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RESEARCH ARTICLE

Pigeons use distinct stop phases to control pecking

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ABSTRACT

Pecking at small targets requires accurate spatial coordination of the head. Planning of the peck has been proposed to occur in two distinct stop phases, but although this idea has now been around for a long time, the specific functional roles of these stop phases remain unsolved. Here, we investigated the characteristics of the two stop phases using high-speed motion capture and examined their functions with two experiments. In experiment 1, we tested the hypothesis that the second stop phase is used to pre-program the final approach to a target and analyzed head movements while pigeons (*Columba livia*) pecked at targets of different size. Our results show that the duration of both stop phases significantly increased as stimulus size decreased. We also found significant positive correlations between stimulus size and the distances of the beaks to the stimulus during both stop phases. In experiment 2, we used a two-alternative forced choice task with different levels of difficulty to test the hypothesis that the first stop phase is used to decide between targets. The results indicate that the characteristics of the stop phases do not change with an increasing difficulty between the two choices. Therefore, we conclude that the first stop phase is not exclusively used to decide upon a target to peck at, but also contributes to the function of the second stop phase, which is improving pecking accuracy and planning the final approach to the target.

KEY WORDS: Head movement, Motor control, Bird, Pecking, Motion capture, Learning

INTRODUCTION

The characteristic head movements of pigeons and their functional role have puzzled researchers for a long time. Pigeons, like many other bird species, exhibit a specific behavior known as head-bobbing. To the unaided eye, pigeons appear to periodically thrust their heads forwards and then pull them backwards as they walk. In slow motion however, it can be seen that the backwards motion is illusory. Instead of moving their heads backwards, pigeons thrust them forwards and then hold them almost perfectly stationary as the rest of their body catches up (Davies and Green, 1988; Dunlap and Mowrer, 1930; Friedman, 1975; Necker, 2007; Troje and Frost, 2000). In this way, during walking, a pigeon's head undergoes a series of rapid forward movements (thrust phases) and stationary phases (hold phases), while the body moves with a relatively homogenous speed.

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Similarly, the motion of the head is interrupted during pecking by two distinct stop phases that are reminiscent of the hold phases observed during walking (Goodale, 1983a; Zweers, 1982). Pigeons thrust their head forwards, pause (a stop phase Goodale termed F1), thrust their head forwards again, pause again (F2), and then execute the final approach towards the target. On the one hand, the two stop phases were reported to be highly stereotypic: both F1 and F2 always occurred at constant distances from the target and lasted for similar amounts of time across all birds (Goodale, 1983a). On the other hand, it was shown that pecking does not always follow a fixed action pattern, but instead is flexible and adjusted to the location of a seed (Zeigler et al., 1980). Furthermore, pigeons adjust their pecking movement to different circumstances such as seeds mixed with grit, non-removable seeds, hunger, head loads and grain size (Siemann and Delius, 1992). A high flexibility of pecking movements was also observed when different conditioning methods, such as delayed food reward, were applied (Hörster et al., 2002). However, it is not clear how the pigeons control the different pecking movements, and the functions of the two stop phases during pecking remain unsolved.

The thrust and hold phases that occur during head-bobbing have been analyzed in more detail. During the hold phase, not only does the head remain motionless in space, but there are also no movements of the eyes relative to the head (Wallman and Letelier, 1993). It is therefore believed that pigeons use the hold phase of a head-bobbing cycle to fixate and detect objects (Bloch et al., 1988; Davies and Green, 1988). This applies most importantly to moving objects such as predators, whose movement makes them stand out against the otherwise stationary retinal image, but also facilitates the recognition of small, low contrast, stationary objects such as seeds (Davies and Green, 1988; Frost, 1978; Troje and Frost, 2000; Wohlschläger et al., 1993; Zweers, 1982).

During the head-bobbing thrust phase, the pigeons' visual input changes rapidly (Troje and Frost, 2000). This is due to the rapidly moving head, but also to the fact that the majority of eye movements occur during that time (Pratt, 1982; Wohlschläger et al., 1993). This rapid change is likely to provide pigeons with depth information from motion parallax that cannot be obtained from the still retinal images they experience during the hold phase (Frost, 1978; Troje and Frost, 2000; Xiao and Frost, 2013). In support of that theory, it was shown that visual processing is not supressed during the thrust phase. In that regard, the saccadic head movements of birds are different from the eye saccades of mammals during which much of the visual input is suppressed (Jiménez-Ortega et al., 2009).

Obviously, visual feedback also plays a major role in pecking, during which pigeons shift their eyes to converge the visual fields (Martinoya et al., 1984). This convergence starts at the first stop phase (F1), increases to the second stop phase (F2) and continues during the final approach (Martinoya et al., 1984). During this final approach, pigeons open their beak around 25–30 ms after leaving the second stop phase and nearly close their eyes around 5–10 ms later (Delius, 1985; Goodale, 1983a). Closing the eyes just before the impact with a target probably protects them against possible

back-scattering particles (Delius, 1985). The beak opening is proportional to the size of the seed at which the peck is aimed (Deich et al., 1985; LaMon and Zeigler, 1984). However, when pigeons peck at targets on a screen to obtain a water reward, the beak remains closed (LaMon and Zeigler, 1988, 1984).

Because the eyes seemed to be completely closed before impact, it was assumed for a long time that the final approach to a target is a ballistic movement (Wohlschläger et al., 1993). However, the assumption of a ballistic movement was challenged by the discovery that the eyes are not completely closed but instead a slit remains that might allow on-line visual adjustments during the final approach (Ostheim, 1997). So far, it is not clear to what extent the final approach is adjusted through on-line visual feedback, but given that the eyes are closed to a large extent, it can be assumed that the movement needs to be planned in advance.

Goodale (1983a) hypothesised that this planning takes place during the second stop phase, F2. He suggested that pigeons use F2 to obtain information about the finer details of a target (specifically its size and distance). In addition, he suggested that during the first stop phase (F1), pigeons decide whether or not to peck at a target, and also within which area their intended target was located (Goodale, 1983a).

However, the characterization of the two stop phases during pecking was not the main purpose of Goodale's experiments and his suggestions were never tested experimentally. Here, we designed two experiments using high-speed motion capture to empirically examine the specific functional roles of the two distinct stop phases during pecking.

By manipulating the size of disk-shaped targets, we tested whether varying target sizes resulted in different durations of the second stop phase, F2. If pigeons collect visual information to pre-program the final approach, they should spend more time in F2 when smaller targets are presented, because small targets require a higher degree of accuracy than larger ones. In contrast, the duration of the first stop phase (F1) should be independent of target size, if it is only used for deciding on a broad area to peck at.

In experiment 2, we trained pigeons to peck at one of two identical target disks that were each surrounded either by a red or a yellow frame. A food reward was contingent on the color of the frame. By increasing the similarity of the two colors, we increased the difficulty of choosing between the two targets and examined to what extent this manipulation affected pecking accuracy and duration of the two stop phases. We expected prolonged durations of the first stop phase (decision-making phase) with increasing difficulty, but no effect on the duration of the second stop phase.

MATERIALS AND METHODS
Subjects
We used four (three males, one female) rock doves (*Columba livia* Gmelin 1789) in both experiments and a fifth bird (male) that only participated in experiment 2. The birds were obtained from pigeon breeders in Ontario, Canada (Limestone City Flyers) and kept at Queen's University. All experimental protocols conformed to the ethics requirements for animal research of the Canadian Council on Animal Care (CCAC) and were approved by the University Animal Care Committee of Queen's University.

For the duration of the experiments, the birds were separated from the aviary population and housed in metal-wire cages each measuring 39×28×31 cm and kept on a fixed 12 h light:12 h dark cycle. Their diet was restricted in order to maintain their weight at approximately 85% of their free-feeding weight to ensure that they were motivated to participate. Prior to the experiment, the birds were

trained to peck at white disks on a screen using a standard autoshaping procedure (Brown and Jenkins, 1968). Once the pigeons reliably pecked at the disks for three consecutive sessions they were placed into the experiments.

Experimental setup
The experiment was completed on a metal table (233×41 cm). Stimuli were presented on a computer monitor (30.5×23 cm) mounted at one end, and feeders were placed at both ends to provide food rewards. In experiment 1 we used the distant feeder to provide the food reward and in experiment 2, we used the feeder close to the screen. The original purpose of presenting the food reward at a distance away from the screen was to avoid carry-over effects from one trial to the next due to the position of the last stimulus they responded to. Observing the birds in experiment 1, we were convinced that this would not be an issue and decided to only use the proximal feeder in experiment 2, which resulted in shorter experiments. The table was painted with matte black paint and the majority of the surface (except for the recording area) was covered by white absorbent paper that was changed every day. The table was enclosed by a rectangular wooden box frame (40.5 cm high) enclosed with mist netting. The sides were also paneled with opaque black foam board to reduce visual distractions.

An infrared touch screen (Keytec, PPMT-IR-015EL) with the glass back plate removed was fitted over the computer monitor where the stimuli were displayed. The touchscreen had a spatial resolution of 5.2 mm (distance between infrared beams, both vertical and horizontal) and was used to detect peck locations on the screen. Correct pecks at a stimulus caused the respective feeder to provide a food reward.

The feeders consisted of a chamber filled with pigeon grain located below the table and a small circular platform (2 cm in diameter) that was raised up from the food chamber to the table's surface to present grain to the birds. A laser barrier was located 17 cm in front of the feeder at the far end, with the laser beam at a height of 11 cm above the table's surface. The platform descended back to its resting position 3 s after the laser barrier had been tripped, thus terminating access to the food. In experiment 2, no laser barrier was required because the feeder was located in front of the screen where the birds were already standing. The feeder provided food for 3 s.

Motion capture
The pigeons' movements were recorded with a six-camera motion capture system (Qualisys, Oqus 300), which recorded positional data of retro-reflective markers at 360 Hz in 3D space. The system provided a spatial resolution smaller than 1 mm (RMS error).

To record the movements of the pigeons, we designed two lightweight rigid structures, a triangle for the head (2 g) and a rectangle for the back (3 g, see Fig. 1A). Each structure had four retro-reflective markers (3×3 Designs Ltd., 4 mm in diameter) attached to it. In order to attach the structures to the birds, two areas of feathers (one on the head and one on the back) were trimmed and patches of Velcro were attached to them using PVA glue. These patches remained on the birds until data collection was finished. The rigid structures with the motion capture markers were attached to the Velcro patches prior to an experimental session and were removed once it was completed (Fig. 1A).

An additional motion capture marker that consisted of a small piece (2×5 mm) of reflective tape was adhered to the pigeons' beaks below their nostrils for the duration of an experimental day.
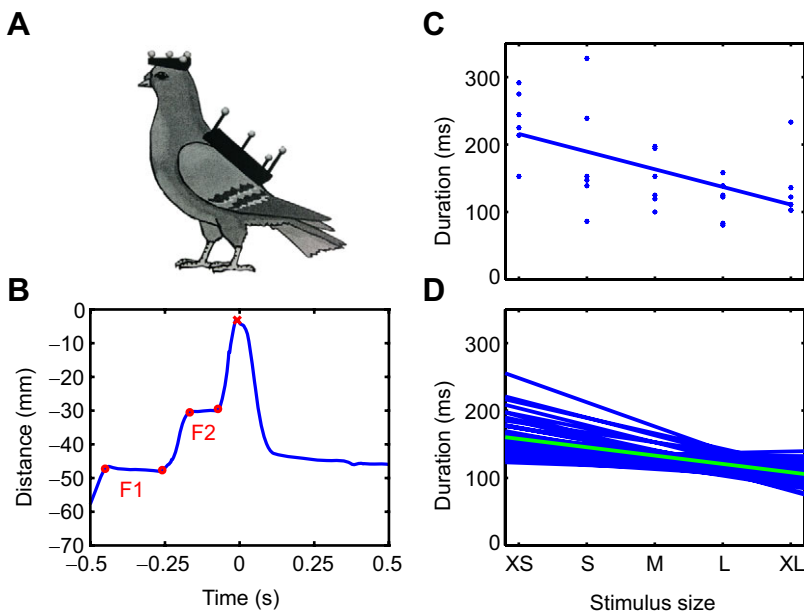
Fig. 1. Pigeon with markers, beak time course of a typical peck and regression analysis. (A) Sketch of a pigeon with marker structures attached to the head and the back to record their movements with the motion capture system. (B) Time course of the distance to the screen of the beak with respect to the impact on the screen (time 0) showing a typical example of a peck. The peck and the starts and endings of the preceding stop phases (F1 and F2) are indicated by a red cross and circles, respectively. (C) Regression line of the F2 stop phase duration of a typical session of Bird 2 with 6 pecks at each stimulus size (XS=5.08, S=8.08, M=12.86, L=20.34, XL=32.3 mm diameter). (D) All regression lines for bird 2 (blue) from which the mean regression line (green) and the 95% confidence intervals were calculated (see Fig. 2, green).

Design and procedure
Experiment 1
In experiment 1, the pecking targets for the pigeons were white disks presented on the computer monitor at a height of 21.5 cm above the table's surface at three locations, either in the center of the screen, or 47 mm to the left or to the right of the center. We used five different stimulus sizes with diameters of: 5.1, 8.1, 12.9, 20.3 and 32.3 mm. The size of the smallest stimulus was based on the resolution of the touch screen (5.2 mm), the largest size was the same as that used in the initial autoshaping session, and the three sizes in between were spaced logarithmically – increasing by a factor of 1.6 (2 dB) from one size to the next.

Each experimental session consisted of ten trials (each stimulus size presented twice), resulting in ten food rewards per session. Each trial consisted of three stimulus presentations of the same size. The first trial was constrained so that it would not use the smallest stimulus size, but apart from that, the order of the sizes was randomized.

In each trial, the first stimulus appeared in the center of the screen. Once this stimulus was pecked correctly it disappeared and the second stimulus appeared after 0.2 s randomly to the left or right of the center stimulus. Once the second stimulus was pecked, the third stimulus appeared on the opposite side as the second stimulus. If a bird pecked outside of the stimulus area (a miss), the stimulus turned green and a tone was played for a penalty period of 3 s. During this time nothing happened if the birds pecked the (green) stimulus or anywhere else on the screen. After 3 s the tone stopped, the stimulus turned white again, and the trial continued. This penalty was added to make the pigeons peck accurately, and not just in the general area of the stimulus. After all three stimuli had been pecked correctly, the birds received a food reward for 3 s from the feeder on the opposite end of the table. After feeding, the next set of stimuli appeared on the screen. The birds then walked back to the screen and the next trial began.

On most days, a second session (with the same procedure) took place immediately after the first. Following completion of the final session for a day, the birds were removed from the experimental arena, the motion capture markers were removed, and they were returned to their cages.

In total, we collected data from at least 50 sessions from each bird (53, 56, 51 and 52, for birds 1 to 4, respectively). A few sessions (in total 22 out of 212) had to be excluded from final analysis because the beak marker was not detected in enough frames to reconstruct the beak position relative to the markers on the head. After removing these sessions, we analyzed 51, 49, 43, and 47 sessions of experiment 1 for birds 1 to 4, respectively.

Experiment 2
In experiment 2, we used the same white disks with a diameter of 20.3 mm, but presented two targets at the same time (each 47 mm to either side of the center). Both targets were placed in the center of a square-shaped frame (side length 44.3 mm, line width 4.5 mm). Only one disk was rewarded when pecked. The color of the surrounding frame (red or yellow, see Fig. S1) cued which one was rewarded.

During training, three of the five birds learned to peck at the target surrounded by a red frame and the other two learned to peck at the target with a yellow frame. After the birds learned to peck at the correct target, we tested them on five different color pairs that became increasingly similar to each other. We achieved that by linearly interpolating between the two starting colors (red [255 0 0] and yellow [255 255 0]) in RGB color space (see Fig. S1).

The design and procedure was very similar to experiment 1. During each session, ten experimental trials were recorded. Each trial started with a single target in the center of the screen. When this stimulus was pecked correctly, the two targets with the colored frames appeared immediately and the pigeon had to decide which side to peck. The side on which the rewarded target appeared and the sequence of the colored pairs were randomized, but the latter was counterbalanced such that each color pair appeared twice during each session. If the pigeon pecked at the correct side and hit the target it received a food reward directly below the screen. When choosing the wrong side or missing the target, pigeons were punished in the same way as in experiment 1, but both targets turned green.

In experiment 2, we recorded 15 sessions of four of the birds and nine sessions of the fifth bird. One session had to be excluded because a marker at the screen fell off during the experiment.

Following the analysis of individual birds, we compared the data to see if the observed behavior was consistent across birds.

Data analysis

The data analysis was the same for both experiments. Marker trajectories were semi-automatically labeled and gaps were filled automatically using Qualisys QTM software. The beak marker especially experienced large gaps. These were filled by exploiting the fact that the beak marker and head markers were all attached to the rigid structure of the skull of the pigeon. Therefore, only a few frames of visible beak marker were needed to reconstruct its location as a linear combination of the locations of the tracking markers on the head. The 3D positional data of the head, the body, and the beak were then combined with data on the size and location of the stimuli, as well as pecks detected by the touchscreen.

To analyze stop phases during pecking, we first identified pecks from the motion capture data. For this identification, beak position data were smoothed using a fourth-order low-pass Butterworth filter with a cut-off frequency of 72 Hz. We then identified pecks as minima of the time series of the distances between beak and screen that occurred within a 5 mm distance from the screen and at a minimum height of 150 mm to avoid the detection of pecks at seeds close to the screen. Each peck was assigned to the stimulus that was presented at the same time. With these parameters, the distance between the peck location and the stimulus center on the screen, and therefore hits and misses, were identified with a higher spatial resolution than the touchscreen was able to provide.

To identify the corresponding stop and thrust phases, the beak velocity was calculated and filtered using a Butterworth filter with a cut-off frequency of 36 Hz. Stop and thrust phases were first identified based on beak velocity and then adjusted by a model that assumes piecewise constant beak velocity that changes only at transitions between the two phases. Model parameters included the location of the transition points in space and time, and the velocities between them. Optimization was achieved according to a least-square criterion and implemented with MATLAB's 'fminsearch' function.

Once the stop and thrust phases were identified, the first stop phase, F1 and the second stop phase, F2, were identified by their timing with respect to the corresponding peck (Fig. 1B). Stop phases occurring immediately before the peck were labeled as F2 phases, and the preceding phases were labeled as F1 (Fig. 1B).

Statistical analysis

We fitted linear mixed-effects (LME) models to the data of experiment 1 to test the effect of stimulus size on stop phase durations and on distances between the beak and the screen. After log-transformation of the duration data, we fitted LME models with stimulus size as fixed effect coefficient and animal as random factor to the data.

For experiment 2, we used the Friedman test to evaluate the level of difficulty to differentiate between the colored frames. To analyze the effect of stimulus difficulty on F1 and F2 durations, we used the same LME models with stimulus difficulty as fixed factor and animal as random factor. However, no log-transformation was required, because the data were already normally distributed.

RESULTS

Stop phase durations are negatively correlated with stimulus size

The motivating question for experiment 1 was whether birds use the final stop phase (F2) to prepare and pre-program the final pecking movement. We hypothesized that F2 duration increases with decreasing target size. To examine this hypothesis, we identified the stop phases preceding each peck (Fig. 1B) and computed for each session the slope of the regression line that relates F2 duration linearly to the logarithm of target size (Fig. 1C). We then calculated the average slope from all sessions (Fig. 1D) along with the 95% confidence interval separately for each bird (Fig. 2A). We found a significant effect of stimulus size on F2 duration (Fig. 2A, LME model: d.f.=5228, t=−6.0, P<0.001). The majority of negative slopes (Fig. 2A; −1.0, −6.1, −1.6 and 0.9 ms dB^{-1}) shows that F2 duration decreased with increasing stimulus size.
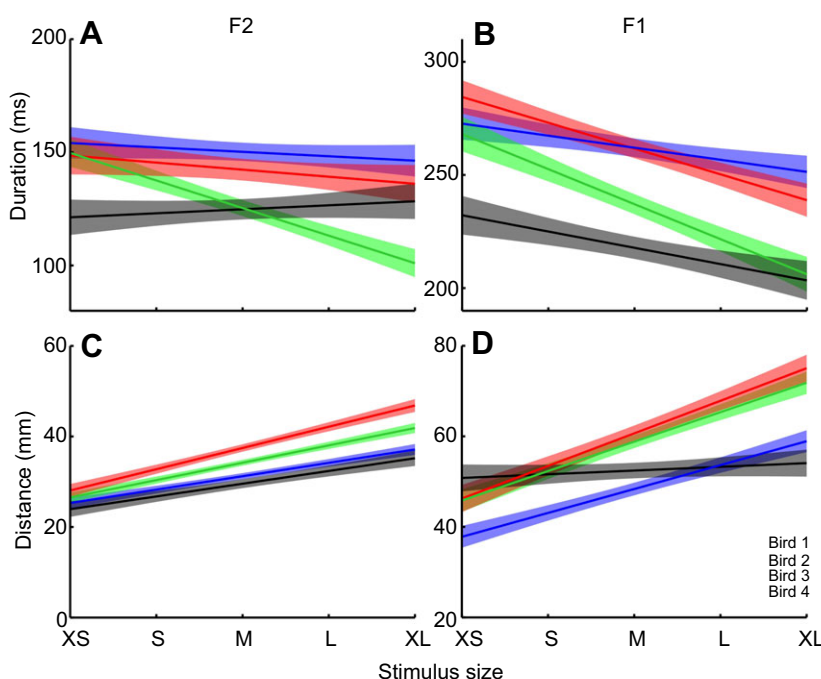

Fig. 2. Stop phase duration and distance to the screen change with stimulus size. Mean regression lines with 95% confidence intervals between stimulus size and stop phase durations (A,B) and beak distance to the screen (C,D) are shown for four birds. (A,B) F2 and F1 stop phase duration as a function of the log of stimulus size. Both were found to decrease with stimulus size in the four birds (three significantly for F2 and all four significantly for F1, P<0.05). (C,D) F2 and F1 distance over the log of stimulus size. Both were found to increase significantly with stimulus size in all four birds (P<0.05).

We then followed up by examining the duration of the preceding stop phase (F1) as a function of stimulus size in order to assess the hypothesized functional role of F1: that pigeons use this stop phase to decide between separate stimuli. Since we only presented the birds with one stimulus, we expected them to spend the same amount of time deciding where to peck (duration of F1) regardless of stimulus size.

However, the LME model showed that stimulus size significantly affected F1 duration (d.f.=5228, $t=-13.9$, $P<0.001$). The corresponding regression lines for F1 duration as a function of stimulus size showed that F1 duration was negatively correlated with stimulus size (Fig. 2B; slopes: -2.7, -7.8, -5.7, -3.6 ms dB^{-1}).

Distance to the screen increases with stimulus size
In addition to stop phase durations, we assumed that the distance between the beak and the screen during the respective stop phases might play an important role for accurate pecking. Closer distances result in a larger retinal image of the stimulus and might reduce the noise of the final movement. We therefore reasoned that in order to have an optimal retinal image for calculating the final motor movement, the pigeons would hold their heads closer to the screen for small stimuli than for large stimuli.

The LME models confirmed this expectation and showed that stimulus size significantly affected the distance to the screen during both F2 stop phases (d.f.=5228, $t=34.4$, $P<0.001$) and F1 stop phases (d.f.=5228, $t=24.5$, $P<0.001$). As shown by the regression lines in Fig. 2C (1.5, 1.9, 2.4, 1.4 mm dB^{-1}) and Fig. 2D (2.7, 3.3, 3.6, 0.4 mm dB^{-1}), stimulus size was positively correlated with the distance between the beak and the screen.

To further evaluate the functional roles of the two stop phases during pecking, we analyzed how pigeons orientated their head during pecking. In experiment 1, head orientation during pecking naturally changed because the birds needed to adapt to the lateral positions of the stimuli, left or right, respectively. To evaluate when this adaptation takes place, we calculated the average head orientation angles at three points in time: during the first stop phase (F1), during the second stop phase (F2) and at the time when the beak touched the screen (Fig. 3, Peck).

Head orientation was changed in yaw and roll significantly between F1 and F2 independent of the side of the stimulus (Fig. 3, LME models: $P<0.001$; see Table S1 for statistical details). Thus, head orientation was already partly adjusted to stimulus location during the thrust phase following F1. After F2, head orientation in roll was further adjusted until the beak touched the screen: i.e. the roll angle changed significantly after F2 independent of the stimulus position (Fig. 3B, LME models: $P<0.001$, Table S1). In contrast, head yaw angle was only adjusted after F2 for the center and for the right stimuli (Fig. 3A, LME models: $P<0.001$, Table S1), but not for the stimuli that appeared on the left side (Fig. 3A, LME model: $P>0.05$, Table S1). This showed that head orientation in yaw to stimuli that appeared on the left side took place between F1 and F2. Nevertheless, the changes in head orientation angles show overall that the initial adjustment to the stimulus location took place between F1 and F2, and that head orientation was further adjusted after the final stop phase (F2) until the beak touched the screen (Fig. 3, compare angles of F2 and Peck).

Interestingly, head orientation was also adjusted to the center stimulus, which would not have required changes in yaw and roll angles (Fig. 3, Center). The consistent turn to the left shows that the pigeons did not peck straight at the stimuli and might indicate that the birds preferred to look with the right eye (positive yaw, i.e. turn to left).

F1 duration does not increase with increasing similarity of targets
The purpose of experiment 2 was to test the hypothesis that the first stop phase (F1) is used to make the decision between two different targets. Therefore, we trained the birds to peck at one of two
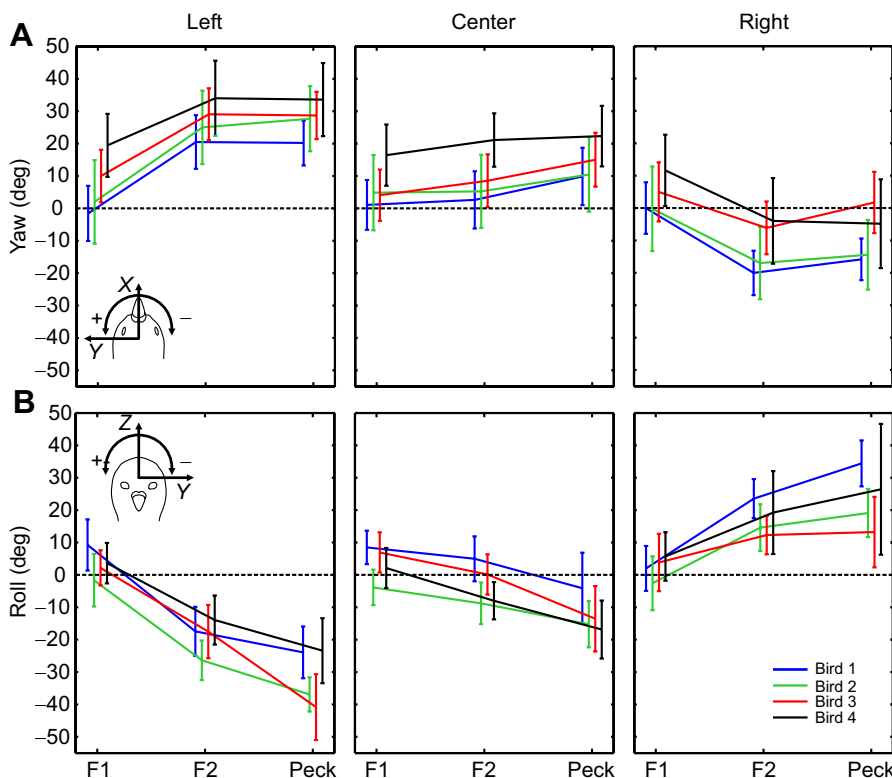

Fig. 3. Head orientation is adjusted to stimulus location. Mean head orientation angles with standard deviations during the stop phases (F1, F2) and at the time of the peck (Peck) for the three different stimulus locations (Left, Center, Right). Mean head yaw (A) and roll (B) angles are shown for each bird (different colors) in global coordinates. Head orientation changes in yaw and roll after both the first (F1) and the second stop phase (F2). Insets indicate positive (counter-clockwise) and negative (clockwise) rotations around the vertical axis (A, yaw) and around the longitudinal axis (B, roll), respectively.
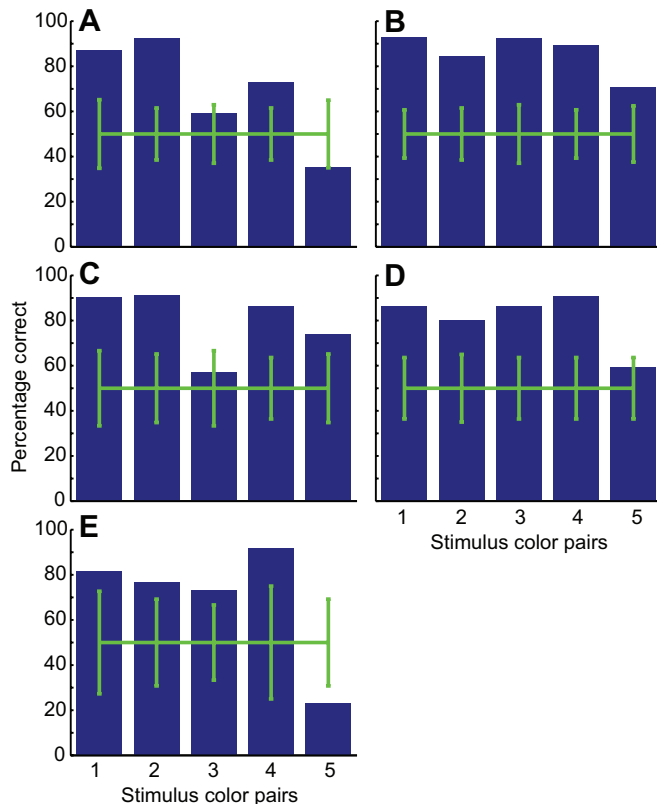
Fig. 4. The ability to choose the correct side decreases with increasing difficulty of the task. (A-E) Percentage of correct choices for each bird (A-E) for the different color pairs (1-5). The correct side was chosen when the respective peck was within the colored frame. The green horizontal line indicates chance level and the vertical lines indicate the area within which a binomial, two-tailed test results in error probabilities larger than 5%. For the four birds with 15 sessions (A-D), the number of pecks per bar ranged from 20 to 28 and for animal five (E), it ranged from 11 to 15.

identical targets whose reward value was cued by the color of a surrounding frame. Three birds learned to peck at a target with a red frame to receive a food reward, and the other two birds learned the same for a yellow frame. After all birds learned the task, we tested them by making the decision between the two targets more difficult, i.e. increasing the similarity of the colored frames (see Fig. S1).

The results show that the birds were not only able to differentiate between the red and yellow frames, but in most cases they also performed above chance for the more difficult stimuli (Fig. 4). Nevertheless, the percentages of choosing the correct side significantly decreased with the increasing difficulty of the discrimination (Friedman-Test: d.f.=4, X^2=11.11, P<0.05). In case of stimulus color pairs 1 and 2, all birds chose the correct side in around 80 to 90% of the pecks. This differed when the colors of the frames were more similar. Two birds seemed to have trouble with color pair 3 and performed at chance level (Fig. 4A) and with the most difficult stimulus, color pair 5, three of five birds performed below or at chance (Fig. 4A,D,E). This indicates that the color pairs worked in principle and that the birds had difficulty in picking the correct side when the task became more difficult. But, did the increased difficulty also affect the duration of F1 stop phases, which were hypothesized to be the decision-making phase?

To test our hypothesis that the F1 stop phase is used to decide between different targets, we calculated the mean stop phase durations for each bird and stimulus color pair (Fig. 5B). It can be seen that, on average, F1 stop phase durations were longer when two

targets were present (color pairs 1–5) compared with the single target (Fig. 5B, single). However, the difficulty of the task had no significant effect on F1 duration (LME model: d.f.=475, t=0.1, P=0.9). This means that although F1 duration was generally longer when a bird was confronted with two stimuli than with only a single target, F1 duration did not increase with the increasing difficulty to differentiate between the colored frames (Fig. 5D).

Regarding the durations of the F2 stop phase, no difference between the single target (Fig. 5A, single) and the two targets surrounded by colored frames could be observed. As expected, differentiation difficulty also had no significant effect on F2 duration (Fig. 5A,C, LME model: d.f.=527, t=0.9, P=0.4). This shows that the duration of the second stop phase was affected neither by the number of possible targets, nor by the increased difficulty to differentiate between two targets.

DISCUSSION

We examined the role of the two stop phases during pecking at a target with two experiments. In experiment 1 we tested the hypothesis that the F2 stop phase is used to pre-program the final approach of the pecking movement by exploring targets of different size. In experiment 2, we presented two targets at the same time and increased the difficulty to differentiate between them in order to test the hypothesis that the function of the first stop phase, F1, is to decide which target to peck at.

Overall, we found average stop phase durations of 122 ms (F2) and 250 ms (F1), which were longer than the average durations found by Goodale (1983a) in two separate experiments that employed different types of targets: a key and seeds (F2: 103 and 93 ms, F1: 140 and 220 ms, respectively). The differences between the current study and Goodale's may result from the different targets that were used and also may be due at least in part to the differences in measurement, i.e. semi-automated, high-speed, marker-based motion capture versus manual film analysis.

Stop phase durations increase with decreasing target size

The results of experiment 1 show that the duration of F2 increased with decreasing stimulus size. The correlation between F2 duration and stimulus size supports our hypothesis that pigeons might use F2 to collect information to pre-program the final peck; if they require higher accuracy to peck smaller stimuli they spend more time in F2.

In contrast, Goodale (1983a) found no significant differences in F2 duration between pecking at illuminated keys (2.5 cm in diameter) or at seeds on the ground. The apparent incompatibility of these results might be explained by the fact that the illuminated keys had a secondary, 2-mm black dot in their center, which served as a cue and at which the pigeons always directed their pecks (Goodale, 1983a,b). If the pigeons considered the black dot (approximately the same size as a seed) to be the target as opposed to the key as a whole, we would not expect large differences in F2 durations.

The function of F1 goes beyond making decisions

We also found that F1 duration increased as stimulus size decreased (Fig. 2B), but it did not increase in experiment 2 when differentiation between two targets became more difficult (Fig. 5). This does not support our hypothesis that F1 is used to decide which target to peck at, but it does not contradict it either. The negative result could also result from the absence of the speed-accuracy trade-off, which our hypothesis implicitly assumed. Discrimination performance did drop as the two stimuli became more similar, but F1 time remained constant. The only hint pointing to a connection
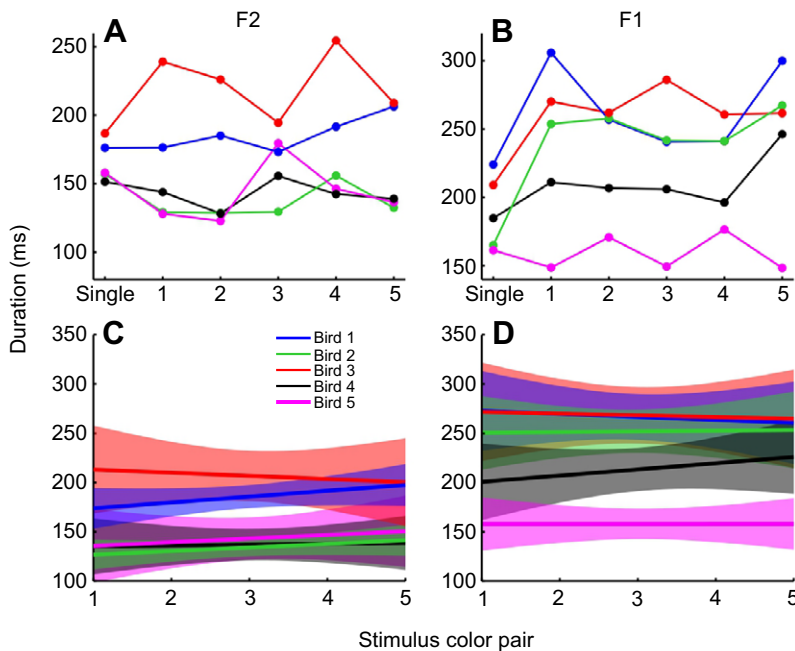
Fig. 5. Stop phase duration does not increase with the difficulty of the color pairs. (A,B) Mean F2 (A) and F1 (B) stop phase durations against a single target without a frame (single) and stimulus color pairs for each animal. (C,D) Mean regression lines with 95% confidence intervals calculated from all pecks that corresponded to the five stimulus color pairs.

between the duration of F1 and the difficulty of the decision that needed to be made is that the duration of F1 was generally longer when birds had to decide between two targets compared to the situation when only a single target was present. Furthermore, the variability of F1 durations was larger in experiment 2 compared to experiment 1 (compare Fig. 5D and Fig. 2B). This indicates that decision making might take place during the F1 stop phase, but as the results of experiment 1 show, the time that pigeons spent in F1 was also influenced by other factors such as the size of the target. The increase of F1 duration with respect to target size even seemed to be more pronounced than the increase of F2 duration. In combination with the finding that the head orientation was partly adjusted following F1 (Fig. 3), we conclude that the function of F1 goes beyond making decisions about which target to peck. Pigeons can discriminate all sorts of different stimulus properties such as shape, size, line orientation, and brightness (Teng et al., 2015; Vyazovska et al., 2014). It would be interesting to see how the characteristics of F1 are affected by a more complex task that includes differentiation of more than one stimulus property and whether its duration increases when more than two stimuli are presented.

Distance to the screen is adjusted to stimulus size
During the stop phases, we found very strong positive correlations between the distance of the head to the screen and stimulus size. Because vision is presumed to be a major function of the head-bobbing hold phases during which objects are detected and identified (Davies and Green, 1988; Jiménez-Ortega et al., 2009), one might assume that the decrease in distance serves to optimize the retinal image size of the stimulus. However, the distance between the beak and the screen increased on average by a factor of 1.3 for F1 and 1.0 for F2 from one target size to the next, whereas the stimulus size increased by a factor of 1.6. This shows that the differences in distance to the screen did not entirely compensate for the change of the retinal image size caused by the different stimuli. The discrepancy might result from limits in distance to the screen from which pigeons are able to peck, i.e. for the largest stimulus, the optimal retinal image might have been obtained from a distance

further away, but initiating a peck from that distance would have been difficult or impossible due to anatomical limitations. Nevertheless, the variability in distance to the screen and head orientation indicates that pecking is adjusted to the given circumstances and supports the view that pecking is not a stereotypic, fixed action pattern (Siemann and Delius, 1992; Zeigler et al., 1980).

Conclusions
The results of experiment 1 show a negative correlation between the length of time pigeons spend in F2 and stimulus size, which supports our main hypothesis that pigeons use F2 to pre-program the final peck. Unexpectedly, we also found a strong negative correlation between F1 duration and stimulus size. In experiment 2 we did not find the hypothesized correlation between F1 duration and the difficulty to differentiate between two targets. This indicates that the function of F1 is not limited to deciding whether or not to peck, but furthermore likely involves planning some part of the final pecking movement. This hypothesis is further supported by the finding that head orientation is partly adjusted to the stimulus during the thrust phase following F1. Significant correlations were also found between the distances from the screen that the pigeons held their heads at during both F1 and F2, giving further areas of pecking behavior that are affected by stimulus size.

Author contributions
L.M.T. designed experiments, supervised experimenters, analyzed data, interpreted the findings and wrote the manuscript. T.R. carried out experiment 1, analyzed data and wrote the manuscript. N.F.T. designed experiments, supervised T.R. and L.M.T., interpreted findings and edited the manuscript.

Supplementary information

Supplementary information available online at
http://jeb.biologists.org/lookup/doi/10.1242/jeb.147850.supplemental

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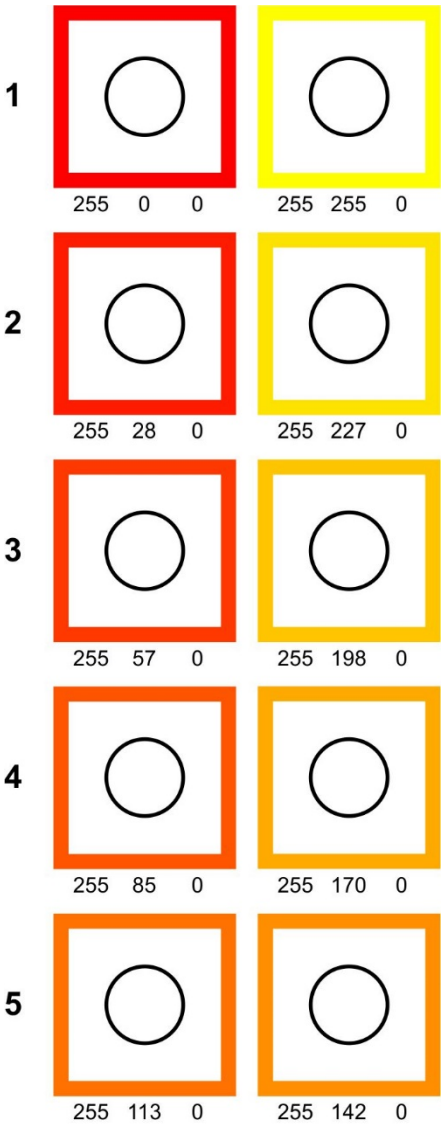
Figure S1: Comparison of the five color pairs used in Experiment 2. The colors become increasingly similar (from 1 to 5) and therefore the decision for the correct target (inner white circle) becomes more difficult. The corresponding RGB values are given under each frame.

Table S1:

Statistics of the LME that fitted best to head yaw and roll angles. We compared the change of the angles from F1 to F2 (F1→F2) and from F2 to peck (F2→Peck) for each side of the stimuli (left, center, right). The LME included stimulus size as fixed and animal as random effect: 'y ~ phase + (1 |animal)'.

	Side	F1→F2			F2→Peck		
		Df	t-stat	p	Df	t-stat	p
Yaw	left	3620	41.8	<0.001	3691	1.5	=0.125
	center	3598	5.6	<0.001	3674	11.5	<0.001
	right	3555	-30.1	<0.001	3679	5.6	<0.001
Roll	left	3620	-53.8	<0.001	3691	-31.1	<0.001
	center	3598	-17.6	<0.001	3674	-20.7	<0.001
	right	3555	31.9	<0.001	3679	13.6	<0.001