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Evidence of non-circadian timing in a low response-cost daily Time-Place Learning task with pigeons *Columba Livia*

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ABSTRACT

Previous research has shown that rats require high response cost in order to display circadian timing in daily Time-Place Learning (TPL) tasks. For many possible reasons, no explicit effort to explore the effects of response cost on the performance of other species in these tasks has been made. Therefore, the present paper explores the effects of response cost on pigeon's performance on a daily TPL task. Head entry responses were reinforced according to a Random Interval schedule of reinforcement on one feeder during morning sessions and on another feeder during afternoon sessions. Feeders were located 8 cm apart for one group of birds (Group Near) and 56 cm apart for another group (Group Far). After 50 training sessions, testing began. Test sessions consisted of skipping either the morning or the afternoon session. Results show that most birds in the near group respond primarily on the opposite feeder during the first 20 s of the test sessions and then they switch to the correct feeder. On the other hand, most birds in Group Far respond at the same rate on both opposite and correct feeders during 20 s, and then they respond primarily on the correct feeder. The possibility of these data revealing non circadian timing for birds in a low response-cost daily TPL task is discussed along with the implications of such a finding for previous literature that claims that this type of performance could be unique to rats.

1. Introduction

Time-Place Learning (TPL) has been conceived as the ability to find and exploit resources with limited temporal and spatial availability (Crystal, 2009). Of course, the evolutionary advantages implied in the ability to anticipate the location and duration of biologically significant events cannot be overstated (Gallistel, 1990; Wilkie, 1995). This can be supported by the fact that a wide variety of species such as pigeons (Wilkie and Wilson, 1992; Saksida and Wilkie, 1994; Garca-Gallardo and Carpio, 2016), rats (Carr and Wilkie, 1997a, 1999; Means et al., 2000a), fish (Gmez-Laplaza and Morgan, 2005; Barreto et al., 2006; Almeida and Luchiari, 2016; Almeida et al., 2017), garden warblers (Biebach et al., 1989, 1994), bees (Breed et al., 2002; Murphy and Breed, 2008) ants (Schatz et al., 1994), mice (Van der Zee et al., 2008; Mulder et al., 2013) and hummingbirds (Tello-Ramos et al., 2015), have been shown to display TPL under different circumstances.

A TPL task is defined by two key features: 1) There is more than one available resource location (i.e. a place where a given resource can be obtained). 2) There is a temporal criterion according to which the correct place changes (Wilkie, 1995; Crystal, 2009; Mulder et al., 2013).

TPL tasks are regularly considered to be of one of two kinds: 1) *Daily TPL*. Food, or any other biologically significant resource, can be obtained for responses in one location at a time, with the correct place changes according to the time of day (e.g. Biebach et al., 1989; Saksida and Wilkie, 1994; Carr and Wilkie, 1997a; Delicio and Barreto, 2008) 2) *Interval TPL*. It is just like daily TPL, with the exception that the correct place changes within minutes or seconds since the start of each session (e.g. Carr et al., 2001; Thorpe et al., 2002; García-Gallardo et al., 2015, 2018).

A widely accepted view of performance of animals when faced with a TPL task is that there are a number of different strategies that they could potentially use to solve it (Wilkie, 1995; Crystal, 2009; Mulder et al., 2013). For instance, in an interval TPL task that awards food for responses on one of four levers according to a fixed sequence, a rat could respond on lever 1 while it provided food and stop responding there when no more food could be obtained on that lever (i.e. A win/stay – lose/shift strategy). However, the overwhelming evidence in the

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field suggests that this is rarely the case. Instead, when faced with an interval TPL task, most species show evidence of anticipating depletion of food in the current location, and anticipating availability of food in the following location, which is usually interpreted as evidence of an interval timing strategy (e.g. Wilkie and Wilson, 1992; Carr and Wilkie, 1998; Carr et al., 2001; Thorpe and Wilkie, 2002; Garca-Gallardo and Carpio, 2016). An interesting finding in this regard comes from the use of a related task: The Mid Session Reversal (MSR) task (Cook and Rosen, 2010; Rayburn-Reeves et al., 2011; McMillan et al., 2016). A MSR task consists of arranging a particular contingency of reinforcement (i.e. a simple discrimination) that is reversed after a fixed number of trials every session (Rayburn-Reeves and Zentall, 2013; Rayburn- Reeves and Cook, 2017; Rayburn-Reeves et al., 2017). For instance, a bird could be faced with a red + /green- discrimination for 40 trials and then face a red-/green + problem for the remaining 40 trials of each session. The particularly interesting finding in this field is that evidence suggests that bird´s allocation of responses is typically controlled by the elapsing of time (not the availability of reinforcement), while rats, humans and primates rely on immediate situational cues (i.e. whether reinforcement was obtained last trial) in order to allocate their responses (Rayburn-Reeves et al., 2013; Stagner et al., 2013; McMillan et al., 2014).

On the other hand, a common finding on daily TPL task is the temporal regularity of behavior organized around the time of day, which has been suggested as evidence of circadian timing under these conditions (Biebach et al., 1989, 1994; Saksida and Wilkie, 1994; Gmez-Laplaza and Morgan, 2005).

An early example of a daily TPL task which produced performance that could be described as circadian timing is that of Biebach et al. (1989). In their task, a garden warbler could obtain food for entering in one of four rooms every trial, the correct room (i.e. the one where food could be obtained) changed every three hours. They found that birds obtained high percent correct choices. After training, they ran a series of test sessions, during which food could be obtained at any room each trial; the rationale was that, if birds were following a Win/stay – Lose/shift strategy, they would never stop choosing option 1 during these test trials; on the other hand, if birds were responding according to a Time-Place association, they should visit the feeding places in the same fashion as they did during training. They found the latter scenario to be true, leading them to the conclusion that some sort of Time-Place Learning was in effect.

Of course, Biebach et al (1989) entertained the possibility that circadian timing was not the only viable explanation for their birds' performance. They also considered the possibility of their birds responding to the order in which the feeders provided food (ordinal timing) or an hourglass-like mechanism (Interval timing). More consistent evidence for the circadian hypothesis came from a subsequent study from their laboratory. Biebach et al. (1991) reported an experiment explicitly designed to test the timing mechanism involved in daily TPL. After a training procedure much like the one described above, they used one of two phase shifts for each subject: forwarding the cycle by six hours, or delaying it by the same amount of time. If birds were using an interval based timing mechanism, they should adjust the visiting pattern (forward or backwards) completely; if, on the other hand the mechanism relies on circadian rhythms, then no such adjustment should be observed. They found the latter possibility to be true, for none of their birds forwarded or delayed the pattern of room visits.

Wilkie and his colleagues developed a different training method to explore daily TPL that allowed them to conduct different types of testing (Wilkie and Wilson, 1992; Saksida and Wilkie, 1994; Carr and Wilkie, 1997a,b, 1999). One example of such training and testing was carried by Saksida and Wilkie (1994), who conducted an experiment to test whether pigeons could also display daily TPL. They exposed 4 pigeons to a design in which pecks on one of two keys provided food according to a Variable Interval (VI) schedule of reinforcement on morning sessions, and pecks on the other key provided food according to the same schedule during afternoon sessions. These birds quickly began responding mostly on the correct key for each type of session, then testing began. One test consisted of skipping either the morning or the afternoon session and recording where the pigeon pecked. They found that pigeons still restricted the majority of their responses to the temporally correct key, despite the obvious fact that no reinforcement was available during these tests.

The second test they conducted was displacing the temporal location of the morning and afternoon sessions, either bringing them closer together or farther away. The rationale of this test is that if birds are responding according to an ordinal strategy, they should not be affected by this manipulation, because the order remains the same; on the other hand, if they respond according to a circadian or interval strategy (i.e. according to time of day, or time since a given event), then this test would generate a sensitive increase in the error rate. The authors found the latter case to be true.

The third test conducted by Saksida and Wilkie (1994) was to alter the light-dark cycle for the birds. If birds were using an interval strategy entrained to an event such as Lights on, then there should be a considerable immediate effect of this cycle change. On the other hand, since circadian timing is said to be endogenous and self-sustaining, the effect of this manipulation would have to be developed over time, as the oscillator becomes gradually entrained to the new light-dark cycle. The results were quite clear: There was no effect of the cycle change after 6 days of training. Taken together, the results from training and the three different testing suggests that a circadian strategy is the best option to describe the pigeon´s behavior under these circumstances.

Studies such as those reported above have lead to the overwhelming consensus that daily TPL tasks produce performance that can be accurately characterized as circadian timing for almost all species involved (Saksida and Wilkie, 1994; Gmez-Laplaza and Morgan, 2005; Van der Zee et al., 2008; Mulder et al., 2015). However, a considerable body of evidence suggests that rats do not fit this description (Carr and Wilkie, 1997a, 1999; Means et al., 2000a; Widman et al., 2000; Thorpe et al., 2003; Widman et al., 2004; Thorpe et al., 2012; Deibel et al., 2014).

An early example of failure to find circadian timing in daily-TPL with rats is a study published by Carr and Wilkie (1997a). They conducted an experiment in which rats could obtain food by pressing one lever on morning sessions and another during afternoon sessions according to a Variable Ratio (VR) schedule of reinforcement. They found that rats restricted the majority of their responses to the temporally correct lever; this would suggest that rats were showing TPL. However, they conducted several tests including skipping either the morning or the afternoon session; conducting interpolated sessions in the time between morning and afternoon sessions, and altering the light-dark cycle by leaving the lights on throughout the day. All of the results obtained with these tests pointed to the fact that rats were not relying on a circadian timing strategy, but rather an ordinal one. This result was rather odd, for many species so far were shown to readily use time-of day as a cue to find and exploit resources.

Carr and Wilkie (1999), designed an experiment like the one described above: Rats could obtain food for responses in one of two levers, according to a VR 16. The correct lever changed according to the time of day, so that responses on one lever would be reinforced during morning sessions and on the other during afternoon sessions. However, their study comprised three types of experimental days: 1. Morning only sessions. 2. Afternoon only sessions. 3. Morning and afternoon sessions. During training, all three types of experimental days were administered in a random fashion. This way, they encouraged the use of a circadian timing strategy. They found that, even under these circumstances, rats did not select the lever to press based on the time of day of the session, but rather, on an ordinal fashion. These two studies revealed that a non circadian strategy provides a better description for rat's behavior on TPL tasks, even when faced with conditions in which this strategy is not optimal. The apparent reluctance of rats to use circadian information to guide their choice on TPL tasks has caught the interest of many researchers for it could reveal important species differences in time-sensitivity between them and other species so far studied under TPL tasks (e.g. Thorpe et al., 2003, 2012; Deibel et al., 2014).

An extremely relevant study in this respect was that of Widman et al. (2000), who designed a study to assess the effects of response cost on daily TPL performance of rats in a vertical maze. They conducted a series of studies and they found that, when a low response cost is employed, rats do not rely on time-of-day in order to find and exploit food. However, when response cost is increased, rats start responding according to circadian timing hypotheses.

Increasing response cost for daily TPL tasks has been regarded as a necessary condition for the emergence of circadian timing during daily TPL tasks when using rats (Widman et al., 2000, 2004; Deibel and Thorpe, 2013). A recent example of a study designed under this assumption is that of Thorpe et al. (2012). They explicitly tested for strain differences in the performance of rats under a daily TPL Task. In their study, Long Evans (Experiments, 1,2,3) and Sprague Dawley (Experiment 4) rats had to climb one of four towers in a vertical maze in each of two daily sessions. The correct tower (i.e. the one on top of which food could be obtained) was different in morning and afternoon sessions. Thorpe et al. (2012) found that Long Evans rats were unable to learn the task, as evidenced by chance levels of performance under different conditions, while Sprague Dawley rats did solve the task, as suggested by a significantly above chance performance. The authors then conducted probe tests that, like Carr and Wilkies (1999) consisted of skipping either the morning or afternoon sessions. The rationale is that rats using circadian information to solve the task should still climb the temporally correct tower, while rats using an ordinal timer should climb the opposite tower (the one whose session was skipped). Their rats suffered a post-criterion decline in performance which precluded adequate testing for most of them, and, for those who were appropriately tested, one seemed to be using circadian timing and another seemed to be using ordinal timing. Thus, they found inconclusive evidence of the timing strategy that better described their subjects' performance.

Taken together, these studies have led to the growing consensus that daily time-place learning task is a situation that could reveal important differences between rats and other species (mostly birds) in terms of the mechanisms involved (Carr and Wilkie, 1997a, 1999; Means et al., 2000a, b; Thorpe et al., 2003; Thorpe and Wilkie, 2007; Cain et al., 2004; Deibel and Thorpe, 2013). In general, rats show circadian TPL when high response costs are programmed and fail to do so when low response costs are used. This is not a minor issue; since this general finding could imply that daily TPL task provide a useful experimental situation to explore species differences in animal behavior. However, it is noteworthy that, perhaps due to the relative ease with which birds seem to solve daily TPL tasks, no explicit effort to explore the effects of response cost on their performance in tasks like these has been made, and, while it is true that extensive evidence of circadian timing in daily TPL task with birds (Biebach et al., 1989; Falk et al., 1992; Saksida and Wilkie, 1994; Clayton and Dickinson, 1998), this could have been achieved by inadvertently setting conditions that represent high response costs when using birds as subjects. If this is shown to be true, then there would be a possibility that other species behaved like rats on TPL tasks. While there are a number of different ways to understand response cost: time or energy spent on visiting each feeding location, penalization for wrong responses, etc., the literature shows that increasing the energy expenditure necessary to visit each location, provides an adequate experimental treatment of response cost in TPL situations (e.g. Widman et al., 2000, 2004; Thorpe et al., 2012; Deibel and Thorpe, 2013). Two different scenarios can be foreseen by conducting an experiment assessing the effects of response cost in a daily TPL task when birds are used as experimental subjects: 1) Birds could solve the task and display circadian timing when tested under both low and high response costs. In this scenario, the long developing hypothesis of species differences in daily TPL between rats and birds would be strengthened. 2) Birds could solve the task and show non circadian timing, just as rats have done on previous studies. In this scenario, the species difference hypothesis should be revised and taken carefully, and the possibility that response cost plays a major role in TPL regardless of the species used should at the very least, be considered. Therefore the present paper was designed to provide an explicit test of the effects of response cost on the percent correct responses of pigeons in a daily TPL task.

2. Method

2.1. Subjects

Six experimentally naive Columba Livia pigeons were maintained at 70% of their free-feeding weight +/- 15 g. Birds were individually housed with free access to water in their home cages.

2.2. Apparatus

A Plexiglas experimental chamber 65 cm (wide) x 65 cm (long) x 33 cm (tall) was used, each wall had seven panels of 8 cm. Three feeders were mounted on each of three sides of the chamber (See Fig. 1). Head entry responses were recorded via an infrared beam mounted on each feeder. Also mounted on these feeders was a 5 W light bulb. Reinforcement consisted of 2 s. deliveries of mixed grain through an opening of 7 x 5.5 cm. Each feeder was placed 10 cm above the chamber floor. A 5 W light bulb placed on a One-Plane Readout Industrial Electronic Engineers INC response key was used as a houselight.

The experimental events were operated and recorded through a Lanix 506 computer, equipped with Med-PC II software that was

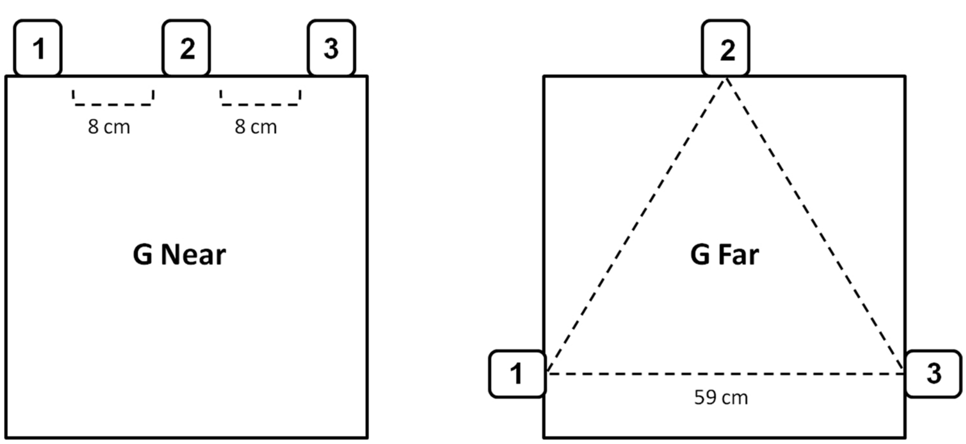

Fig. 1. Position of the feeders for each group.

connected to a Med-SG-6000C interface.

2.3. Procedure

2.3.1. Magazine training and shaping

Feeders were differentially arranged for each group. As seen on Fig. 1, for birds in Group Near feeders were all mounted on the same wall of the chamber and approx 8 cm. apart from each other. On the other hand, for birds in Group Far, each feeder was mounted on a different wall and at a rectilinear distance of 59 cm of each other. This difference in arrangements was kept constant throughout the entire experiment.

All Birds were exposed to magazine training sessions in which all three feeders were turned on since the beginning of the session. Once a bird ate from any given feeder, shaping of the head-entry response started on that feeder and the rest of them were turned off. After 5 responses were made on that feeder, reinforcement stopped and the bird had to respond on any other feeder. This phase was concluded once birds were reliably responding on all three feeders. These sessions had a maximum duration of 30 min. Birds took between 2 and 10 sessions to reach this criterion.

2.3.2. Continuous reinforcement and increasing random ratio schedule of reinforcement

Once birds were reliably responding on all three feeders, they were exposed to a Continuous Reinforcement (CRF) schedule of reinforcement for one session. During this session, birds could obtain up to 20 reinforcers for responses on each feeder (Max Total 60). The response requirement was then increased for the following sessions using a Random Ratio 2, 4, 6, 8 and 12 schedule of reinforcement, one session for each ratio, these sessions concluded when the subject obtained 60 reinforcers or after 30 min.

2.3.3. Training

During this phase, subjects received two sessions per day, seven days a week. Morning sessions were carried out between 11:05 and 12:45 h and afternoon sessions were conducted between 17:05 and 18:45 h. Each bird was introduced to the experimental chamber at the same hour each day. During training sessions, the first head entry response emitted by the subject turned on the house light and initiated all experimental events. Every Session started with a variable nonreinforced period (either 5, 10, 15, 20, 25, 30, 35, 40, 45, 50, 55 or 60 s long; this schedule is similar to a Random Interval 28 s) during which responses were recorded although they did not have any consequence. Responses made during these unreinforced periods are the primary data presented on the Results section, for as has been previously noted these responses show where birds tend to search for food in the absence of local availability cues (Saksida and Wilkie, 1994; Carr and Wilkie, 1997a, 1999). Once the nonreinforced period ended, responses were reinforced according to a Random Interval 20" Schedule of reinforcement (T = 4, p = .2) in only one of the feeders (i.e. *Correct Location*). Table 1 shows the Correct Location assignment for each bird for each type of session.

Table 1
Correct location and Time of day assignment for each bird.

Group	Bird	Correct location for Morning Sessions	Time of Day for Morning Sessions	Correct location for Afternoon sessions	Time of Day for Afternoon Sessions
Near	S1	Feeder 1	11:05	Feeder 2	17:05
	S2	Feeder 2	11:25	Feeder 1	17:25
	S3	Feeder 2	11:45	Feeder 3	17:45
Far	S1	Feeder 1	12:05	Feeder 2	18:05
	S2	Feeder 2	12:25	Feeder 1	18:25
	S3	Feeder 2	12:45	Feeder 3	18:45

Responses during training sessions were recorded according to the following code:

1 *Correct Responses*. Head entry responses made on the correct Feeder, i.e. the one in which responses are reinforced during the reinforced period for that session.
2 *Opposite Responses*. Head entry responses made on the Feeder that serves as the correct one for the opposite session (e.g. For S1 from Group Far a head entry response made to Feeder 2 and not to Feeder 1, during a morning session would be coded as an opposite response).
3 *Incorrect Responses*. Responses made to the Feeder that never serves as the correct one. (e.g. For S1 from Group Far, a response to Feeder 3 would be coded as an incorrect response).

Each bird completed a total of 100 training sessions (50 Morning and 50 Afternoon sessions) prior to testing.

2.3.4. Skipped session tests

Testing sessions were identical to those conducted during training with two main exceptions: 1) during testing, a fixed duration of 120 s for the nonreinforced period was implemented. The purpose of this change was to ensure time enough to collect a vast number of unreinforced responses. 2) The prior session was skipped. That is, before conducting a morning test session, the prior afternoon training session was not conducted; on the other hand, if an afternoon test session was to be conducted, the prior morning training session was skipped. A total of 5 morning tests and 5 afternoon tests were conducted for each bird. Testing sessions were separated by four regular training days (conducting both morning and afternoon sessions). The rationale behind this test was: If birds are relying on a circadian strategy to solve this TPL task, then they should respond primarily on the correct Feeder during test sessions, regardless of the skipped session. On the other hand, if birds were using a non circadian strategy, then their responses should be allocated on the opposite Feeder (i.e. the one that would have been the correct one during the skipped session).

3. Results

The first question that needs to be answered was whether birds were at all able to solve the task. Fig. 2 displays the percent correct responses for each subject in both groups in 10 session blocks for both Morning (Top Panel) and Afternoon (Bottom Panel) training sessions. Data for subjects in Group Near is represented by dotted lines and open markers, while data for Group Far by continuous lines and filled markers.

A clear increase in percent correct levels throughout the experiment is visible for all subjects, from near chance levels (33%) to near 90% correct in morning sessions, and 80% correct for afternoon sessions. The evident superposition of all lines in this plot suggests a lack of difference in the course of learning between groups. These impressions were confirmed by two Mixed Effects ANOVA's with Block as a within subjects factor and Group as a between subjects factor, one for morning sessions and one for afternoon sessions. The Morning Session Mixed Effects ANOVA revealed a significant main effect of Block, F (4, 16) = 7.23, p = .001. partial η^2 = .64, but no main effect of Group, F (1, 4) = 3.44, p = .13, nor interaction, F = (4, 16) = 1.77, p = .28. The same scenario holds true for the Afternoon Sessions ANOVA, a significant main effect of Block, F (4,16) = 4.10, p =.01, partial η^2 = .50 was obtained in the absence of both a significant main effect of group, F (1,4) = .56, p = .49, and interaction, F (4,16) = .36, p = .83. A small, but significant difference in performance can be noted between morning and afternoon sessions A mixed effects ANOVA with the Session Type as a within subjects factor and Group as a Between subjects factor revealed a significant main effect of Session Type, F (1,4) = 8.35, p = .04, partial η^2 = .67, but no main effect of group, F

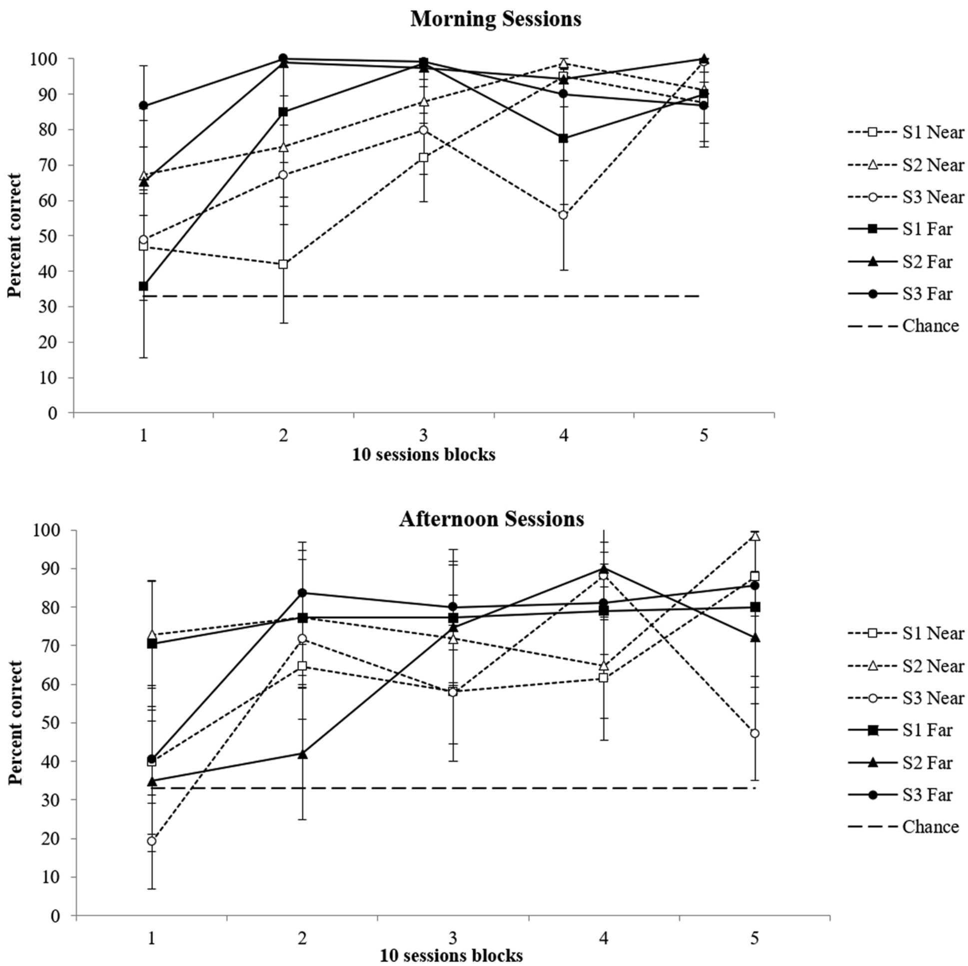

Fig. 2. Percent correct responses during training in 10 sessions blocks for each subject in both groups. Top Panel shows data for morning sessions, and bottom panel shows data for afternoon sessions. Open markers show data for Group Near, and filled markers show data for Group Far. The dashed line shows the expected chance level. Error bars represent the Standard Error of the Mean (SEM).

(1, 4) = 2.47, p = .19, nor interaction, F(1, 28) = .702, p = .44. This differences are to be expected considering that a widely established practice in previous literature was implemented for this study: establishing a six (plus minus one) hours interval between morning and afternoon sessions(e.g. Reeb, 1993; Saksida and Wilkie, 1994; Carr and Wilkie, 1997a, 1999; Widman et al., 2000; Thorpe et al., 2003; Gmez-Laplaza and Morgan, 2005; Thorpe and Wilkie, 2007; Thorpe et al., 2012; Deibel and Thorpe, 2013), thus rendering somewhat different motivational states in morning and afternoon sessions as a likely possibility. However, since performance in both types of sessions is well above chance for all subjects, this does not imply any major concerns for data analysis.

Overall, data from Fig. 2 shows that birds from both groups learned to solve the daily TPL task. However, these data do not allow differentiating between circadian timing and non circadian strategies. Therefore, Fig. 3 was obtained; this figure shows the average percent of correct, opposite and incorrect responses during the first 30 s of the non-reinforced period for morning and afternoon test sessions for each subject in both groups. A number of important facts must be noted on these figures: 1) there is a noticeable drop in percent correct responses, between training and testing for most subjects. This drop seems more noticeable in morning sessions, which go from around 90% in training (Fig. 2 Top Panel) to around 40% in testing (Fig. 3 Left Panel). The drop for afternoon sessions seems somewhat minor, from around 80% in training (Fig. 2 Bottom Panel) to around 55% in testing (Fig. 3 Right Panel). 2) While differences between subjects exist, there is an important pattern in these data: Percent Opposite responses are persistently higher for birds in Group Near than for birds in Group Far in both session types, on the other hand, the reverse is true for percent correct responses, these are overall higher for birds in Group Far. 3) 2 of 3 birds in Group Near obtained a higher percent opposite than correct responses in morning sessions while this is true for only 1 bird in Group Far, and, moreover, the magnitude of these differences are completely asymmetric: around 40% for the two birds in Group Near and around 10% for the one bird in Group Far. 4) although only one bird in Group Near shows a higher percent opposite than correct responses in afternoon sessions, this difference is extreme: 70%. On the other hand, none of the birds in Group Far obtained higher percent opposite than correct responses, although S2 Far obtained very similar scores. 5) Overall, percent correct responses is around 15% lower for birds in Group Near than for birds in Group Far, in both types of training sessions, although this difference is not statistically significant for Morning, t (4) = -.53, p = . .62, d = .43, but it is significant for Afternoon sessions, t (4) = -2.82, p = .048, d = .2.30. On the other hand, percent opposite responses are higher for birds in Group Near than those in Group Far, although, again, these differences were not statistically significant, t (4) = .085, p =. .93, d = .07, for morning sessions, and, t (4) = .20, p = .84, d = .17, for afternoon sessions. Overall, the data shown in Fig. 3 does not seem entirely conclusive, because although there is a clear reduction in percent correct responses between training and testing, which would suggest a non circadian strategy; correct responses are still well above chance levels for most birds in Group Far, which would suggest a circadian strategy, but not necessarily so for birds in Group Near. Moreover, the scores observed in this figure could be the

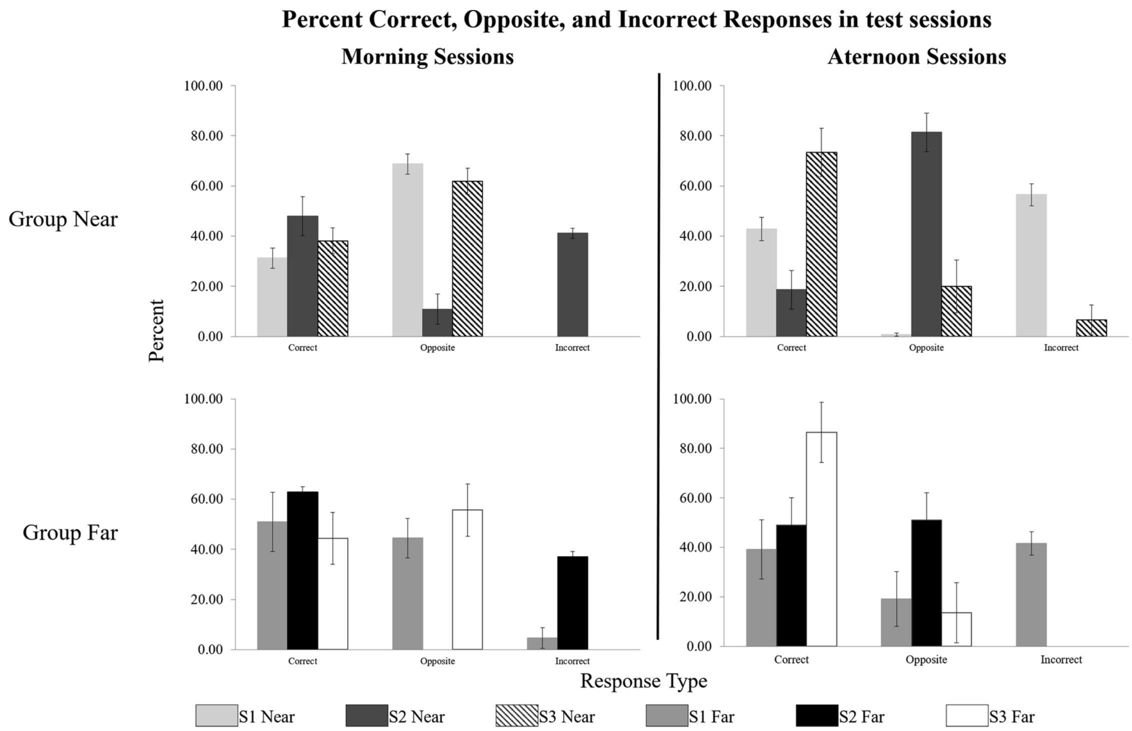

Fig. 3. Average percent correct, opposite and incorrect responses during both morning (left panel) and afternoon (right panel) for the first 30 s of test sessions for each subject in both groups. Error bars represent the SEM.

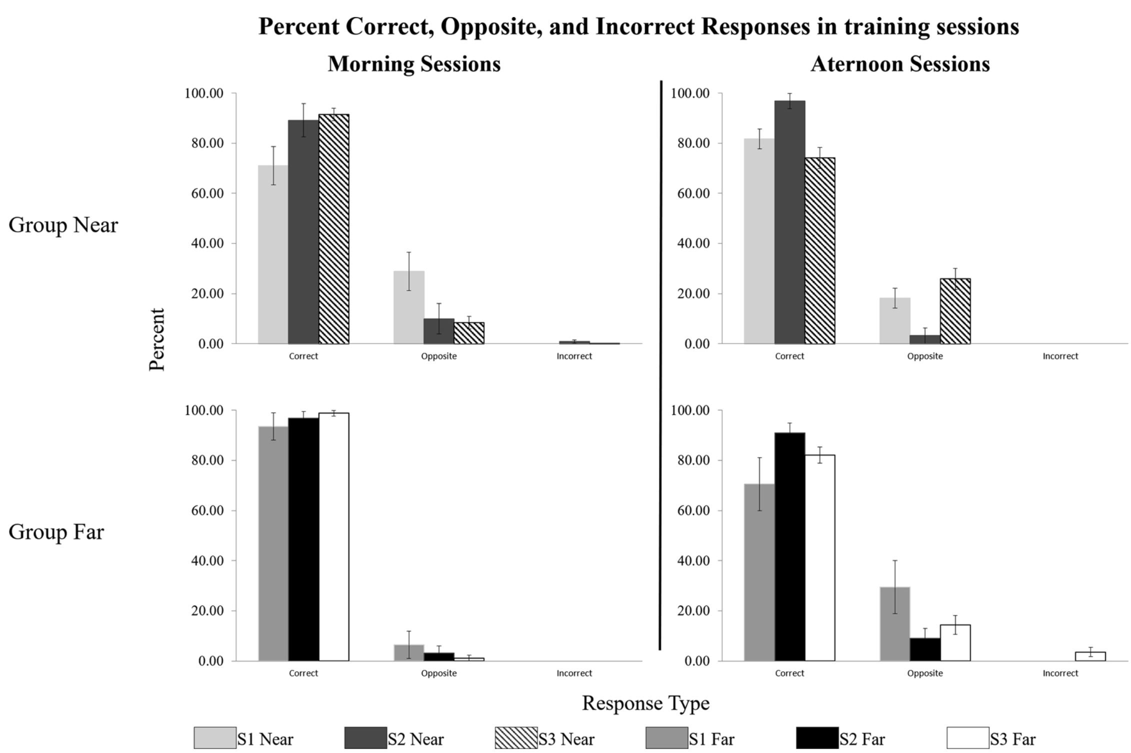

Fig. 4. Average percent correct, opposite and incorrect responses morning (left panel) and afternoon (right panel) for the first 30 s of the training sessions interspersed between test sessions for each subject in both groups. Error bars represent the SEM.

product of a generalized performance disruption due to the occasional skipping of a session. To discard this possibility, Fig. 4 was obtained. This figure shows the exact same data as Fig. 3, but for the training sessions that were interspersed with the testing session. As this figure shows, there is a clear difference between performance during training and testing, for all birds show above 70% correct responses in any type of session. Therefore, the results obtained during testing cannot be attributed to a generalized performance disruption.

Overall, Figs. 3 and 4 show that during test sessions, birds from both groups show a clear tendency to obtain increased percent opposite responses and fewer correct responses. Moreover, this effect is specific to test sessions (as shown by the difference in performance that can clearly

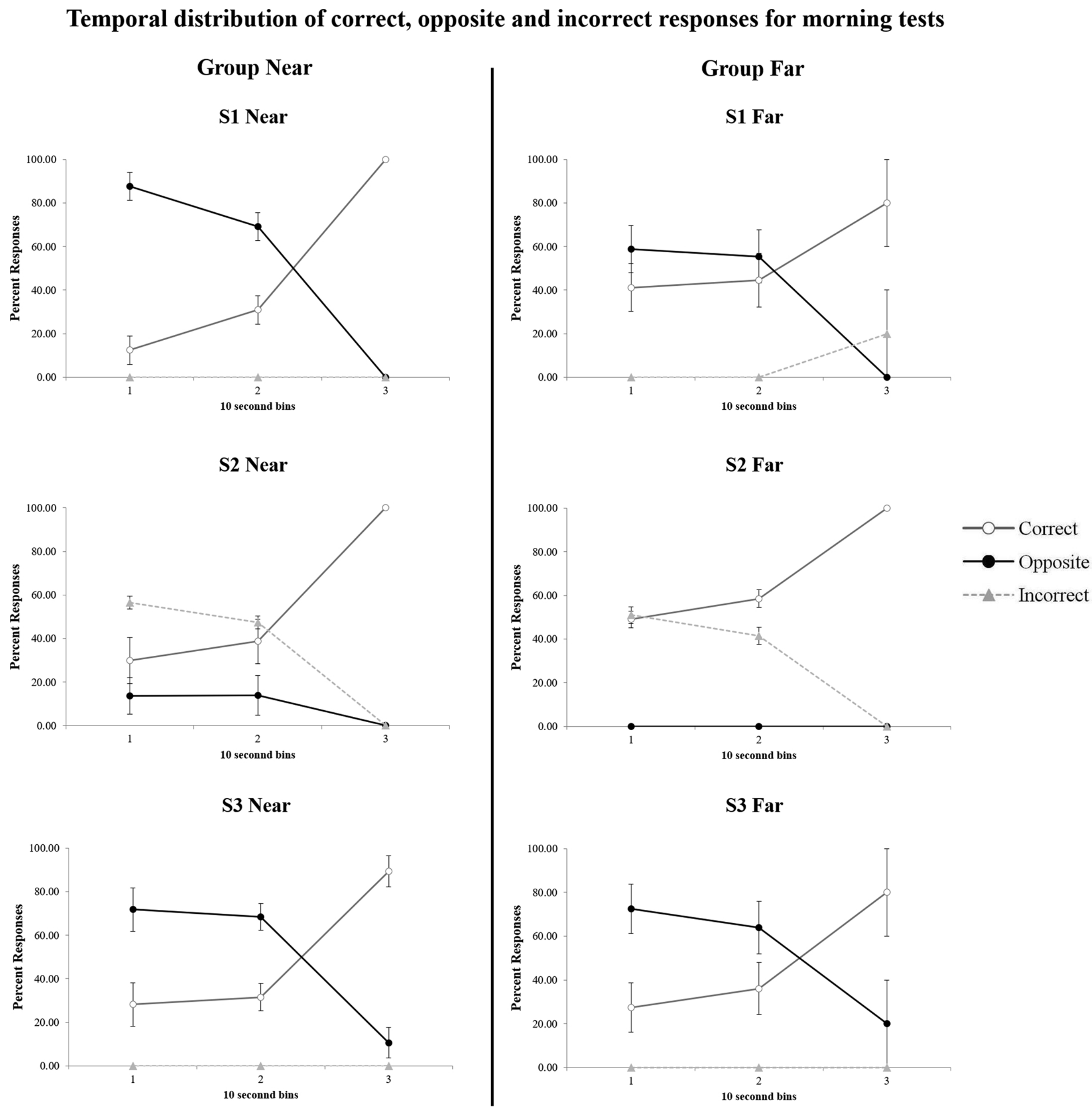

Fig. 5. Average percent correct, opposite, and incorrect responses in 10 sond bins for the first 30 s of the nonreinforced period of morning test sessions for each subject. Left column shows data for birds in Group Near and right column shows data for Group Far. Error bars represent the SEM.

be seen between Figs. 3 and 4). However, since there is still a well-above-chance level of percent correct responses during test sessions, it becomes crucial to know exactly when were this opposite responses emitted, for, if they are emitted early during the session, this could imply that birds were using a non circadian strategy.

Fig. 5 shows the percent correct, opposite, and incorrect responses in 10 s bins for the first 30 s of the nonreinforced period of morning test sessions for each subject. Left panel shows data for Group Near, and right panel shows data for Group Far. As this plot clearly shows, early during the session, most of the responses made by most birds on Group Near are opposite, and then, 20 s into the session, these birds reverse their pattern, switching to an overall majority of correct responses. On the other hand, a somewhat similar scenario holds true for birds in Group Far, although in their case, during the first 20 s of morning test sessions, the difference between correct and opposite responses is not as great as that of birds in Group Near. Overall then, data for both groups suggest that birds start responding primarily on the opposite Feeder and then they switch. This effect was considerably more powerful for birds the Group Near, for, even tough a paired samples t test comparing percent correct vs percent opposite responses for the first 20 s of the morning test sessions revealed non statistically significant differences, $t(2) = -1.08$, $p = .18$, $d = .1.01$ for birds in group Near, the extreme d value for this particular test suggests a strong effect that does not reach significance level due to reduced sample size. On the other hand, The same test conducted on the afternoon sessions revealed a much less considerable t score and a minor effect size indicator, $t(2) = .036$, $p = .97$. $d = .04$. Another noteworthy finding is that there is one bird in each group that allocates a high percentage of incorrect responses, which suggests some sort of disruption coming from the test itself.

Fig. 6 shows the exact same data as Fig. 5 but for the afternoon sessions. This plot shows that one of the birds in Group Near has a clear reversal pattern as those seen in morning tests, on the other hand, the remaining two subjects in this group show a different response pattern: one of them starts responding more in the incorrect option, while the other one allocates most of its responses on the correct option, although the superimposing error bars in this plot (S3 Near), particularly in the

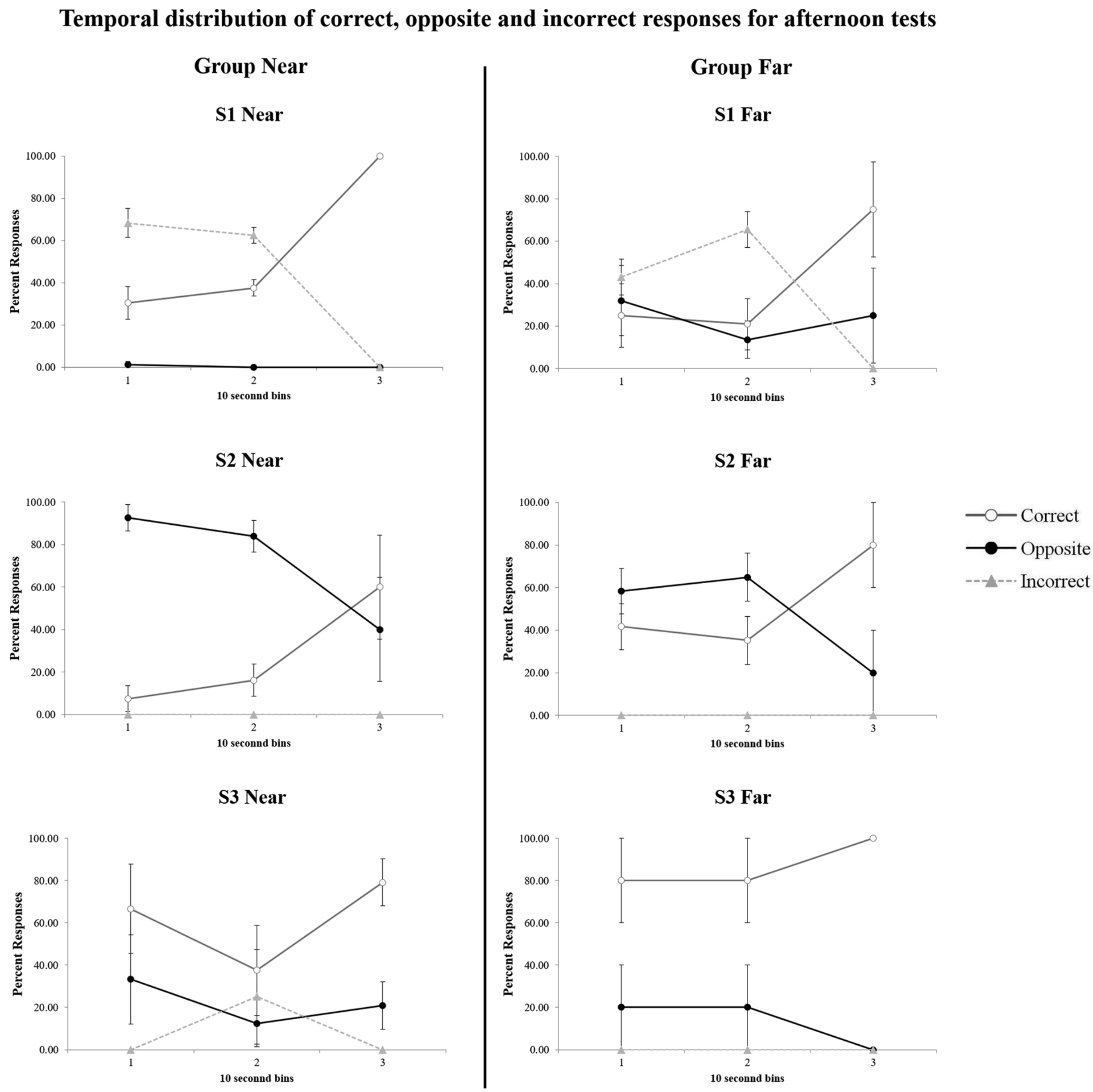

Fig. 6. Average percent correct, opposite, and incorrect responses in 10 sond bins for the first 30 s of the nonreinforced period of afternoon test sessions for each subject. Left column shows data for birds in Group Near and right column shows data for Group Far. Error bars represent the SEM.

first 20 s, do not suggest a clear circadian timing strategy. The same plot shows a similar pattern for birds in Group Far: One bird (S2 Far) responds more on the opposite Feeder, although, in this case, as it was for morning tests, the difference between percent opposite and percent correct responses is much smaller than that seen for birds in Group Near. Another bird shows a disrupted pattern, as that showed by two birds in the last figure. And, finally, another bird shows a clear and absolute majority of its responses being allocated to the correct option from the start. The same *t* tests as for morning sessions were conducted, none of them showed statistically significant differences, although, once again, group near, $t\ (2) = .49$, $p\ =\ .66$, $d = .46$ shows a more powerful difference than group far, $t(2)\ =\ -.12$, $p\ =\ .90$, $d\ = .13$.

Overall, Figs. 5 and 6 show several interesting findings. First of all, three recognizably different patterns of response can be identified:

1 *Majority of correct responses*. Birds allocate most of their responses on the correct option from the start of the session, the difference between correct and opposite responses increases dramatically by the 3rd ten second bin. This would be the expectable pattern when birds were using a circadian strategy. 3 of the plots show a pattern like this.

2 *Majority of opposite responses*. Birds allocate most of their responses on the opposite option for the first 20 s of the test session. Interestingly, a clear reversal can be seen in all cases during the 3rd bin. This is the expectable pattern from a non circadian strategy. This was actually the most frequent pattern found throughout the experiment: 6 of the plots show it.

3 *Increased incorrect responses*. Birds allocate a high percentage of their responses on the incorrect option, such that there is either a clear majority of incorrect responses, or indistinguishable response levels in all options. The existence of these patterns suggests the possibility of a disruption effect brought about by the act of skipping one training sessions. These patterns are difficult to interpret, specially because there are no studies in the Daily TPL field that report a measure like these temporal distributions.

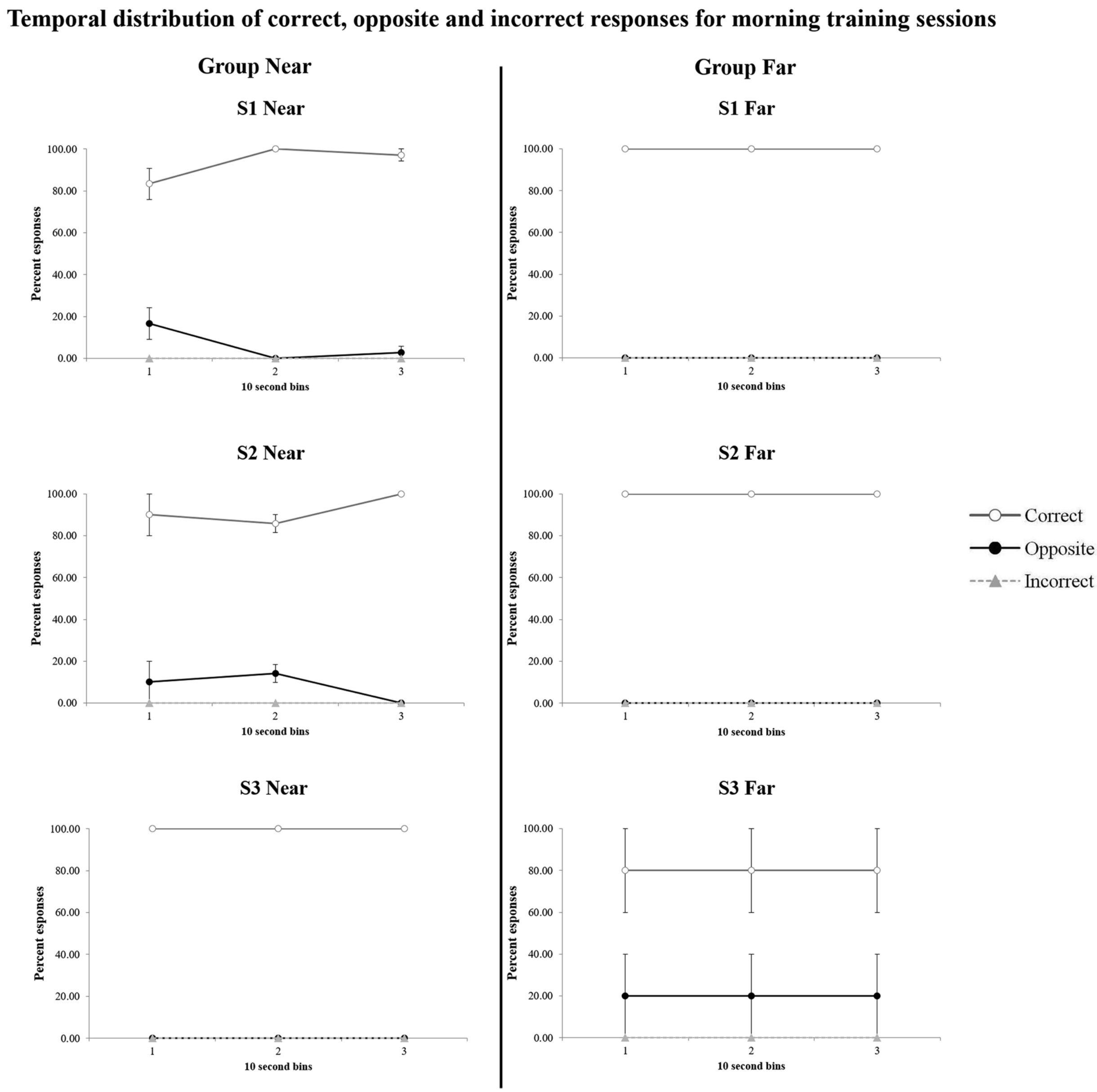

Fig. 7. Average percent correct, opposite, and incorrect responses in 10 sond bins for the first 30 s of morning training sessions for each subject. Left column shows data for Group Near and right column row shows data for Group Far. Error bars represent the SEM.

Overall, data suggests that birds in both groups show a majority of number 2 patterns, which would be in line with a non-circadian strategy, however, a consideration must be done about this particular finding: While the *shape* of the pattern is similar in all cases, the difference between opposite and correct responses is far superior in birds of Group Near than birds in Group Far, thus strengthening the conclusion that, when low response costs are involved, birds, like rats, might also resort to non circadian strategies in solving a daily TPL task. Finally, note that, in all cases, there is an important difference in performance between the first 20 s and the last 10 s of testing. One possibility could be that this change is somehow controlled by the RI 28" imposed for the first reinforcement during training.

Of course, another possibility would be that the temporal distribution of responses observed during test sessions is merely a replication of a response pattern learned during training. That is, maybe during training, birds responded on many different Feeders as part of a *searching pattern* maintained by the RI 28" schedule of reinforcement. Figs. 7 and 8 were obtained to further explore this possibility. These figures show the percent correct, opposite and incorrect responses for the first 30 s of morning (Fig. 7) and afternoon (Fig. 8) training sessions for each subject. In obtaining these plots, special care was taken to discard any and all responses emitted after the first reinforcement in each session, thus ensuring contrastability with the data presented in Figs. 5 and 6 (in all cases, in Figs. 5–8, all responses considered occur before the first reinforcement).

If the temporal distribution observed in Figs. 5 and 6 evolved as a searching pattern during training, then the pairs of Figs. 5 and 7 (morning) and 6 and 8 (afternoon) should show similar data. As can clearly be seen in Figs. 7 and 8, the temporal distributions of correct, opposite, and incorrect responses during the non-reinforced period of training sessions are quite different from those obtained in testing sessions. During training, practically all birds from both groups allocate the vast majority of their responses on the correct option from the very start of the session. The only exception to this finding is S3 Near during afternoon sessions, for whom, most responses occur to the opposite option, however, even this pattern of responding does not mirror that obtained during test sessions for this particular bird. Therefore, the most appropriate conclusion is that the response patterns observed

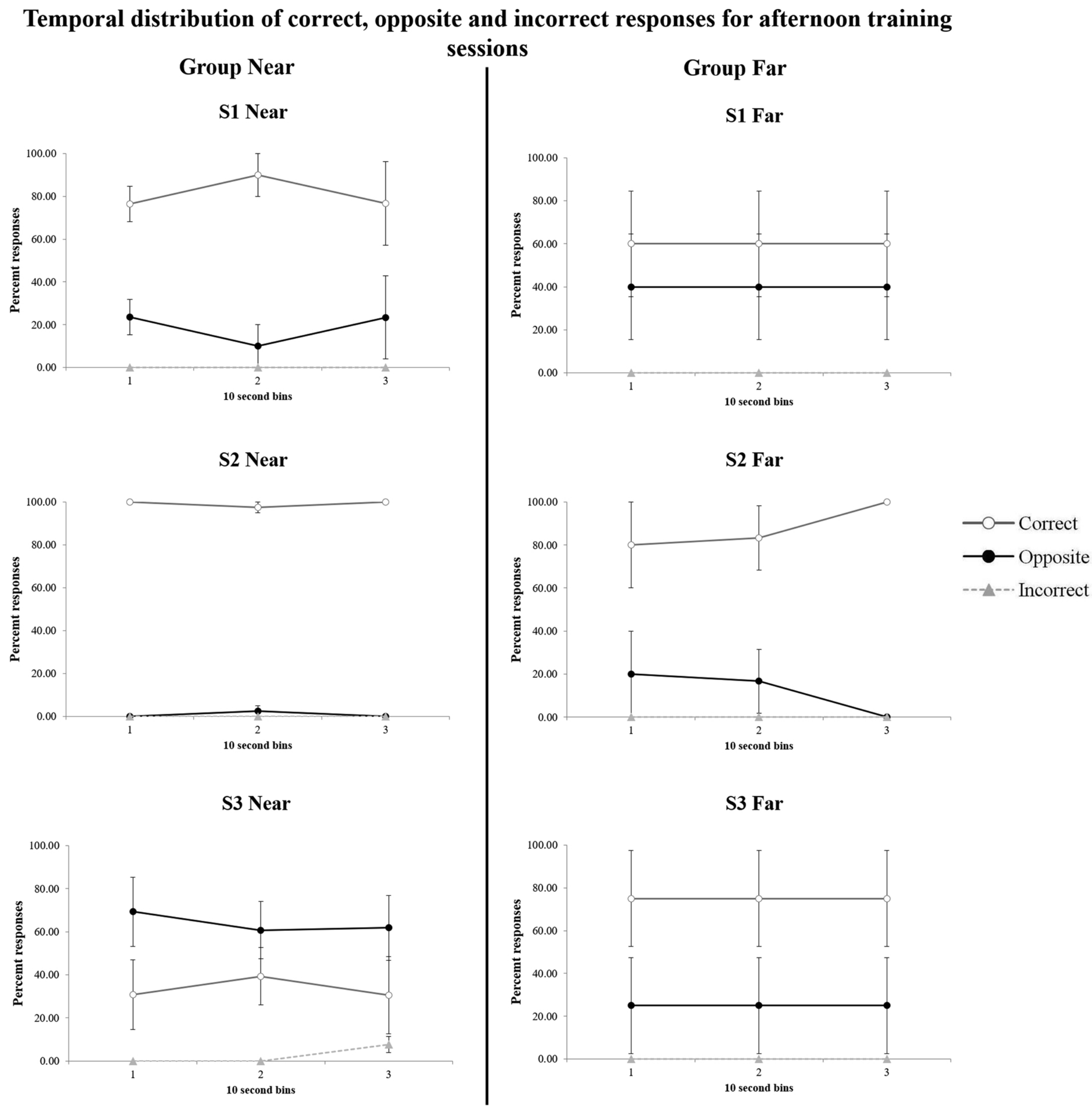

Fig. 8. Average percent correct, opposite, and incorrect responses in 10 sond bins for the first 30 s of afternoon training sessions for each subject. Left column shows data for Group Near and right column row shows data for Group Far. Error bars represent the SEM.

during testing do not reflect a *searching pattern* evolved during training.

4. Discussion

Previous research has shown that many different species can successfully exploit resources with a limited spatial and temporal availability. Pigeons (Wilkie and Wilson, 1992; Saksida and Wilkie, 1994; Garca-Gallardo and Carpio, 2016), rats (Carr and Wilkie, 1997a, 1999; Means et al., 2000a), fish (Reeb, 1993; Reebs, 1999; Gmez-Laplaza and Morgan, 2005), garden warblers (Biebach et al., 1989, 1994), ants (Schatz et al., 1994), and mice (Van der Zee, Havekes, Barf, Hut, Nijholt, Jacobs & Gerkema, 2008; Mulder et al., 2013) have all been shown to display TPL under different circumstances.

However, an interesting finding has been repeatedly reported: rats seem to require high response costs in order to solve the daily TPL task via circadian timing. This is not a minor issue, for, just as findings from the MSR task seem to imply (Cook and Rosen, 2010; McMillan et al., 2014; McMillan et al., 2016), it could show an important species difference in time-controlled behavior between rats and other widely explored species, such as the pigeon. Therefore, the present study was designed to bridge a gap in the current literature in daily TPL: exploring whether or not, response cost has a similar effect on pigeons as it does on rats (i.e. Non circadian timing under low response costs, and circadian timing under a high response cost task).

During this study, six birds were exposed to a typical daily TPL task: food could be obtained by responses in one location during morning sessions, and another location during afternoon sessions. During test sessions, the previous session was skipped, so that, if birds were relying on a non circadian strategy, their level of responding on the Opposite location would increase. On the other hand, the use of a circadian strategy would predict that most responses would be allocated in the Correct location. The only difference between groups was the distance between locations, for one group, feeding locations were 8 cm apart (Group Near), and, for the second group of birds, this distance was set to 59 cm (Group Far). The rationale is that this arrangement entails differential response costs in the switchover between feeding sites, going from the correct to the opposite option takes as much as 7 times longer for birds in Group Far than birds in the Group Near.

Our data showed a number of interesting findings. First, as anticipated, birds were able to successfully learn the task in the course of 50 training sessions. As shown by percent correct responses around 90 for morning sessions and 80 for afternoon sessions. Second, when faced with test sessions, birds in Group Near show a majority of opposite responses in morning sessions and very similar percent opposite and correct responses during afternoon sessions. On the other hand, birds in Group Far still show a majority of percent correct responses although with a noticeable drop in this measure. Altogether, these findings raised the question: When are the opposite responses being made?

As shown by the temporal distribution of responses, the most frequent pattern of temporal distribution of responses consists of birds allocating most of their responses in the opposite location, and, between the 2nd and 3rd 10 s bins, they switch to the correct option. Another interesting finding about this particular response pattern is that, although it appears for birds in both groups, the difference between opposite and correct responses during the first 20 s is much greater for birds in Group Near than for birds in Group Far. This finding is particularly relevant, since it does not agree with a circadian strategy. However, an important question must be considered: Why do birds switch between the 20th and 30th second of the test session? Note that the nonreinforced period used during training was roughly 28 s in average; therefore, birds could start responding on the opposite location and then, around the time that reinforcement would have usually occurred during training, switch to the correct option. It is interesting that, while some birds in the Group Far do not show this clear reversal, they do show a 20–30 sec period of increased opposite and incorrect responses, which would suggest confusion. In both cases, an interval timing strategy that times the lapse between the start of the session and the first reinforcement could explain why there is an abrupt change in response allocation after 30 s elapsed for both groups (Wilkie, 1995; Carr and Wilkie, 1997b; Crystal, 2009). If this rationale is true, then the data shown in this study would strongly suggest that birds in both response cost conditions could come to rely on a non circadian strategy, although this conclusion would be stronger for birds in Group Near than for birds in Group Far.

This conclusion is strengthened when analyzing temporal distribution of responses during training. Figs. 6 and 7 show that there is a clear difference in response patterns during training and testing, therefore, the temporal distribution of responses observed during test sessions, cannot be considered as a search or exploratory pattern developed during training.

Overall, the soundest explanation for the data presented in this experiment is that birds' performance under the low response cost condition is better described by a non circadian strategy, as shown by the allocation of their responses on the opposite option at the start of the test sessions; however, when the average reinforcement time encountered during training has elapsed, birds alter their allocation and start responding on the correct option. On the other hand, the same explanation could apply for one of the birds in the high response cost condition, although the somewhat chaotic allocation of responses observed during the first 20 s for some birds in this group suggests that the skipping of a session entails disruptive effects in the performance of our birds but it does not necessarily suggests a non circadian strategy for them. This disruption in performance could be in line with the literature, since methodologically similar studies have shown that there is usually a slight decrease in percent correct responses (Saksida and Wilkie, 1994; Thorpe and Wilkie, 2007; Mulder et al., 2015). However, direct comparison with these studies is not possible, since they do not report the temporal distribution of responses during testing.

In short, the present experiment could very well be the first to document that pigeons, like rats, show a tendency to rely on a non circadian strategy when faced with low response costs in a daily TPL task. As mentioned above, this issue is not minor, since, it has been hitherto considered that this tendency was exclusive to rats and that it might show a species difference in time-sensitivity, when it could be a generalized effect of a specific task parameter. Of course, additional research is required to shed light into the matter. First of all, more species should be exposed to explicit manipulations of different levels of response costs. Second, note that response cost can be mapped by many different ways into an experimental design, for the purposes of this task, this was accomplished via the distance between feeding locations; however, increasing response requirements, the use of aversive stimulation, or even physical obstacles between feeding locations could all be viable ways to further explore the effect of response cost on the performance of pigeons under TPL tasks. Last but not least, a number of additional manipulations can be conducted in order to differentiate between different types of non circadian strategies in solving a daily TPL task (i.e. Alternation vs ordinal timing). Overall, in terms of Carr and Wilkie's (1999) influential paper, our data strongly suggests that rats are not alone in their "reluctance" to solve daily TPL via circadian timing when low response costs are involved, a conclusion that could be greatly strengthened by future research.

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