



Reward history modulates visual attention in an avian model

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Abstract

Attention can be biased towards previously reward-associated stimuli even when they are task-irrelevant and physically non-salient, although studies of reward-modulated attention have been largely limited to primate (including human and nonhuman) models. Birds have been shown to have the capacity to discriminate reward and spatial cues in a manner similar to primates, but whether reward history involuntarily affects their attention in the same way remains unclear. We adapted a spatial cueing paradigm with differential rewards to investigate how reward modulates the allocation of attention in peafowl (*Pavo cristatus*). The birds were required to locate and peck a target on a computer screen that was preceded by a high-value or low-value color cue that was uninformative with respect to the location of the upcoming target. All birds exhibited a validity effect (performance enhanced on valid compared to invalid cue), and an interaction effect between value and validity was evident at the group level, being particularly pronounced in the birds with the greatest amount of reward training. The time course of reward learning was conspicuously incremental, phenomenologically slower compared to primates. Our findings suggest a similar influence of reward history on attention across phylogeny despite a significant difference in neuroanatomy.

Keywords Reward learning · Visual search · Attentional bias · Selective attention · Avian attention

Introduction

Natural environments are perceptually dense and complex, requiring organisms to use their attention to selectively filter information for further processing. What is ultimately prioritized by attention is the outcome of a trichotomous

competition between current goals, physical salience, and selection history (e.g., Anderson et al. 2021; Awh et al. 2012; Desimone and Duncan 1995). Observers can voluntarily direct their attention to task-relevant locations (e.g., Posner 1980; Yantis and Johnston 1990), and stimuli that possess a task-relevant feature (e.g., Folk et al. 1992; Irons et al. 2012; Reynolds et al. 1999; Wolfe et al. 1989). However, attention can also be involuntarily drawn towards physically

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salient information (e.g., the only red flower in a field of green grass because of the high feature contrast, e.g., Itti and Koch 2001; Theeuwes 1992, 1994; Yantis and Jonides, 1984), or personally relevant, experience-driven sources of information (e.g., your favorite dessert in the restaurant display case; Anderson et al. 2021; Awh et al. 2012). Selection history has recently emerged as a source of attentional bias in which prior experiences can exert a direct influence on the control of attention (e.g., Anderson et al. 2021; Awh et al. 2012). Reward history is one component of selection history, and Anderson et al. (2011) demonstrated that previously reward-associated features continue to capture attention in a subsequent task even when those features are non-salient and task-irrelevant. Such value-driven attentional capture has been demonstrated across a variety of stimulus features including color (Anderson et al. 2011; Le Pelley et al. 2015), orientation (Laurent et al. 2015; Theeuwes and Belopolsky 2012), shape (Della Libera and Chelazzi 2009; Della Libera et al. 2011), and object category (Donohue et al. 2016; Hickey et al. 2015), in addition to value-driven prioritization of regions in space (Anderson and Kim 2018a, b) and directional eye movements (Liao and Anderson 2020; see also Liao et al. 2023). The study of reward history effects on attention has been largely limited to primate (human and nonhuman) models (Anderson 2019) and it is unknown whether the involuntary influence of reward on attention generalizes to other biological classes.

Like primates, eyesight is a critical sensory modality for many birds, allowing them to fly, evade predators, forage for food, and evaluate potential mating partners. Unlike primates, however, birds have four types of cones in their eyes instead of three (Bowmaker et al. 1997), which allows them to see parts of the light spectrum that primates cannot. In addition, they also have superior temporal sensitivity for fast-changing visual stimuli. Hodos et al. (2003) demonstrated that pigeons can detect temporal resolution thresholds up to 100 Hz compared to 60 Hz in humans. Bird brains are generally smaller than their body size-matched primate counterparts (Clayton and Emery 2015), but the most salient neuroanatomical difference is the lack of a multilayered cortex and a much smaller cerebellum. However, forebrain organization remains similar (Güntürkün, 2005; Kirsch, et al. 2008; Olkowitz et al. 2016), and avian visuo-cognitive abilities are comparable to their primate counterparts, making them an ideal comparative cognition model for investigating how different neuroanatomy supports the same functions (Knudsen 2018).

In a relevant study, Sridharan and colleagues used a spatial cueing paradigm to demonstrate that chickens are capable of extracting information from a spatial cue to improve accuracy and reaction time for target detection (Sridharan et al. 2014; but see also Blough 1989, 2000; Quest et al. 2022; Shimp and Friedrich 1993). Classical spatial cueing

experiments involve a salient cue that precedes target onset at either the same (valid) or a different (invalid) location (e.g., Folk and Remington 1998; Posner 1980). In the event that attention is directed to the cue, response time in target identification should be faster on valid trials, since attention has already been oriented to the location of the target when it appears, which reduces processing time. In Sridharan et al. (2014), the birds pecked at a cross to begin each trial, which was followed by either valid, invalid, or no cue in the form of a red circle that predicted only the horizontal placement of the target stimuli. The target and distractor were identical except in contrast and were presented simultaneously for 50 ms, after which the bird had to report the vertical position of the target by pecking at one of two response boxes. The birds were rewarded after making correct responses, or they could opt-out of the trial and receive a reward ~ 33% of the time. Consistent with primates, spatial cueing increased task performance on valid trials with increased target localization accuracy and decreased response times (Folk and Remington 1998; Herbranson and Stanton 2011; Posner 1980; Tomonaga 1997).

In addition to similar spatial attention capabilities, avian attention more generally has been shown to be sensitive to rewards for many decades, as pigeons were sensitive to different features that predict reward as measured by pecking responses (Reynolds 1961). Although they were reinforced on a combination of two features (color and shape), the pigeons actually only selected one feature to prioritize (e.g., color over shape or vice versa), showing an inherent ability to prioritize important features while ignoring features that are either task-irrelevant or provide redundant information. Reward-modulated attention also extended to cued visual search, as reaction time decreased for the target associated with a higher reinforcement ratio at the expense of performance for other targets (Blough 2000; see also Blough 1989). In this case, however, the target and the reward-associated cue were combined such that reward was not an independent source of attentional bias but a means to promote motivational engagement (Shen and Chun 2011; Small et al. 2005; see also Chelazzi et al. 2013 and Pessoa 2009 for reviews).

Here we used the Indian Peafowl (*Pavo cristatus*) as our avian model and adapted a spatial cueing paradigm to investigate how involuntary attentional control is influenced by reward history, which has not been previously investigated in birds. In addition to common pressures on survival such as predator and prey detection, peafowl are also a lekking species where peacocks with a more elaborate train have greater mating success (Petrie and Halliday 1994). Like many other birds, peafowl have a tetrachromatic color vision system with four different types of cones in their retina as well as a homolog to the human fovea (Hart 2002). Although not as ubiquitous as pigeons or chickens, peafowl have been the

subject of many experiments (e.g., Yorzinski et al. 2017a, b) including those investigating ecologically relevant attentional orienting (Yorzinski and Platt 2014; Yorzinski et al. 2017a, b; Yorzinski 2019). We focused our investigation on the differences in performance in target localization following a high-value and low-value color cue that was uninformative with respect to the location of the upcoming target. Faster responses on valid compared to invalid trials for uninformative cues is a robust and commonly used indicator of involuntary attentional processing of the cue in both humans and birds (e.g., Folk et al. 1992; Folk and Remington 1998; Irons et al. 2012; Quest et al. 2022). Where prior studies have manipulated cue validity (i.e., how often the cue predicts target location) or stimulus onset asynchrony (i.e., time between the onset of cue and target stimuli; Folk and Remington 1998; Posner et al. 1978; Shimp and Friedrich 1993; Tomonaga 1997), we opted to manipulate reward by using two cues of different colors. We predicted performance to mirror that of primates (e.g., Hickey et al. 2011; Peck et al. 2009; Preciado et al. 2017; Failing and Theeuwes 2014) with larger cueing effects when the uninformative cues are associated with reward.

Method

Subjects

A total of seven adult peafowl (five peahens and two peacocks) were trained to perform the task, four of whom contributed behavioral data. One peahen died before testing could begin, and the peacocks learned the task but stopped participating once the mating season began (due to time constraints, we did not have time to re-train the males after the mating season ended). Of the remaining four peahens, two became uncooperative partway through the study, completing comparatively fewer trials. The birds were housed in an outdoor aviary ($18.3 \times 24.4 \times 2.1$ m) and the experiment was

conducted in a separate enclosure ($5.8 \times 5.9 \times 2.1$ m; testing area; see S1 for diagram) within the aviary. All of the birds were caught from free-ranging populations in Florida, North Carolina, and California between 2009 and 2019 (see Yorzinski et al. 2013 for further details of this population), and were given food and water ad libitum. None of the birds exhibited any signs of cognitive or physical abnormality. The study took place over a 2-year period, beginning in January 2021 and concluding in November 2022 (Figs. 1 and 2).

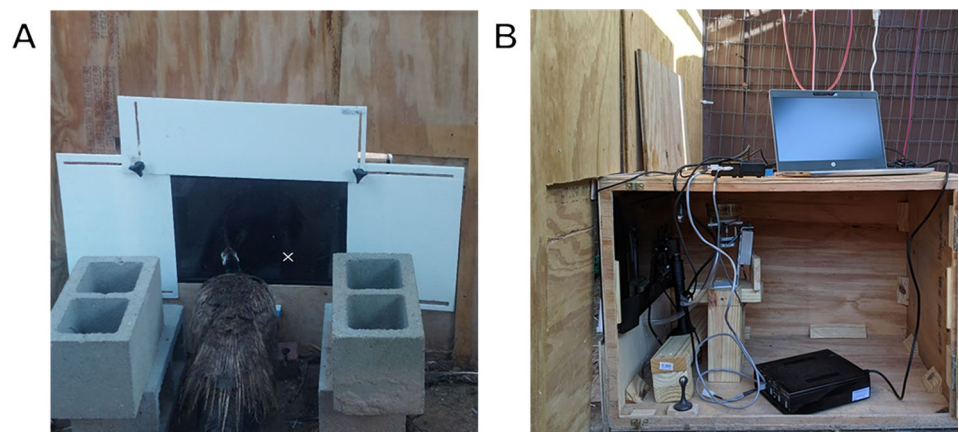
Apparatus: the touchscreen-equipped operant chamber

Behavioral testing was conducted with our touchscreen-equipped operant chamber (TOC), which was an open



Fig. 2 Time course of trial of events during the experiment. The subjects pecked the central fixation cross to initiate the trial, before pecking at the target 'X' which appeared after the reward-predictive color cue. The cue and target could appear in one of four locations on the screen, and reward-color associations were counterbalanced

Fig. 1 Experimental setup, which included a touchscreen-equipped operant chamber (TOC) and a wall to separate the experimenter and subject. The front facing side of our setup (A) included cinderblocks to limit peafowl position during the experiment and the task, both of which were controlled by the experimenter on the other side of the wall (B)



chamber as in Seitz et al. (2021) to allow the peafowl to engage with the apparatus at will. The TOC was constructed out of commercially available plywood sheaths, water-proofed with a wood sealer, and cut to size with a circular saw and a computerized numerical control cutter. The TOC was constructed to hold a touchscreen sensor (TouchWindow) and a clear polycarbonate sheet in front of a monitor (Dell S2417DG, replaced with Sceptre E248B-FPN168 during the course of the study; both with 144 Hz refresh rates), which were connected to a laptop (HP ProBook 445R G6) that also controlled a pellet dispenser (Med Associates ENV-203-190IR) that delivered food (BioServ 190 mg Bacon Yummies) to an external pellet receptacle (Med-Associates ENV-200R6). The food used was considered a treat that was withheld from the peafowl outside of experiment purposes. A wall was constructed out of plywood sheaths to form a barrier between the experimenter and the peafowl to minimize distractions, although a hole (2.54 cm in diameter, 152.4 cm off the ground; see S1) was drilled that allowed the experimenter to observe the peafowl at all times. Additionally, cinderblocks were stacked to limit peafowl position during the experiment.

Training procedure

Similar to Seitz et al. (2021), peafowl were trained to interact with the TOC through three distinct steps: habituation to the TOC, stimulus engagement training, and experimental paradigm training. The Matlab code for the procedures (as well as the experiment) is available at https://osf.io/dvzqh/?view_only=28bcf725882548e8acb36a06adea7960.

Habituation to TOC

We manually dispensed food pellets to encourage peafowl to approach the TOC monitor and eat out of the receptacle. Pellet dispensing was preceded by a 500-Hz tone for 100 ms, and the delay between tone and food reward was less than 100 ms. Habituation initially occurred with the entire flock to alleviate potential anxiety or fear of being separated from the flock. Afterwards, birds that voluntarily interacted with the TOC were individually guided into the testing area (by slowly walking behind them and directing them towards the testing area) for individual habituation training, as well as all other training that followed.

TOC engagement training

Peafowl were trained to peck the screen to gain access to a food reward. Like Seitz et al. (2021), we found that instrumental learning (peck a stimulus to receive a reward) worked best. We employed a variety of shaping tasks in which the experimenter would manually reward the birds

while incrementally adjusting the difficulty of obtaining food (i.e., encouraging more accurate responses). We found that different birds responded to different shaping procedures, with *peckMouse* (experimenter-controlled square) and *peckCricket* (biologically relevant stimuli like crickets;) being the most effective (see S2 File for detailed description of these methods and a general overview of the approaches to shaping used).

Experimental paradigm training

After the peafowl had learned to peck at stimuli for food reward, they began training on individual components of our experimental paradigm. They first learned to peck at the central fixation cross (2.5 × 2.5 cm). After learning this component, they learned to peck at the central fixation to initiate the trial then to peck at a target 'X' (1.8 × 1.8 cm) that randomly appeared within one quadrant of the screen. Lastly, the peafowl continued training with the entire sequence (pecking at an initial fixation cross and then pecking at a peripheral target) within a four second time limit until performance was stable. After we finalized our shaping procedure, taking the peafowl from naïve to experiment-ready took approximately four months of consistent training (sessions at least twice a week, weather permitting). The typical eye-to-screen distance was 15.2 cm for a bird using our apparatus, although the birds could move freely, and thus eye-to-screen distance was not controlled.

General TOC training rules

We replicated the general guidelines in Seitz et al. (2021) by making the TOC apparatus (see S3 File) available only during training or experimentation, removing the bird from the testing area if they did not engage within five minutes, and ending the session early if they became distracted and did not return to the task within five minutes. In addition, if a bird was exhibiting any signs of distress at any stage of the training procedure, it was immediately returned to the flock. With the TOC set up outdoors, we only ran trials on days when there was no rain/snow, and wind gusts were low (below 15mph).

Experimental paradigm

We combined a contingent capture task (Folk and Remington 1998) and a value-modulated attentional capture task (Le Pelley et al. 2015) with peck-sensitive responses where a color cue (1 cm × 1 cm) precedes a target "X" that the bird must peck on every trial. The peafowl were randomly assigned to a color–reward association pairing (red, green, and blue; high-value and low-value reward). One cue color predicted an 80% probability of large reward and

20% probability of small reward (high-value cue), whereas the other color predicted a 20% probability of small reward and 80% probability of no reward (low-value cue). Both color cues were uninformative with respect to the upcoming target location (25% valid and 75% invalid).

The color cue appeared for 50 ms in one of four cartesian quadrants, 250 ms after a peck on the fixation cross. Following a 250-ms inter-stimulus interval, the target “X” appeared in one of four cartesian quadrants for 6000 ms or until the bird pecked at the target, whichever came first. The color cue and target appeared only in the center of each quadrant. The trial ended with a blank screen and food dispersal (if any) that occurred after a 500 Hz tone for 100 ms. The next trial began immediately after the previous one ended. The bird only received a food reward if it pecked at the target within 6000 ms. The cue and target locations were fully crossed and counterbalanced such that the cues were uninformative with respect to the upcoming target location, resulting in 25% of the trials being valid and 75% of the trials being invalid. The color–reward association was pseudo-counterbalanced across birds (1: blue–high, red–low, 2: green–high, blue–low, 3: red–high, green–low, 4: blue–high, green–low), and the experiment was programmed in Matlab with Psychophysics Toolbox extensions (Brainard 1997). An ideal block of trials was composed of 160 trials with the color of the uninformative cue, the location of the cue, and the location of the target fully counterbalanced. After the 160 trials, there was a delay as the data saved, during which the birds would often leave. The birds participated voluntarily, so our stopping rule was whenever the birds stopped participating (i.e., walked away or laid down), but we would run as many trials as the birds wanted. See supplemental Table 1 for information about the dates of each session, along with the number of trials in each session. Whenever the birds ceased engaging with the apparatus or pecking became suboptimal (e.g., getting too close to the screen for a point of contact to be registered), we would return the bird to the shaping procedures to encourage voluntary pecks that could be registered by our apparatus.

Table 1 Detailed breakdown of trials excluded from analyses, for each bird

Bird	Total Trials	Misses	RT < 150 ms	RT > 2000 ms
1	8976	516	241	2713
2	1994	430	1	609
3	9589	1350	62	2925
4	4176	671	49	1536

Misses refer to trials where no pecks on the target were registered within the 6-s window. RTs < 150 ms reflect anticipatory responses that were trimmed, and RTs > 2000 ms reflect trials that were trimmed for low task engagement

Measurements and statistical analyses

Only responses faster than 2000 ms were analyzed to account for low task engagement (the measurement of attentional capture assumes speeded responses), external distractions, and touch screen insensitivity. Responses under 150 ms were also excluded from analyses as anticipatory responses. Overall, 47.5% of trials were excluded from analyses (bird 1: 38.7%, bird 2: 52.2%, bird 3: 45.2%, bird 4: 54.0%; Table 1). Proportion of trials missed and proportion of trials trimmed due to fast responses did not significantly differ as a function of validity or value ($p > 0.1$), and the proportion of trials excluded due to slow responses generally mirrored the pattern observed in mean RT, with the conditions that were the slowest also tending to have more delayed responses removed (S4). We compared the effects of value and validity on response times (RTs) with 2×2 ANOVAs for each peahen individually, then all together with a 2 (high vs low-value) $\times 2$ (valid vs invalid) $\times 4$ (birds 1–4) ANOVA. Faster responses on valid trials compared to invalid trials is indicative of attentional capture by the uninformative cue (Folk and Remington 1998), whereby the cue is attended in spite of its irrelevance to the behavior required to obtain reward (pecking on the target). Analyses focus on RT, as pecks on locations other than the target (pecking errors, including pecks at the cued location on invalid trials) were not observed.

We conducted post hoc analyses investigating reward-modulated cueing effects over the first and second half of trials for each bird separately to examine the unfolding of trends in reward-related biases. We also binned trials into blocks of 50 and ran a multiple regression to investigate how the trends emerge on a finer temporal scale. All analyses were conducted in R.

Results

Aggregate analyses

Each of the birds exhibited a validity effect, with faster response time for valid compared to invalid trials (i.e., validity effect; Bird 1: $F(1, 5502) = 17.98$, $p < 0.001$, $\eta_p^2 = 0.003$, Bird 2: $F(1, 950) = 13.80$, $p < 0.001$, $\eta_p^2 = 0.014$, Bird 3: $F(1, 5248) = 138.30$, $p < 0.001$, $\eta_p^2 = 0.026$, bird 4: $F(1, 1916) = 3.69$, $p = 0.055$, $\eta_p^2 = 0.002$; Fig. 3). The validity effect increased from first to second half for Bird 1, $F(1, 5498) = 27.09$, $p < 0.001$, $\eta_p^2 < 0.001$, and marginally so for Bird 2, $F(1, 946) = 2.99$, $p = 0.084$, $\eta_p^2 = 0.003$, and Bird 3, $F(1, 5244) = 3.29$, $p = 0.070$, $\eta_p^2 = 0.001$, but not for Bird 4, $F(1, 1912) = 0.04$, $p = 0.846$, $\eta_p^2 < 0.001$. For Bird 1 and Bird 3, there was an interaction between value and validity in which the validity effect was larger for high-value compared

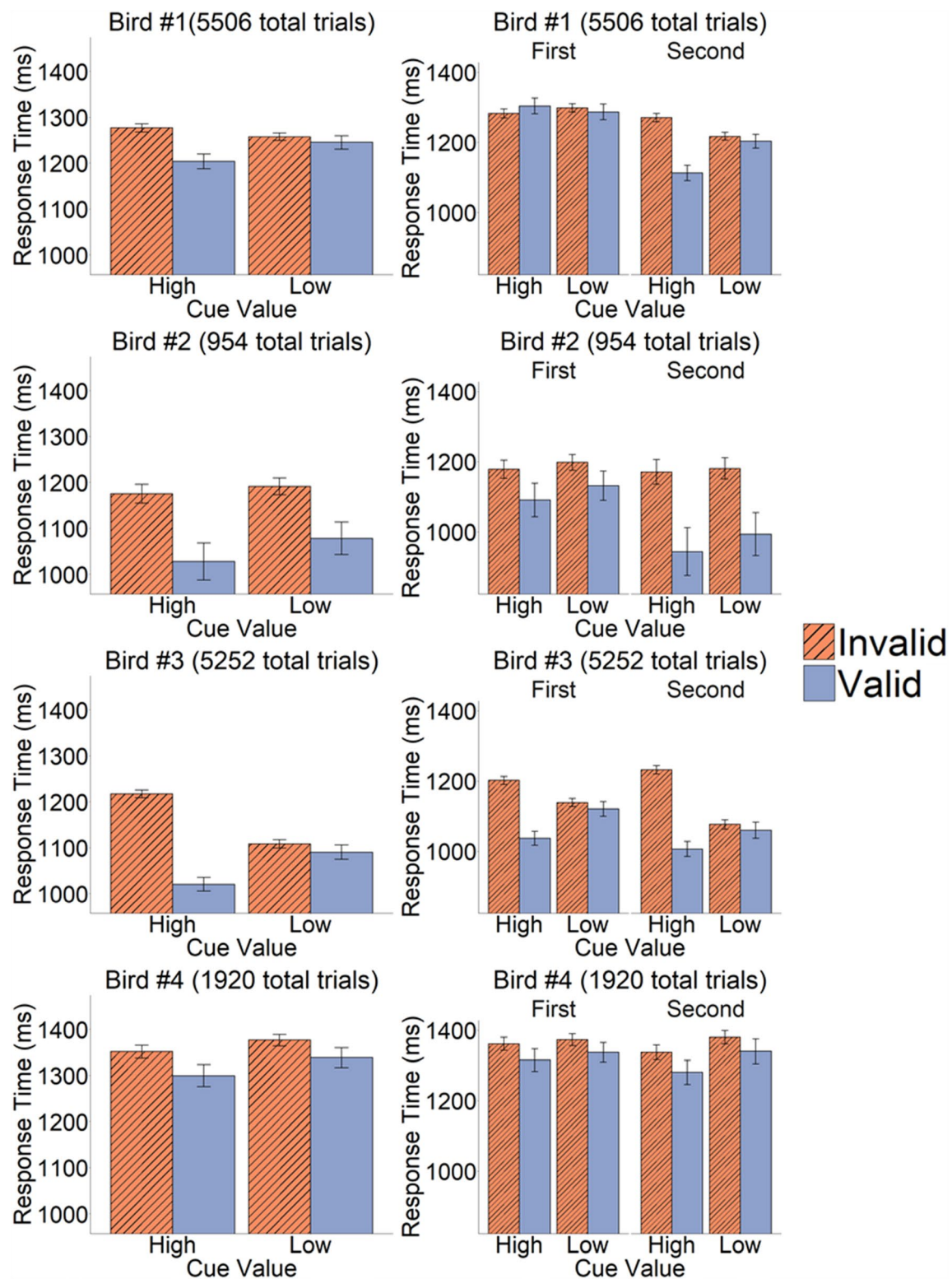


Fig. 3 Response times as a function of the value and validity of the cue for **A** each subject, and **B** for each subject broken down into the first and second half of testing. Error bars represent standard error of the mean

to low-value cues, $F(1, 5502) = 6.25$, $p = 0.012$, $\eta_p^2 = 0.001$, and $F(1, 5248) = 55.13$, $p < 0.001$, $\eta_p^2 = 0.010$, respectively ($ps > 0.5$ for the other birds).

Only Bird 3 exhibited a main effect of value, with faster response time for high-value compared to low-value trials, $F(1, 5248) = 77.38$, $p < 0.001$, $\eta_p^2 = 0.015$ ($ps > 0.1$ for the other birds). The difference in high-value and low-value response times increased between halves for Bird 1, $F(1, 5498) = 8.09$, $p = 0.004$, $\eta_p^2 < 0.001$, and Bird 3, $F(1, 5244) = 14.09$, $p < 0.001$, $\eta_p^2 = 0.003$ ($ps > 0.4$ for the other birds), but only Bird 1 showed an interaction between validity and value that increased between halves, $F(1, 5498) = 13.26$, $p < 0.001$, $\eta_p^2 < 0.001$ ($ps > 0.1$ for the other birds). See supplemental Tables 2A,B for a complete report of the statistics for each individual bird.

With the data for all four birds combined (Fig. 4), we observed differences in performance depending on the bird, $F(3, 13,625) = 188.35$, $p < 0.001$, $\eta_p^2 = 0.04$. Altogether, validity effects were greater for high-value compared to low-value cues, reflected in a significant interaction between value and validity, $F(1, 13,625) = 42.82$, $p < 0.001$, $\eta_p^2 = 0.003$. A post hoc Tukey test showed that all comparisons were significant, $ps < 0.04$. Critically, responses were faster for valid high-value ($M = 1128$ ms, $SD = 423$ ms) compared to valid low-value trials ($M = 1186$ ms, $SD = 399$ ms), and slower for invalid high-value ($M = 1258$ ms, $SD = 378$ ms) compared to invalid low-value ($M = 1212$ ms, $SD = 394$ ms) trials. See Table S2C–E for full analyses.

Progression of effect analyses

We then investigated how the effects across each bird developed over individual testing sessions (Fig. 5 and Table S3). A multiple linear regression was calculated for each bird to predict RT based on validity, value, and block. A significant equation was found that explained the variance in RT

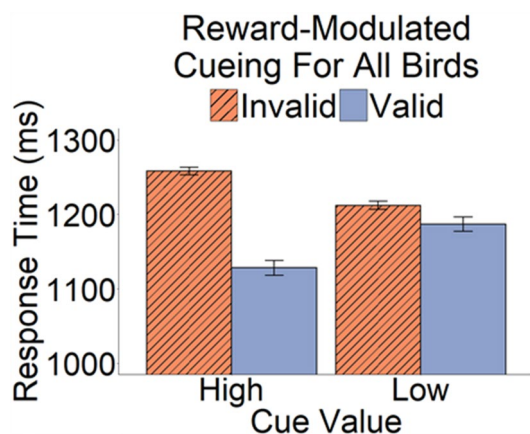


Fig. 4 Response time as a function of the value and validity of the cue for all trials for all birds combined

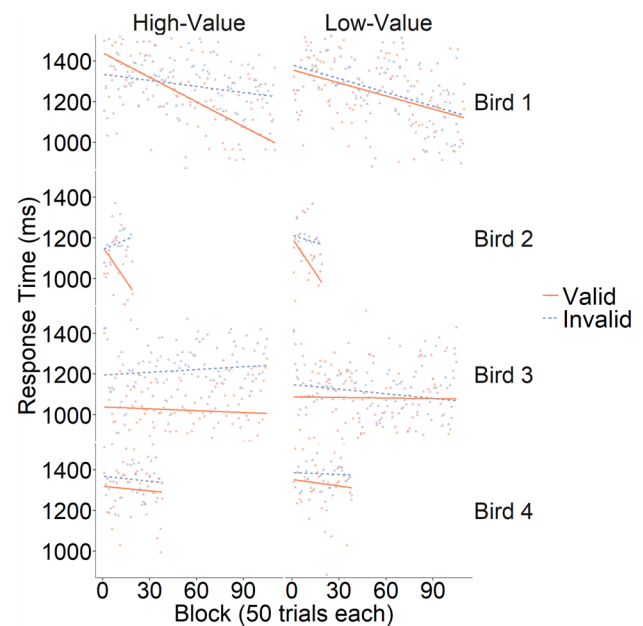


Fig. 5 Mean response time over sequential 50 trial bins for each bird (1–4) with slopes indicated

for bird 1, $R^2 = 0.19$, $F(7, 432) = 14.13$, $p < 0.001$, bird 2, $R^2 = 0.24$, $F(7, 68) = 4.46$, $p < 0.001$, and bird 3, $R^2 = 0.18$, $F(7, 412) = 13.87$, $p < 0.001$, but not for bird 4, $R^2 = 0.01$, $F(7, 144) = 1.143$, $p = 0.340$. Bird 1 and bird 3 exhibited significant effects of validity [10.00, 202.08], $p = 0.031$, [− 239.23, − 74.16], $p < 0.001$, respectively, reflecting the validity effect observed in the earlier analyses with faster responses on valid compared to invalid trials.

Bird 1 exhibited marginally significant effects of block, ([− 2.06, 0.07], $p = 0.066$), and the interaction between validity and value, ([− 266.07, 5.58], $p = 0.060$), as well as a significant interaction between validity and block, ([− 4.53, − 1.52], $p < 0.001$), and the interaction between validity, value, and block, ([1.01, 5.26], $p = 0.004$). In other words, performance was different for high-value and low-value trials throughout all blocks, but the validity effect for the high-value trials increased while it remained comparable for the low-value trials. The validity effect increased over blocks of trials for bird 2, ([− 28.39, − 0.50], $p = 0.043$), and the difference in RT between high and low-value trials increased over blocks for bird 3, ([− 2.56, 0.15], $p = 0.08$). The effects not mentioned for birds 1–3 were not significant, $ps > 0.1$, and all effects for bird 4 were not significant, $ps > 0.4$ (see Table S3A–D for full analyses).

To investigate how the effects developed over time for all birds, we added bird as an intercept term to the multiple linear regression above. A significant regression equation was found that explained 28.84% of the variance in RT ($R^2 = 0.29$, $F(10, 1077) = 45.04$, $p < 0.001$). Although RT over time differed between all birds, $p < 0.007$, there was

a significant three-way interaction between validity, value, and block, $[1.05, 3.47]$, $p < 0.001$, suggesting that reward-modulated cueing effects developed over time for all birds. See supplemental Table 3E for full analyses.

Discussion

We corroborated prior studies demonstrating that birds exhibit the same signatures of spatial attention as seen in human and non-human primates (e.g., Folk and Remington 1998; Posner 1980; Shimp and Friedrich 1993; Sridharan et al. 2014; Tomonaga 1997), and extend those findings to the modulatory influence of reward history, a component of selection history (e.g., Anderson et al. 2021, Awh et al. 2012). The peafowl exhibited validity effects in which they were faster to respond to targets appearing in the same location as a preceding uninformative cue (valid trial), compared to trials in which the target appeared in a different location (invalid trials). Importantly, reward history markedly increased this validity effect for high-value compared to low-value cues, a finding not previously demonstrated in birds (see Blough 1989, 2000 for related findings). The four birds in our study were assigned different color–reward associations such that our findings cannot be explained by color-specific biases and only by the associated value of the color cue. The similarities between primates and birds in this respect (e.g., Hickey et al. 2011; Peck et al. 2009; Preciado et al. 2017; Failing and Theeuwes 2014) suggests that the mechanism for the value-dependent modulation of attention may have appeared early in evolution and has been conserved across phylogeny.

We observed a robust interaction effect between value and validity consistent with behaviors typical of humans (Preciado et al. 2017; Failing and Theeuwes 2014) collapsed across all trials for all birds. When tested separately, however, this interaction was only significant in the two most frequently trained birds (total trials greater than 5000 each). We then tested the emergence of effects over sequential blocks of 50 trials and found that only bird 1 exhibited an interaction effect that emerged gradually across testing sessions, while the validity effect emerged over testing sessions for bird 2, and the value effect emerged over testing sessions for bird 3. Although the effect of value continued to emerge across halves for bird 3, the effect of validity and the interaction effect between validity and value seemed to have stagnated as evidenced by first and second half comparisons. Our results suggest there to be a ceiling in the modulatory effect of reward on selective attention, and that there exist individual differences in birds with respect to the time course of learning-dependent influences on attention.

The emergence of value-modulated attentional capture in our sample was conspicuously slower than that in humans,

which can be evidenced in a single testing session (e.g., 400 trials in Le Pelley et al. 2015). It is important to note that most studies examining the effects of reward history on attention closely and consistently pair the reinforcement with the predictive cue with respect to temporal occurrence (e.g., Anderson et al. 2011; Le Pelley et al. 2015), but our paradigm included an extra 250 ms after the cue along with up to 6000 ms before receiving the reinforcement (but see also Small et al. 2005 for a similar paradigm). The value of the reinforcer is discounted with delay (Odum 2011), so learning may have been inherently more difficult in this task. Although there are cross-species variation in perceptual systems such as tetrachromacy and an increased temporal sensitivity in birds (Bowmaker et al. 1997; Hodos et al. 2003), these differences are unlikely to be the reason for suboptimal learning. Birds can discriminate colors just as well as humans (Olsson et al. 2015), robustly learn color–reward associations (e.g., Reynolds 1961), and exhibit similar patterns of delay discounting compared to humans (Calvert et al. 2011). Whether a more sensitive temporal sensitivity would result in a less robust linking of the high-value cue to reward, particularly on trials with slower responses, remains unclear. Along with differences in task demands, impediments in learning may be due to incomplete task understanding and naturalistic environments in which there were greater sources of external distractions.

Although avian brains contain a much smaller cerebellum and no neocortex (Krazulis et al. 2018), how their brains support selective attention, and potentially the learning-dependent modulation thereof, are remarkably similar. In birds, visual information flows along two main pathways that are homologous to the dorsal and ventral stream in mammals (Niu et al. 2022), and visual selection is handled in the forebrain through the arcopallial gaze field (Winkowski and Knudsen 2007, 2008) which is analogous to the frontal eye field in primates (Squier et al. 2013). Similar to primates, birds also learn through dopamine-mediated reward prediction errors (Güntürkün et al. 2018; Schultz 2016; Soto and Wasserman 2011), which enables them to focus their attention on relevant features (Watanabe 1992; 2003; Knudsen 2018; Krazulis et al. 2018). Since the strength of attentional orienting to reward-associated stimuli was shown to be positively correlated with dopamine release in the striatum (Anderson et al. 2016, 2017), and visual information from both dorsal and ventral streams flow through the striatum in bird brains (Güntürkün et al. 2018), it is very likely that the neurobiology of value-driven attention (Anderson 2019) is preserved across species. Further research would be required to substantiate this prediction, and it would be interesting to see how other types of selection history effects are encoded in the avian brain.

Ultimately, we were unable to investigate potential sex differences in value-driven attention. Our study period

substantially overlapped with the birds' breeding season and the males would not participate in trials during the breeding season (likely because of their interest in mating and defending their mating arena against competitors; Harikrishan et al. 2010). Regardless, we would not expect major differences in attentional processing since both peacocks and peahens have the capacity for selective attention as they attend to peacock trains for both mate and rival assessment (Yorzinski et al. 2013, Yorzinski et al. 2017a, b). Administration of exogenous testosterone during breeding season did lead to increases in aggression in birds (Beletsky et al. 1990; Wingfield 1984; Wingfield et al. 1987) so additional studies that examine sex and hormonal differences in cognition would be valuable in order to explore this idea further.

The present study demonstrates the capacity for peahens to exhibit properties of value-driven attention commonly seen in primates, whereby attention towards task-relevant stimuli can be influenced by task-irrelevant reward-associated stimuli. Such reward-modulated attention may reflect an adaptive mechanism of biased information processing with respect to ecologically relevant behaviors such as foraging, where the allocation of attention guides a bird towards an area with plentiful food, and mate selection, in which a bird focuses their attention on key features that are predictive of reproductive fitness (Anderson 2021). We also establish a robust methodology for testing the learning-dependent attentional processes in birds that can be implemented in enclosed animal housing outside of the laboratory. Cognitive enrichment is an important component of captive animal welfare (Meehan and Mench 2007; Millar 2013) and can be combined with research data collection to benefit both the animal and researchers.

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Author contributions M-RL, BAA, and JYL wrote the main manuscript text. M-RL, JJH, BAA, and JYL reviewed the manuscript text. M-RL, MHD, JLH, LAB, JSW, and ACV collected data. M-RL, BAA, and JYL designed the experiment. M-RL and BAA designed the testing apparatus. M-RL programmed the experiment, prepared the figures, and ran the analyses.

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Data availability Raw data and all experiment and analysis code are available via the Open Science Framework (OSF) at https://osf.io/dvzqh/?view_only=28bcf725882548e8acb36a06adea7960.

Declarations

Conflict of interest The authors declare no conflicts of interest.

Ethical approval This research was approved by Texas A&M University's Animal Care and Use Committee (#2019-0203).

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