

Unihemispheric Evidence Accumulation in Pigeons

Neslihan Wittek¹, Hiroshi Matsui¹, Mehdi Behroozi¹, Tobias Otto², Kevin Wittek^{3, 4}, Nurullah Sarı⁵,
Sven Stoecker⁶, Sara Letzner¹, Vikash Choudhary⁷, Jutta Peterburs⁸, and Onur Güntürkün¹

¹ Faculty of Psychology, Department of Biopsychology, Institute of Cognitive Neuroscience, Ruhr University Bochum

² Faculty of Psychology, Department of Cognitive Psychology, Ruhr University Bochum

³ Institute for Internet Security, Westphalian University of Applied Sciences

⁴ Faculty of Mathematics, Computer Science and Natural Sciences, Department of Computer Science, RWTH Aachen University

⁵ Psychology Department, Faculty of Science, Avrasya University

⁶ Faculty of Psychology, Werkstatt, Ruhr University Bochum

⁷ Institut du Cerveau et de la Moelle épinière (ICM), CNRS UMR 7225 – Inserm U1127, Sorbonne Université

⁸ Department of Medicine, Medical Psychology, MSH Medical School Hamburg

Perceptual decision making involves choices between alternatives based on sensory information. Studies in primates and rodents revealed a stochastic perceptual evidence accumulation process that, after reaching threshold, results in action execution. Birds represent a cognitively highly successful vertebrate class that has been evolving independent from mammals for more than 300 million years. The present study investigated whether perceptual decision making in pigeons shows behavioral and computational dynamics comparable to those in mammals and rodents. Using a novel “pigeon helmet” with liquid shutter displays that controls visual input to individual eyes/hemispheres with precise timing, we indeed revealed highly similar dynamics of perceptual decision making. Thus, both mammals and birds seem to share this core cognitive process that possibly represents a fundamental constituent of decision making throughout vertebrates. Interestingly, in our experiments we additionally discovered that both avian hemispheres start independent sensory accumulation processes without any major interhemispheric exchange. Because birds lack a corpus callosum and have only a small anterior commissure, they seem to be forced to decide on motor responses based on unihemispheric decisions under conditions of time pressure.

Keywords: perceptual-decision, evidence accumulation, unihemispheric, pigeons

Neslihan Wittek  <https://orcid.org/0000-0002-6282-6209>

Hiroshi Matsui  <https://orcid.org/0000-0001-7585-7699>

Mehdi Behroozi  <https://orcid.org/0000-0001-8373-6168>

Tobias Otto  <https://orcid.org/0000-0002-9994-0910>

Kevin Wittek  <https://orcid.org/0000-0003-1245-9970>

Vikash Choudhary  <https://orcid.org/0000-0002-4586-0931>

Jutta Peterburs  <https://orcid.org/0000-0003-3571-126X>

Onur Güntürkün  <https://orcid.org/0000-0003-4173-5233>

Neslihan Wittek and Hiroshi Matsui have contributed equally to this work.

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The code that was used for the experimental paradigms and calculation of the results is available here: <https://github.com/neslihanedes/Unihemispheric-Evidence-Accumulation-in-Pigeons>

Correspondence concerning this article should be addressed to Neslihan Wittek, Faculty of Psychology, Department of Biopsychology, Institute of Cognitive Neuroscience, Ruhr University Bochum, Universitätsstraße 150, 44801 Bochum, Germany. Email: Neslihan.Wittek@rub.de

Living in complex and dynamic environments, animals constantly have to make decisions. Faced with lacking predictability, they often have to choose between foraging strategies (Anselme & Güntürkün, 2019; Bateson, 2002; Protas & Jeffery, 2012; Stephens & Krebs, 1986); mates (Bateson & Bateson, 1983; Ryan et al., 2008); territories (Aubret & Shine, 2008; Pimm & Rosenzweig, 1981; Tetzlaff et al., 2018); and social partners (Almeling et al., 2016; Weinstein & Capitanio, 2012). Thus, proper decision making, by which animals swiftly and accurately detect, discriminate, and categorize all incoming sensory inputs to contextually interpret them, is fundamental for survival. Accordingly, decision-making is a core area of research in both psychology and neuroscience. Currently, the most innovative results are yielded by studies on perceptual decision making which focuses on the combination and evaluation of sensory inputs and corresponding actions (Bitzer et al., 2014; Heekeren et al., 2008).

How long does it take to make a perceptual decision? Consider being a goalkeeper during the penalty shootout of a soccer match. Jumping too fast into the wrong corner is as fatal as jumping too late toward the correct one. Hence, you wait for some evidence about the trajectory of the approaching ball to incrementally accumulate until a decision threshold is reached and you jump (Brunton et al., 2013; Morcos & Harvey, 2016; Odoemene et al., 2018;

Pedersen et al., 2015). This exemplary situation illustrates most of the elements of the evidence accumulation framework that posits three successive steps of information processing: First, an animal receives noisy sensory input from the environment (e.g., visual cues). Second, this accumulating input contains sensory evidence that enables decision making (e.g., the decision to execute or inhibit a response). Third, the perceptual decision is made once the accumulating evidence reaches a threshold (e.g., response execution). This framework of perceptual decision making is well supported by various empirical studies with humans, nonhuman primates, or rodents (Brunton et al., 2013; de Lafuente et al., 2015; Gold & Shadlen, 2001; Huk & Shadlen, 2005; Kelly & O'Connell, 2013; Kira et al., 2015; Lee & Cummins, 2004; Odoemene et al., 2018; Piet et al., 2018; Philiastides et al., 2011; Purcell et al., 2010; Shadlen & Newsome, 1996; Zuo & Diamond, 2019). Moreover, mathematical models based on this framework have been applied successfully in a number of cognitive studies (Brown & Heathcote, 2008; Ratcliff, & Rouder, 2000). In addition, both fMRI and single unit studies indicate that sensorimotor regions including prefrontal and intraparietal areas are involved in evidence accumulation during perceptual decision making (Kim & Shadlen, 1999; Liu & Pleskac, 2011; Shadlen & Newsome, 2001).

Do birds engage in similar perceptual decision making? There is no doubt that birds make decisions (Bartonicsek & Colombo, 2020), but the question is whether they use the same mechanisms as mammals. There are good reasons to ask this question. First, birds and mammals diverged around 312 million years ago (Nei et al., 2001) and have since developed different forebrain organizations (Güntürkün & Bugnyar, 2016); although their sensory areas resemble each other (Stacho et al., 2020). Second, bird brains have no corpus callosum but instead only an anterior commissure that is constituted by a small number of pallial commissural neurons (Letzner et al., 2016). Although interhemispheric communication in birds thus seems to be severely limited in comparison to placental mammals (Aboitiz & Montiel, 2003); pigeons can in principle exchange information between the hemispheres during tasks that involve color or pattern cues (Manns & Römling, 2012; Ünver et al., 2019; Watanabe, 1985). However, especially in tasks that involve response selection based on spatial cues, pigeons face severe limitations of interhemispheric transmission (Nottelmann et al., 2002; Watanabe, 1980; Watanabe & Weis, 1984; Xiao & Güntürkün, 2009). Because birds also have laterally placed eyes, tasks involving incremental perceptual evidence accumulation can be expected to be particularly challenging for them. For instance, fast moving targets that cross from the field of view of one eye into the field of view of the other eye would be expected to require a restart of decision-making in the other hemisphere, which would prolong response time.

Thus, we are faced with two questions: First, are birds using a similar sensory evidence accumulation mechanism as mammals? Second, how do birds cope with the problem of interhemispheric transfer of sensory decisions? The present study aimed to answer both questions by using a GO-NOGO task in pigeons while applying a novel methodology which allowed us to test pigeons in monocular and binocular conditions using precise stimulus on- and offset timing. To this end, pigeons wore a helmet with liquid shutter displays that could open or close input to each eye with high temporal resolution. Findings in humans have suggested that evidence accumulation is distributed over sensorimotor and associative cortical

areas (Liu & Pleskac, 2011) and different timescales (Werkle-Bergner et al., 2014). To date, the corresponding processes in birds are still largely unclear. In the present study, we first aimed to identify the underlying temporal dynamics of evidence accumulation. In Experiment 1, we therefore examined the temporal aspects of sensory evidence accumulation under monocular and binocular conditions by using variable GO stimulus durations. Gradual evidence accumulation was expected to be reflected particularly in gradually increasing accuracy with increasing duration of the GO stimulus. In Experiment 2, we switched the viewing eye during the trial in order to examine whether the sensory information gathered by one hemisphere could be transferred to the other during perceptual decision making. Three outcome options are conceivable: (a) The hemispheres transfer the current status of evidence accumulation to the other side such that the receiving hemisphere can start from there. In this case, we would expect a constant transfer time across conditions. (b) If shutter switches would force the receiving hemisphere to start from zero, we should expect the beginning of a new evidence accumulation function after each shutter switch. (c) If the hemisphere that had received the first stimulus would simply go on to control the response despite meanwhile being devoid of visual input, we expect identical result patterns for Experiments 1 and 2.

Materials and Methods

Animals and Housing Conditions

Nine naive homing pigeons (*Columba livia*) of undetermined sex which were obtained from local breeders were used in this study. Animals were housed in individual cages under a 12 hr/12 hr light/dark schedule (the light was turned on at 7:00 a.m. daily). They were maintained at approximately 80–85% of their free-feeding body weight for the duration of the experiment and had access to water ad libitum. All procedures followed the German guidelines for the care and use of animals in science and were in accordance with the European Communities Council Directive 86/609/EEC concerning the care and use of animals for experimentation.

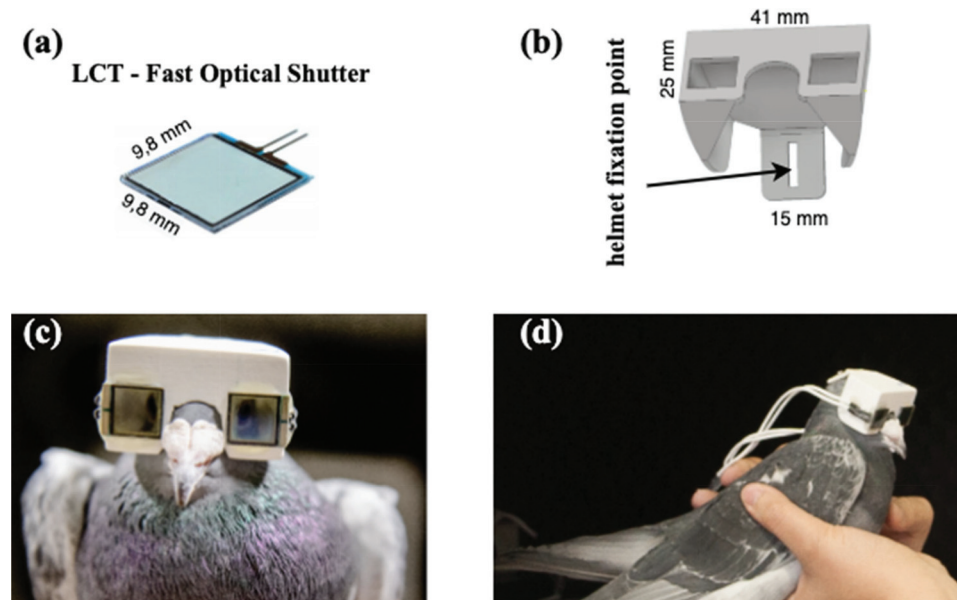
Apparatus

The pigeons were tested in individual operant chambers (34 cm width × 34 cm depth × 32 cm height) which were equipped with a white house light. On the front panel, one transparent pecking key (4 cm × 4 cm), coupled with an electric switch, allowed the animal to respond to the conditioned stimulus displayed on an LCD screen located behind the panel. A food hopper was centered below the keys, approximately 5 cm above floor level, providing access to one food pellet in the rewarded trials. On the back panel, a camera allowed the experimenter to monitor the pigeons' activity during the experiment. A custom written MATLAB program and the Biopsychology Toolbox (Rose et al., 2008) were used to control the apparatus.

Helmet

The pigeon helmet had two frontally oriented shutter displays (LC-Tec.-Fast Optical Shutters, LC-Tec Displays AB, Börlänge, Sweden; closing time ≤ 6 ms, opening time ≤ 30 ms, Figure 1a),

Figure 1
Helmet Design



Note. (a) Fast Optical Shutters as integrated into the helmet. From LC-Tec website by LC-Tec Displays AB, 2021 (<https://www.lc-tec.se/fast-optical-shutters/>). Reprinted with permission. (b) 3D printed white colored PLA helmet; (c) frontal view of pigeon wearing helmet (©RUB, Marquard); and (d) 45° view of pigeon wearing helmet (Christine Heinemann, photographer). See the online article for the color version of this figure.

with each pigeon eye looking through one of these displays (Figure 1c–1d). The shutters could turn the display opaque or transparent, and these changes could be synchronized with the pigeon's pecking on the pecking key. The helmet was manufactured by 3D printing. White colored PLA Polylactide Filament (German RepRap GmbH, Feldkirchen, Germany) with 1.75 mm diameter was used (Figure 1b). The shutter connections with the power supply were constructed using a highly flexible single wire cable (diameter 1×0.25 mm, Stäubli Electrical Connectors, Allschwil, Switzerland). Based on the trial type and the pigeon's response, the state of the shutters was controlled with the custom-written MATLAB program. The helmet design occluded the lateral field of view and thus enforced frontal viewing. Helmets were attached to small plastic pedestals on the pigeon's skull as shown in Figure 1c–1d. The 3D printing code for the helmet is available upon request from the corresponding author.

Surgery

We used a similar method as described by Behroozi et al. (2020) to implant a plastic pedestal to attach the helmet to. In brief, birds were anesthetized with a mixture of ketamine (100 g/ml; Pfizer GmbH, Berlin, Germany) and xylazine (20 mg/ml Rompun, Bayer Vital GmbH, Leverkusen, Germany) and were injected i.m. with .075 ml per 100 g body weight (70% ketamine and 30% xylazine). To maintain a stable anesthesia during surgery, isoflurane as an inhalational anesthetic was provided through a breathing mask (100% (volume/volume percentage), Mark 5, Medical Developments International Abbott GmbH and Co KG, Wiesbaden, Germany). Dental cement (OmniCeram) was used to fix the custom-made pedestals to the animal's skull. Immediately

after surgery, all pigeons received analgesic treatment twice a day on three consecutive days. During the recovery period (1 month), the animals had water and food ad libitum in their home cage. Before starting the behavioral training, the pigeons' food intake was controlled to maintain 80–85% of their free-feeding body weight.

Pretraining

Training started with autoshaping. The pigeons learned to associate food reward with stimulus presentation (key light) in daily sessions for several days until they reliably pecked the lit response key. Then the GO paradigm started, consisting of 150 daily trials. Each trial began with the white initial stimulus presentation (5 s), and after a single key peck, a square-shaped green GO stimulus was shown on the response key for 5 s. Pecking on the GO stimulus was rewarded with one food pellet. GO training was continued until each pigeon responded within the permissible response latency (5 s) in at least 80% of the trials. Then, GO-NOGO training started. Again, each trial started with a white initial stimulus that had to be pecked. Thereafter, either a GO (green) or a NOGO stimulus (red) followed for 5 s. Pecking on NOGO was followed by a 2 s time out as punishment. Pecking on GO was rewarded as described above. After achieving a response accuracy of at least 80%, the animals were habituated to the helmets. To this end, the pigeons were kept in their home cages wearing the helmets to confirm that they moved, pecked, and ate normally. Individual helmet designs were slightly adjusted, depending on each pigeon's needs. Once the pigeons started to consume food while wearing their helmet, we retrained them again in the GO-NOGO paradigm as described above. Training was continued with the helmet until the former response accuracy was reached. As the

last stage of helmet habituation, monocular GO-NOGO trials were introduced. Here, the left or right shutter was turned off and the stimulus was only visible through the open shutter. This training was continued 10 consecutive days.

Experiment 1

Method

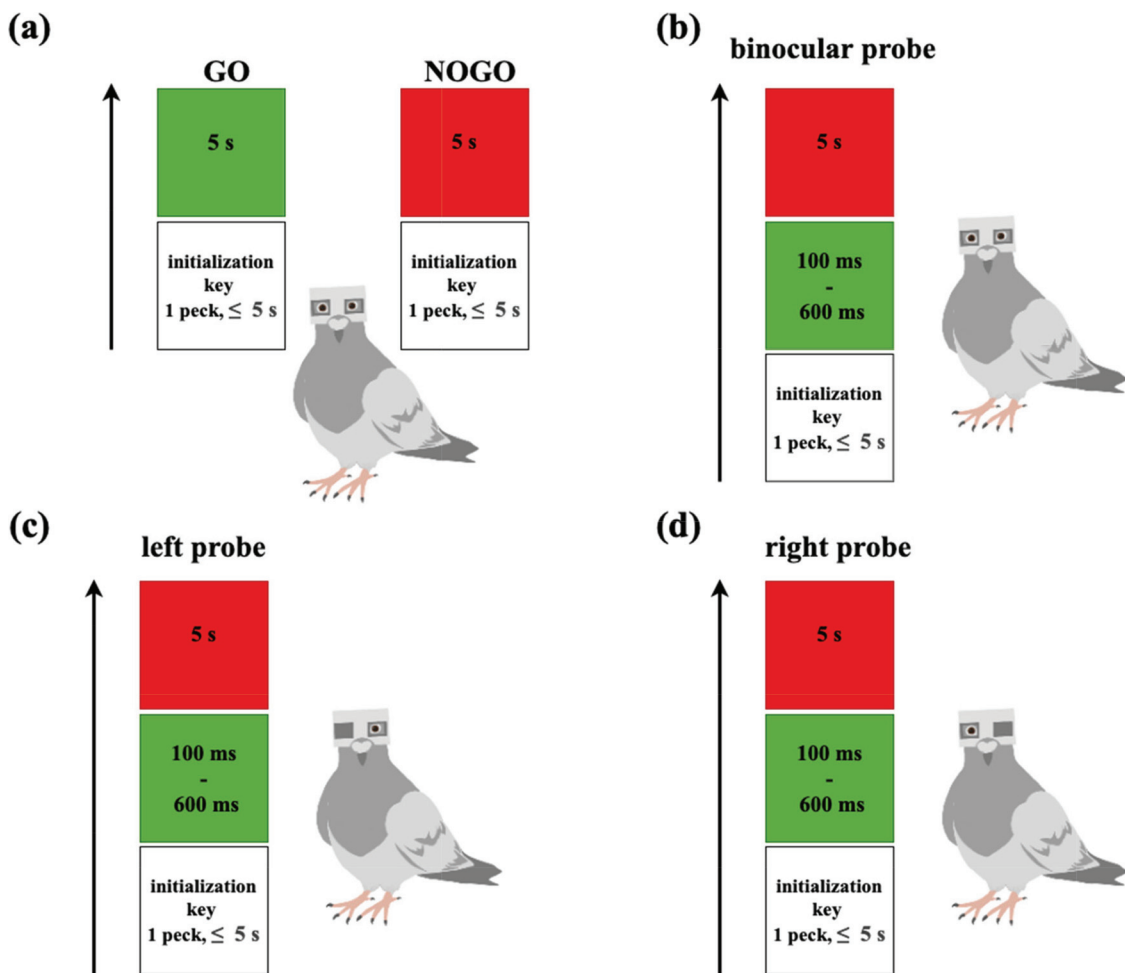
For Experiment 1, probe trials, performed binocularly as well as monocularly, were included in the sessions. Probe trials also started with a white initialization stimulus that had to be pecked within 5 s. After a single peck, the GO stimulus appeared for a duration of 100 ms, 125 ms, 175 ms, 200 ms, 225 ms, 275 ms, 300 ms, 325 ms, 375 ms, 400 ms, 500 ms, or 600 ms. The sequence of stimulus presentation in Experiment 1 is illustrated in Figure 2b–2c. If pigeons pecked the GO stimulus while it was presented, they were rewarded. Otherwise, the NOGO stimulus was immediately switched on for 5 s, and if it was pecked, the house lights

were turned off for 2 s (time out). Thus, by initiating a peck late during the GO-time slot pigeons risked erroneously pecking the NOGO stimulus. Aside from the probe trials described above, training consisted of normal binocular GO and NOGO trials, identical to the pretraining phase (Figure 2a). Because difficulty was lower for these trials than for probe trials due to the lack of time constraint for GO responses, we could ensure the pigeons' motivation to work fast on the task and at the same time keep the average reward rate per session high enough. Normal and probe trials were presented randomly. Each pigeon received, on average, 1,200 normal, binocular GO and NOGO trials and at least 100 trials of each type of probe trial (12 different durations for the GO stimulus; binocular and monocular left/right performance).

Data Analysis

Calculation of correct and incorrect choice ratios was based on responses in probe trials. The *correct rate* was calculated from responses to the GO stimulus that were given, while the GO stimulus

Figure 2
Overview of Experiment 1



Note. Pigeons received (a) binocularly presented GO-NOGO trials and had to peck the Go-stimulus within 5 s; (b) binocularly presented binocular probe trials; (c) left shutter open presented left-monocular probe trials; and (d) right shutter open presented right-monocular probe trials. See the online article for the color version of this figure.

was presented (as explained above, presentation duration varied between 100–600 ms), whereas the *incorrect rate* was derived from responses that occurred while the NOGO stimulus was presented. Please note that since the NOGO stimulus appeared immediately after the offset of the probe trial GO-stimulus, it was possible that responses which were initiated during GO ended in the NOGO phase. To exclude these trials from analysis, we implemented a response latency criterion during off-line data analysis (see below).

Correct and incorrect rates were analyzed with repeated-measures analyses of variance (ANOVAs) and Holm's posthoc multiple comparison method. The ANOVAs included two within-subjects factors: GO duration (100–600 ms; 12 levels) and visual condition (binocular, left monocular, right monocular; three levels). To infer a possible evidence accumulation time, we applied logistic regression for GO response rates of each individual. The logistic model is a sigmoidal-shape regression, and our model incorporated the correct response rates as dependent variable. The GO duration and visual condition were used as independent variables, resulting in fitting three logistic functions for each visual conditions. The resulting logistic functions were used to estimate the GO durations at which pigeons produced 50% correct responses. These durations were considered as evidence accumulation times. Accumulation times were compared between binocular, left-, and right-monocular condition by means of univariate repeated-measures ANOVA.

Responses with latencies below 50 ms were excluded from analysis because eyelid closure during a pecking movement is initiated roughly 30 ms before impact (Goodale, 1983), and because the monitor refresh rate of 60 Hz (i.e., a new image was presented on the screen every 16 ms) needed to be taken into account. This procedure ensured that fast responses under unclear stimulus presentation conditions as well as responses that were initiated during GO stimulus presentation but registered during the NOGO period were not analyzed.

Results

In total, 10,578 correct and 6,650 incorrect responses occurred in probe trials. The ANOVA for correct rates revealed a significant

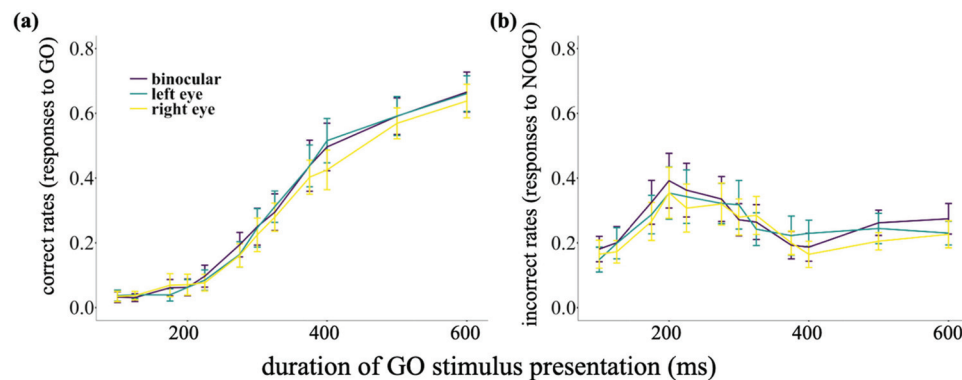
effect of GO duration, $F(11, 88) = 42.53, p < .0001$. As shown in Figure 3a, correct rates increased in a sigmoidal fashion as a function of GO duration. The main effect of visual condition was not significant, $F(2, 16) = 1.70, p = .21$. However, a significant interaction between GO duration and visual condition, $F(22, 176) = 1.622, p = .046$, indicated that correct rates differed between binocular and monocular left and/or right condition as a function of GO duration. To resolve the interaction and clarify this effect, a test for simple main effects was performed, revealing a significant albeit small difference at 400 ms GO duration, $F(2, 16) = 5.69, p = .01$. Here, posthoc comparisons revealed a significantly higher correct rate for monocular-left relative to monocular-right, $t(8) = 3.05, p_{\text{corr}} = .047$.

The average accumulation times for the binocular, monocular-left, and monocular-right condition as inferred from logistic regression were 450 ms \pm 11.42 (mean \pm SE), 449 ms \pm 9.84, and 465 ms \pm 8.37, respectively. The ANOVA did not yield evidence for differences in evidence accumulation times between the three visual conditions, $F(2, 21) = .05, p = .95$.

As shown in Figure 3b, incorrect rates assumed a bitonic function. The ANOVA yielded significant main effects of GO duration, $F(11, 88) = 4.17, p < .0001$, and visual condition, $F(2, 16) = 3.64, p = .0496$. The interaction was not significant, $F(22, 176) = .87, p = .64$. The significant main effect of GO duration indicated that incorrect rates were affected by the GO duration. As depicted in Figure 3b, a peak can be observed around 200 ms. Posthoc multiple comparisons indicated that there was only a significant difference between binocular and monocular-right conditions (binocular vs monocular-right: $t(8) = 3.175, p_{\text{corr}} = .039$; binocular vs monocular-left: $t(8) = .97, p_{\text{corr}} = .36$; monocular-left vs monocular-right: $t(8) = 1.49, p_{\text{corr}} = .35$), with higher incorrect rates for binocular trials.

Results revealed that correct rates increased monotonically as a function of GO duration. This monotonic increase is in accordance with the notion of an evidence accumulation process, that is, with gradually increasing sensory evidence for decision making. In contrast, incorrect rates only increased monotonically between 100 ms and 200 ms, followed by a decrease after the 200 ms peak, irrespective

Figure 3
Results of Experiment 1



Note. (a) Accuracy rates for probe trials in Experiment 1: correct rates increased as a function of stimulus duration in a sigmoidal fashion. A significant interaction between GO duration and visual condition was observed, without an overall significant difference between visual conditions. (b) Incorrect rates for probe trials in Experiment 1: incorrect rates showed a bitonic function. Both GO duration and visual condition showed significant main effects, but their interaction was not significant. See the online article for the color version of this figure.

of binocular or monocular conditions. This counterintuitive observation raises the question about the underlying processes. One possibility is that a GO duration of 200 ms is not enough to accumulate sufficient sensory evidence and to subsequently finalize a peck. In this case, a peck that was initiated very late within the GO-period would fall into the NOGO-phase. The closer to the 200 ms time point pigeons decided to peck, the more likely this scenario is. This hypothesis will be further examined by using model simulations in the last part of this article.

In our task, pigeons had to decide on their responses based on stimulus color. Usually, birds such as pigeons (Prior & Güntürkün, 2001; Skiba et al., 2000, 2002) or chicks (Rogers, 2014; Vallortigara et al., 1996) show right eye (left hemisphere) superiority for color discrimination. Somewhat contrary to this, correct rates of the monocular and binocular conditions did not differ at the overall level. We detected, however, a local left eye (right hemisphere) superiority at 400 ms GO duration for correct responses. This might hint at a minute color discrimination advantage in speeded responses for the right hemisphere (Güntürkün, 1997). However, this interpretation is posthoc and we also cannot exclude a false positive result.

Our pigeon helmet restrained the animals' field of view to the frontal view. This is of relevance because pigeons have two retinal areas of enhanced vision of which the central one points to the lateral field and is used when fixating distant objects (Blough, 1971). The frontal field is served by the dorsotemporal retina and plays a role for close-up vision like during pecking for food (Martin, 2017) or at keys during discrimination tasks (Goodale, 1983). This frontal view is mostly served by the tectofugal visual pathway which is the largest visual system in pigeons (Güntürkün & Hahmann, 1999; Remy & Güntürkün, 1991). Taken together, we are well aware that we restrained the field of view of our animals, but it has to be emphasized that they still could comfortably use the part of their visual field that is naturally preferred under such conditions.

Overall, binocular and monocular conditions resulted in comparable response accuracy and evidence accumulation values. For incorrect rates, binocular trials even showed a local disadvantage. Assuming that the two eyes give rise to two independent visuomotor systems, horse race models would predict a binocular advantage (Marley & Colonius, 1992). This is due to the assumption that the final response time under binocular conditions would result from trial-by-trial latencies of the faster of the two eyes. While some studies indeed found evidence for such an effect in pigeons (Kusmic et al., 1991); others found no evidence (Ünver & Güntürkün, 2014; Ünver et al., 2019). But why were monocular trials at least as successful and sometimes even more successful than binocular trials? One possibility is that even binocular trials were, in fact, governed by only one hemisphere, the left or the right. Indeed, several studies in pigeons could show that binocularly learned tasks can result in pure monocular learning with a subsequent lack of interhemispheric transfer (Nottelmann et al., 2002; Xiao & Güntürkün, 2009). The second experiment aimed to test this possibility.

Experiment 2

Method

In Experiment 2, we aimed to test the hypothesis that a single hemisphere governs the animals' behavior and processes sensory

evidence accumulation and response initiation on its own. We planned to test this idea by forcing the birds to transfer information between the hemispheres to come up with a proper decision. To this end, the critical difference between Experiment 1 and Experiment 2 was a switch between left- and right-eye shutters within a trial. If, for example, a pigeon did not peck the GO stimulus during the given time period with the left shutter open, simultaneously (a) the left shutter was switched off, (b) the right shutter was turned on, and (c) the NOGO stimulus was presented (see Figure 4). Thus, decisions based on incremental evidence had to either be transferred to the other hemisphere or had to start anew. In case of transfer, we would expect a small and possibly constant transfer time. Without interhemispheric information transfer, we expect a restart of evidence accumulation and therefore an increase in response time. But there is also a third option: If the initial hemisphere (in this case the right hemisphere because the left shutter is initially open) controls the action even after the switch, the result patterns should not differ between Experiment 2 and Experiment 1.

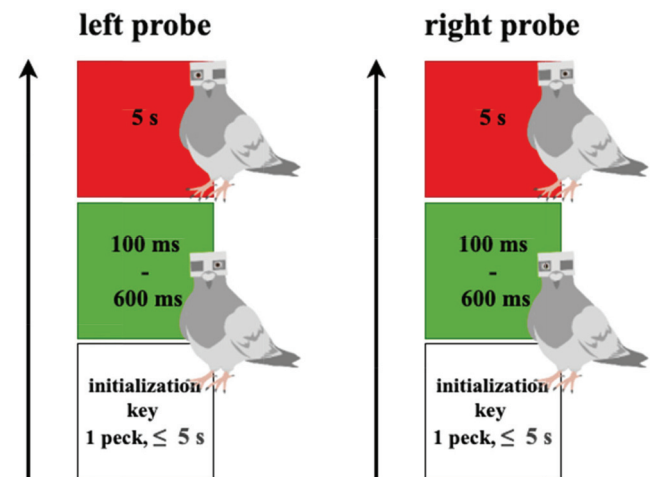
Data Analysis

As in Experiment 1, responses with latencies below 50 ms were excluded from analysis. Please note that this also eliminates possible effects related to shutter switching time (≤ 30 ms). All other analysis procedures were performed as outlined for Experiment 1.

Results

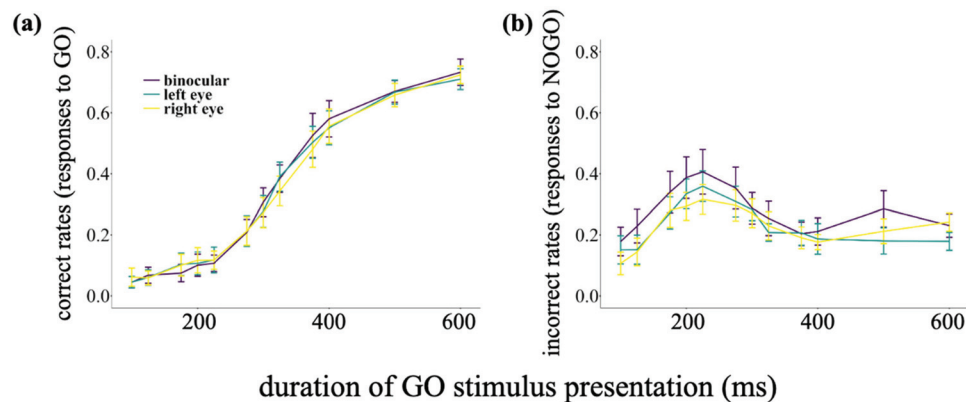
A total of 11,726 correct and 5,444 incorrect probe trial responses were entered into the analysis. Similar to Experiment 1, correct rates showed sigmoidal shapes as a function of GO duration (Figure 5a). The ANOVA revealed a significant effect of GO duration, $F(11, 88) = 75.98, p < .0001$, but did not yield significant effects for visual condition, $F(2, 16) = .25, p = .79$, and the interaction, $F(22, 176) = 1.02, p = .44$. Of note, the correct rates were also comparable to Experiment 1, as confirmed by

Figure 4
Left- and Right-Probe-Trials in Experiment 2



Note. In Experiment 2, the shutters toggled their status with the onset of the NOGO stimulus if no peck was recorded on the GO stimulus. See the online article for the color version of this figure.

Figure 5
Results of Experiment 2



Note. (a) Accuracy rates for probe trials in Experiment 2: Correct rates were increased as a function of GO duration in sigmoidal fashion. A significant main effect of GO duration was observed, but neither visual conditions nor the interaction between visual condition and GO duration was significant. (b) Incorrect rates for probe trials in Experiment 2 showed a bitonic function. Note that in the monocular-right condition the right eye (and thus the left hemisphere) received the GO and the left eye (and thus the right hemisphere) received the NOGO stimulus. See the online article for the color version of this figure.

dependent-sample *t* tests for correct rates according to visual condition—binocular: $t(8) = 1.71$, $p_{\text{corr}} = .252$; left-monocular: $t(8) = 1.466$, $p_{\text{corr}} = .252$; right-monocular: $t(8) = 2.252$, $p_{\text{corr}} = .163$. This is not surprising, given that shutter switching did not occur if pigeons responded before GO turned to NOGO, thereby rendering trial procedures identical to Experiment 1.

The average accumulation times for the binocular, monocular-left, and monocular-right condition, which were inferred from logistic regressions to GO response rates, were 396 ms \pm 7.09, 399 ms \pm 6.85, and 402 ms \pm 6.82, respectively. The ANOVA did not indicate significant differences between conditions, $F(2, 21) = .14$, $p = .87$.

Incorrect rates showed a bitonic function, similar to Experiment 1 (Figure 5b). The ANOVA showed significant effects of GO duration, $F(11, 88) = 5.082$, $p < .0001$, and visual condition, $F(2, 16) = 6.92$, $p = .007$, but there was no significant interaction, $F(22, 176) = .941$, $p = .54$. Because shutter switching did not occur in the binocular condition, the incorrect rates of both experiments were equal, $F(1, 8) = .29$, $p = .60$, with no interaction between stimulus duration, $F(11, 88) = .51$, $p = .89$. Similar to Experiment 1, incorrect rates revealed poorer performance in the binocular condition, with the subsequent posthoc comparisons statistically confirming higher incorrect rates for binocular compared to right-monocular, $t(8) = 3.30$, $p_{\text{corr}} = .033$, whereas the other comparisons were not significant—binocular vs left-monocular: $t(8) = 2.54$, $p_{\text{corr}} = .069$; left-monocular vs right-monocular: $t(8) = .47$, $p_{\text{corr}} = .651$. Note that right-monocular for incorrect rates means that the right eye (and thus the left hemisphere) received the GO stimulus and the left eye (and thus the right hemisphere) subsequently saw the NOGO stimulus. This result pattern is in line with Experiment 1: Again, it was the left hemisphere that was superior in stopping an incorrect response if it had received the initial GO stimulus.

Overall, incorrect rates in Experiment 2 were virtually identical to those in Experiment 1, as confirmed by paired-sample *t* tests between

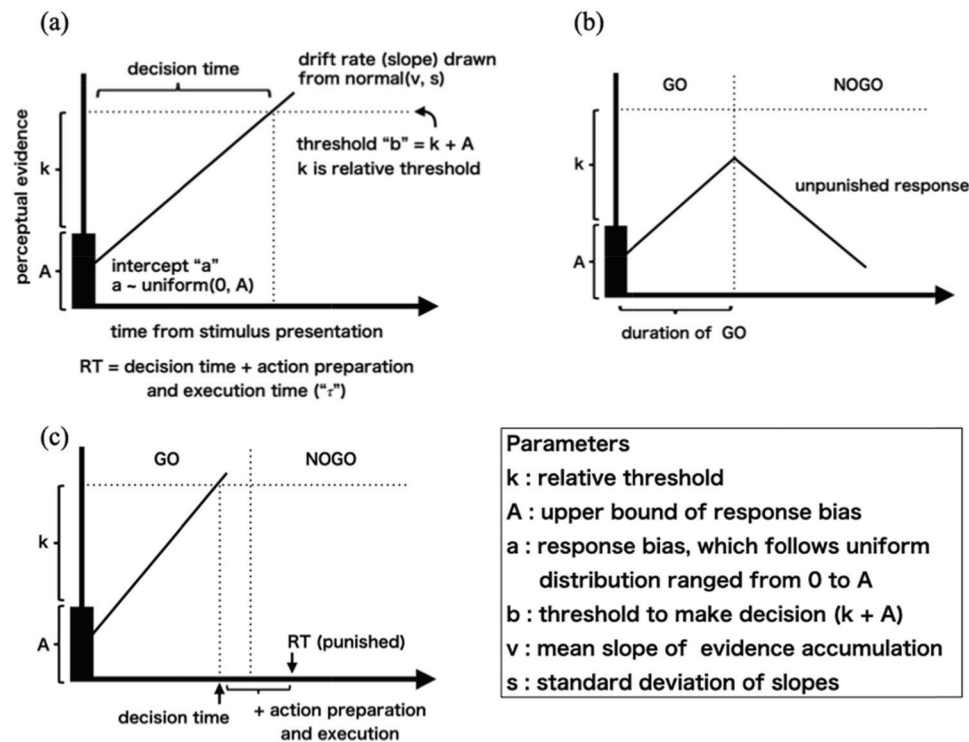
the experiments for the three conditions—binocular: $t(8) = .54$, $p = .604$; left-monocular: $t(8) = 1.071$, $p = .315$; right-monocular: $t(8) = .897$, $p = .395$ —although we had induced a within-trial hemispheric switch in perceptual access to the stimuli. We therefore compared the NOGO response times of the monocular conditions between the experiments to check for possible differences due to hemispheric transfer. Results showed virtually identical response times in both experiments: left-monocular: $F(1, 17) = .017$, $p = .897$; right-monocular: $F(1, 17) = .016$, $p = .90$. Because interhemispheric transfer should require additional time, the present result pattern seems to indicate a lack of interhemispheric transfer and thus unihemispheric decision making.

Computational Modeling and Simulation

Method

In both experiments, correct rates increased with a sigmoid shape as a function of GO duration (Figures 3a, 5a) and thus resemble perceptual evidence accumulation curves in primates (de Lafuente et al., 2015; Ding & Gold, 2010; Katz et al., 2016; Rorie et al., 2010). To understand and quantify the processes that drive evidence accumulation, various mathematical models have been established. Most of these models integrate both response time (RT) and response accuracy (Brown & Heathcote, 2008; Dmochowski & Norcia, 2015; Donkin & Brown, 2018; Ratcliff & Rouder, 1998). To elucidate the information process of perceptual decision making in pigeons, we utilized a linear ballistic accumulator model (LBA model; Brown & Heathcote, 2008) to study information processing of response execution. The LBA model was originally proposed for decision making in a choice situation as reflected in response times. Here, we used it to account for correct and incorrect rates by modeling response times to GO stimuli, since especially incorrect rates showed an unexpected function across the different durations of GO stimuli. Since correct rates in

Figure 6
Schematic Representation of our Simulation



Note. (a) Graphical illustration of the linear ballistic accumulator model, and (b) the possible scenario for correct rejection responses (no-response to NOGO). The simulation assumed that a pigeon can stop evidence accumulation before it reaches threshold, therefore generating no response to NOGO. (c) Alternative possible scenario for punished responses (peck at NOGO). Here, our model simulated processes that generate incorrect responses to NOGO due to late decision times. The simulation assumed that most of the action preparation and execution in pigeons is governed by feedforward control. As a consequence, an initiated response cannot be retracted, once evidence reaches threshold.

both experiments showed a monotonic increase in performance and LBA assumes linear increase of sensory evidence, usage of an LBA model seems to be appropriate.

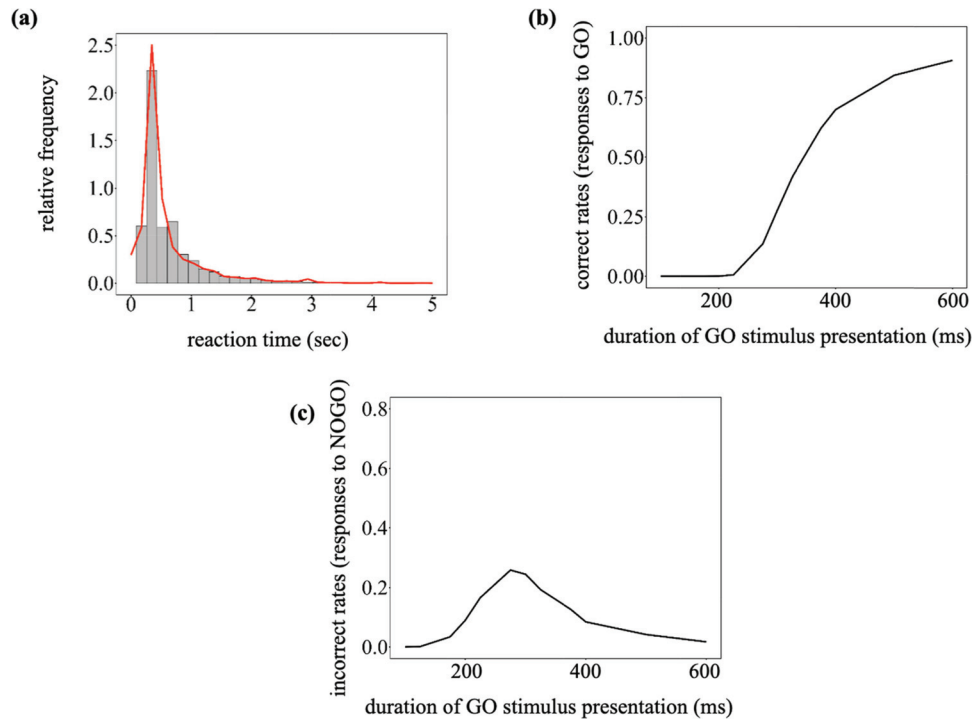
A schematic illustration of the LBA model is shown in Figure 6a. In brief, the model assumes that an agent accumulates sensory evidence across time after stimulus presentation. The decision to respond is made when the accumulated evidence reaches a certain criterion (threshold “b”). The parameter “b” consists of the sum of the relative threshold “k” and an upper bound as the starting point “A” ($b = k + A$). The parameter A can be regarded as an upper bound of a bias term toward threshold before starting to accumulate evidence. The bias “a” is assumed to be sampled from a uniform distribution from 0 to A. The model assumes that the animal responds once the evidence accumulated reaches threshold “b.” Response time is then a sum of decision time, which reflects the total duration of evidence accumulation, and the parameter “ τ ” which represents the time taken for action preparation and execution other than decision making. This information processing model mathematically results in an “LBA distribution”, and thus permits to statistically estimate the relevant parameters (Brown & Heathcote, 2008).

We used the response times normal GO trials, rather than probe trials, in order to avoid a truncation of the LBA distribution as was

happening in many probe trials. For the same reason we also did not remove responses with latencies < 50 ms. However, fitting the overall LBA distribution also includes biologically implausible fast responses. To avoid this, we built a mixed distribution of exponential and LBA distributions to circumvent the influence from such fast response times. The rationale to use the mixture distribution is the following: since an exponential distribution has a peak at 0, occasional fast response times are absorbed in it, and thus can be statistically ignored. In other words, the influence of containing fast response times on estimation of LBA parameters were alleviated by the exponential distribution. As a result, the fitting (posterior predictive distribution) nicely mimicked the real response time distribution (Figure 7a).

The parameters of the model were estimated using the Markov Chain Monte Carlo (MCMC) method with 50,500 iterations, 50,000 burn-in periods, and four chains. The relative threshold “k” was fixed to be 1 to permit estimation convergence. Computation was regarded as converged once Gelman-Rubin R-hat statistics were below 1.1. The modeling source code was obtained from Annis et al. (2017). After performing the parameter estimation using response time values, we simulated the probe trial condition to verify whether the model would reproduce similar correct and incorrect rates. To mimic the probe trial, we simulated the

Figure 7
Simulation Results



Note. (a) The posterior predictive distribution, which simulates the response times of normal trials. Histograms represent the real response times from normal trials in Experiment 1, and the red line represents the response times generated by the model; (b) correct rates to GO; (c) incorrect rates to NOGO. See the online article for the color version of this figure.

evidence accumulation process by sampling MCMC samples of parameters. Specifically, we calculated the simulated response times from the model, and compared them with the varying GO stimulus durations used in the experimental conditions (from 100 to 600 ms). If the simulated response time was lower than the stimulus duration, it was regarded as a “correct response” of the simulated pigeon. If the evidence did not reach the threshold until the end of the stimulus duration, it was regarded as a response to neither GO nor NOGO stimuli of the simulated pigeon (Figure 6b). If the simulated evidence accumulated to a threshold until the end of the stimulus duration while response time exceeded that duration, it was regarded as a NOGO response (i.e., incorrect; Figure 6c). This means that our simulated pigeon did or could not interrupt its response during action preparation and execution. The simulation was performed 10,000 times for each stimulus duration, and the simulated data were analyzed in the same way as the real data. All analyses and simulations were conducted using R 3.5.3 (R Core Team, 2019). Bayesian modeling was performed using the Stan probabilistic language (Carpenter et al., 2017).

Results

The posterior predictive distribution of the model was similar to the empirical response time distribution (Figure 7a). The simulated correct responses also showed a sigmoidal curve as a function of GO duration, akin to those observed in real data (Figure 7b).

Similarly, simulated incorrect rates produced a bitonic function, with the peak of incorrect responses observed at the intermediate stimulus duration, also mimicking the real data (Figure 7c). The simulation produced a maximum incorrect rate at the 275 ms condition, similar to the 200 ms and 225 ms maxima in Experiment 1 and 2, respectively. These incorrect responses were produced by the assumption that pigeons did not retract their response after it was initiated, even if the GO stimulus subsequently turned to NOGO. No further model assumptions were necessary.

Although the LBA model itself is only estimated from response time data, the simulation produced response curves for correct and incorrect rates similar to those obtained from real pigeons. This leads to two conclusions: (a) the evidence accumulation process itself might be a common cognitive operation between pigeons and mammals, (b) the shape of the curve for incorrect responses as observed in both Experiment 1 and 2 (Figure 3b and 5) was indeed likely due to the inability of pigeons to stop their peck once movement was initiated. We will discuss these points in the general discussion.

General Discussion

The current study examined perceptual decision making and inter-hemispheric transfer in pigeons by using a GO-NOGO task in two separate experiments. With the possibilities provided by our pigeon-helmet, we were able to control with high temporal precision the viewing eyes during task performance. In Experiment 1, we compared the

performance for left-, right-monocular, and binocular viewing conditions. In Experiment 2, we studied interhemispheric information transmission by toggling the seeing eye in accordance with stimulus alterations. Our findings reveal that the dynamics of perceptual decision making in pigeons strongly resemble evidence accumulation processes in mammals. However, our data also indicate the presence of a unique pattern of unihemispheric decisions without any indication for interhemispheric transfer.

Evidence Accumulation in Birds

In a stochastic physical and social environment, input-based decision making needs to capture optimal prioritization of actions in a timely manner. Evidence accumulation is a key process in this regard, and has been studied in different animal groups such as rats, monkeys, and humans, resulting in multiple but overlapping evidence accumulation models (Brunton et al., 2013; Gold & Shadlen, 2001; Kelly & O'Connell, 2013; Kira et al., 2015; Lee & Cummins, 2004; Philiastides et al., 2011; Piet et al., 2018; Purcell et al., 2010). These models have been applied to various domains of human cognition and perception (e.g., perceptual choice: Forstmann et al., 2010; Goldfarb et al., 2014; lexical decision: Brown, & Heathcote, 2008; attention: Nishiguchi et al., 2019; multiattribute decision making: Donkin et al., 2011; Trueblood et al., 2014). Taken together, evidence accumulation processes have been recognized as a ubiquitous cognitive operation that is evident in rodents and primates.

Here, we set out to test if decisions based on perceptual input follow similar principles in birds. Indeed, we could show for the first time that despite more than 300 million years of separate evolution (Nei et al., 2001); evidence accumulation processes in pigeons strongly resemble those in mammals. The correct rates from probe trials showed a sigmoidal pattern along increasing durations of the GO stimulus, suggesting the presence of a stochastic accumulation process in pigeons. A recent study revealed a cortex-like wiring pattern in the pigeon pallium, making similar computational dynamics in the mammalian and avian perceptual forebrain likely (Stacho et al., 2020). Our results perfectly fit to this interpretation.

The analysis of evidence accumulation times and response times revealed that the whole process takes between 400–450 ms in pigeons, leading to response times of approximately 450 ms. In rhesus monkeys, response times ranged from 350 ms and 850 ms in a motion-discrimination task, depending on motion strength (Roitman & Shadlen, 2002). Humans had response times between 550 ms and 650 ms in visual discrimination tasks, but more difficult trials typically resulted in slower responses (Pedersen et al., 2015). We assume that our stimuli were easy to discriminate and therefore resulted in rather short response times. In principle, the present results could also hint at faster computation times in birds due to their densely packed pallial neurons with very short interneuron distances (Olkowicz et al., 2016). Generally, accumulation times for pigeons and mammals appear to fall into largely the same order of magnitude, with pigeons more at the lower end. Consequently, the present findings make similarities between mammals and birds in this core decision making process likely.

We used an LBA model to explain dynamics of correct and incorrect rates from the response time data. The LBA model produced not only a response time distribution similar to the empirical data, but

also generated qualitatively similar curves for correct and incorrect rates. Specifically, incorrect rates had a peak at an intermediate delay rather than showing monotonic increases or decreases both in Experiment 1 and 2. We thereby departed from the assumption that our simulated pigeons cannot stop their peck after perceptual evidence is accumulated to threshold levels, even if the stimulus turned to NOGO while the peck was initiated. This assumption corresponds to the previous motor control studies, which suggested that pecking in pigeons is governed by feedforward control (Delius, 1985; Matsui & Izawa, 2017, 2019). By incorporating such a feedforward control mechanism, the simulation mimicked the actual behavior on incorrect trials.

Pigeons Make Unihemispheric Decisions

Contrary to mammals, in pigeons practically all optic fibers to the nucleus geniculatus lateralis pars dorsalis (GLd) and the optic tectum cross completely at the optic chiasm (Güntürkün & Karten, 1991; Manns & Güntürkün, 1997). Because both GLd and tectum constitute starting points of the ascending thalamo- and tectofugal systems, respectively, avian hemispheres only receive direct visual input from the contralateral eye. There are, however, small secondary back-projections both at midbrain (the inhibitory tectal and posterior commissures; Stacho et al., 2016) and at thalamic level (dorsal supraoptic decussation; Letzner et al., 2020) that can transfer visual information between hemispheres. Because birds lack a corpus callosum and have a rather small anterior and a minute hippocampal commissure (Jonckers et al., 2015; Letzner et al., 2016; Schmidt, 2008); channels to exchange information between hemispheres do exist in pigeons, but these are rather limited (Valencia-Alfonso et al., 2009; Watanabe, 1985; Watanabe & Weis, 1984; Xiao & Güntürkün, 2018). These pallial commissures do not have a predefined sensory visual function but can exchange all kinds of behaviorally relevant information, including visual information (Xiao & Güntürkün, 2018). In line with these findings, the uniform performance of GO responses in both experiments and in all viewing conditions might indicate an underlying unihemispheric decision mechanism.

Experiment 2 examined whether information would be conveyed from one hemisphere to the other by using shutter alternation. Of the three outcomes that were hypothesized in the introduction, we discovered (c) to come into effect through the occurrence of identical result patterns for Experiments 1 and 2. There is also further indication that the initially “seeing” hemisphere still controlled the response after the shutter switch: both in Experiment 1 and 2, the hemisphere that showed lower incorrect rates than the binocular condition was the one that initially “saw” the GO-response with the right eye. However, in Experiment 2, the right eye was behind a dark shutter after shutter switch. Possibly, in this case the left hemisphere (right eye) was still controlling the feedforward-based response (Matsui & Izawa, 2017, 2019), thereby producing lower incorrect rates than under binocular conditions.

This lack of interhemispheric transfer is in line with earlier findings, pointing out that the absence of a corpus callosum restrains or reduces the transfer of information from one hemisphere to the other in pigeons (Nottelmann et al., 2002; Watanabe & Weis, 1984; Xiao & Güntürkün, 2009) and chicks (Gaston, 1984). The present data show that the absence of a corpus callosum in birds

and the presence of a rather small anterior commissure (Letzner et al., 2016) results in limitations of interhemispheric transfer. This limitation consequently forces birds to execute motor responses based on unihemispheric processes (Palmer & Zeier, 1974). Although this may look like a unique avian specialization, there is also evidence that time-pressured sensorimotor decision making can also result in strictly unihemispheric processes in humans (Hadar et al., 2016).

Binocular Disadvantage

When monocular and binocular reaction times are compared in humans, the latter ones are faster for a wide range of diverse stimuli (Blake et al., 1980). This binocular visual advantage is also observed in driving performance tests during racing, in which response times increased twofold under monocular condition (Adrian et al., 2019). In contrast to these examples, our pigeons showed higher incorrect rates under binocular conditions, both in Experiment 1 and 2. Although this effect was small, it occurred twice and is counterintuitive in light of previous studies that had observed binocular advantage in pigeons (di Stefano et al., 1987; Watanabe et al., 1984). What could be the reason? Given the specificities of our experimental design, this effect could result from simple neurobiological mechanisms. Under binocular conditions, both eyes see the GO stimulus and possibly both hemispheres start an evidence accumulation process that eventually results in movement initiation. Anatomically, this implies that descending forebrain motor neurons drive brainstem pre/motor structures via the tractus septomesencephalicus (TSM) and the tractus occipitomesencephalicus (TOM) to activate head and body pre/motor neurons to produce pecking behavior (Dubbeldam & Den Boer-Visser, 1994; Hellmann et al., 2004; Mouritsen et al., 2016; Wild et al., 1985). The projections of TOM and TSM are bilateral and are descending from both hemispheres since both eyes see the GO-stimulus (Fernández et al., 2020). The activation of forebrain motor areas to initiate pecking movements will have a much higher impact on brainstem neurons after binocular (activation by both hemispheres) than after monocular conditions (activation by one hemisphere). As a result, under binocular conditions, membrane potentials of brainstem motor neurons will reach action potential thresholds faster, thereby resulting in shorter response times for pecking movements (Garrido et al., 2003). These shorter latencies in the binocular condition are, however, associated with higher incorrect rates when shutter switches happen early, explaining the present pattern of results.

Conclusion

Our experimental and computational results reveal the dynamics of stochastic evidence accumulation as a core cognitive decision-making process in birds. Given that highly similar result patterns have been observed in various mammalian species, including humans, our results could imply that sensory evidence accumulation represents a ubiquitous fundament of decision making in vertebrate brains. In addition, we discovered a lack of interhemispheric transfer during perceptual decision making. This finding implies that, at least under time pressure, perceptual decisions are taken unihemispherically in pigeons. Because our pigeon helmet enabled fast switches between the eyes, this created the unique

situation that the hemisphere that had initiated the response could no longer see its effect. Because pecking is under feedforward control in pigeons, we assume that this experimentally induced condition possibly created no major sensorimotor difference to normal pecking maneuvers.

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