Universidade do Minho
Escola de Psicologia

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Unveiling the usage of time: Exploring pigeons' temporal strategy in the midsession reversal task

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Professor Doutor Carlos Pinto
e coorientação do
Professor Doutor Armando Machado

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DIREITOS DE AUTOR E CONDIÇÕES DE UTILIZAÇÃO DO TRABALHO POR TERCEIROS

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STATEMENT OF INTEGRITY

I hereby declare having conducted this academic work with integrity. I confirm that I have not used plagiarism or any form of undue use of information or falsification of results along the process leading to its elaboration.

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Universidade do Minho, 06 de junho de 2024



(João Antônio Queiroz Silva)

Revelando o uso do tempo: Explorando a estratégia temporal de pombos na tarefa de *midsession reversal*.

Resumo

Em uma tarefa chamada *midsession reversal*, as contingências são invertidas ao meio da sessão. Em uma sessão com 80 ensaios, os primeiros 40 são reforçados quando o pombo escolhe o estímulo S1, e os restantes são reforçados quando escolhe o estímulo S2. Os pombos consistentemente cometem erros antes da inversão, escolhendo S2 antes do ensaio 40, e após a inversão, continuando a escolher S1 depois do ensaio 40. Para analisar qual estratégia os pombos realizam nessa tarefa, o intervalo entre ensaios (ITI) no teste é geralmente dobrado ou reduzido pela metade em comparação com o ITI no treino. Ao contrário dos humanos, que tipicamente mudam de S1 para S2 quando param de receber reforço no S1, os pombos geralmente dependem do tempo decorrido na sessão para prever o ponto de inversão. Em nosso estudo, tornamos o ITI variável, com o ITI médio no teste sendo ou dobrado ou reduzido pela metade em comparação com o ITI médio no treino. Ao tornar o ITI variável, procuramos atenuar a principal diferença entre as fases de treino e teste (o tempo do ITI) dificultando que os pombos detetem mudanças na tarefa ao passarem para o teste.

Palavras-Chave: Midsession reversal, Tempo, Decremento da Generalização, Pombo, ITI variável.

Unveiling the usage of time: Exploring pigeons' temporal strategy in the midsession reversal task

Abstract

In a midsession reversal task, the contingencies of the session are reversed at its midpoint. For instance, in a session with 80 trials, the first 40 are reinforced when the pigeon chooses stimulus S1, and the remaining are reinforced when choosing stimulus S2. Pigeons consistently make errors before the reversal, choosing S2 before trial 40, and after the reversal, continuing to choose S1 after trial 40. To assess what strategy pigeons adopt in this task, the inter-trial interval (ITI) in testing is usually doubled or halved the ITI in training. Unlike humans, who typically switch from S1 to S2 when they stop receiving reinforcement for choosing S1, pigeons usually rely on the elapsed time to predict the reversal point. In our procedure, we made the ITI variable, with the average ITI in testing being either doubled or halved the average ITI in training. By making the ITI variable, we aimed to attenuate the main difference between the training and test phases, making it harder for the pigeons to notice changes in the task when they are transferred to testing.

Keywords: Midsession reversal, Timing, Generalization decrement, Pigeon, Variable ITI.

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Introduction

Imagine a recruiter receiving countless job applications. Instead of extensively evaluating all candidates to find the best possible hire, the recruiter is likely to stop as soon as he finds one application that meets the company's requirements. This illustrates how when dealing with problems, humans frequently fail to adopt the optimal strategy. Instead, we go for approximations to the best solution, performing in a way that provides a merely satisfactory outcome. Herbet Simon (1956, 1957) proposed the concept of a bounded rationality, which suggests that the capacities of the individual and the structure of the environment play a fundamental role in our ability to solve problems. This is a well-grounded idea in the study of human decision-making (e.g., Gigerenzer & Todd, 1999, p. 13; Jones, 1999), and it would be unreasonable to presume that nonhuman animals do not act similarly.

Studies that explore how nonhuman animals adapt to changes in their environment regularly support the idea of a bounded rationality. Cook and Rosen (2010) developed a procedure in which the environmental contingency changes mid-session. The task was done with pigeons in an operant chamber containing three horizontally displaced keys. It started with the presentation of a sample stimulus at the middle key that could be one of two colors. The sample was then turned off and the two colors appeared simultaneously at the side keys. The sessions had 96 trials, and during the first 48 trials, the animal had to choose the color that corresponded to the sample (identity matching). During the remaining 48 trials, they had to choose the color that was different from the sample (oddity matching). Interestingly, the authors found that the pigeons consistently made two types of errors. Sometimes they started oddity matching before the contingency switch (anticipating the moment of reversal), and sometimes they continued identity matching even after the session rule had changed (persevering on their choice after the reversal had occurred).

Rayburn-Reeves et al. (2011) simplified the task and presented pigeons with a choice between two keys (S1 and S2), one illuminated green and the other red. In the first half of the session, only choices of S1 were reinforced, and in the second half of the session, only choices of S2 were reinforced. This procedure, the midsession reversal (MSR) task, can be learned in different ways: choices can be made based on the outcome of the previous trial (i.e., start the session by always choosing S1, and when choices of S1 cease to be reinforced, switch to S2), on numerical cues (i.e., count the trials to know when to choose S1 or S2), or on temporal cues (i.e., estimate when in the session the reversal occurs). Given the error associated with estimations of both number and time, the adoption of either strategy could explain the results observed by Cook and Rosen (2010), with pigeons anticipating the reversal or perseverating

the choice after the reversal occurred. Therefore, basing the choices on the trial outcome (known as a win-stay/lose-shift strategy) would be the optimal strategy, given that it would result in the loss of only one reinforcer (following the first incorrect choice of S1). Rayburn-Reeves et al. (2011) found similar results to Cook and Rosen (2010), with pigeons consistently making anticipatory and perseverative errors.

The procedure employed by Rayburn-Reeves et al. (2011) involved a visual discrimination (i.e., S1 and S2 were fixed in position without counterbalancing the samples between the left and right keys), which could cause a weaker sensitivity to the moment of the reversal since there is evidence that performance on serial reversal is better when using spatial discrimination (Bullock & Bitterman, 1962). In a follow-up study, Rayburn-Reeves et al. (2013) did the same procedure, but now using spatial discrimination, and found that pigeons made similar patterns of errors. This suggests that the pigeons were using either a timing or a counting strategy.

As mentioned, the preference for using numerical or temporal cues is not the most efficient strategy. Rayburn-Reeves et al. (2013) tried to argue that the win-stay/lose-shift rule is harder to acquire than it seems since it requires remembering both the last key chosen and the outcome of that choice. Although remembering the events of the last trial could be considered fairly easy, pigeons show considerable forgetting with delays of just a few seconds (Randall & Zentall, 1997). Therefore, if counting or timing strategies are based solely on estimates of how much time has passed or what trial the animal is currently in, those strategies could be considered easier to use since they do not require remembering the outcome of previous trials in order to switch.

McMillan and Roberts (2012) tried to assess if pigeons were using a timing or a counting strategy by either doubling or halving the inter-trial interval (ITI) on test sessions. The procedure was similar to Rayburn-Reeves et al. (2011), with 80 trials per session and the reversal on trial 41. If pigeons were timing the reversal point to decide when they should switch from S1 to S2, testing with a doubled ITI would increase the session duration, reducing the trial number in which the pigeon would prefer S2 over S1. To further illustrate how the trial estimate of the reversal would be reduced, in training with a 5 s ITI the pigeon will time the reversal point, say at 10 minutes into the session. In other words, during training, trial 41 occurs after 10 minutes into the session. By doubling the ITI in testing to 10 s, the session time is longer, with the real reversal (trial 41) being after 20 minutes. But since the pigeon is expecting the reversal after 10 minutes, it will reverse its preference from S1 to S2 after 10 minutes, which in testing corresponds to trial 20. The opposite would happen when testing with a halved ITI (the expected reversal would be around trial 80). If pigeons were counting to predict the reversal, the sole manipulation of time

should not influence the number of errors, therefore, if the errors in test sessions were similar to the errors in training, it would suggest that pigeons were counting. The results showed an effect consistent with the use of timing. In training, the point of subjective equality (PSE) – the trial where pigeons were indifferent between S1 or S2 – was around trial 40. However, in testing, the PSE was close to trial 20 for the doubled ITI (showing more anticipatory errors) and close to trial 50 for the halved ITI (showing more perseverative errors) (see also Soares et al., 2020).

Rayburn-Reeves et al. (2013) showed that pigeons had a better performance when trained with shorter ITIs in the MSR. When training with 1.5 s ITI, the animals showed fewer errors compared to training with 5 or 10 s ITIs, with psychometric functions showing an almost perfect use of a win-stay/lose-shift strategy. This result suggests that with shorter ITIs, the pigeon can better remember the outcome of the last trial, resulting in a better opportunity to use this outcome as the predictor of the reversal, which could be the reason for the obtained function being similar to a win-stay/lose-shift strategy. With longer ITIs, remembering the outcome of the last trial is harder, perhaps leading the pigeon to also rely on other cues that are not as precise, possibly interfering with its performance.

Although the manipulation of ITIs suggests that the pigeons adopt a timing strategy in the MSR, an asymmetry between the magnitudes of anticipatory and perseverative errors was observed. When doubling the ITI, the PSE decreased by a factor of 2, but halving the ITI increased the PSE only by a factor of approximately 1.21 (Soares et al., 2020; Machado et al., 2023). An argument that tries to explain the asymmetry found is the competition between cues. Rayburn-Reeves et al. (2017) argue that as a session approaches the reversal, the time cue becomes less reliable (since time estimation is not a precise process), reducing the utility of that cue. Consequently, other cues (such as the feedback from the previous trial) may exert a stronger influence on pigeon behavior at this point in the session. This was somewhat verified when they increased the salience of a cue or added other external cues to the task, and that improved accuracy across a session. McMillan and Roberts (2012) also suggested that pigeons do not use a single strategy to predict the reversal, with results showing that pigeons using timing, also use trial-outcome cues to some degree. The competition between cues is more substantial in the halved ITI condition. In the test phase of the halved ITI condition, a pigeon that uses timing to predict the reversal, will expect the reversal to occur around trial 80. After the session reversal (trial 41) the timing strategy would conflict with the outcomes of the previous trials, meaning that the timing would encourage the pigeon to keep choosing S1 after trial 40, but it would cease to be reinforced. The trials after the reversal where the pigeon is no longer reinforced could cause the decision to switch from S1 to S2 to occur earlier

than a timing strategy suggested, resulting in the asymmetry found. This is not a problem in the doubled ITI condition, because using timing, the decision to switch from S1 to S2 happens at trial 20, which is before the actual reversal of the task. So timing is not anticipated by the task reversal, allowing the pigeon to use only timing to decide when to switch.

A potential fix to avoid competition between timing and the trial-outcome cue would be to reinforce both S1 and S2 after trial 40 in test sessions, so that no choice would be subject to extinction, and timing could be expressed without interference. This would help determine if the magnitude of changes in the PSE would be the same for both halved and doubled ITI conditions. Therefore, when the ITI is halved, a pigeon following a timing strategy would prefer S1 from trials 41 to 80 and would still be reinforced, so the outcomes after trial 40 would not be preventing timing-controlled behavior from being expressed. With this manipulation, Soares et al. (2023) no longer found an asymmetry with a PSE around trial 25 for the doubled ITI condition and around trial 75 for the halved ITI condition. This result suggests that most of the subjects were indeed following a timing strategy (see also Machado et al., 2023, for a similar procedure with starlings).

In conclusion, pigeons were found to exhibit anticipatory and perseverative errors when faced with the MSR task, indicating that they were using a strategy that was not very effective. To investigate the preferred strategy, manipulations of the duration of the task suggested the use of a strategy based on temporal cues. Although this manipulation showed strong evidence for the use of timing, some components of the task indicated that other types of cues could be influencing the strategy chosen by the animals, so controlling for competing cues was necessary. Besides this, since the ITI from training is noticeably different from test sessions, the generalization decrement from training to testing needs to be considered. Due to the lack of control over some aspects of the task, the study of the timing hypothesis as the primary strategy chosen by pigeons can be further improved.

In previous MSR procedures, the different ITI durations between training and testing sessions should be easily perceptible by the pigeon, possibly giving rise to a generalization decrement when going to the test phase. Hence, the present study tries to minimize the generalization decrement of the task by using a variable ITI that has shared durations between training and testing but with different proportions, so that the test session is either doubled or halved the duration of training. By making the ITI variable, it will be arguably harder for pigeons to perceive a difference between training and test sessions, consequently, diminishing the generalization decrement of the task. Thus, this procedure tries to be more

effective in measuring the timing hypothesis, providing a more definitive answer to the use of this strategy by pigeons.

Another aspect of our procedure is that we purposedly destroyed the regularity of the trials while maintaining only the point of the reversal stable. In other words, by making the ITI variable, the pigeon can only time the reversal of the session since the time of each trial is unpredictable. By doing this, our study tries to elucidate what temporal markers the pigeons use to predict the reversal, since this is still not clear (i.e., does the pigeon count the session time as a whole or count (or sum) the various discrete portions of the session (the time passed in each trial)?) It is expected that if the pigeon counts the session time as a whole, the ITI being variable will not have an effect on its estimate, producing results close to what previous studies found. Otherwise, if the discrete portions are also considered when timing the reversal, by making the ITI variable, we expect the performance to be worsened.

Methods

Subjects

Twelve pigeons (*Columba livia*) participated in the experiment, divided into two groups of six. The determination of sample size was conducted using a priori power analysis (G*Power 3.1). A t-test for paired samples was employed to compare the PSEs from training and testing. The significance level was set at .05 (two-tailed), with a power of .80. The estimated effect size, which was derived from a previous study (Soares et al., submitted), was established at 2.03 for the 10–5 condition and 2.12 for the 5–10 condition.

Pigeons were maintained at approximately 80% of their free-feeding weight. They were housed in individual cages with access to water and grit on a 13:11h light/dark cycle, with a room temperature between 21° and 22°C. In each group of six pigeons, five had previous experience with midsession tasks.

Apparatus

The experiment was run in four operant chambers, with three birds assigned to each. One was a homemade chamber, while the other three were LVE (Lehigh Valley Electronics) chambers. The homemade chamber measured 31 x 33 x 33 cm (h x l x w) and was enclosed in a PVC sound-attenuating cubicle (Med Associates, ENV-018V) equipped with an exhaust fan to mask the noise and circulate air in the chamber. The front wall was equipped with three circular response keys, arranged horizontally, 2.5 cm in diameter, 9 cm apart (center to center), and 21 cm above the floor. The keys had a 12-stimulus IEE (Industrial Electronics Engineers) in-line projector illuminated with a 28-V, 0.1-A lamp. Access to the

LVE food hopper with mixed grains was through a 6-cm wide x 4.5-cm high opening centered horizontally in the front panel (below the response keys), 6.5 cm above the floor. The food hopper was illuminated with a 28-V, 0.04-A light when activated. All other walls were made of acrylic, and a wire mesh served as the floor.

The LVE chambers were all 34 x 35 x 31 cm (h x l x w). They were equipped with an exhaust fan, and the walls were made of aluminum. A wire mesh also served as the floor. The front wall had three horizontally aligned response keys, 2.5 cm in diameter, 8.5 cm apart center to center, and placed 22.5 cm above the wire mesh floor. The keys were illuminated by a 12-stimulus IEE in-line projector, and each stimulus was illuminated with a 28-V, 0.1-A lamp. The LVE food hopper with mixed grains was illuminated with a 28-V, 0.04-A light, and it was accessible by a 6-cm wide, 5-cm high opening. The food hopper was centered horizontally in the front panel, below the keys, and 8.5 cm above the floor.

Experimental events were controlled and data was recorded by the ABET II software (Lafayette Instrument Company).

Procedure

Table 1

Procedure structure

	I		II	
Pigeons	Avg ITI Training (s)	Avg ITI Test (s)	Avg ITI Training (s)	Avg ITI Test (s)
P283 PG39 P458 PG29 P960 PG47	5 ⇨	10	10 ⇨	5
P449 P918 P456 P234 P902 P588	10 ⇨	5	5 ⇨	10

All pigeons were exposed to two conditions (5–10 and 10–5). Pigeons who completed condition 5–10 were then placed in condition 10–5. Conversely, pigeons that started in condition 10–5 were moved to 5–10 after completion. Table 1 illustrates the order of the conditions that the pigeons were exposed to. For example, pigeon P283 began training with an average ITI of 5 seconds, followed by testing with an average ITI of 10 seconds – Condition 5-10 (I). After completing this condition, P283 started its second condition, training with an average ITI of 10 seconds and then being tested with an average ITI of 5 seconds – Condition 10-5 (II).

Each training session consisted of 80 trials. At the beginning of a trial, both side keys were illuminated with the stimuli, one with a red hue and the other with a green hue. During trials 1 to 40, only responses on one color were correct (S1); from trial 41 to 80, only responses on the other color were correct (S2). After selecting a stimulus, both side keys were turned off, and an inter-trial interval (ITI) commenced. If the choice was correct, during the first two seconds of this ITI, the food hopper was raised and illuminated, granting access to the reinforcer.

The positions of the colors on the side keys of the box were counterbalanced within sessions, and the assignment of which color was S1 and S2 was counterbalanced among pigeons.

Order group II was used to increase the sample size of each condition, offering the possibility of comparing 12 pigeons in condition 5–10 with 12 pigeons in condition 10–5.

Training occurred six days a week for a minimum of 20 sessions, and lasted until the proportion of correct responses in each half of the session was at least .80 in three consecutive sessions, or until a maximum of 40 sessions was reached.

Condition 5–10 (I):

In training, the ITI was variable and had an average of 5s during training. The 20 values of the ITI (see Table 2, Appendix) were constructed following the Flescher and Hoffman (1962) distribution. The sessions were divided into blocks of 20 trials, with each block showing all 20 ITI values. So, in 80 trials, they saw each ITI value 4 times. The minimum ITI duration was 3s; this was done to ensure that if a correct response was made, the pigeon had time to access food (available for 2s) and still experience an ITI.

After training, the subjects were exposed to two test sessions. During testing, the ITI distribution was constructed in the same way as training, but now with a doubled average of 10s (see Table 2, Appendix). To control possible competing cues in testing, two manipulations were done. Firstly, choices were only reinforced after the 20th trial, to have an additional control for pigeons that opt for timing (because the moment the 20th trial occurs in a test session should roughly correspond to the moment in a training session when reinforcement for S2 started). And choices of S1 were always reinforcement, to guarantee that the change from S1 to S2 was not due to an interruption of reinforcement on S1. The test sessions consisted of 120 trials.

Condition 10–5 (I):

The procedure resembled Condition 5–10, with a few distinctions. Firstly, the training and test phases had the opposite ITI distribution as the previous condition (i.e., during training, pigeons experienced a distribution with an average ITI of 10 seconds, while testing had a distribution of ITI averaging 5 seconds). Another distinction was that during testing, S2 choices were only reinforced after trial 40. This was to guarantee that pigeons that used counting to predict the reversal were not affected by the possibility of reinforcements before trial 40 resulting in competing cues; also, pigeons that used timing were not affected by this change, because for them the reversal was expected to happen later into the session (around trial 80).

Condition 5–10 (II):

After completing the test sessions in condition 10–5 (I), the same group of pigeons now started a condition with the same characteristics of training and testing as condition 5–10 (I).

Condition 10–5 (II):

After completing the test sessions in condition 5–10 (I), the same group of pigeons now started a condition with the same characteristics of training and testing as condition 10–5 (I).

Data Analysis

For each condition, we plotted the average psychometric function with proportion of S1 choices plotted against trial number for the last session of training and the first session of testing. To calculate which trial corresponded to the PSE of each pigeon, we fitted a cumulative Gaussian curve with two free parameters (mean and standard deviation) to the psychometric functions of each subject using the least-squares method and the mean parameter as the PSE. For subjects where the Gaussian curve could not be fitted (due to the psychometric function not crossing 50%), the PSE was not estimated. Psychometric functions where the Gaussian curve fit the data poorly ($R^2 < 0.5$) were truncated after trial 80, and a second fitting was performed to check if it was improved. An order analysis was performed to verify if the order of the conditions made a difference (e.g., 5–10 (I) vs. 5–10 (II)). Another order analysis for the test sessions (first test session vs. second) was performed to see if the second session of the test was significantly different from the first. Besides PSE comparisons, we also compared when in the session those PSEs occurred. We also analyzed the ratio for trial- and time-based PSEs with a 95% Confidence Interval, using the *t* distribution.

All statistical tests were conducted with the Jamovi software for Windows (version 2.3.21), with the Type-1 error rate set to 0.05. For order analysis, we performed repeated-measures ANOVAs. For PSE

and time comparisons between training and test we conducted paired-samples *t* tests with the standardized Cohen's *d* for effect sizes (*dz*, e.g., Cohen, 1988, p. 48; Lakens, 2013).

Results

Testing was run for two sessions, and a repeated measures ANOVA, for one of the groups [5–10 (I)], showed a significant main effect of test (two levels), $F(1, 5) = 17.09$, $p = 0.009$. Due to this difference, suggesting that performance on the second test session could have been affected by the first test session, we only considered the first test session for the analysis of all conditions. To make the comparisons between training and test sessions equivalent, we used only the last session of training.

To increase the sample size, all 12 pigeons did both conditions (5–10 and 10–5), by doing this, we could compare 12 subjects in condition 5–10 with 12 subjects in 10–5. In the following analysis of the conditions, this grouping was not implemented due to both groups having during test significant main effects of order and interaction in a repeated measures ANOVA with order (2 levels) and subjects (12 levels): conditions 5–10 (I) vs. 5–10 (II) main effect of order, $F(1, 10) = 5.08$, $p = 0.048$, and interaction, $F(23, 230) = 1.70$, $p = 0.027$. Conditions 10–5 (I) vs. 10–5 (II) main effect of order, $F(1, 10) = 9.69$, $p = 0.011$, and interaction, $F(23, 230) = 3.67$, $p = 0.011$. As the groups were not combined, we analyzed each condition and order group separately.

The figures show the average psychometric functions of the last session of training and the first session of testing. To group the training sessions of Conditions 5–10 (I and II) we compared the PSEs of the training sessions with an independent samples *t* test, revealing that the conditions were not statistically different, $t(10) = -1.77$, $p = 0.107$, $d_z = -1.02$. The same was done for Conditions 10–5 (I and II), also revealing not to be statistically different, $t(10) = -0.647$, $p = 0.532$, $d_z = -0.374$. Therefore, the training curves in Fig. 1 and Fig. 2 have the average training functions of the order groups I and II.

Condition 5-10 (I)

Pigeons required from 20 to 40 training sessions (average = 27.83). Fig. 1 shows the average proportion of responses to S1 in the training and testing phases; each point represents a block of five trials (for individual functions see Fig 3, Appendix). Initially, the Gaussian curve was not a good fit for pigeons PG39, PG29, and PG47 during the test phase ($R^2 < 0.5$). This could be due to the variability of responses after trial 80, which were not seen during training, possibly producing some generalization decrement after such trial. Since trials after trial 80 are not especially important, we truncated the function at such trial, producing a Gaussian curve that had a better fit to the data; therefore, for this condition,

Fig. 1 only shows responses until trial 80. Table 1 shows the PSEs of the last training session and test, as well as the time into the session where the PSE trial occurred (the PSEs for subjects PG39, PG29, and PG47 were calculated by cutting the data after trial 80). In the last session of training, the average PSE was at trial 37.69 – approximately 223 s into the session. In the test session, with an ITI twice as long, the average PSE was at trial 30.11 – approximately 334 s into the session. A paired sample *t* test showed that the PSEs during the test phase differed significantly from the PSEs during the training phase, $t(5) = 3.95$, $p = 0.005$, $d_z = 1.61$. A paired sample *t* test showed that the time the pigeons switched preferences from S1 to S2 differed from training to testing, $t(5) = -5.79$, $p = 0.002$, $d_z = -2.36$.

The use of a timing strategy predicts a trial-based ratio close to 0.5 and a time-based ratio close to 1. Table 1 shows that the values do not seem to follow strictly a timing account, with trial-based ratios averaging 0.8 and 95% CI [0.7, 0.9] and time-based ratios averaging 1.5 and 95% CI [1.3, 1.7]. PG29 had an interesting performance, with the PSE of both training and test being close to each other (35 for training and 34 for test), while the time where the PSE occurred for training was almost 2 times less than the test (194 s for training and 360 s for test). These results are close to what is expected when the reversal is predicted by counting trials.

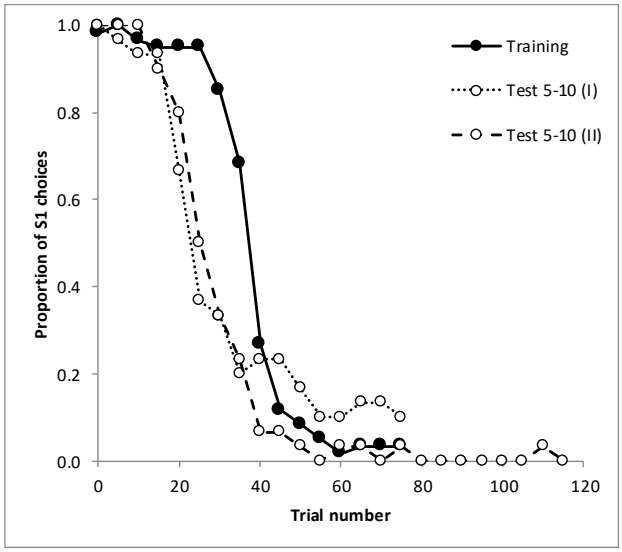
Condition 5-10 (II)

For the pigeons that ran this condition after completing Condition 10–5 (I), training ranged from 20 to 21 sessions. Fig. 1 shows the proportion of S1 choices across trials in training and test phases (for individual functions see Fig 4, Appendix). The average PSE of training was at trial 41.10 – approximately 244 s into the session. in the test session, similarly to condition 5-10(I), the average PSE was at trial 29.27 – approximately 307 s into the session. A paired sample *t* test showed that the moment of the switch of preference from S1 to S2 was significantly different from training to test sessions, $t(5) = 4.18$, $p = 0.004$, $d_z = 1.71$. An analysis of the time when this switch occurred revealed that it was not significantly different in training versus testing, $t(5) = -2.11$, $p = 0.089$, $d_z = -0.861$.

The ratio analysis showed that pigeons here opted for a strategy closer to timing in comparison with group order I. With an average trial-based ratio of 0.72 and 95% CI [0.5, 0.9] and an average time-based ratio of 1.27 and 95% CI [0.9, 1.6]. In this condition, one subject (P234) also seemed to follow a counting strategy with a trial ratio of 1.02 and a time ratio of 1.76.

Figure 1

Average psychometric functions of the last session of training (average of the last training session of both conditions) and the first test session of conditions 5-10 (I and II)



Note. The psychometric function of the test phase of Condition 5–10 (I) stops at trial 80 because of the necessity to cut the function at this trial in order to calculate the PSEs of three pigeons (PG39, PG29 and PG47).

Condition 10-5 (I)

The pigeons required from 20 to 37 sessions to complete training (average = 24.83). The response functions in Fig. 2 present the average proportion of S1 choices across training and test phases (for individual functions see Fig 5, Appendix). For pigeons P449 and P588, the fitting of a Gaussian curve was not possible because the psychometric function never crossed 50%; therefore, the PSEs of these subjects were not calculated. The average PSE of training was at trial 43.87 – approximately 469 s into the session. In test, when the ITI was halved, the average PSE was at trial 89.84 – approximately 550 s into the session. The average PSEs of training and test differed significantly, $t(3) = -6.95$, $p = 0.003$, $d_z = -3.47$. The average time when the PSEs occurred in training and test was not statistically different, $t(3) = -2.08$, $p = 0.129$, $d_z = -1.04$.

For Conditions 10–5, the expected trial-based ratio for the adoption of a timing strategy is 2 and the time-based ratio is 1. The average performance appears to follow a timing strategy, with a trial-based ratio of 2.10 and 95% CI [1.7, 2.5] and a time-based ratio of 1.2 and 95% CI [1, 1.4].

Condition 10-5 (II)

The pigeons needed 20 to 35 sessions to complete the training requirement (average = 24.16). Fig. 2 shows the proportion of choices of S1 across trials in training and test (for individual functions see

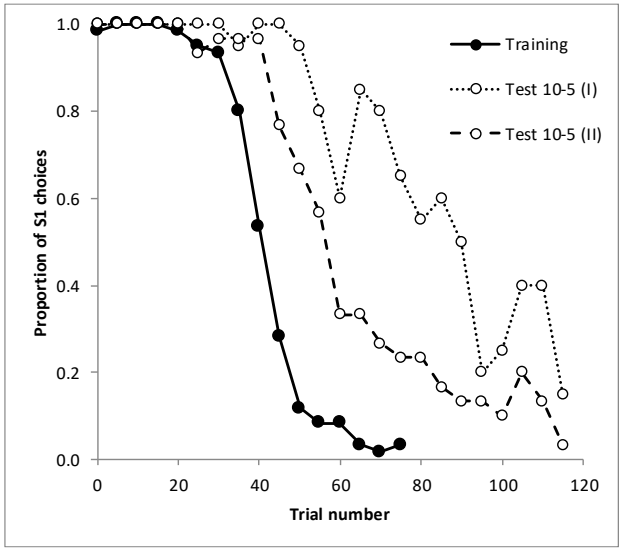
Fig 6, Appendix). Pigeon P960 stopped responding after trial 37, which happens before the task reversal. Since this stoppage could interfere with the timing strategy (assuming it was following a timing cue), we decided to eliminate this test session and run another test session the next day. Therefore, for this pigeon, the time and trial in which it switched preferences from S1 to S2 were calculated based on this second session.

Contrary to condition 10-5 (I), the PSE in test occurred much earlier (trial 66.25), with responses in S1 being close to 0 after trial 80. The average PSE of training was at trial 43.05 – around 479 s into the session. The average PSE of the test was at trial 66.25 – around 408 s into the session. The PSEs from training and test differed significantly, $t(5) = -2.56$, $p = 0.025$, $d_z = -1.04$. The time when the PSE happened in training and testing did not differ, $t(5) = 1.39$, $p = 0.224$, $d_z = 0.566$.

The ratio analysis showed that, similarly to condition 5–10 (I), pigeons did not strongly follow a timing strategy. The trial-based ratio was, on average, 1.54 with 95% CI [1, 2.1], while the time-based ratio had an average of 0.84 with 95% CI [0.6, 1.1]. The individual analysis suggests that pigeons P458 and PG39 had strategies that resembled a counting rule, with trial-based ratios close to 1 while time-based ratios were close to 0.5.

Figure 2

Average psychometric functions of the last session of training (average of the last training session of both conditions) and the first test session of conditions 10-5 (I and II)



Note. The psychometric function of the test phase of Condition 10–5 (I) does not include pigeons P449 and P588.

Table 2

Individual PSEs and time estimates for the last training session and the first test session for Conditions 5-10 (I), 5-10 (II), 10-5 (I) and 10-5 (II)

	Condition 5–10 (I)						Condition 10–5 (II)					
	Trial			Time (s)			Trial			Time (s)		
Pigeon	Train	Test	Ratio	Train	Test	Ratio	Train	Test	Ratio	Train	Test	Ratio
P283	36	27	0.75	212	270	1.27	42	56	1.35	456	340	0.75
P458	35	29	0.82	195	307	1.57	45	52	1.15	478	302	0.63
P960	40	27	0.68	241	316	1.31	42	65	1.54	462	397	0.86
PG39	43	39	0.91	275	444	1.62	41	47	1.13	467	301	0.64
PG29	35	34	0.97	194	360	1.85	45	70	1.55	478	408	0.85
PG47	38	25	0.66	219	306	1.40	43	109	2.50	534	701	1.31
Avg.	37.69	30.11	0.80	223	334	1.50	43.05	66.25	1.54	479	408	0.84
Std.	3.06	5.28	0.12	30.78	61.35	0.22	1.75	22.45	0.51	28.19	150.67	0.25
95% CI $\begin{cases} LL \\ \square \\ UL \end{cases}$	34.5 40.9	24.6 35.7	0.7 0.9	190.4 255	269.5 398.3	1.3 1.7	41.2 44.9	42.7 89.8	1 2.1	449.3 508.5	250.1 566.4	0.6 1.1

	Condition 10–5 (I)						Condition 5–10 (II)					
	Trial			Time (s)			Trial			Time (s)		
Pigeon	Train	Test	Ratio	Train	Test	Ratio	Train	Test	Ratio	Train	Test	Ratio
P449	48	-	-	513	-	-	38	19	0.50	213	189	0.89
P456	45	88	1.95	487	531	1.09	43	33	0.78	260	385	1.48
P902	42	107	2.56	444	649	1.46	42	31	0.75	237	324	1.37
P918	43	76	1.75	473	483	1.02	42	25	0.61	259	277	1.07
P234	41	88	2.13	445	541	1.22	37	37	1.02	216	380	1.76
P588	43	-	-	455	-	-	47	30	0.64	281	291	1.03
Avg.	43.87	89.84	2.10	469.5	550.9	1.20	41.10	29.27	0.72	244.2	307.8	1.27
Std.	2.55	13.03	0.35	27.34	70.15	0.19	3.59	6.48	0.18	27.03	73.20	0.33
95% CI $\begin{cases} LL \\ \square \\ UL \end{cases}$	41.2 46.5	76.2 103.5	1.7 2.5	440.8 498.2	477.3 624.5	1 1.4	37.3 44.9	22.5 36.1	0.5 0.9	215.9 272.6	231 384.6	0.9 1.6

Note. The PSEs (and consequently time) of pigeons PG39, PG29 and PG47 in Condition 5-10 (I) were calculated based on a 80 trial test session. PSEs of pigeons P449 and P588 could not be estimated because the psychometric function never crossed 50% (the indifference point).

Discussion

The purpose of the present study was to reduce the generalization decrement from the training to the test phase in a midsession reversal task. Previous studies showed that the use of time to predict the switching point of the task was the strategy primarily adopted by pigeons. This conclusion comes with some issues because if pigeons were solely using time to predict the reversal, when the ITI was doubled or halved in test, the trial where they should be indifferent to choosing S1 or S2 should also be doubled or halved. Previous results consistently showed an asymmetry between the conditions, with the psychometric curve being close to the expected values for the doubled ITI condition but not for the halved. Soares et al. (2023) and Machado et al. (2023) fixed this problem by controlling for competing cues that could be happening in the halved ITI condition. Our study applied the same manipulation as well as making the ITI variable in both training and testing. By controlling for competing cues and reducing the generalization decrement of the task, we expected the results to show more consistent patterns of pigeons who adopt a timing strategy.

In an MSR task with 80 trials, it is expected that the point of subject equality (PSE) will be around trial 40 for training, trial 20 for Condition 5–10 and trial 80 for Condition 10–5 in testing. Controlling for competing cues has already been demonstrated to be a good way to observe an almost exclusively use of a timing strategy by pigeons, with PSEs going to trial 25.3 for condition 5–10 and to trial 75.4 for condition 10–5 (Soares et al., 2023). In our experiment, besides controlling for competing cues, pigeons learned the task in a 5 s variable ITI and were tested in a 10 s variable ITI (Conditions 5–10), or vice versa (Conditions 10–5). Our results showed that pigeons still adopt a timing strategy in a MSR with variable ITIs, with the psychometric functions in testing going to the expected directions (to the right of the training function for Conditions 10–5 and to the left of the training function for Conditions 5–10). Although the functions go to the expected directions and suggests the use of timing, by making the ITI variable we may have introduced other complications to the task, since the average PSEs obtained were further from the expected values in comparison with the results obtained by Soares et al. (2023) – trials 30.11 and 29.27 for Conditions 5–10 (I and II respectively) and trials 89.84 and 66.25 for Conditions 10–5 (I and II respectively).

A possible explanation for the results being further away from the expected values is that with a variable ITI, the timing of the task becomes harder to estimate than when the ITI has a fixed duration. Previous studies showed that pigeons manage to time simultaneously two different intervals in a session (e.g., Plowright, 1996; Vieira de Castro and Machado, 2010). Therefore, in the MSR, to estimate the

moment of the reversal, the pigeons could count the duration of the session as a whole, count (or sum) the different sections of the task (in this case, the ITI) or count both simultaneously. If pigeons consider each section of the task to estimate the reversal, in a fixed ITI condition, the measure of the ITI should be effortless after a few trials. With variable ITIs, each trial has a different duration, so considering each section of the task should demand a higher level of attention. As the time estimates of the reversal in testing was worsened in our manipulation, it seems that the pigeon considerer discrete sections of the task in order to make its estimation.

With the time of the session being harder to estimate, searching for other cues that could help predict the reversal should be a better strategy. Some studies suggest that the midsession reversal task with shorter ITIs results in better performance by pigeons, with the argument that there is a shorter interval between trials, allowing the animal to remember the previous outcome and use that information for their next choice (Rayburn-Reeves et al., 2013; McMillan et al., 2014). Rayburn-Reeves et al. (2013) had pigeons in a midsession with 1.5 s of ITI, and their performance resembles a win-stay/lose-shift strategy (i.e., the outcome of the previous trial was the most salient cue). Regular midsession procedures use longer ITIs, usually 5 to 10 seconds (as was the average values used in our procedure), and the usual result is the adoption of timing to predict the reversal. Previous studies also proposed that, in the MSR, time is not the only strategy being followed (McMillan and Roberts, 2012). Assuming that pigeons can use multiple strategies simultaneously, we can view the previous assumption as a spectrum, where with an ITI of 1.5 s pigeons use mostly the trial-outcome cue to change from S1 to S2 and as we increase the time of the ITI pigeons will progressively opt for the timing strategy, because the trial-outcome cue becomes less salient. Applying this view to our results, we should see subjects in both Conditions using timing, but pigeons in Conditions 5–10 (assuming that the strategy adopted in training is the one used in the test) should put more weight on the outcome of the previous trial than in Conditions 10–5. One way to check this account is by the ratio of the PSE in training to the PSE in testing; ratios closer to 1 should demonstrate a stronger importance given to the trial-outcome cue (or the use of counting). This is verified in our results, where Conditions 5–10 have log ratios of the PSE closer to 1 (-0.22 and -0.33 for I and II respectively) than Conditions 10–5 (0.43 and 0.74 for I and II respectively).

In testing, all responses were reinforced after trial 40 for conditions 10–5 and after trial 20 for conditions 5–10. This nondifferential reinforcement could be the reason why the PSEs could not be estimated for 2 pigeons in Condition 10–5 (I), since both pigeons stuck to choosing S1 throughout the whole session, suggesting that they followed reinforcement contingencies. In Condition 5–10 (I), the PSE

could not initially be estimated for 3 pigeons, arguably for the same reason, but leading to different patterns of response (with pigeons not having a preferred sample after trial 80). The different pattern may be due to the reversal in Condition 5–10 occurring much earlier in the session (trial 20 for pigeons that use timing), thus the nondifferential reinforcement seemed to initially not be a problem, but started to be after trial 80, since when cutting the psychometric function after that trial we were able to estimate the PSE.

An interesting result was the order effect observed between the order groups I and II for both 5–10 and 10–5 conditions. Analyzing the amount of training required to first meet the 80% correct criteria for 3 consecutive days, we see a big difference in the order in which the task was done. Pigeons who were in Condition 5–10 (I) also did Condition 10–5 (II); the criteria for order group I was first met on average after 24 sessions, while for order group II, it was first met on average after 11 sessions. The decrease in the number of sessions where the criteria was first met also happened for Conditions 10-5 (I) and 5-10 (II), where the average number of sessions was 17.17 for order group I and 5.33 for order group II, also being less than half. Assuming that it is harder to time a session with a variable ITI, the faster speed of learning the training phase in order groups I could be an indicator that the pigeons initially had some trouble developing a strategy, but after enough training, the strategy adopted is transferred to other durations of the task (either doubling or halving the session).

In summary, our aim was to mitigate the impact of generalization decrement when changing ITI duration in a MSR task. We hypothesized that by introducing a variable ITI, we could achieve PSEs that align more closely with the theoretical values of pigeons relying on timing as their primary cue for transitioning from S1 to S2. However, in attempting to mitigate generalization decrement effects, we may have introduced other complexities to the procedure. Specifically, time estimation of the session could have become more challenging, thereby complicating the adoption of a timing strategy, or introducing more estimation errors. Interestingly, despite the potential difficulty in time estimation with variable ITIs, it seems that pigeons still use this cue to estimate the reversal but also consider others, perhaps more salient at some points of the session (i.e., the outcome of previous trials or counting).

Data availability

All data are available at: https://doi.org/10.34622/datarepositorium/KYIUIK. This study's design and data analyses were not preregistered.

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Appendix

Table 3

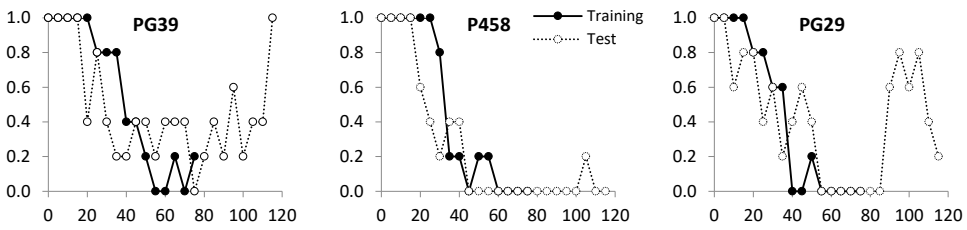
Distribution of the ITIs presented in training and testing for conditions with an average of 5 s and 10 s

5 s ITI distribution	10 s ITI distribution
3.05	3.18
3.16	3.55
3.27	3.94
3.39	4.35
3.51	4.79
3.64	5.25
3.79	5.75
3.94	6.29
4.11	6.88
4.29	7.51
4.49	8.21
4.71	8.99
4.96	9.87
5.25	10.87
5.58	12.05
5.99	13.46
6.49	15.22
7.17	17.60
8.22	21.27
10.99	30.97

Note. The ITI distribution comprises 20 values. During training, these 20 values were presented in a completely random order. Once all values had been shown, the same set of 20 values was reshuffled and presented again, with this cycle repeating 4 times per session, resulting in 80 trials. The testing phase followed the same procedure, but the set of 20 values was repeated 6 times per session, totaling 120 trials.

Figure 3

Individual psychometric function for pigeons in Conditions 5–10 (I)



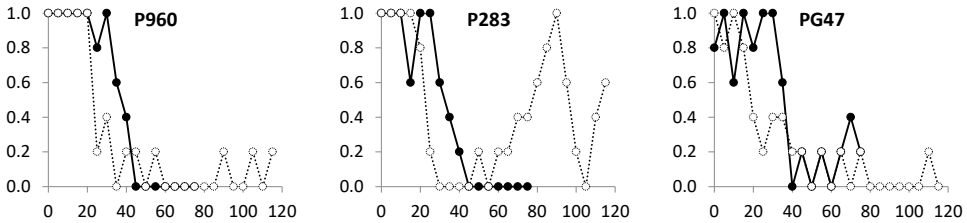


Figure 4

Individual psychometric function for pigeons in Conditions 5–10 (II)

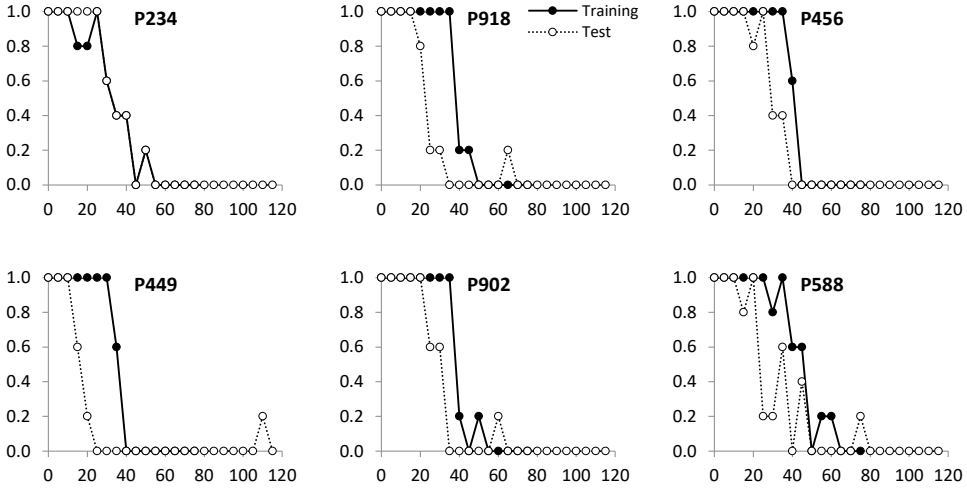


Figure 5

Individual psychometric function for pigeons in Conditions 10–5 (I)

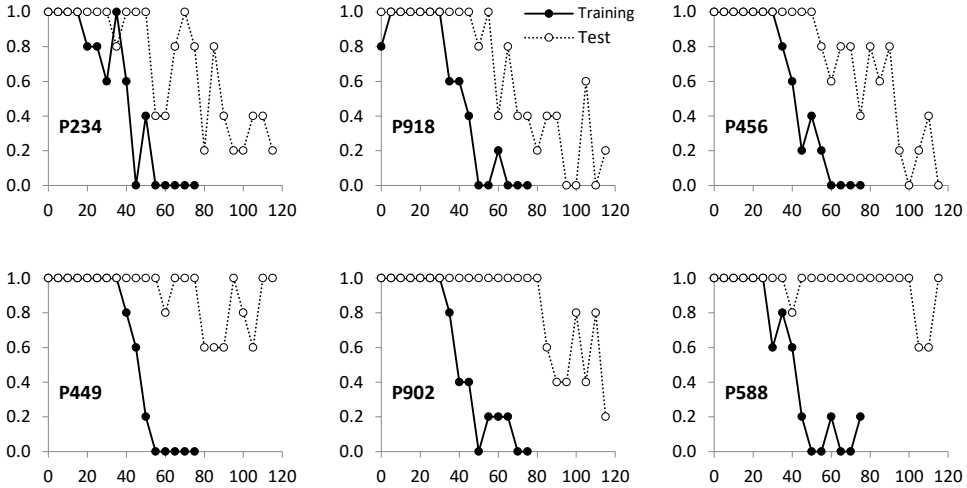
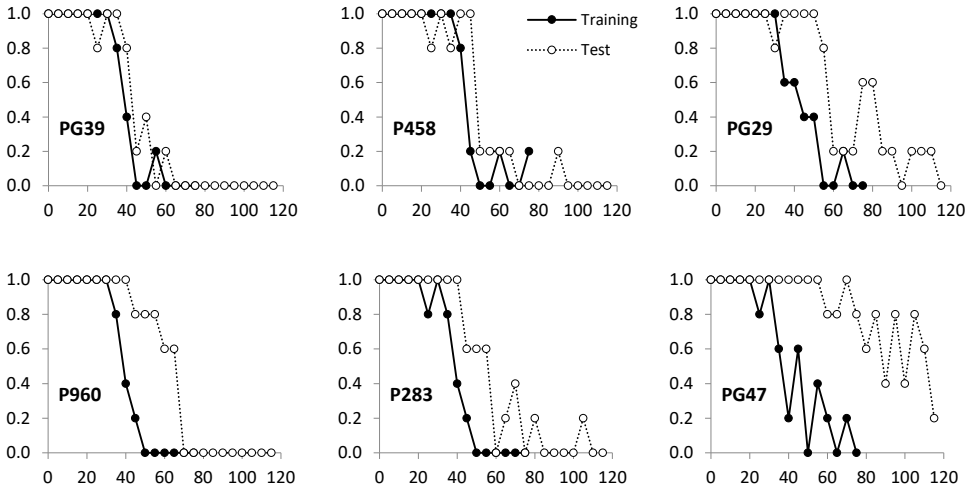


Figure 6

Individual psychometric function for pigeons in Conditions 10–5 (II)



Declaração do orientador acerca da Comissão de Ética

Clarificação sobre parecer da Comissão de Ética

A presente tese ("Unveiling the usage of time: Exploring pigeons' temporal strategy in the midsession reversal task") fez parte de um projeto de investigação intitulado "Comportamento animal e adaptação ao ambiente: discriminação temporal, escolha e raciocínio causal" que, por se tratar de um trabalho que envolveu participantes não-humanos, não é do âmbito da Comissão de Ética para a Investigação em Ciências Sociais e Humanas (CEICSH), tendo sido submetido e aprovado internamente pela Subcomissão de Ética para as Ciências da Vida e da Saúde (SECVS; documento SECVS 044/2017) e externamente pela Direção Geral de Alimentação e Veterinária (DGAV; autorização #024946). De acordo com o Decreto-Lei n.º 113/2013 de 7 de agosto, a autorização legal de projetos de investigação/experimentação animal é feita pela DGAV.

O Orientador,

Assinado por: **CARLOS ANDRÉ RIBEIRO OLIVEIRA PINTO**
Num. de Identificação: 15745089