom as it allows for life-saving orienting responses (6). The second type is endogenous (voluntary) attention, which operates in an active, slow, sustained, volitional, goal-driven, and top-down manner. Endogenous attention is under cognitive control and allows us to willfully monitor currently relevant information at the expense of irrelevant distractors (11,12). Due to its higher demand of attentional resources, endogenous attention is phylogenetically more exclusive and found in cognitively flexible animals (13).

The most common approach for studying both exogenous and endogenous (spatial) attention effects is Posner's spatial cueing task (14). In this task, subjects are required to detect as quickly as possible a peripheral target stimulus that was preceded by a cue stimulus (Fig. 1). The task design allows the comparison of performance (as measured by reaction times (RT) and detection accuracy) in trials in which attention is either directed to a given location (attended condition), away from that location (unattended condition), or to distributed or random locations (neutral or control condition; 11). In the attended condition, performance is typically better (i.e., more accurate, faster, or both). Importantly, the nature of the cue determines whether exogenous or endogenous attention is being addressed. Exogenous attention is addressed if the cue is nonpredictive (i.e., could not have previously been associated with the location of the upcoming target) and is presented at the same location as the upcoming target. However, if the cue is predictive because the subjects had learned that it forecasts a particular location of an upcoming stimulus, endogenous attention is engaged (11).

Significance

Attention is a crucial ingredient of intelligent behavior because it allows for selective processing of one aspect of the environment at the expense of others. We hypothesized that carrion crows exhibit both reflex-like driven (exogenous) attentional orienting responses in addition to cognitive control over (endogenous) attentional resources. We adopted the influential Posner spatial attention protocol using four crows. We found two separate attentional mechanisms at work in crows: a moderate, transient exogenous attention process and a strong, long-lasting endogenous attention system. While reflexive exogenous attention is widespread in the animal kingdom, enduring endogenous attention is seldom found. Its prominent effects in crows suggest substantial attentional capacity and robust cognitive control in this species.
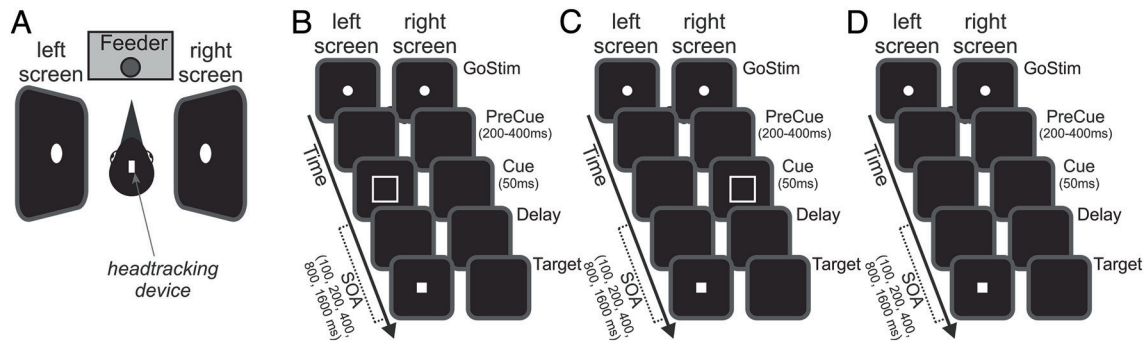
Fig. 1. Setup layout and spatial cueing task. (A) Setup layout. Visual stimuli were shown monocularly on two laterally placed screens. During the trial, the crow was placed on a perch and required to center its head between the screens with the beak pointing straight forward. Head position was measured real time with a two-camera headtracking system. After each correct trial, food reward was delivered by a feeder. (B–D) Variants of spatial cueing task. Sequence of stimuli displayed on the left and right screens is shown from *Top* to *Bottom*. The display of Go-stimuli (filled white circles) on both screens instructed the crow to center its head between the screens in order to start a trial. After the crow had positioned its head, the disappearing Go-stimuli on both screens signaled the start of a trial. After a precue period with black screens, the cue period followed. The cue period was followed by a varying delay period resulting in five different stimulus onset asynchronies (SOA) before the target was displayed. The crow was rewarded for detecting the target (indicated by a "nodding" head movement) on either side within 550 ms after target onset. (B) Valid cueing condition. Cue (white square outline) and target (filled white square) are shown on the same side (in the example on the left side) and in corresponding positions. (C) Invalid cueing condition. Cue and target are shown on opposite sides and in disparate positions. (D) No-cue condition. No cue is shown during the cue period, only the target. All the cueing conditions were shown in either the "nonpredictive cue protocol" (crows 1 and 2) or the "predictive cue protocol" (crows 3 and 4).

Based on results from Posner-like spatial cueing tasks, it is generally accepted that nonhuman primates exhibit endogenous attention (5, 15, 16) In addition, evidence suggests that also other species of mammals (17, 18, 19), birds (20, 21, 22), and perhaps even fish (23) show aspects of endogenous attention. However, the respective contributions of exogenous and endogenous attention effects are often difficult to disentangle due to specificities of the task designs and behavioral repertoires of animal species.

In the current study, we explored selective spatial attention in carrion crows, a species of corvid songbirds. Corvids are renowned for their flexible and goal-directed behaviors suggestive of a toolkit of elaborate cognitive processes (24, 25, 26, 27, 28). However, the components and scope of their selective attention capabilities have never been explored in controlled and standardized behavioral protocols, allowing comparison with human and nonhuman species. We tested two groups of subjects in two different versions of a Posner-like spatial attention task, demonstrating and characterizing the workings of both exogenous and endogenous spatial attention in crows.

Results

We trained four carrion crows on a Posner-like spatial cueing task to detect a visual target as quickly and as accurately as possible (Fig. 1). Stimulation of the crow's left and right eye was strictly monocular as the stimuli were shown on two lateral monitor screens. The crow's centered head orientation between the two screens was ensured by tracking the head's position throughout the trial (Fig. 1A) (29). Once the crow oriented its head straight between the screens, a trial started. After a brief variable waiting period without visual stimuli, a cue period followed. A cue (the outline of a square) was flashed for 50 ms either on the same side as the subsequent target (valid condition) (Fig. 1B), opposite to where the subsequent target was shown (invalid condition) (Fig. 1C), or a cue was not shown at all (neutral no-cue condition) (Fig. 1D). After a variable delay period showing a blank screen, a filled white square was presented as the target stimulus on one of the screens. The target appeared with different stimulus onset asynchronies (SOA) of between 100 ms and 1,600 ms relative to cue onset. The crow was required to respond to the target as quickly as possible and

within 550 ms after target onset by moving its head out of the center position to receive a reward.

This spatial cueing task was presented in two versions that differed concerning the significance of the cue. Two of the crows (crow 1 and crow 2) performed the first version of the task (nonpredictive cue protocol) and had no experience with the cue and its cooccurrence with the target. Both valid and invalid trials were each shown just as often in 25% of the trials per session, while the rest of the trials were no-cue trials (50%). This prevented the crows from being able to learn any predictive value of the cue. The aim of this version was to explore an automatic, bottom-up, and reflex-like (exogenous) attention-capturing effect of the cue.

In contrast, crow 3 and crow 4 performed the second version of the task (predictive cue protocol) and were trained to learn the predictive value of the cue. During training and testing, the valid trial condition was presented in 80% of the trials, which allowed the crows to learn that the side of cue appearance signaled with high confidence the side of target appearance. Invalid trials and no-cue trials made up 10% of the trials, respectively. With this version, a top-down and volitional (endogenous) attentional orientation of the crows could be explored. The behavioral results as measured by RT and detection accuracies for the nonpredictive and the predictive cue protocols are first reported separately and later compared.

Performance in the Nonpredictive Cue Protocol. We first analyzed the RT effects of two crows (crows 1 and 2) performing the nonpredictive cue protocol. The average RTs across SOAs and intensities were 321 ms for crow 1 and 337 ms for crow 2 (Fig. 2 A and B). Irrespective of the cue condition and overall differences in response speed, both crows showed shortest RTs at SOAs of 400 ms and increasing RTs toward shorter and longer SOAs (Fig. 2 A and B). As a measure of putative attention effects, we calculated the RT difference between the invalid and valid cue conditions (i.e., RT invalid minus RT valid) at the five SOAs. If the cue captures attention to one side, the crow is expected to respond faster for the valid cue condition when compared to the invalid condition, resulting in a positive RT difference.

The RT differences and the accompanying statistics for each of the two crows are shown in Fig. 2C. The two crows exhibited opposing effects for the shortest SOAs: crow 1 showed shorter RTs for the valid cue at SOA 100 ms and 200 ms ($P < 0.001$, n = 50
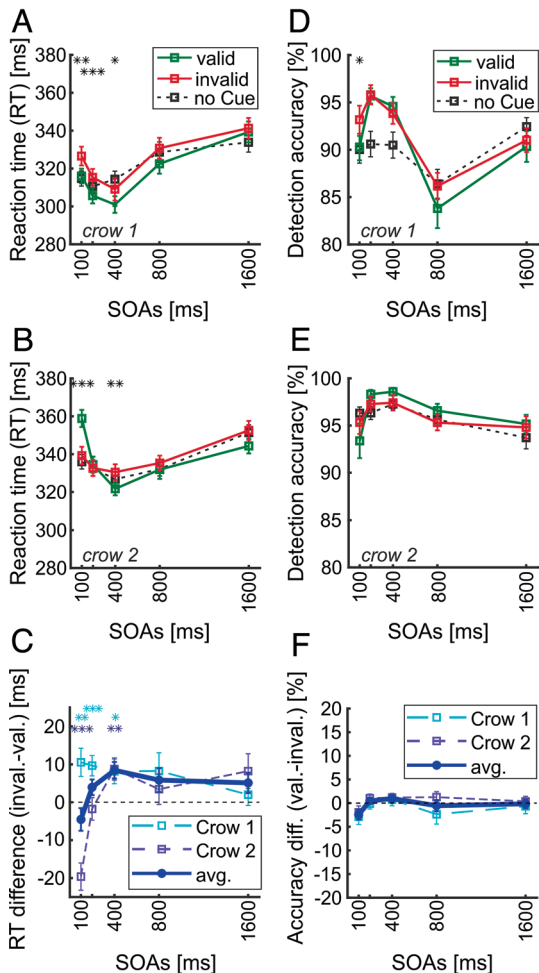
Fig. 2. Performance in the nonpredictive cue task. (*A, B*) RTs for crow 1 and crow 2 to every SOA. Both crows showed fastest RTs in the 400 ms SOA. Furthermore, both crows reacted faster in valid cue conditions compared to invalid cue conditions in the 400 ms SOA. (*C*) The RT differences between valid and invalid cue conditions. With 400 ms SOA, both crows individually reacted significantly faster in valid conditions. (*D, E*) Detection accuracies for each crow in every SOA. No consistent differences between valid and invalid cue conditions were found. (*F*) No differences in detection accuracies were found. All graphs show the mean and the error bars the SEM (n = 50). The stars indicate significant differences between valid and invalid cue conditions (Wilcoxon test, $P < 0.05 = *$, $P < 0.01 = **$, $P < 0.001 = ***$).

sessions, all tested target intensities averaged; Wilcoxon test), whereas crow 2 showed shorter RTs for the invalid cue at 100 ms ($P < 0.001$, n = 50 sessions, all tested target intensities averaged; Wilcoxon test). However, both crows individually showed shorter RTs and thus a speed advantage for valid cues for an SOA of 400 ms. (RT difference 8 and 9 ms for crows 1 and 2, respectively; crow 1: $P = 0.015$, n = 50 sessions; crow 2: $P = 0.004$, n = 50 sessions, all tested target intensities averaged; Wilcoxon test). For SOAs longer than 400 ms, no significant RT differences between valid and invalid trials were noticeable.

This overall RT difference pattern across SOAs was present for all the three tested target intensities in the individual crows, albeit more variable due to the sample sizes split into thirds (*SI Appendix,* Fig. S1 *A–C*). The pooled RT functions of both crows display a mild increase in RT difference up to an SOA of 400 ms, followed by a progressive drop for longer SOAs (i.e., 800 and 1,600 ms) (Fig. 2*C*). This indicates that the nonpredictive cue resulted in a mild but significant target detection advantage at an SOA of 400 ms in the crows; shorter and longer time intervals between nonpredictive cue and target had no consistent RT effects.

As a second behavioral parameter, we analyzed correct target detection accuracy, i.e., the percentage of correct (i.e., timely) target detection responses relative to all responses (i.e., the sum of correct and late responses). The hypothesis here is that the valid cue condition may provide an advantage for detection accuracy when compared to the invalid condition. Both crows showed high average detection accuracy of 90% (crow 1) and 96% (crow 2) across SOAs and cue conditions, with minor and individual variability across SOAs (Fig. 2 *D* and *E*). We calculated the target detection accuracy difference between the valid and invalid cue conditions at the five SOAs. No significant accuracy differences between the valid and invalid cue conditions across SOAs were seen in the data pooled across both crows (Fig. 2*F*) (both crows: $P > 0.05$, n = 50 sessions per crow; all the three tested target intensities averaged; Wilcoxon test). Accuracy differences were also absent for the three tested target intensities separately (*SI Appendix,* Fig. S1 *D–F*).

To further assess spatial cueing effects in the nonpredictive cue task, valid and invalid cue performance (percent correct) for the two crows was plotted against overall proportion correct for each signal strength (i.e., intensity) condition (30). No cueing effect, defined as the difference in proportion correct between valid and invalid trials, was observed in the nonpredictive cue task for sessions pooled across the three target intensities for either crow (*SI Appendix,* Fig. S2*A*) ($P > 0.05$, Wilcoxon test, n = 150 sessions). Because the cueing effect is based on percent correct performance, this finding correlates with the above-reported absence of accuracy differences between the valid and invalid cue conditions across SOAs in the nonpredictive cue task.

Performance in the Predictive Cue Protocol. Next, we analyzed the same performance parameters for crows 3 and 4 that had learned that the cue predicted the side of the impending target. The average RTs across SOAs and intensities were 374 ms for crow 3 and 325 ms for crow 4 (Fig. 3 *A* and *B*), and thus comparable to crows 1 and 2 performing the nonpredictive cue task. The absolute RTs to the valid, invalid, and no-cue conditions showed both a facilitation in the valid cue conditions and an increase in the invalid condition relative to the neutral condition (Fig. 3 *A* and *B*). When we calculated the RT differences between the invalid and valid cue conditions at the five SOAs, we found strong effects even with long SOAs (Fig. 3*C*). Crow 3 showed significantly faster responses for valid as compared to invalid trials for SOAs of 200–1,600 ms ($P < 0.001$, n = 25; all tested target intensities averaged; Wilcoxon test). RT advantages of crow 3 in valid trials were 16 ms (SOA 200 ms), 35 ms (SOA 400 ms), 42 ms (SOA 800 ms), and 25 ms (SOA 1,600 ms). Crow 4 also showed significantly faster responses for valid as compared to invalid trials for all the tested SOAs from 100 to 1,600 ms ($P < 0.001$, n = 25 sessions; all tested target intensities averaged; Wilcoxon test). RT advantages of crow 4 in valid trials were 14 ms (SOA 100 ms), 28 ms (SOA 200 ms), 25 ms (SOA 400 ms), 30 ms (SOA 800 ms), and 30 ms (SOA 1,600 ms). Thus, for SOAs of 200–1,600 ms, both crows individually responded faster to the target in valid conditions, and with almost identical average RT differences of 29 ms and 28 ms, respectively. This overall RT advantage for valid trials across SOAs was present for all the three tested target intensities (*SI Appendix,* Fig. S3 *A–C*).

In addition to the RT difference, we analyzed target detection accuracies as a second performance parameter. Crows 3 and 4 made almost no errors when detecting the targets. This resulted in almost perfect average detection accuracies of 97% (crow 3) and 98% (crow 2) across SOAs and cue conditions (Fig. 3 *D* and *E*). Detection accuracy differences between the valid and invalid
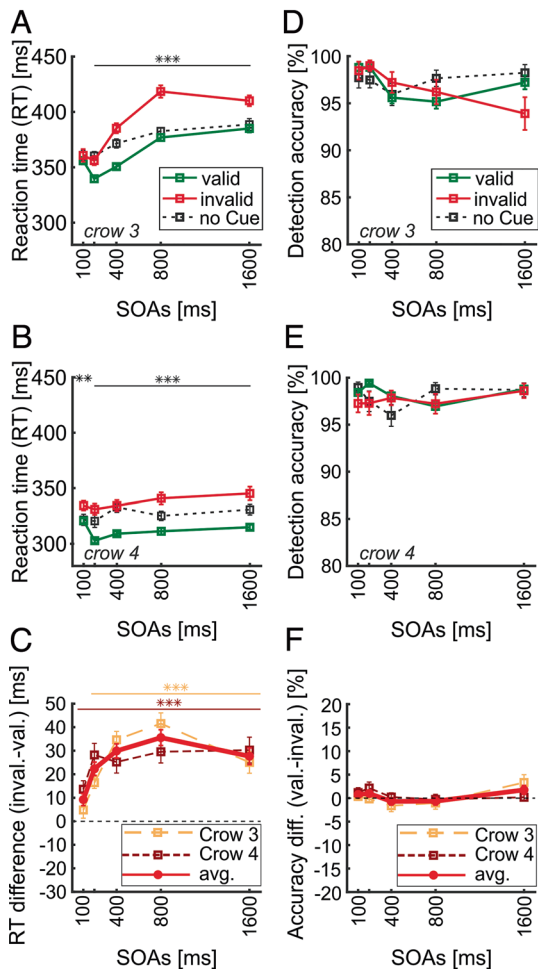
Fig. 3. Performance in the predictive cue task. (*A*, *B*) Reaction times for crows 3 and 4 to every SOA. Both crows showed consistently faster RTs in valid cue conditions when compared to invalid cue conditions for SOAs of 200 ms and higher. (*C*) Reaction time differences between valid and invalid conditions. While crow 3 was faster in valid cue conditions in all but the shortest SOA, crow 4 was faster across all SOAs. Their average RT difference was 29 ms and 28 ms, respectively. (*D*, *E*) Detection accuracies for each crow in every SOA. No differences between valid and invalid conditions were found. (*F*) Detection accuracy differences between valid and invalid conditions. The crows did not show any effects of SOA or cue validity. All graphs show the mean and the error bars the SEM (n = 25). The stars indicate significant differences between valid and invalid trials (Wilcoxon test, $P < 0.05$ = *, $P < 0.01$ = **, $P < 0.001$ = ***).

cue conditions were absent across SOAs in either of the two crows (both crows: $P > 0.05$, n = 25 sessions per crow; all tested target intensities averaged; Wilcoxon test). Accuracy differences were also largely absent in the data pooled across both crows (Fig. 3*F*) and for the three tested target intensities separately (*SI Appendix*, Fig. S3 *D–F*).

Despite clear RT effects between valid and invalid trials, differences in detection accuracy were absent. We hypothesized that the crows' nearly perfect detection rates reaching the upper limit of the accuracy scale in all conditions prevented uncovering of accuracy differences. To lower detection accuracy, we therefore increased task difficulty and retested crows 3 and 4 in the (reduced) predictive cue protocol with even lower target intensities ("*follow-up task*"; only valid and invalid conditions; 11 sessions). The pattern of RT differences remained comparable to the previously seen effects across decreasing target intensities, albeit noisier due to a smaller number of sessions (Fig. 4 *A–C*). However, the average detection accuracies dropped notably to 81% in crow 3 and 66% in crow 4 with fainter target stimuli. More importantly, with increasing task difficulty (due to fainter

target stimuli), detection accuracy became significantly better for valid compared to invalid trials in both crows individually (Fig. 4 *D–F*). For SOAs 200 and 800 ms, both crows individually showed significant accuracy differences (all $P < 0.05$; n = 11 sessions per crow; Wilcoxon test). For SOA 800 ms, the crows showed an accuracy advantage of almost 20% in the valid over the invalid condition (Fig. 4*F*). Thus, with increased task difficulty, a clear accuracy advantage in addition to a significant RT advantage for the valid cue condition over the invalid cue condition is seen.

To further assess the spatial cueing effects in the predictive cue task and the follow-up task, valid and invalid cue performance for the two crows was plotted against overall proportion correct for each signal strength condition. A significant cueing effect (i.e., a significant difference in proportion correct between valid and invalid trials) was observed in the predictive cue task for each crow individually for sessions pooled across the three target intensities in the follow-up task (*SI Appendix*, Fig. S2*B*) ($P < 0.001$, Wilcoxon test, n = 33 sessions). Significantly stronger cueing effects of 9% (crow 3) and 12% (crow 4) for valid trials compared to invalid trials were present for the smallest target intensities compared to higher target intensities (follow-up task; $P = 0.001$, Friedman test across both crows, n = 22 sessions). The presence of a cueing effect in the follow-up task concurs with the discovered accuracy advantage in the valid over the invalid condition described above. These findings indicate that both crows were utilizing the predictive cue to control and enhance their detection performance via endogenous attention.

Comparison of RT Performance in the Nonpredictive and Predictive Cue Protocols. In the main task, both the nonpredictive and the predictive cue protocols resulted in significant RT advantages for valid as compared to invalid trials at selected SOAs. We, therefore, compared the average RTs of crows 1 and 2 (nonpredictive cue protocol) and crows 3 and 4 (predictive cue protocol) as a function of SOAs. We found that RT differences (between invalid and valid trials) were significantly greater and longer lasting in the predictive cue protocol (Fig. 5) ($P < 0.001$, Mann–Whitney U test). At SOA 800 ms, the SOA with the strongest RT difference between the two cue protocols, the crows responded 30 ms faster to the valid condition in the predictive cue protocol compared to the nonpredictive cue protocol. This indicates that the predictive cue quantitatively and qualitatively improved the performance speed of the crows relative to the nonpredictive cue.

Because the crows contributing the data for the noninformative cue task were considerably younger compared to those performing the informative cue task, we tested whether these age differences might have caused the observed differences in performance between the two conditions. To that aim, we trained two more young crows (aged 1.5 and 2 y old; the latter was crow 2 originally trained on the nonpredictive cue task) on the predictive cue task. Just as the older crows tested before, both young crows showed significant attention effects in RT differences for valid versus invalid trials (*SI Appendix*, Fig. S4*A*), with RT values and SOA profiles comparable to those of the older crows (*SI Appendix*, Fig. S4*C*). In addition, the young crows showed almost no significant differences in correct performances for valid versus invalid trials (*SI Appendix*, Fig. S4*B*), which was also equivalent to the findings in the older crows (*SI Appendix*, Fig. S3*F*). Systematic difference in age between the crows used in the different experiments thus cannot explain the different patterns of results between the noninformative and the informative cue conditions.
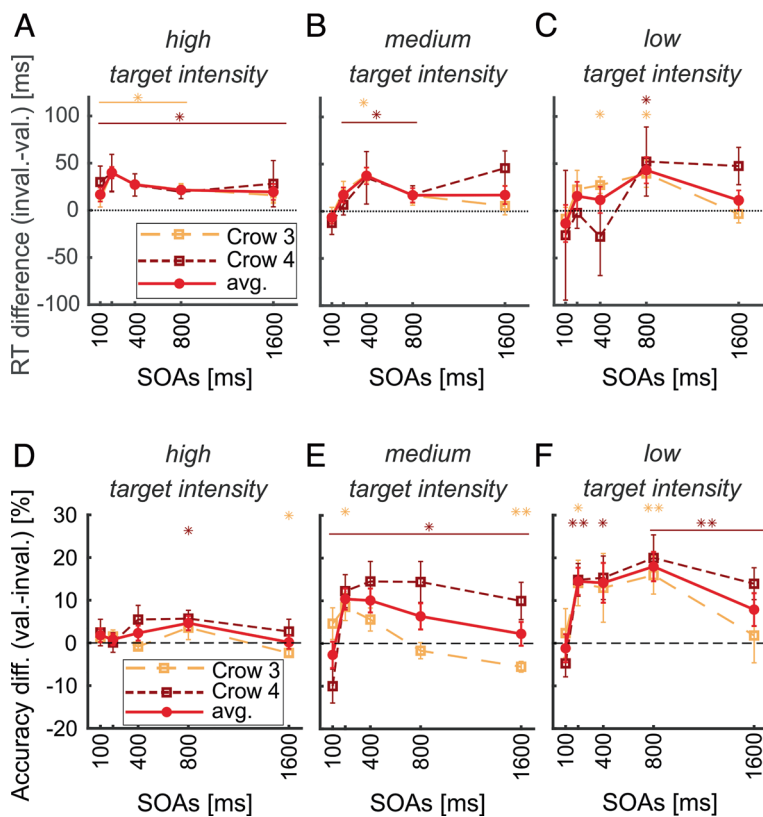
Fig. 4. Follow-up task to the original predictive cue task with lower target intensities. (*A*, *B*, and *C*) RT difference for high (*A*), medium (*B*), and low (*C*) target intensities. (*D*, *E*, and *F*) Accuracy difference for high (*D*), medium (*E*), and low (*F*) target intensities. Initially, the accuracy difference is again missing. However, at medium target intensity, an accuracy difference starts to emerge from the 200 ms SOA onward. At low target intensities, this difference becomes more prominent and consistent across SOAs. The graphs show the mean and the error bars the SEM (n = 11). The stars indicate significant differences between valid and invalid trials (Wilcoxon test, $P < 0.05$ = *, $P < 0.01$ = **, $P < 0.001$ = ***).

Discussion

We report two separate attention mechanisms at work in crows: a moderate and transient exogenous attention process, and a strong

Fig. 5. Comparison of the RT difference between the nonpredictive and predictive cue tasks. The crows in the nonpredictive cue task (blue colors) showed only a relatively small but significant RT difference at 400 ms SOA (n = 50). The crows in the predictive cue task (red colors) showed stronger and longer lasting RT differences (n = 25). The graphs show the mean and the error bars the SEM. The stars indicate significant differences between nonpredictive and predictive cue tasks (Mann–Whitney *U* test, $P < 0.05$ = *, $P < 0.01$ = **, $P < 0.001$ = ***).

and long-lasting endogenous attention system. While reflexive exogenous attention is widespread in the animal kingdom, the prominent and enduring endogenous attention effects in crows suggest substantial attentional capacity and robust cognitive control over attention allocation in this corvid songbird species.
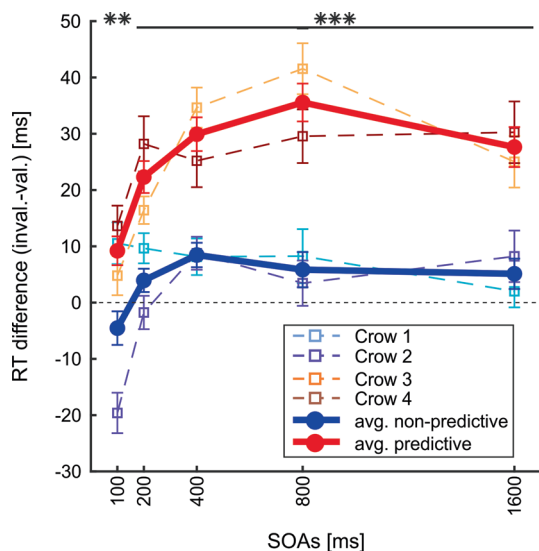
Evidence for, and Characteristics of, Exogenous Attention in Crows. With a nonpredictive cue that the crows had not learned to associate with the appearance of the target, both crows showed an RT advantage for the valid cue condition at an SOA of 400 ms. An arbitrary stimulus flashing 400 ms before and on the same side as the target automatically captured the crows' attention to the side of the cue; this allowed the crows to respond faster to the target if nonpredictive cue and target were on the same side. For longer SOAs, this RT advantage decayed and was no longer significant. SOAs shorter than 400 ms showed inconsistent RT effects between the two tested crows with an RT disadvantage for valid cues in one crow (crow 1). The rapid onset and fast decay of an RT advantage for nonpredictive cues in valid conditions are both typical signatures of exogenous (bottom-up, automatic, involuntary) attention.

Similar effects of exogenous attention have been found in other animals, such as macaques (5), pigeons (20), and archerfish (31). Compared to humans and macaques with exogenous attention effects as early as 40 ms and 100 ms of SOA, respectively (5, 32), the RT advantage occurred relatively late in two pigeons (20) and in our crows. Because cue and target were presented in the same location in both studies, the cue might have masked the target at very short SOAs. Alternatively, exogenous attention may work slower in birds.

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For SOAs longer than 200 ms, humans usually show a peculiar reversal of RT effects in exogenous attention tasks and respond faster to invalid trials compared to valid trials (33, 34). This effect has been termed "inhibition of return (IOR)." In our crows, IOR was absent. The demonstration of an IOR in animal subjects is generally variable. While IOR was demonstrated in studies with macaques (5), archerfish (31), and one of the two tested barn owls (35), no IOR was found in studies with rats (36), mice (37), or pigeons (38). The significance of the IOR, which is present even in a predictive cue task protocol in archerfish (23), as a signature of exogenous attention remains unclear.

In contrast to our expectation, a performance advantage for valid conditions was not mirrored in the crows' detection accuracy; valid and invalid conditions were reported with equal and almost perfect accuracy, and a cueing effect was absent. In similar spatial cueing tasks, humans (39) and rodents (17, 19) showed the expected accuracy advantages for the valid condition due to exogenous attention. We suspect this lack of accuracy differences between valid and invalid conditions in our crows was a result of the crows' proficiency resulting in a "ceiling effect;" with almost 100% accuracy in both valid and invalid conditions, accuracy differences cannot be deciphered. This is reminiscent to a study in macaques for which an absence of an exogenous attention effect for accuracy may similarly be explained by relative ease of target detection (5). We suspect that an accuracy effect for exogenous attention would have emerged in our crows with higher task difficulty (by lowering target intensity or shortening the response interval); we were able to verify this hypothesis for the predictive cue task.

Evidence for, and Characteristics of, Endogenous Attention in Crows. In the predictive cue task, both crows showed strong and long-lasting RT advantages to valid cues. One of the tested crows showed a significant effect starting at the earliest SOA of 100 ms; both crows exhibited clear RT effects for SOAs from 200 ms up to the longest tested SOA of 1,600 ms. With a validity effect of 30 ms in the predictive cue protocol relative to the nonpredictive cue protocol, the magnitude of the attention effect in crows was comparable to the attention effects of macaques (5). When we further decreased target stimulus intensity and thereby increased task difficulty (in the predictive-cue follow-up task), the crows exhibited clear cueing effects and considerable accuracy advantages for valid trials for SOAs between 200 ms and 800 ms. This temporal pattern of the accuracy effect mirrored the pattern found for RT effects already at higher target intensities, thus corroborating the attentional advantage caused by the predictive cue. This finding argues for a ceiling effect in detection accuracy for targets that are easy to detect.

Strong and long-lasting facilitatory effects of the valid cue on performance speed and accuracy are clear signatures of endogenous (top-down, volitional) attention in our crows. We can rule out age as a factor responsible for the behavioral differences found between the nonpredictive and the predictive cue tasks, because the two young crows (one of them retrained from the nonpredictive to the predictive cue task) showed the same endogenous attention effects with similar effect magnitudes and temporal patterns as the older crows.

Since we did not measure eye movements, we cannot exclude that the crows' behavioral advantage in the predictive cue protocol may reflect a combination of top-down attention and perceptual enhancement. It is possible that the crows made eye movements to the cued stimulus location and thereby allocated foveal processing to the stimulus that resulted in enhanced visual processing of the target stimulus. The most convincing argument against perceptual enhancement by target-directed eye movements comes from the time course of endogenous attention effects. With short SOAs of 100 and 200 ms, the interval between the cue and the target was brief enough to prevent target-directed eye movements, as about 250 ms are needed for a saccade to occur (40). Despite such short SOAs faster than eye movements, we see significant RT advantages for the cued location in both crows, and at magnitudes approaching RT effects seen for longer SOAs. In addition, we speculate that the salient cue might have prompted eye movements not only in the predictive, but also in the nonpredictive cue task, which would have also helped the crows to detect the target better in the exogenous condition; however, the crows only showed weak RT effects in this exogenous condition. It is, therefore, unlikely that perceptual enhancement by target-directed eye movements can explain all the witnessed effects.

Endogenous attention shows a delayed time course. In humans, it requires 300–500 ms to take effect (41). Our crows showed a full-blown endogenous attention effect already from 200 ms SOA onward. This could indicate faster top-down mechanisms in crows. Alternatively, or in addition, early mild exogenous attention effects might overlay and facilitate target detection in valid conditions with short SOAs. The latter explanation cannot be excluded as the location of the predictive cue and the target coincided in our protocol. To dissociate potential exogenous and endogenous effects, cue and target location need to be spatially disparate.

Given that cue validity was the main difference between the nonpredictive and the predictive task protocols, the result implies that crows are very responsive to the validity of the cue in the endogenous condition. Crows are known to flexibly grasp the meaning of spatial and nonspatial cues 29,42. With respect to cue validity, crows concur with human and nonhuman primates that also show a strong validity effect (5, 43, 44), but differ from other nonprimate species, such as pigeons and rats, in which cue validity only mildly affects RT differences 17,20. The strong and lasting cue validity effects in crows imply robust cognitive control over attention allocation and considerable attention capacity in these corvids. It would be interesting to know for how much longer SOAs the crows can maintain endogenous attention before the effects vanish as a result of the cognitively exhausting vigilance (45).

Explicit endogenous attention has been rarely studied in birds. Using a crossmodal spatial cueing paradigm, attentional influence on sound localization behavior was demonstrated in barn owls (21). In another study with owls trained to search for visual Gabor patterns on a computer screen, owls' attention was automatically captured by task-irrelevant distractors (46). Both studies argue for the presence of top-down attention mechanisms in addition to bottom-up effects in owls. Detailed endogenous attention effects in a Posner-like spatial cueing task in which cue and target locations were not identical were shown in chickens, especially when trials were difficult (22).

Because corvids have laterally placed eyes with mainly monocular visual fields (47) and because other songbirds can perform simultaneous eye movements toward two different targets (48), one may speculate that crows can attend to stimuli in each monocular visual field independently. In our approach with exactly laterally placed monitors, each stimulation side could only be viewed with one eye only. Inconsistent with this hypothesis, a cue on one side resulted not only in facilitation of targets on the same side, but also in behavioral degradation (i.e., increase in RT) on the opposite side relative to no-cue conditions. The most parsimonious explanation of these results is a unitary locus of endogenous attention effective in spatial selective attention. A similar conclusion was reached for spatial attention in chickens (22).

Besides some bird species, rats and mice show robust endogenous attention effects in spatial cueing protocols (17, 18, 19), complementing endogenous attention findings in nonhuman primates (5, 15, 16). Archerfish so far are the only species of fish that have succeeded in an endogenous Posner-like spatial cueing task (23). As expected for attention effects, archerfish's RTs to targets on the cued side were faster compared to RTs to un-cued targets. However, the fish showed IOR, a behavioral signature unexpected for endogenous attention but predictive for exogenous attention. Archerfish may possess a shorter attention time constant and may only be capable of short-lasting cognitive control over attention. Alternatively, archerfish may not show an implicit (unconscious) associative learning of cue–target contingencies; the latter explanation would not invoke attention at all (23).

Neural Origin of Endogenous Attention in Birds. Our crows showed a clear cueing effect in the predictive cue task and a decline in the cueing effect with increasing target intensity. Spatial cueing effects have been observed in a variety of species, such as monkeys (49), rats (17), and pigeons (20), and in different tasks. Among protostomes, honeybees trained on a spatial two-alternative forced-choice association task with a cue and a distractor can use predictive cues to aid visual discrimination (30). Similar to the observations in our crows, the magnitude of the cueing effect vanishes with increasing signal detectability in humans (50), monkeys (30), and, to a lesser degree, bees (30). Our results add crows to the list of species that can use informative spatial cues to optimize their behavioral choices.

The similarity of the effects and mechanisms of endogenous spatial attention in crows compared to primates is also remarkable from the perspective of brain evolution. In mammals, top-down attention and other cognitive control functions are thought to emerge from the six-layered neocortex (51, 52). Birds, however, independently evolved distinct telencephalic integration centers since they diverged from the last common ancestor with mammals around 320 Mio years ago. The avian telencephalic integration centers that play a major role in avian cognitive functions, such as the *nidopallium caudolaterale* (26, 28, 53, 54, 55), originate embryonically from different pallial territories (56), lack a layered architecture characteristic for the cerebral cortex (56), and exhibit independently evolved pallial cell types (57). Our findings in crows therefore contradict the hypothesis that neocortical circuitry is indispensable for endogenous attention in all vertebrates (see also refs. 6 and 13). Rather, it suggests that overarching anatomical and physiological principles of the telencephalic pallium offer this structure as a substrate for endogenous attention to evolve independently across vertebrate phylogeny (58).

Methods

Subjects. We used four male carrion crows (*Corvus corone corone*) from the university's facilities. Crow 1 and crow 2 were 1.5 y and 1 y old, respectively. Prior to the current experiments, crow 1 was unexperienced in attention tasks and crow 2 was a completely naïve crow; they participated in the noninformative cue task. Crows 3 and 4 participated in the informative cue task and were experienced crows. At the time of data collection, they were 6 and 4 y old. They lived in indoor aviaries in social groups with visual and auditory contact to the crows in the other aviaries. During training, the crows worked in a controlled feeding protocol and earned food as reward for correct trials. All animal experiments followed the National Institute of Health's Guide for Care and Use of Laboratory Animals and were authorized by the national authority (Regierungspräsidium).

Experimental Setup. During sessions, the crows were placed on a perch in an operant conditioning chamber. The crow sat in front of a feeder. Two stimulation

monitors (Joy-it RB-LCD10-2, 10.1″, 60-Hz-refresh rate) were mounted to the left and right of the crow 35 cm away from the crow at the same height as the crow's head. To track the crow's head position online and in 3D during the task, the setup was equipped with two cameras (Body: FLIR CM3-U3-13y3M, Lens: Fujinon DF6HA-1B). One camera was fixed to the roof and the other one to the left wall of the chamber. Each camera was accompanied by an IR emitter (Kingbright BL0106-15-28, 940 nm). This camera system allowed tracking a reflector attached to the crow's head in the darkened setup. The top camera tracked in the horizontal plane and the side camera in the vertical plane. The headtracking was done via a custom-written Matlab script (Matlab R2017b). During the sessions, the crow initiated trials by keeping its head still in the predefined center position between–and parallel to–the two side monitors. The crow was required to keep its head within ± 1.35 cm (in anterior-posterior, left-right, and up-down positions) relative to the center between the two side monitors (each 35 cm away from the crow) throughout the trial (including SOAs) until the target stimulus appeared. In addition, the crow was required to keep its head straight within an angle of ± 20° throughout the trial until target appearance. Head position and orientation were measured in real time at a sampling rate of 60 Hz. The crow reported the detection of the target stimulus by briefly moving its head ("nodding"), which was again automatically detected by the computer-controlled setup. With every correct answer, food reward was presented at the briefly illuminated feeder.

Behavioral Protocol. The tasks followed the Posner spatial cueing protocol. Two versions of the protocol were used that only differed in the cue validity. Task 1 (nonpredictive cue task) used a cue that was not predictive of the target (50% validity), while task 2 (Predictive cue task) employed a highly predictive cue (89% validity). The "follow-up task" was a repetition of task 2 with lower target intensities. During the tasks, the items presented consisted of white dots, white outlined squares (cue), or white filled squares (target) on a black background (Fig. 1). The crows initiated the trials and gave their responses via changes of their head positions. During pretraining, the crows had learned to move and hold the head in the required central position and to respond to the target stimulus.

Task 1: Nonpredictive cue task. In the first version of the spatial cueing task, the crow had to maintain the head exactly between the two side monitors with the beak pointing straight forward and parallel to the monitors. The crow had to respond to a target appearing on either the left or right monitor. All the presented items appeared on their respective side in the same location. A white dot (0.7° visual angle) on each of the side monitors served as a Go-stimulus and indicated that the crow could start a new trial. After moving the head into the predefined position, the white Go-stimulus disappeared. From now on, the crow's head had to remain in the predefined position. Leaving this predefined position resulted in the abortion of the trial and green flashing monitors as visual feedback. After the disappearance of the go-cue, the pre-cue phase with blank monitors for 200–400 ms followed. With the following cue period, three different cue conditions were possible.

The trial either continued with or without a cue. In trials with a cue, the cue was presented during the 50 ms long cue phase. It appeared in the same location as the previous go-cue. The cue was presented as a white outline of a square (2.95° visual angle). In "valid" trials, the cue was flashed on the same side and monitor as the subsequent target. In the "invalid" trials, the cue was flashed on the opposite side as the subsequent target. In "no-cue" trials, no cue was shown and the monitor stayed black.

The cue phase was followed by a delay phase with black monitors. Five different delays were used. The 50 ms cue phase and the delay phase add up to the "stimulus onset asynchrony," or SOA. We used SOAs of 100, 200, 400, 800, and 1,600 ms. A trial ended with the target and response phase. In this phase, the target appeared either on the left side or on the right side (left and right monitors, respectively) at the position of the go-cue and cue. The target was a filled white square (1.15° visual angle). The crow now had to answer by moving the head out of the allowed area. For the response, a time window between 150 ms and 550 ms after the target onset was defined. A response shorter than 150 ms (indicating responses too early to be caused by stimulus detection) resulted in trial abortion, while no responses or responses later than 550 ms were counted as error and elicited a yellow flash on the monitor. This resulted in three categories of trial outcomes: All trials in which the crow accidentally moved the head outside of the position borders (as set by the head tracking system)

between cue onset and target onset plus 150 ms were counted as "abortion" trial. Abortion frequency for the four crows was as follows: crow 1: 9.4%, crow 2: 27.5%; crow 3: 27.9%; crow 4: 33.8%. Abortion trials were excluded from the calculation of detection accuracy. All trials in which the crow failed to detect a target (i.e., missed to detect a target) and did not respond between 150 ms and 550 ms after the target onset were counted as "error" trials. All trials in which the crow responded in a time window between 150 ms and 550 ms after the target onset were counted as "correct" trials. Every error or aborted trial was followed by a timeout of 2,000 ms.

The relation between cue and target defined the condition. If cue and target appeared on the same side, the trial was a "valid" trial. If the cue appeared on the opposite side, it was an "invalid" trial. These possible combinations amount to six different conditions for each SOA (target left valid or invalid, target right valid or invalid, target left or right without cue). In this nonpredictive cue task, the sessions consisted of 25% valid cue trials, 25% invalid cue trials, and 50% no-cue trials. This means that in this task, the cue was nonpredictive and the participating crows could never have learned any meaning of the cue.

Furthermore, three different target intensities were used. These were a "high" intensity of 10.2 cd/m^2, a "medium" intensity of 3.1 cd/m^2, and a "low" intensity of 0.43 cd/m^2 (measured with a Konica Minolta luminance meter LS-100). In each daily session, the conditions were pseudorandomized and balanced for the SOA, the target side, and the intensity. The erroneous and aborted trials were repeated after a random number of trials. Crows 1 and 2 each participated for a total of 50 sessions in this task. Each session consisted of 210 correct trials, on average.

Task 2: Predictive cue task. Task 2 differed from task 1 only in the validity of the cue. That is, the crows had learned that the cue predicted with high probability the location where the target would appear. Sessions with 80% valid cue trials, 10% invalid cue trials, and 10% no cue trials made the cue highly predictive in this task. Crows 3 and 4 participated in the predictive cue task for a total of 25 sessions each.

Variation of task 2: Follow-up task. The follow-up task was identical to task 2 except for reduced target intensities. The intent was to see whether even lower target intensities would elicit accuracy differences between valid and invalid trials. We were specifically interested to find a stimulus condition that elicited strongest possible attention effects. Because exogenous attention seemed limited in crows, this follow-up task was only done with the two crows from the predictive cue task (crows 3 and 4) and only for 11 sessions each. Two of the three target intensities used in this follow-up task were lower than the low intensity in the previous tasks. The used

target intensities were 0.43 cd/m^2, 0.38 cd/m^2, and 0.32 cd/m^2. Furthermore, there were no "no-cue" trials in this task. Instead, the sessions consisted of 80% valid and 20% invalid trials.

Data Analysis. Custom-written MATLAB programs (version R2021a, MathWorks Inc.) were used for data analysis. Nonparametric statistics was exclusively used. The two typical behavioral parameters of RT and detection accuracy were analyzed for different conditions.

The analysis of the RT was done with correct trials only. First, median RTs per SOA and session were calculated. These session medians were then averaged to achieve the results referred to in text and figures. For the RT difference, the session medians for correct valid trials were subtracted from the respective session medians for correct invalid trials. The average RT differences were calculated by first combining session RT differences for both crows, and then calculating the average. This resulted in n = 50 in task 1 and n = 25 in task 2 for the individual birds. In the follow-up task 2, the individual crows had n = 11 sessions, and the average was n = 22 sessions. The RT difference was also calculated for each session across all SOAs. The session's RT differences were then again averaged.

The detection accuracy was calculated as the number of correct trials divided by the sum of correct and error trials. Aborted trials were not considered. The detection accuracy was first calculated for each session and then averaged across sessions. The accuracy difference resulted from subtracting the detection accuracy in correct invalid trials from the detection accuracy in correct valid trials. Just as the RT difference, the accuracy difference was first calculated for each session and then averaged across sessions. The calculations for individual crows and the average per task were done in the same way as for the RT difference. As in the case of the RT difference, an average accuracy difference for each intensity was also calculated and tested in the same way.

To further analyze cueing effect across signal amplitude, we plotted accuracy valid– accuracy invalid vs. overall performance across the tested target stimulus intensities. A cueing effect was defined as the difference in proportion correct between valid and invalid trials. This was done separately for the nonpredictive cue task and the predictive cue task.

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