



# Through the eyes of a bird: modelling visually guided obstacle flight

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*Obstacle flight by pigeons* H-T Lin et al.

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4 1 **Title.** Through the eyes of a bird: Modeling visually guided obstacle flight

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For Review Only

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3 9 **SUMMARY.** Various flight navigation strategies for birds have been identified at the large  
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6 10 spatial scales of migratory and homing behaviors. However, relatively little is known about close-  
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8 11 range obstacle negotiation through cluttered environments. To examine obstacle flight guidance,  
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10 12 we tracked pigeons (*C. livea*) flying through an artificial forest of vertical poles. Interestingly,  
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12 13 pigeons adjusted their flight path only ~1.5m from the forest entry, suggesting a reactive mode of  
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14 14 path planning. Combining flight trajectories with obstacle pole positions, we reconstructed the  
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16 15 visual experience of the pigeons throughout obstacle flights. Assuming proportional-derivative  
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18 16 (PD) control with a constant delay, we searched the relevant parameter space of steering gains and  
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20 17 visuomotor delays that best explained the observed steering. We found that a pigeon's steering  
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22 18 resembles proportional control driven by the error angle between the flight direction and the  
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24 19 desired opening, or gap, between obstacles. Using this pigeon steering controller, we simulated  
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26 20 obstacle flights and showed that pigeons do not simply steer to the nearest opening in the  
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28 21 direction of flight or destination. Pigeons bias their flight direction toward larger visual gaps when  
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30 22 making fast steering decisions. The proposed behavioral modeling method converts the obstacle  
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32 23 avoidance behavior into a (piece-wise) target-aiming behavior, which is better defined and  
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34 24 understood. This study demonstrates how such an approach decomposes open-loop free-flight  
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36 25 behaviors into components that can be independently evaluated.  
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44 26 **Keywords:** pigeon flight; flight guidance; obstacle negotiation; path planning; PD controller  
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## 1. INTRODUCTION

Animals moving in the natural environment need to routinely avoid obstacles on route to a destination. This task becomes critically challenging when moving at high speeds, such as in flight. Many flying animals have evolved impressive abilities to avoid obstacle collisions (1). For example, echolocating big brown bats (*Eptesicus fuscus*) forage at night, avoiding obstacles while tracking flying insects, whereas diurnal goshawks (*Accipiter gentilis*) chase aerial preys through dense woodlands at high speed. Apart from these specialists, other flying birds and bats must also routinely deal with obstacles. For example, sparrows and pigeons have successfully colonized cities, which are highly three-dimensional (3D) environments, similar to their natural habitats (2). These birds maneuver around lampposts, buildings and vehicles with proficiency, relying on vision to navigate through their environment. Here, we examine guidance strategies that pigeons (*Columba livia*) use to successfully navigate cluttered environments using a combined experimental and modeling approach.

Limitations of the visual system necessarily affect any visually guided locomotion. Similar to other birds at risk of aerial predators, pigeons have a wide  $>300^\circ$  panoramic field of view for predator detection. The associated retinotopic trade-off limits a pigeon's binocular field to  $\sim 20^\circ$  (3-5). Binocular stereoscopic depth perception has been demonstrated in falcons, owls and pigeons, but only in close-range discrimination tasks (6-8). Hence, binocular vision is unlikely to provide depth sensing for flight. A pigeon's broad panoramic visual field also reduces their overall visual acuity: pigeons can resolve up to 12 sinusoidal cycles/degree within their lateral visual field, which declines toward their frontal view, much less than predatory eagles ( $\sim 140$  cycles/deg) and humans ( $\sim 70$  cycles/deg) (9). Although high resolution is important for distant target tracking (which raptors do routinely), it is not a requirement for flight control. Most insect

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3 54 compound eyes have even worse visual acuity (<4 cycles/deg) (10), yet flying insects have quite  
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5 55 robust flight control (11-15). Finally, in order to perceive rapid motion in flight, birds generally  
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7 56 possess flicker fusion frequencies above 100 Hz (pigeon: 116-146Hz) (16). Taken together, these  
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9 57 properties of pigeon vision suggest a more reactive approach to obstacle negotiation. In contrast  
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11 58 to a conventional path-planning paradigm where sensory information is used to construct an  
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13 59 internal model of the world for evaluation (17-19), we hypothesize that pigeons may react to  
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15 60 obstacles over short distances and time scales based on local information and simple rules.

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20 61 Such a view of visual guidance is shared by others in the field. In particular, Warren and  
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22 62 colleagues termed this “information-based control”, which they used to derive various behavioral  
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24 63 models for humans navigating in virtual reality (20-23). These models treat goals as attractors and  
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26 64 obstacles as repellers. The superposition of attraction/repulsion potential fields continuously  
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28 65 shapes steering, causing the locomotor trajectories to “emerge” (23). This **potential field method**  
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30 66 describes human goal-directed walking well (22) and also is a classic approach in reactive robotic  
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32 67 obstacle avoidance (24-27). However the main limitation to this method (attractor-repeller) is the  
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34 68 treatment of multiple goals and obstacles (28). For instance, if there are two goals affecting the  
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36 69 agent (robot, human or other animal), the model might predict an average path that misses both  
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38 70 targets. Similarly, an agent approaching three obstacles might steer head-on to the middle obstacle  
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40 71 due to the average repulsion from the two side obstacles. This so-called “cancellation effect”, as  
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42 72 recognized by Fajen et al. (29), can be solved by differentiating the “valence” of different  
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44 73 obstacles and goals. Indeed, it seems conceptually unlikely that a navigating agent would avoid  
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46 74 all obstacles simultaneously or steer toward an average goal direction, in which no real goal exists.  
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48 75 In practice, the agent only needs to guide movement through one opening (or gap) at a time. A  
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50 76 natural alternative to the potential field method is to always aim for a gap (30). Although all  
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3 77 available gaps affect the gap selection process, once the choice is made the actual steering should  
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5 78 be unaffected by the other, non-selected gaps. Here, we propose a new procedure for modeling  
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8 79 avian obstacle flight by introducing the **gap-aiming method** with two underlying assumptions: 1)  
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10 80 we treat obstacle avoidance as a series of gap aiming behaviors; and 2) we assume that the agent  
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12 81 steers toward one selected opening (gap) at each instance and never attempts to simultaneously  
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14 82 aim for multiple openings. Under these assumptions, obstacle flight becomes a piece-wise target-  
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16 83 aiming behavior, in which the selected gaps are the steering aims.

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20 84 In this study, we examine short-range guidance of pigeons flying through randomized sets of  
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22 85 vertical obstacles. Under our proposed framework, the pigeon must first identify relevant  
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24 86 obstacles and then select a suitable gap aim. A general strategy for gap selection may be  
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26 87 decomposed into two concurrent and possibly competing objectives (31): maximizing clearance  
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28 88 between obstacles and minimizing required steering (i.e. change in path trajectory). Whereas a  
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30 89 bird should select the largest gap to maximize clearance, it should simultaneously select the gap  
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32 90 most aligned with its flight direction in order to minimize steering. We refer this decision process  
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34 91 as the **guidance rule**. Once the desired flight direction is chosen, the bird must implement the  
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36 92 steering that changes the flight path. A **steering controller** that dictates the motor behaviors and  
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38 93 ultimately the flight dynamics is needed to accomplish the required steering. Sensory and  
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40 94 biomechanical delays exist for any motor controller. Here, we formulate the steering controller by  
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42 95 simply combining the delays and steering dynamics into a generic proportional-derivative  
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44 96 controller with a constant visuomotor delay.

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50 97 We strategically simplified the sensory task by presenting the pigeons with a vertical pole  
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52 98 array of relatively short depth (Fig. 1), minimizing the birds' depth perception challenge and  
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54 99 inducing steering cues only about the yaw axis. The scale of the flight corridor also minimized the  
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4 100 global navigation challenge for the pigeon. The direction along the corridor is practically the  
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6 101 direction of the destination (Fig. 1a). Using proportional-derivative (PD) control theory (32), we  
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8 102 established a steering controller assuming that the pigeon steers to one gap at a time. We  
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10 103 subsequently reproduced pigeon flight trajectories using several different guidance rules, each  
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12 104 based on the same, established steering controller, with varying levels of perception noise. In  
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14 105 particular, we ask whether pigeons prioritize clearance over steering minimization during the  
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16 106 obstacle flights.

## 107 **2. MATERIALS AND METHODS**

### 108 *2.1. Animal training and the obstacle course*

109 Seven wild-caught adult pigeons (*Columba livia*) were trained to fly through an indoor corridor  
110 without obstacles. The four birds that flew most consistently between the perches were selected  
111 for experiments. All pigeons were housed, trained, and studied at the Concord Field Station  
112 (Bedford, MA) according to protocols approved by Harvard University's Institutional Animal  
113 Care and Use Committee.

114 To study path planning and maneuvering flight in a cluttered environment, we challenged  
115 pigeons to fly between two perches (1.2 m high) through an indoor flight corridor (20 m long, 3 m  
116 high, 3 m wide) with an obstacle field located 10 m from the take-off perch (Fig. 1a). The  
117 obstacle field comprised a  $3 \times 3$  m area over which 15 PVC poles (3.81 cm o.d.) were erected  
118 vertically in predetermined random distributions. In order to maintain the overall obstacle density  
119 while introducing random variations, random pole distributions were based on a standard grid, in  
120 which each pole had an equal probability of being placed at one of 5 positions: At the center  
121 position or at one of four corner positions  $\sim 30$ cm from the center position (Fig. 1b). For every  
122 obstacle flight, the poles were repositioned according to this randomizing procedure, so that the

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3 123 pigeons experienced a new obstacle distribution for each flight. Each obstacle pole was digitized  
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6 124 every flight to verify its placement. The walls of the flight corridor were lined with translucent  
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8 125 white plastic sheeting to provide a homogenous visual environment. The front and rear borders of  
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10 126 the obstacle field were guarded by 0.9m high paper to ensure the pigeon flight paths remained  
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13 127 within a calibrated 3D volume (Fig. 1e).

## 14 15 128 *2.2. Pigeon flight tracking*

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18 129 Each pigeon carried two pairs of infrared, surface mount high-intensity LED markers (Vishay  
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20 130 Intertechnology, Inc., Malvern, PA) for tracking purposes: one pair defined the head vector and  
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23 131 one pair defined the body vector (Fig. 1c). These were securely strapped on the head and torso  
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25 132 along with a battery (overall weight: 16.5 g). We limited the added components to less than 5% of  
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27 133 the pigeon's body mass to minimize the effect on maneuvering. Multiple views of the flight  
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30 134 trajectories were obtained by five synchronized Photron high speed cameras (three SA3; two PCI-  
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32 135 1024, Photron USA, Inc. San Diego, CA) mounted on the ceiling, operating at 500Hz. This  
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34 136 provided a calibrated volume covering the obstacle field and 5 m of the flight corridor leading up  
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37 137 to the obstacle field (Fig. 1a). 3D reconstruction of the marker trajectories was achieved using  
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39 138 *DLTdv5* and *EasyWand2* Matlab scripts (33).

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41 139 To establish the birds' indoor flight characteristics, 8 flights per bird were recorded without  
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44 140 obstacles (32 flights total). Following this, a total of 64 obstacle flights were recorded for novel  
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46 141 obstacle distributions from the four birds, after training the birds with 5-8 obstacle flights. The 32  
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48 142 initial flights without obstacles were used to establish a behavioral reference. From the 64  
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50 143 obstacle flights, we used 8 flights per bird from the first three pigeons to tune the steering  
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52 144 controller (24 flights). The remainder of the flights from the first three pigeons and ten obstacle  
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55 145 flights from the fourth pigeon were used to test the guidance strategy simulations (10 obstacle  
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3 146 flights per bird). This data allocation allowed us to demonstrate the universality of the PD  
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6 147 controller, as well as test for the robustness of the guidance rules simulations.  
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### 8 148 *2.3. Data processing and flight path analysis*

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10  
11 149 Pigeons' body and head positions were computed from sampled 500 Hz 3D marker data. Because  
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13 150 we were only interested in the body trajectory and the visual experience determined by the body  
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15 151 velocity vector (the flight direction), head and body orientations were not computed for this study.  
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18 152 Specifically, we used the rear head marker to compute in-flight visual information (i.e. obstacle  
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20 153 angular position, angular velocities and distance), and the rear body marker (close to the estimated  
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22 154 body center of mass) to derive the pigeon trajectory. The visual input data were down-sampled to  
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25 155 100 Hz (or 10 ms time-steps) to approximate a pigeon's flicker fusion frequency of 116-146 Hz  
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27 156 (16).  $t = 0$  was defined when the pigeon's rear body marker crossed the entry line of the obstacle  
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30 157 field. In order to generate continuous steering dynamics, we evaluated steering using the same 10  
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32 158 ms time-step for all modeling procedures.  
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## 34 159 **3. EXPERIMENTAL RESULTS**

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37 160 Without obstacles, the four pigeons flew in straight lines near the central axis of the corridor (Fig.  
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39 161 2a, light grey paths). When randomly distributed obstacles were introduced, pigeons deviated  
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41 162 from the center straight path to avoid obstacles, by initiating maneuvers  $\sim 1.5$ m before the obstacle  
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43 163 field (Fig. 2b, dark grey paths). Occasional head turns were observed during obstacle flights.  
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45 164 However, previous work suggests that head turns are more relevant to visual stabilization than  
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47 165 targeting during obstacle avoidance (34).  
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51 166 Despite pronounced maneuvers, pigeon obstacle flight paths were only up to 8% longer than  
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53 167 straight-line paths (Fig. 2c). Summed changes in flight direction over a flight, or total steering,  
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55 168 ranged from  $10^\circ$  to  $80^\circ$  for obstacle flights (Fig. 2d). 87% of these obstacle flights contained  $<60^\circ$   
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4 169 of steering. Pigeons generally re-aligned their flight direction with the corridor central axis, which  
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6 170 suggests a maximum of 30° steering to either left or right. The pigeons flew by obstacles with a  
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8 171 clearance of 15.6±5 cm (referenced to the bird's body midline), with a minimum of 9.3 cm. Given  
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10 172 that a pigeon's torso is ~10 cm wide, this represents a surprisingly tight clearance for obstacle  
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13 173 avoidance.

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15 174 Cruising speeds of pigeons exceed 10 m/s in open space (35). In our 20 m indoor flight  
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17 175 corridor, however, pigeons only achieved an average speed of 6.95±0.64 m/s (Fig. 2e). When  
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20 176 obstacles were introduced, pigeons reduced their average flight speed to 3.86±0.52 m/s and  
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22 177 increased their wingbeat frequency from 6.58±0.63 Hz during straight corridor flights (Fig. 2f) to  
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24 178 7.95±0.59 Hz when negotiating obstacles, a typical wingbeat frequency for maneuvering flights  
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27 179 (36). This higher frequency likely satisfied the additional power demand of slower flight and  
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29 180 increased maneuverability by providing more opportunity for changing flight direction. Without  
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32 181 obstacles, the four pigeons maintained flight altitude at 88.1±3.3cm, 111.1±4.8cm, 63.5±2.3cm,  
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34 182 and 78.0±1.9cm respectively. Maneuvering through the obstacles, the four pigeons flew at similar  
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36 183 heights but displayed more altitude fluctuation (75.8±42.5 cm; 103.7±41.8 cm; 106.1±45.6 cm;  
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38 184 110.7±39.4 cm). However, given that the flight negotiation task was to steer around vertical  
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41 185 obstacles, we ignored these altitude fluctuations and analyzed only the horizontal components of  
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44 186 the flight trajectories for developing and evaluating the following guidance modeling work.

#### 46 187 **4. PIGEON OBSTACLE FLIGHT MODEL**

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49 188 According to our framework, we consider obstacle avoidance behavior as two levels of control:  
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51 189 the **steering controller**, which directly produces the flight trajectories, is embedded within an  
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53 190 outer **guidance rule** loop that determines the gap selection and thus steering direction (Fig. 3a).  
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3 191 In the following sub-sections, we introduce each component and the underlying assumptions of  
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5 192 the model.  
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#### 8 193 *4.1. The attention zone*

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10 194 To limit the parameter space, we first considered only  $30^\circ$  on either side of the pigeon's flight  
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12 195 direction as obstacles to which the pigeon must attend. Since most flights (87%) exhibited  $<60^\circ$   
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14 196 total turning ( $\sim 30^\circ$  left or right) (Fig. 2d), we assumed that pigeons only considered steering  
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16 197 within that  $60^\circ$  zone centered about their flight direction (Fig. 3b, solid lines). We estimated the  
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18 198 effective range of this "attention zone" by considering the typical response time of the looming  
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20 199 sensitive neurons of 0.48 s (37) in the pigeon's tectofugal pathway (38). For the free-flight indoor  
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22 200 flight speed (6.95 m/s) of the pigeons in our study, 0.48s converts into a detection range of 3.34  
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24 201 m. Because the obstacle array was only 3 m in depth, we assumed that the pigeon could  
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26 202 practically attend to all obstacles within the specified  $60^\circ$  attention zone, once it arrived at the  
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28 203 obstacle forest.  
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#### 34 204 *4.2. Gap aiming behavior and side wall avoidance*

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37 205 There is some established evidence regarding gap aiming behaviors in birds, especially in the  
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39 206 context of flying through tight spaces. Budgerigars balance contra-lateral optical flow when  
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41 207 choosing a flight path through narrow spaces (39). This is consistent with aiming at the angular  
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43 208 center between two poles when flying through a gap. Thus, we represented potential steering aims  
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45 209 by the angular centers (and not the geometric center) of available gaps (Fig. 3b, dashed lines).  
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47 210 This assumption discretized the steering aims into a handful of gap choices. In addition, the flight  
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49 211 corridor had side-walls with homogeneous visual texture, which the pigeon clearly could see (as  
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51 212 observed during training). In order to impose this boundary constraint in the guidance model, we  
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53 213 represented the side-walls as two dense arrays of vertical obstacle poles spaced 20 cm apart (Fig.  
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214 3b). These virtual obstacles created extremely small visual gaps that the model pigeons would  
 215 never attempt to fly through.

### 216 4.3. Steering controller approximation

217 To test and compare gap selection strategies, we first identified a steering controller that captured  
 218 the steering dynamics of the pigeons under the experimental conditions. We incorporated  
 219 visuomotor delay in this phenomenological model. Even though such delay is sometimes  
 220 negligible in low-speed locomotion such as human walking (23), or tracking a distant target such  
 221 as prey interception by raptors (40), it is likely non-trivial for a pigeon in flight through a  
 222 relatively densely cluttered environment. According to the convention in flight guidance (41), we  
 223 identified the pigeon's flight direction angular velocity  $\dot{\theta}_{pigeon}$  as the control variable and  
 224 constructed a simple proportional-derivative (PD) controller with a visuomotor delay  $\tau_d$  and three  
 225 constant steering gains (Fig. 3c): the proportional gain for the steering aim  $K_P$ , the derivative gain  
 226 for the steering aim  $K_D$  and the stabilizing gain for self-motion  $K_S$ . This steering controller is  
 227 given by:

$$228 \quad \dot{\theta}_{pigeon}(t) = K_P \cdot \theta(t - \tau_d) + K_D \cdot \dot{\theta}(t - \tau_d) + K_S \cdot \dot{\theta}_{pigeon}(t - \tau_d), \quad (4.1)$$

229 where  $t$  is time and  $\theta_{pigeon}$  is the flight direction.  $\theta$  is the angular deviation from the steering aim  
 230  $\theta_{aim}$  given by:

$$231 \quad \theta = \theta_{pigeon} - \theta_{aim}, \quad (4.2)$$

232 Similar controllers (frequently implemented without the derivative terms) have been applied to  
 233 houseflies (42), blowflies (43), bats (44), and tiger beetles (Gilbert *et al*, in preparation).  
 234 However, these controllers were developed in the context of pursuit or flight stabilization, in  
 235 which the animal has a clear steering aim ( $\theta_{aim}$ ). In the context of obstacle negotiation, however,  
 236 both the controller parameters and steering aim need to be determined. Consequently, here we

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3 237 first determine the steering controller parameters with a PD controller tuning procedure and  
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6 238 subsequently test between several potential guidance rules by means of simulations.

#### 8 239 *4.4. PD controller tuning*

10 240 Unlike in a conventional controller tuning process, our parameters for the steering controller were  
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13 241 determined without *a priori* knowledge of the steering aims. Instead, our controller tuning relied  
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16 242 on a fitting procedure using all possible candidate gaps. In essence, we tested every possible  
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18 243 combination of gain-delay on every possible gap steering aim. This was done by first imposing a  
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20 244 specific set of controller parameters (three gains and one delay) for one particular flight. Gap  
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22 245 angular centers that fell within the attention zone ( $\pm 30^\circ$  of current flight direction) were identified  
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25 246 as candidate gaps. At each time step (10 ms), the angular centers of all candidate gaps were  
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27 247 determined. The specific set of gains and delays were then applied to each candidate gap angular  
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29 248 center to predict the necessary steering angular velocity, which was in turn compared with the  
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31 249 observed pigeon angular velocity. We picked the candidate gap that gave the minimum deviation  
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34 250 for that time step and proceeded to the next time step. The average deviation over the entire  
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37 251 trajectory became a fitting index for this set of controller parameters. We repeated this process for  
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39 252 every possible combination of the four controller parameters within the relevant ranges (21 delays,  
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41 253 21 proportional gains, 21 derivative gains, and 21 stabilization gain values; yielding 194481 sets  
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44 254 total). To tune the controller that governs turning, time steps in which there was no appreciable  
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46 255 steering ( $< 10$  deg/s) were excluded, covering maneuvering sections from 0.5m before entering the  
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49 256 forest to 0.2m before exiting the forest. This tuning process resulted in a four-dimensional map of  
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51 257 the PD controller fit in the parameter space for each flight and the weighted average (weighted  
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53 258 flights by the time steps with steering) across trails gave the animal specific map. From this map  
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3 259 we could extract the controller parameters that best described the pigeon's steering (see Modeling  
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5 260 Results for details).

#### 8 261 *4.5. Guidance rule simulations*

10 262 To study guidance rules, we used the determined steering controller (derived from pooled data  
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13 263 from three pigeons) to simulate pigeon flights based on different guidance rules. The complete set  
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15 264 of rules used by pigeons for obstacle flight guidance likely includes many behavioral variables  
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18 265 and their interactions. Here, we merely ask which of the following two navigation objectives is  
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20 266 more important: maximizing clearance or minimizing steering. We tested three simple rules for  
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22 267 gap selection: 1) choosing the gap most aligned with the flight direction; 2) choosing the gap most  
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25 268 aligned with the destination direction; or 3) choosing the gap with the largest visual size (Fig. 5a).

27 269 A simple way to test these different guidance rules is to apply the steering controller (with the  
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29 270 parameters from Table 1) with each rule and simulate the pigeon's flight paths given only the  
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31 271 initial conditions (position, flight direction and speed). In each time step, the guidance rule  
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33 272 determined the steering aim, which was subsequently implemented by the steering controller that  
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35 273 determined the steering angular velocity as described in Eqn 4.1. The flight speed was assumed  
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37 274 constant at the average speed of the particular flight being simulated. The simulations produced  
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39 275 some trajectories that closely matched the actual pigeon obstacle flights (blue trace in Fig. 5d).  
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42 276 Others led to different navigation paths (green trace in Fig. 5d). Based on the modeled pigeon  
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44 277 flight trajectories, we quantified the model match to observed flight paths by evaluating the poles  
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46 278 which the model pigeon 'correctly' passed by on the observed side. We then quantified the  
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48 279 percentage of flights that each guidance rule predicted (termed **predictive power**) from  
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50 280 simulations of a separate set of 40 pigeon obstacle flights. For clarity, we define one **simulation**  
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281 set as the ensemble of these 40 flights simulated under the same condition, such as a particular  
 282 guidance rule. Each **simulation set** thus produced a predictive power value.

#### 283 4.6. Obstacle repulsion model as a reference

284 For comparison, we reconstructed a more conventional obstacle repulsion model in relation to  
 285 the gap-aiming paradigm proposed here. In order to do so, we established an obstacle repulsion  
 286 function similar to (23), which can fit into our PD controller (equation 4.1):

$$287 \alpha_i = (\theta_{pigeon} - \theta_i) \cdot \frac{\theta_{th}}{\theta_{pigeon} - \theta_i} \cdot \frac{R_{th}}{R_i} \quad (4.3)$$

288 where  $\alpha_i$  is the desired steering aim relative to the obstacle to avoid,  $\theta_i$  is the angular location of a  
 289 particular obstacle,  $R_i$  is the distance from this obstacle. We only considered this repellent  
 290 function when the obstacle was within the avoidance attention zone thresholds (Fig. 5b). This  
 291 avoidance attention zone had the same angular threshold ( $\theta_{th} = \pm 30^\circ$ ) as the gap-aiming model.  
 292 We empirically varied the range threshold  $R_{th}$  (from 1.5m to 0.25m) in the guidance rule  
 293 simulation and found the best range to be 0.5m. If an obstacle sat at  $30^\circ$  to either side and 0.5m  
 294 away from the model pigeon,  $\alpha_i$  became  $\theta_{pigeon} - \theta_i$  and the steering aim became the pigeon's  
 295 flight direction (no steering). As the obstacle distance and angle decreased,  $\alpha_i$  increased rapidly  
 296 and drove the steering aim away from the obstacle(s). We summed the contributions from all  
 297 obstacles within the attention zone to find the steering aim:

$$298 \theta_{atm} = \sum(\theta_i + \alpha_i) \quad (4.4)$$

299 We used this model to establish a baseline comparison with respect to our gap aiming simulations.

#### 300 4.7. Sensory uncertainty

301 Deterministic behavior models with exact inputs often fail to capture real-world decision  
 302 processes, which involve tolerating sensory uncertainties. For instance, the pigeon might choose



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3 303 either of two gaps with similar qualities in real-life due to sensory uncertainty, but the model will  
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5 304 always choose the slightly better one consistently. To address this discrepancy, we introduced  
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8 305 random noise into the sensory information of guidance rule simulations, following the approach  
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10 306 of Warren and Fajen (23). For our application, we assumed a Gaussian distribution of the obstacle  
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12 307 angular position centering at the actual angular position of each obstacle (Fig. 5c). At each  
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15 308 modeling time step, we randomly sampled from this Gaussian distribution as the sensory input of  
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17 309 each obstacle position. We varied the standard deviation of this Gaussian distribution from 0° (no  
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19 310 sensory noise) to 30° (sufficient noise that obstacle locations are virtually unknown) at 1°  
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21 311 increments to determine whether the introduction of noise resolved this modeling discrepancy. To  
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23 312 obtain statistics for the effect of sensory noise, we ran each sensory noise condition 100 times for  
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25 313 each simulation set. From these 100 simulation sets, we extracted the mean and maximum  
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27 314 predictive power (Fig. 5e-g).

## 315 316 **5. MODELING RESULTS**

317 The steering controller tuning process generated a four-dimensional steering deviation map in the  
318 parameter space. We found the minimum deviation in this map and generated heat-maps for two  
319 parameters at a time in order to examine the gradient around this minimum in the 4D parameter  
320 space (Fig. 4). The proportional controller was broadly tuned with the gain centered at  $\sim 4 \text{ s}^{-1}$  that  
321 varied only slightly across different delays (Fig. 4, column 1). In contrast, the derivative term  
322 showed much less variation with respect to visuomotor delay, being centered at  $\sim 130 \text{ ms}$  (Fig. 4,  
323 column 2). The stabilizing gain (negative by definition) showed a small contribution to the  
324 steering (Fig. 4, column 3).

325 To extract parameter values from the controller tuning maps, we first recognized the  
326 pronounced visuomotor delay selection in the derivative controller map. We averaged the delay



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3 327 values across the range of derivative gains reported in (Table 1). From this delay value, we found  
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5 328 the corresponding proportional gain (Fig. 4, column 1) for each pigeon individually and for the  
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8 329 three-pigeon-pooled data set. This analysis showed that the controller was dominated by the  
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10 330 proportional term, with negligible derivative gain and small stabilizing gain (Table 1). These PD  
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12 331 controller parameters were then used in the steering simulations. We could also evaluate the  
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15 332 steering controller tuning by re-running the tuning procedure with these near-optimal controller  
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17 333 parameters. As before, the steering aim could be any gap that gave the most consistent fit given  
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19 334 these parameters. We plotted the observed flight angular velocity of individual pigeons against  
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21 335 the model predicted angular velocity derived for each pigeon. The resulting regressions showed  
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23 336 extremely strong fits ( $R^2 = 0.97$  for all cases; Fig. 4, column 4). The pooled data for all three  
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25 337 pigeons showed similar fits for controller tuning and predictive performance as for the individual  
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27 338 data (Fig. 4, row 4).

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32 339 The guidance rule simulations produced interesting predictive power tuning curves with  
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34 340 respect to sensory uncertainty (Fig. 5e-g). For clarity, we present the smoothed data for both the  
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36 341 mean predictive power (thick solid traces) and maximum predictive power (dashed traces). The  
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38 342 behavior of the simulation was similar for the three pigeons on which the steering controller  
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40 343 tuning was based, as well as for the fourth pigeon. Thus we considered the pooled steering  
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42 344 controller parameters generic to pigeon flight under the experimental conditions. The  
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44 345 conventional obstacle avoidance paradigm produced a best mean predictive power of 58% at a  
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46 346 threshold reaction range of 0.5m (Fig. 5e). As the sensory uncertainty increased, the predictive  
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48 347 power decreased steadily. The maximum predictive power never exceeded 65%. With  
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50 348 inappropriate reaction range (e.g. 1m), the mean predictive power started below 30% and  
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52 349 approached 40% with increasing sensory uncertainty. A comparable set of simulations using the  
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3 350 gap-aiming paradigm would be a random gap selection model with a minimum gap size threshold  
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5 351 (Fig. 5f). The best mean predictive power for the random gap model with a 5° threshold averaged  
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8 352 close to 60% at zero sensory uncertainty and exhibited a maximum of ~70%. The predictive  
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11 353 power dropped quickly with increasing sensory uncertainty. Simulations with different gap size  
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13 354 threshold values all converged to a predictive power of ~44% at maximum sensory uncertainty.  
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15 355 Instead of randomly selecting gaps above a certain size threshold, we individually applied the  
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17 356 three different gap selection rules (Fig. 5a) as previously described. At zero sensory uncertainty,  
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20 357 the flight direction aim strategy predicted 32.5% of the flights, whereas the destination aim  
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22 358 strategy predicted 42.4% (Fig. 5g), showing that these gap selection rules perform worse than  
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25 359 random gap selection. The maximum predictive power of these two gap selection rules  
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27 360 approached 44%, similar to that observed for random gap selection (Fig. 5f). In contrast, the  
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29 361 largest gap strategy predicted 70% of the flights accurately. With increasing sensory uncertainty,  
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32 362 the maximum predictive power approached 80% (at ~6° noise). The largest gap selection strategy  
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34 363 (Fig. 5g) therefore performed significantly better than any of the other strategies (including those  
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36 364 for obstacle avoidance (Fig. 5e).  
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## 38 365 **6. DISCUSSION**

### 39 366 *6.1. Flight trajectory planning versus reactive navigation*

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42 367 We observe that pigeons can negotiate through a forest-like vertical obstacle field with <60 cm  
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45 368 typical gap spacing at near 100% proficiency. Despite prior training and repeated trials recorded  
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48 369 to negotiate the obstacle field, the pigeons showed no evidence of maneuvering until 1.5 m before  
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51 370 the obstacle field (Fig. 2a, b) and tolerated frequent wing-obstacle collisions. We did find that  
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54 371 pigeons fly slower and use higher wingbeat frequencies during obstacle flights, compared to  
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56 372 unobstructed flights (Fig. 2e). These flight changes likely reflect the demand for enhanced  
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3 373 maneuverability to steer between obstacles. In general, flight paths through obstacle fields were  
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6 374 only 8% longer than straight paths, and 87% of these flights exhibited  $<60^\circ$  of total steering (Fig.  
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8 375 2d).  
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10 376 The lack of steering could be an energetic strategy or a consequence of the bird's relatively  
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12 377 fast entry speed. However, once in close range of the obstacles, pigeons showed deliberate  
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14 378 steering. Pigeons also timed their wingbeats or folded their wings to avoid contact with nearby  
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16 379 obstacles. The closest fly-by relative to the bird's midline body axis was measured at 9.3 cm  
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18 380 (providing  $\sim 4.3$  cm clearance from the obstacle to the side of the body). These observations  
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20 381 suggest that, under our experimental conditions, obstacle flight is a reactive behavior that relies  
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22 382 on local information, rather than following a pre-planned trajectory.  
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## 27 383 *6.2. Proportional versus derivative control*

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29 384 The steering controller tuning showed that obstacle negotiation is best described as proportional  
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31 385 control with a constant delay. The visuomotor delay of  $\sim 130$  ms (Table 1) was comparable to, yet  
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33 386 slightly greater than, the delay measured for the pigeon's peak flight muscle activity after the  
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35 387 firing onset of looming-sensitive cells (38). The visual angular velocities of obstacles did not  
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37 388 seem to affect this control. This is an interesting and somewhat unexpected result given that most  
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39 389 flying animals use angular velocity-based optical flow to assess their flight states, such as ground  
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41 390 speed and drift (45-47). However, during flights through the obstacle 'forests' employed in our  
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43 391 experiments, the angular drifts of obstacles were fast and highly nonlinear. Consequently, our  
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45 392 results suggest that pigeons focus on the angular positions of the obstacles, rather than their  
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47 393 angular velocities induced by the bird's self-motion. This feature distinguishes obstacle flights  
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49 394 from normal cruising flight, particularly at altitude, when most optical flow arises from distant  
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51 395 visual features.  
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### 6.3. *The effect of sensory noise*

An effective obstacle negotiation strategy must tolerate some sensory noise. In principle, the increase of sensory uncertainty should reduce the mean predictive power (Fig. 5f, blue trace). However, in the case of a weak or poor guidance rule, increasing the sensory uncertainty allows the model to occasionally obtain correct steering aims by chance. This leads to an increase of mean predictive power with sensory uncertainty (Fig. 5f, magenta trace). When the sensory uncertainty increases dramatically, the model loses any knowledge of obstacle position, leading all guidance rules to converge to a baseline predictive power that represents random steering. These simulated flight trajectories are generally straight since it is equally probable to steer left or right. As a result, the baseline predictive power is slightly below 50% (almost half of the flights match the observed trajectories, which were generally fairly straight). Interestingly, in the case of the largest visual gap strategy, the maximum predictive power actually increases with a sensory uncertainty of up to  $6^\circ$ , after which predictive power decreases as expected. Closer inspection reveals that the increase in predictive power at low sensory uncertainty is associated with instances of choice degeneracy. Specifically, when two gaps are close in visual size, the model lacking sensory uncertainty always aims for the slightly larger gap. However, this may not be the actual choice of the pigeon due to the naturally present sensory uncertainty. These instances are captured by the maximum predictive power. Based on this, our simulations indicate that pigeon obstacle negotiation can be best described by a largest visual gap aiming strategy (given the obstacle field is short) with a sensory uncertainty of  $\sim 6^\circ$ .

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### 6.4. *Steering to a gap as a navigational objective for obstacle negotiation*

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3 419 Modeling obstacle negotiation as avoiding individual obstacles (e.g. 20-24) has a major difficulty  
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6 420 when more than two obstacles must be considered at the same time (high obstacle density), in  
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8 421 which the summation of the obstacle repulsion may lead to unreasonable guidance. This problem  
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10 422 can be avoided by limiting the avoidance attention to a small region in the flight direction, as we  
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12 423 demonstrate here. However, in a dense obstacle field, in which multiple obstacles must often be  
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14 424 attended to, the superposition of multiple repellent effects ultimately degrades the predictive  
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16 425 power of an obstacle avoidance model. As described here, we instead treat obstacle negotiation as  
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18 426 a gap-aiming behavior. This allows us to transform the avoidance problem (which can be  
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20 427 challenging to define) to a guidance problem. There are two major advantages to this alternative  
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22 428 approach for phenomenological modeling of animal guidance behaviors. First, the local minima  
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24 429 of the steering potential field due to superposition of conflicting obstacle repellence no longer  
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26 430 exist. The agent selects an opening at any given time and, when there is no immediate need to  
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28 431 steer, aims for the destination. Second having one steering aim at any given time enables PD  
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30 432 controller tuning and allows separation of the fundamentally different guidance rule and the  
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32 433 steering controller. The guidance rule comprises decision criteria, which dictate where the agent  
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34 434 chooses to go, whereas the steering controller represents the mechanics and skills that allow the  
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36 435 agent to implement the steering. This separation allows for examination of different guidance  
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38 436 rules for one individual and for comparison of the same guidance rule in different individuals.  
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40 437 Different individuals may share the same guidance rule, but may have differing steering ability.

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48 The gap-aiming method has additional benefits in practice. For example, the attention zone  
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50 439 can incorporate steering as well as the sensory constraints of an agent. Gap-aiming is also  
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52 440 fundamentally safe, because the agent always heads toward a safe direction and not just turns  
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54 441 away from potential obstacles. A very similar gap aiming model has been implemented on a  
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3 442 robotic vehicle with great success (30). In essence, we methodically decompose obstacle flight  
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5 443 into a well-defined target reference-point and a controller, so that we can apply what has been  
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8 444 learned from studies of target aiming/pursuit (21, 48).  
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### 10 445 *6.5. Modeling animal obstacle flights*

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12 446 Obstacle flight is perhaps more difficult to model than other flight behaviors, such as fixation or  
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15 447 optomotor responses, largely because it requires the animal to make consecutive decisions. Our  
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18 448 study shows that a simple strategy of aiming to the largest visual gap seems to capture the  
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20 449 pigeons' obstacle flight behavior. However, such a simple strategy is likely only one of many  
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22 450 decision criteria. Nevertheless, in the short obstacle field setting of our experiments, this strategy  
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25 451 dominated the steering behavior. Most decision processes by an animal involve the integration of  
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27 452 multiple behavioral parameters and sensory inputs. Optimal control theories are powerful tools  
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29 453 that can be used to interpret animal behavior in relation to motor control and trajectory planning  
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32 454 (49). In general, this approach involves evaluating a cost function that contains all variables  
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34 455 relevant to the behavior and determining the optimal output based on some weighting of these  
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36 456 variables. Modeling guidance, therefore, may well require construction of a decision function, in  
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39 457 which most, if not all possible decision criteria (e.g. obstacle identification, visual gap size,  
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41 458 destination direction, flight direction, steering bias, as well as internal states of the animal), are  
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44 459 included (with different weights) to determine the steering decision. A good example of such an  
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46 460 approach is the "open space algorithm" previously proposed to describe the guidance strategy  
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48 461 used by echolocating bats to fly through an obstacle field (50, 51). This algorithm divides 360  
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51 462 degrees into an arbitrary number of steering directions and computes the desirability of each  
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53 463 direction based on a target direction and all detected obstacles. Then, a so called "winner-take-all"  
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55 464 process selects the direction with maximum evaluation. This is similar to our approach, in that the  
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3 465 agent never steers to a summed direction of all the steering directions considered but instead only  
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5 466 steers to a single “winner” direction. Using such a framework to integrate multiple decision  
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8 467 criteria might be something worth-pursuing in the future.  
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10 468 Another inherent challenge in studying obstacle flight is the treatment of free flight data. Due  
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12 469 to the difficulty in providing full in-flight sensory feedback, virtual reality does not always work  
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14 470 for complex flight behaviors. Interpreting free flight data is challenging because, although the  
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16 471 behavioral objective of avoiding obstacles is clear, the steering aims are far less so. Additionally,  
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18 472 under free flight conditions, animals generate sensory input via self-motion, making it difficult to  
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20 473 independently manipulate and evaluate the visual stimuli experienced by the flying animal. Our  
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22 474 current study provides a new modeling procedure for describing obstacle negotiation in a flying  
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24 475 bird. It does so by first extracting the steering controller from the observed flight behavior and  
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26 476 then testing different guidance rules by means of simulation-observation comparison. Such a  
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28 477 framework was enabled by treating the obstacle negotiation as a gap aiming behavior instead of  
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30 478 an obstacle avoidance behavior. The results not only help identify the visuomotor control  
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32 479 properties of obstacle flight in birds, but also may inspire simple ways to develop real-time  
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34 480 controllers for guiding flying robots through cluttered environments (52).  
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Table 1. Steering controller tuning results for pigeon obstacle flights.

	Visuomotor delay (ms)	Proportional gain (s <sup>-1</sup> )	Derivative gain	Stabilizing gain	Controller fit (R <sup>2</sup> )
Pigeon 1	161±8.8	4.31	Irrelevant	<1	0.97
Pigeon 2	159±6.3	4.56	Irrelevant	<0.5	0.97
Pigeon 3	120±5.7	4.95	Irrelevant	<0.5	0.97
Pooled	134±5.0	4.74	Irrelevant	<0.5	0.97

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44 600 **Figure 1. Obstacle avoidance flight corridor and motion tracking.** (a) Pigeons were trained to fly  
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46 601 between two perches located at either end of a 20 m indoor flight corridor. An obstacle ‘pole forest’ was  
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48 602 erected 10m from the take-off perch to elicit obstacle negotiation. Five high-speed cameras captured the  
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50 603 flight trajectories (green section) throughout the entire obstacle forest, including 5 m of the approach. (b)  
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52 604 Starting from a standard grid (red dots), for each flight obstacles were randomly assigned one of five  
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54 605 positions (the grid center or one of four orthogonal locations 0.3 m from the grid center (illustrated by red  
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56 606 arrows). (c) Four 2.4 mm LEDs were attached to the pigeon in combination with a small battery-pack (16.5  
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3 607 g total) to facilitate positional tracking of the head and body. (d) 3D flight trajectories were reconstructed  
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5 608 from the high-speed videos. An example trajectory (green trace) is marked every 200 ms (blue circles). To  
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7 609 model steering through the obstacle field, we considered a section of the flight from 50 cm in front of the  
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9 610 obstacle field to 20 cm before the pigeon left the obstacle field (blue arrow). (e) 3D head positions and  
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11 611 pole-distributions were used to reconstruct the in-flight visual motion of obstacles with respect to the  
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13 612 pigeon's head (and eyes). The modeling process assumed that pigeons always aimed toward visual centers  
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15 613 of gaps.  
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19 614 **Figure 2. Characteristics of pigeon obstacle flight.** (a) The pigeons flew straight, close to the corridor  
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21 615 midline in the absence of obstacles (light grey traces). When challenged with obstacles (dark grey traces),  
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23 616 flight trajectories diverged within the obstacle field. (b) Steering was first observed 1.5 m in advance of  
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25 617 obstacles, determined when the standard deviation (dark grey dash lines) and the limit (dark grey solid  
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27 618 lines) exceeded control trajectories (light grey dash lines and solid lines). (c) Flight trajectories without  
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29 619 obstacles were extremely straight over the 6 m calibrated section of the flight corridor, with a normalized  
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31 620 path length of  $1.00 \pm 0.002$ . Obstacle flights were slightly longer, with a normalized path length of  
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33 621  $1.03 \pm 0.025$ . The path length was normalized to the straight-line reference. (d) Control flights normally  
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35 622 contained  $< 5^\circ$  of total steering; whereas obstacle flights involved total steering summing up to  $\sim 80^\circ$ .  
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37 623 However, 87% of obstacle flights contained  $< 60^\circ$  of total steering (thick arrow). (e) Flight speed was  
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39 624 reduced 44.5% from  $6.95 \pm 0.64$  m/s to  $3.86 \pm 0.52$  m/s, and wing-beat frequency (f) increased by  $\sim 21\%$  from  
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41 625  $6.58 \pm 0.63$  Hz to  $7.95 \pm 0.59$  Hz when pigeons flew through the obstacles.  
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46 626 **Figure 3. Modeling framework for pigeon obstacle negotiation.** (a) The pigeon's obstacle negotiation is  
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48 627 expressed as a feedback control system with a steering controller embedded within a guidance rule (gap  
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50 628 selection). The model determines a steering aim at each time step based on a guidance rule. Gap aiming  
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52 629 behavior suggests that this aim is represented by one of the available gaps in the obstacle field, which then  
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54 630 becomes the reference for the steering controller. The steering controller subsequently generates a steering  
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56 631 command based on a given set of proportional and derivative gains. After a given visuomotor delay, the  
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3 632 steering is implemented under the influence of steering inertia. (b-d) The obstacle navigation behavior can  
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5 633 be broken down into three subsequent steps: Obstacle detection, steering decision and steering  
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7 634 implementation. (b) For each time step relevant obstacles are identified within a given attention zone,  
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9 635 establishing the available gaps (dashed lines). The model pigeon focuses on those that fall within  $\pm 30^\circ$  of  
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11 636 the flight direction, which the model considers its 'attention zone' (solid lines; see texts for details). The  
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13 637 side-walls were modeled as very dense rows of obstacles (black squares). (c) Depending on the guidance  
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15 638 rule, one of the available gaps is selected as the steering aim. The deviation angle  $\theta$  and its derivative are  
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17 639 calculated based on flight direction and the steering aim. (d) The steering controller determines the amount  
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19 640 of steering that occurs after the visuomotor delay  $\tau_d$ .

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24 641 **Figure 4. Steering controller tuning.** Tuning was based on the average deviation between model-  
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26 642 predicted and observed flight directions, determined every 10 ms time step for the best steering aim, for *all*  
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28 643 possible combinations of gains and delay, and for *all* obstacle flights. To make the flight controller  
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30 644 independent of the guidance rule, the tuning process assumed that the pigeon always aimed to one of the  
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32 645 available gaps without imposing an *a priori* rule on gap selection, but instead selected the gap that resulted  
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34 646 in the best fit with the observed flight path. The proportional controller was broadly tuned with a minimum  
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36 647 deviation band centered about a gain of  $\sim 4 \text{ s}^{-1}$  (column 1). For the derivative control, however, a  
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38 648 visuomotor delay of  $\sim 130 \text{ ms}$  was strongly selected but with a broadly tuned derivative gain (column 2).  
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40 649 We implemented steering inertia as a stabilizing term. The stabilization gain is, by definition, negative and  
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42 650 is generally quite small (column 3). We extracted the controller parameters that provided the best fit to the  
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44 651 observed data; these are presented in Table 1 (see text for details). We then demonstrated that pigeon  
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46 652 obstacle flights can be modeled as aiming to a gap by regressing the observed angular rate of change of  
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48 653 flight direction against that predicted by the best fitting controller parameters. The steering controller  
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50 654 predicted the observed steering extremely well ( $R^2 0.97$  for all four cases; column 4), under the paradigm  
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52 655 of gap aiming.

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4 656 **Figure 5. Pigeons bias their flight paths towards largest gaps.** (a) Based on the gap aiming paradigm,  
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6 657 we proposed three potential guidance rules: 1) steer to the gap closest to the destination direction (red); 2)  
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8 658 steer to the gap in the existing flight direction (magenta); or 3) steer to the largest visual gap (blue). (b) To  
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10 659 establish a reference for our gap aiming paradigm, we reconstructed a conventional obstacle repulsion  
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12 660 model with a variable range attention zone (marked by dashed lines), in which the repellent effects from all  
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14 661 obstacles within that threshold range and angle were summed. (c) To provide the simulations with more  
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16 662 realistic sensory information, we incorporated sensory uncertainty by assuming a Gaussian distribution  
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18 663 centered at each obstacle position for the model to sample from. The standard deviation of this Gaussian  
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20 664 distribution was varied to test each steering strategy across a range of noise levels. (d) We simulated 40  
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22 665 pigeon flights (not used for steering controller tuning) given only the initial conditions (*i.e.* body position,  
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24 666 flight direction, entry speed) 0.5m before the obstacle field. Some simulations recapitulated the observed  
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26 667 flight trajectories (blue trace), and some did not (green trace). We quantified the percentage of flight  
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28 668 trajectory matches for each guidance rule in each simulation set (40 flights). To examine the effect of  
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30 669 sensory uncertainty, we ran each simulation set 100 times under each sensory uncertainty condition. (e)  
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32 670 We varied the threshold range of the obstacle repulsion model and found that a threshold of 0.5 m yielded  
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34 671 the greatest mean predictive power of 58% with zero noise (solid blue line). The corresponding maximum  
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36 672 predictive power (blue dashed line) reached 64% at 6° sensory uncertainty. The obstacle repulsion  
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38 673 model's predictive power was lower when reacting to the obstacles too late (<0.25m) or too early (<1m).  
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40 674 (f) The gap aiming navigational paradigm requires that pigeons always aim to a gap between two obstacles.  
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42 675 In this set of simulations, the modeled pigeon randomly aims to a gap over a given angular size threshold.  
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44 676 As the threshold increases, the predictive power increases for sensory uncertainty ranging from 0 to 20°,  
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46 677 signifying the importance of gap size in the decision making process. (g) Maintaining the gap size  
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48 678 threshold at 5°, we ran simulations using the three basic guidance rules described in (a). The destination  
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50 679 gap rule and flight direction gap rule both underperformed compared to random gap selection as in (f). The  
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52 680 maximum predictive power of those simulations where the model pigeons aimed for the largest visual gap,  
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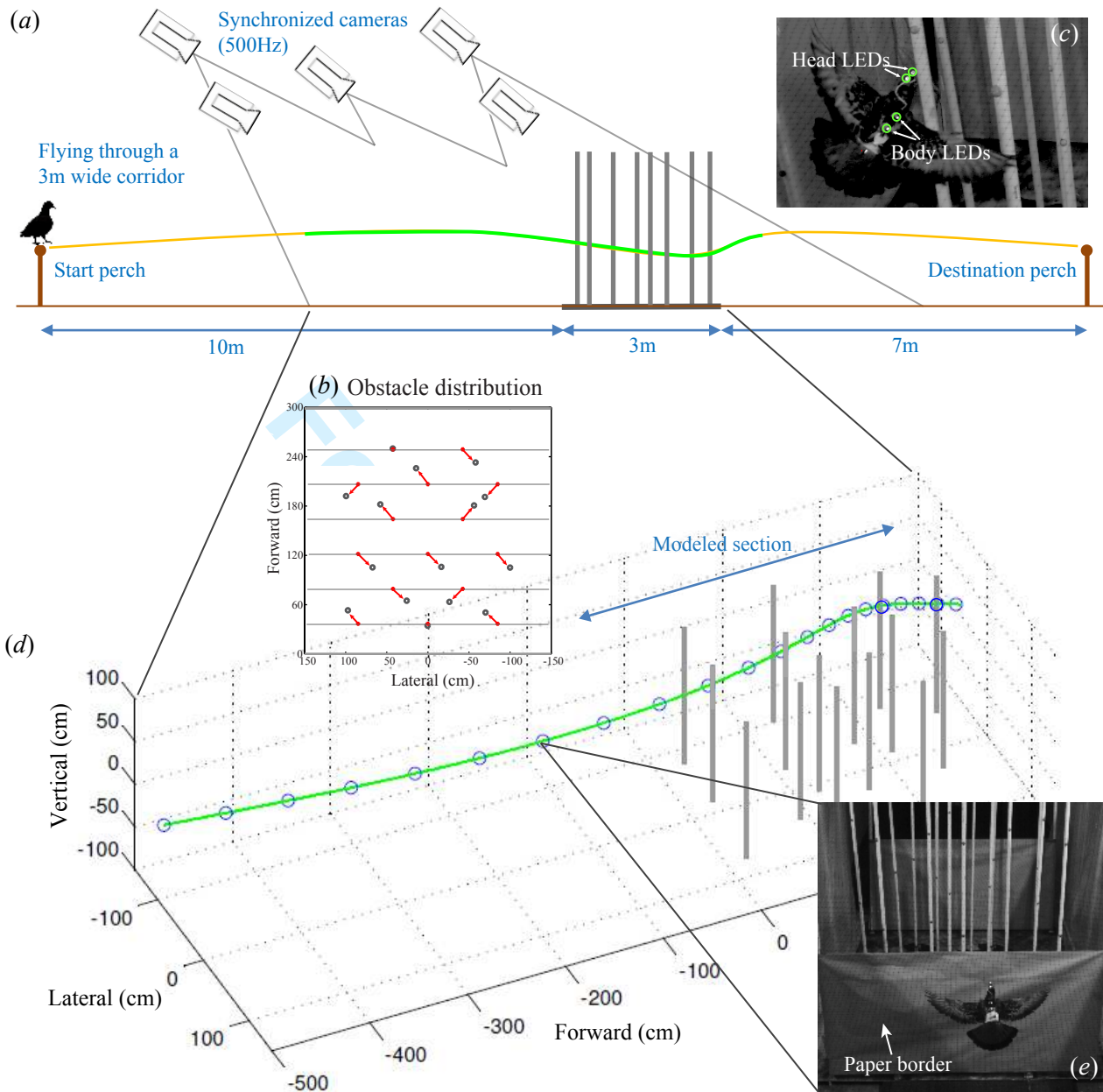
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3 681 however, approached 80% around a noise level of 6°, outperforming the alternative gap selection rules,  
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5 682 random gap selection (*f*), and the obstacle repellence model (*e*).  
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