Learning & Behavior (2022) 50:273–282
https://doi.org/10.3758/s13420-022-00533-5

Time will tell: Temporal processing in the sexual behavior system

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Accepted: 1 June 2022 / Published online: 14 June 2022

Abstract

This paper describes several temporal factors that appear to play a role in sexual conditioning including the conditioned stimulus (CS)-unconditioned stimulus (US) interval, the C/T ratio, and trace conditioning. One commonality among these studies is the attention given to the stimuli and responses involved. This is contrary to traditional learning theories such as the general process theory. The general process theory is focused on identifying universal principles and commonalities of learning, without regard to the stimuli and responses involved. The research described in this paper has taken a different approach and made specific considerations of the stimuli and responses such as with the type of conditioned stimuli used and the use of more than one, and sometimes multiple, response measures with which to identify conditioned responding. The findings of these studies are best accounted for by the behavior systems approach. For example, one of the main findings is that during long-delay learning, a new conditioned response may emerge (increased locomotor activity) in lieu of a decrease or absence of the target conditioned response (approach behavior). The behavior systems approach accounts for this by describing the sexual behavior system as being on a continuum from consummatory behavior to focal search and general search. The nature of the conditioned response depends on where the CS is introduced along the continuum. This example and several other sexual conditioning experiments are described within this paper with an emphasis on their interpretation from a behavior systems perspective.

Keywords Temporal processing · Sexual conditioning · Behavior systems approach · General process theory

Brief overview of general process theory

General process theory assumes that principles of learning are universal, apply to all species, and occur in a wide variety of learning situations (see Domjan, 2000, for a review). It has been a widely accepted scientific approach because it allows for identification and explanations of "universal principles" across different situations. In addition, the theory has been tied to some of our most distinguished learning theorists including Skinner, Thorndike, Hull, and Pavlov (e.g., Bower & Hilgard, 1981). These learning theorists were most interested in identifying commonalities and general principles of learning. For example, Skinner developed the operant chamber to allow for the presentation of arbitrary stimuli so that researchers could study general laws of learning (Skinner, 1938). Thus, early learning theorists were focused on general mechanisms of learning regardless of the stimuli and responses involved.

In 1961, two former graduate students of Skinner, Marian and Keller Breland, published *The Misbehavior of Organisms* (Breland & Breland, 1961). In it, they describe several cases of animal learning that appeared to be at odds with general laws of learning. One of the most well-known cases was a raccoon that failed to learn how to put a token in the slot of a piggy bank. At first, the raccoon placed the coin in the jar, but over time, it rubbed the coins together and appeared to dunk them in the jar but without letting go, so called "washing behavior" (Breland & Breland, 1961). The Brelands explained this as a problem with instinctive drift that interfered with the learned behavior that was being conditioned. They trained and observed thousands of animals and, in their publication, stated (though they said with reluctance) that "the behavior of a species could not be understood without knowledge of its instinctive patterns, evolutionary history, and ecological niche" (Breland & Breland, 1961). In spite of their provocative statements, these examples of "misbehavior" were

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considered exceptions or were later labeled as “biological constraints on learning,” and as such, general process theory continued to be widely accepted and irrefutable in the field of learning (see Domjan, 1983, for a review).

General process theory and the conditioned stimulus (CS)-unconditioned stimulus (US) interval

In the typical Pavlovian conditioning procedure, an initially neutral stimulus is paired with an unconditioned stimulus (US) and after several pairings, the neutral stimulus becomes a conditioned stimulus (CS) and elicits a conditioned response (CR). Typically, conditioning occurs when the interval between the onset of the CS and the onset of the US, the CS-US interval, is relatively short (Riley & Kohut, 2010). Some early studies found that acquisition of responding was inversely related to the CS-US interval. For example, Schneiderman and Gormezano (1964) studied the conditioning of the nictitating membrane and found that a 250-ms CS-US interval resulted in nearly 100% of conditioned responding whereas a 4,000-ms CS-US interval resulted in about 25% of conditioned responding. In a conditioned suppression preparation, Kamin (1965) presented various durations of a noise CS to rats (0.5–3 min) followed by brief shock (US), and he found an inverse relationship between the duration of the noise CS and the US. Later, Revusky and Garcia (1970) demonstrated a similar reverse relationship in conditioned taste aversion. The interpretation of these findings was that increasing the CS-US interval reduces the strength of the CS-US association and thereby reduces the likelihood of learning. The findings are in support of the general process theory because they provide evidence for a reduction of learning as the CS-US interval is increased, regardless of the preparation and/or stimuli and responses involved.

Manipulations of the CS-US interval

Sexual conditioning has been studied by Domjan and his associates for several decades. In a typical sexual conditioning experiment, a stimulus (CS) is paired with copulatory opportunity with a female quail (US). After several pairings, presentation of the CS alone elicits a conditioned response (CR) in male quail. Prior to studies investigating the CS-US interval, early investigations of sexual conditioning (e.g., Domjan et al., 1986, 1988) typically used a CS-US interval of 30 s and were focused on varying the features of the CS. For example, one study (Domjan et al., 1988) investigated conditioned responding to either a toy dog or a female quail adorned with bright orange feathers. Both CSs elicited conditioned approach behavior but only the adorned hen (CS) elicited copulatory behavior with a female quail (US). More recent studies have replicated this finding and have demonstrated that localized conditioned stimuli that contain species-typical cues of a potential sexual partner elicit conditioned copulatory responses such as grabbing, mounting, and attempting to make cloacal contact (Cusato & Domjan, 2012). However, stimuli that are localized and arbitrary (i.e., not relevant to the sexual behavior system) typically elicit conditioned approach behavior (e.g., Domjan et al., 1986, 1988).

Domjan and his associates investigated the effect of the length of the CS-US interval on conditioned sexual approach behavior in male quail (Akins, 1994; Akins et al., 1994). Consistent with general process theory, the prediction was that as the CS-US interval increased, conditioned sexual approach behavior would decrease. In the first experiment of her dissertation, Akins (Akins, 1994; Akins et al., 1994) paired a localized arbitrary CS (a gray foam block) with copulatory opportunity with a female quail. The CS was presented for 30, 150, 300, 600, 900, or 1,200 s and was followed by presentation of the female. The test chambers were double the size of the typical sexual conditioning chambers and three zones were marked off (see Fig. 1).

Zone 0 was directly in front of the door where the CS was presented (the CS zone) and served as a measure of approach behavior. Zone 1 was the rest of the large chamber adjacent to the CS zone, and Zone 2 was the large chamber furthest away from the CS zone. The latter Zone allowed quail an option to move further away from the CS. A sampling procedure was used to determine the percentage of time male quail spent in each zone. Figure 2 shows the percentage of time male quail spent in Zone 0, in front of the CS, during CS presentation across blocks of trials as a function of their CS-US interval.

Relatively long CS-US intervals resulted in male quail spending less time near the CS during CS presentation. As

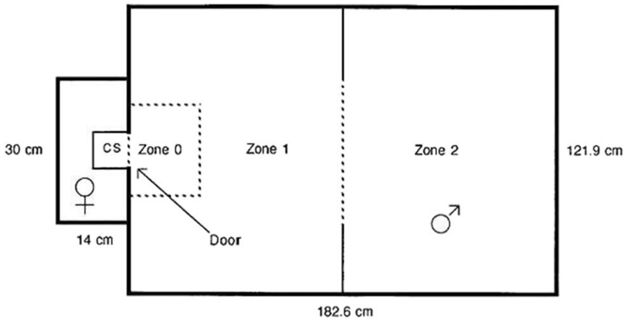

Fig. 1 Floor plan of the apparatus used in Akins et al. (1994). Large chambers were divided into two compartments by a wall containing a large permanent opening, allowing subjects access to both chambers (from Akins et al.,1994)

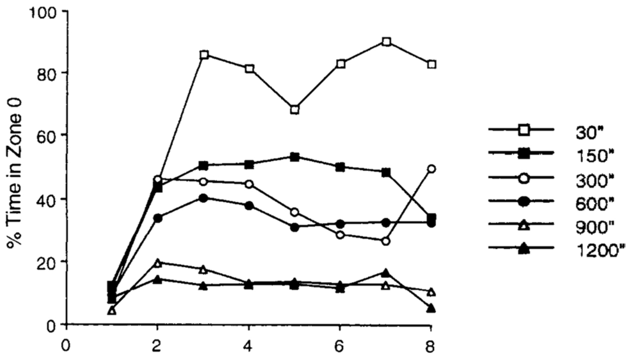

Fig. 2 Mean percentage of time (s) spent in Zone 0, the zone closest to the conditioned stimulus (CS) as a function of CS-unconditioned stimulus (US) interval (from Akins et al., 1994)

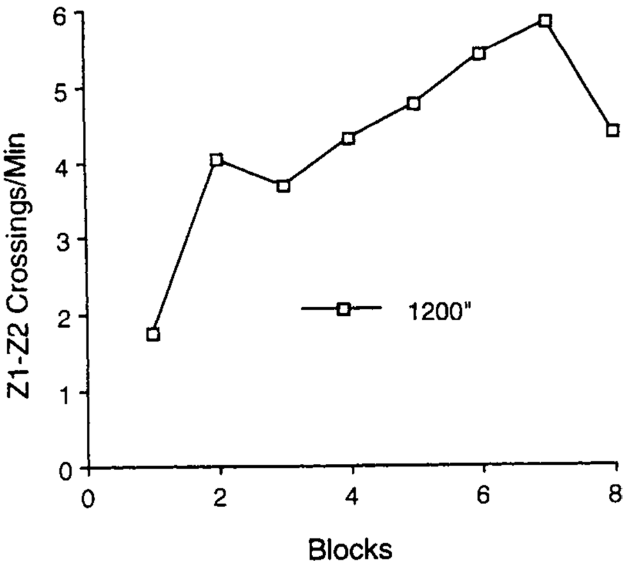

Fig. 3 Mean frequency of crossings per minute between Zones 1 and 2 across two-trial blocks for the last four subjects that received a 1,200-s conditioned stimulus (CS)-unconditioned stimulus (US) interval (from Akins et al., 1994)

predicted, there was less conditioned approach behavior as the CS-US interval increased. During the experiment, it was observed anecdotally that male quail that were given the 1,200-s CS-US interval were moving toward the CS and then moving away from the CS into the zone furthest away in somewhat of a pacing manner. In addition, individual quail appeared to have idiosyncratic patterns of locomotor activity. For example, one quail ran toward and away from the CS along the same side wall while another ran around the entire chamber in a circle moving in and out of each zone. To quantify this incidental observation, locomotor activity was measured as frequency of crossings between Zones 1 and 2, the two furthest zones, in the last four subjects of the 1,200-s group. Figure 3 represents Zone 1 to Zone 2 crossings for the last four subjects in the 1,200-s group across blocks of trials. The results showed that these subjects had a consistent pattern of increased locomotor activity between the zones furthest from the CS across trials.

In a more systematic follow-up experiment (Akins, 1994; Akins et al., 1994), a short CS-US interval (60 s) was compared to a long CS-US interval (1,200-s) and approach behavior and zone crossings were measured using the same large chambers and arbitrary localized CS as in Experiment 1. The design of the current experiment was a 2 X 2 factorial design in which an unpaired control that received the US 2 h prior to the CS was included for each CS-US interval assignment. Thus, the groups were Short-Unpaired, Long-Unpaired, Short-Paired, and Long-Paired. Figure 4 represents the percentage of time each group spent in Zone 0 near the CS during the CS presentation across blocks (top figure) and locomotor activity between the two zones farthest from the CS for each group across blocks (bottom figure).

Male quail that received the 60-s CS followed by the US (Short-Paired) spent significantly more time near the CS than male quail that received the 1,200-s CS followed by the US (Long-Paired) and more than both unpaired groups, overall and across blocks. In contrast, male quail that received the 1,200-s CS (Long-Paired) had significantly greater locomotor activity than the other groups, and this activity increased across trial blocks.

The findings are remarkably consistent with the behavior systems approach, originally proposed by Timberlake (Timberlake & Lucas, 1989; Timberlake, 1994; Timberlake 2001). The behavior systems approach proposes that behavior systems consist of a series of modules that are organized in a temporal-spatial sequence. These modules are assumed to be on a continuum from general search behavior to consummatory behavior, with focal search behavior in the middle. The theory provides an inclusive approach that combines the theoretical frameworks of ethology and learning. For example, one aspect of the sexual behavior of male quail might be viewed as a foraging opportunity to seek out a mate. As such, the sexual behavior sequence might consist of general search for a potential mate, followed by approach to a female (focal search), and direct social interactions once a female is encountered (consummatory behavior).

Pavlovian conditioning occurs with the integration of the CS into the behavior sequence. The conditioned response that is elicited by the CS depends on which module is activated at the time of CS presentation, which to a large extent depends on when the CS is presented relative to the US, the CS-US interval. Varying the CS-US interval alters the timing of when the CS becomes integrated into the behavior sequence such that short CS-US intervals may activate more focal search and consummatory responses and long CS-US intervals may activate more general search behaviors. The findings above are indicative of male quail demonstrating

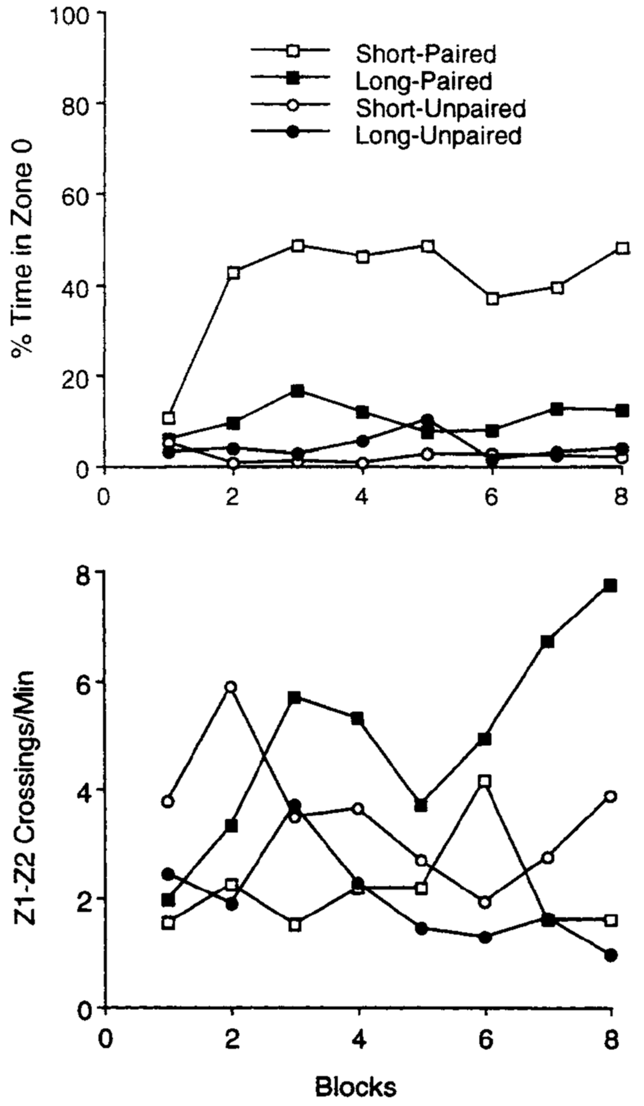

Fig. 4 Mean percentage of time spent in Zone 0, the zone closest to the CS, across two-trial blocks (**top panel**) and mean frequency of crossings/min between Zones 1 and 2, the two furthest zones from the CS across two-trial blocks (**bottom panel**) (from Akins et al., 1994)

approach behavior or focal search behavior when given a relatively short CS-US interval and increased locomotor activity or general search behavior when given a long CS-US interval.

Admittedly, the interpretation of conditioned pacing during the long CS-US interval as "general search" behavior was/is post hoc. Another possible interpretation is that the pacing activity reflects adjunctive or schedule-induced behavior (e.g., Staddon, 1987). Adjunctive behaviors typically occur when a stimulus is presented according to a temporally defined schedule. For example, in one study (Falk, 1961), rats received a food pellet for pressing a lever but they had to wait another minute before pressing the lever for another pellet. The rats developed the habit of drinking water during these intervals and their consumption far exceeded what was expected. The pacing behavior in the Akins study (Akins et al., 1994) was significantly greater in the experimental group compared to the control group, thus it is possible that the pacing behavior in the present experiment may be characterized as adjunctive behavior. An alternative explanation might be that adjunctive behavior is an expression of general search behavior within the sexual behavior system, and therefore the pacing behavior could have been accounted for by both explanations.

Manipulations of CS features in conjunction with the CS-US interval

Previous studies have shown that the features of a CS influence the topography of the conditioned response (e.g., Garcia & Koelling, 1966; Hearst & Jenkins, 1974; Holland, 1977, 1980a; Timberlake & Grant, 1975; see Silva, 2018, for a review). For example, Holland (1980a) presented rats with visual or auditory cues as CSs paired with a food US. Visual CSs evoked rearing and orientation toward a food location but auditory CSs evoked head jerks and startle responses. Timberlake and Grant (1975) presented rats with a live rat as a CS paired with a food US. The live rat CS evoked conditioned social contact behavior such as approaching, pawing, and grooming behavior, whereas a block of wood as a CS (the size of a live rat) elicited orienting toward the CS. In a recent review, Silva (2018) describes numerous experiments in which the nature of the CS alters the form of the CR and he provides a conceptual analysis of neutral CSs and ecologically relevant CSs.

As previously discussed, another major determinant of the topography of conditioned responding is the CS-US interval. Holland (1980b) investigated how both the nature of the CS and the length of the CS-US interval would affect the topography of the CR by presenting visual and auditory CSs to rats and using food as a US. Similar to his previous research (Holland, 1977, 1980a), he found that auditory and visual CSs paired with food evoked different response topographies, but in addition, the topography of the conditioned behaviors elicited by those stimuli depended on the length of the CS-US interval. Auditory CSs evoked high frequencies of startle and head-jerk responses when the CS-US interval was short but less startle and head-jerk movements and more magazine-directed responding when the CS-US interval was long.

The findings of Akins et al. (1994) indicate that male quail will approach and remain near an arbitrary localized CS that predicts a US when the CS-US interval is relatively short, but when it is long, male quail show increased generalized locomotor activity. It has also previously been shown that male quail demonstrate conditioned copulatory behaviors toward a terrycloth model that contains species-typical female head and neck cues when the environmental context becomes associated with the presentation of a live female quail (Domjan et al., 1989).

Akins (2000) investigated how the presence or absence of species typical cues and varying the CS-US interval would alter the topography of the CR. The experiment was a replication of Akins et al. (1994) but with two different CSs (see Fig. 5).

Both CSs contained terrycloth vertical and horizontal pads, similar to the shape of a female quail, but in addition, one CS (a) contained a taxidermically prepared head and neck of a female quail attached to the top of the vertical pad. The same procedure was used as in a previous study (Akins et al., 1994) and multiple behavioral measures such as grabs and pecks, mounts, cloacal contact movements, approach behavior, and zone crossings were collected. Short (1 min) and long (20 min) CS–US intervals were tested.

During conditioning, paired group subjects were presented with either a

terry cloth model (T) or a head and neck model (HN) for either 1 min (Short) or 20 min (Long). After exposure to the model, the door to the female's side cage was opened and subjects received copulatory opportunity with a female quail for 5 min. Unpaired group subjects received the same treatment as paired group subjects except they were given copulatory opportunity with a female 2 h prior to exposure to the model. Thus, the groups were HN-Short Paired, HN-Short Unpaired, HN-Long Paired, HN-Long Unpaired, T-Short Paired, T-Short Unpaired, T-Long Paired, and T-Long Unpaired (*n*s 5–6).

Figure 6 shows the mean frequency of crossings between Zones 1 and 2 per min for each group across trials (top) and the percentage of time paired and unpaired groups spent near the CS across trials (bottom).

Results showed that only the terry cloth model presented for 20 min before the US elicited an increase in locomotor activity between the two zones furthest from the CS across trials (top panel). Both the terry cloth CS and the head and neck CS elicited conditioned approach behavior when the CS-US interval was short but the head and neck CS elicited greater approach and a stronger acquisition of approach behavior than the terrycloth model (Fig. 6; bottom panel). Interestingly, when the head and neck CS was presented for a long CS-US interval and paired with the US, it also elicited

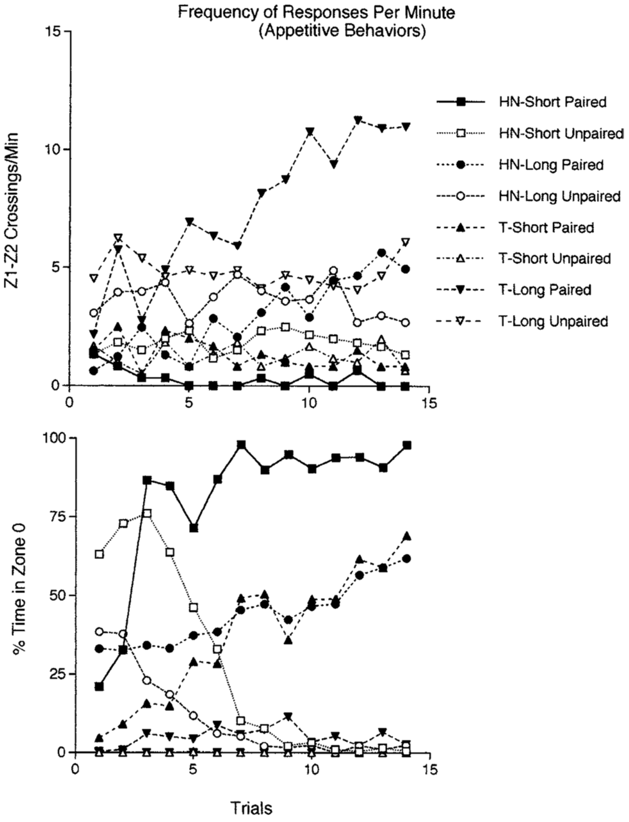

Fig. 6 The frequency of crossings between Zones 1 and 2 per min (**top**) and the percentage of time subjects spent in Zone 0 per min as a function of trials (**bottom**) (from Akins, 2000)

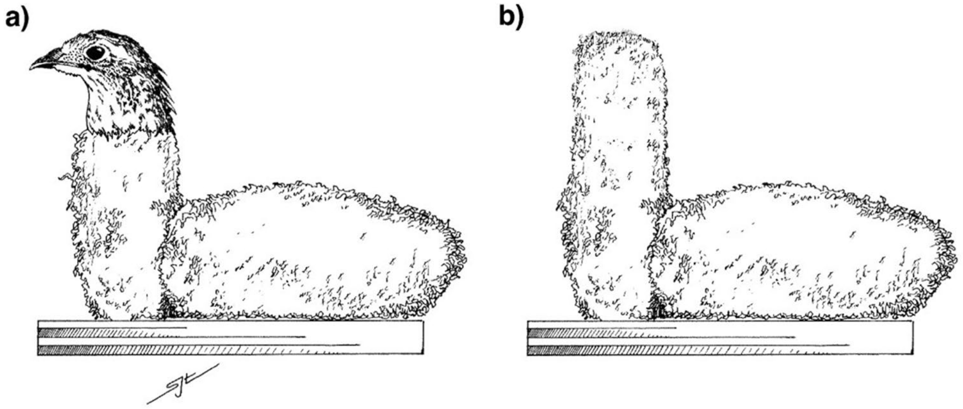

Fig. 5 Terrycloth models with a taxidermic model of a female quail's head and neck (**a**) and one without (**b**) (from Cusato & Domjan, 1998)

approach to the CS rather than an increase in locomotor activity.

In the present experiment, in the absence of species-typical cues of the female, the CS elicited conditioned approach behavior when the CS-US interval was short and increased locomotor activity when the CS-US interval was long. This is consistent with previous research (e.g., Akins et al., 1994). In contrast, when the CS contained species-typical features of a female quail, conditioned approach behavior was even greater and resulted in a stronger acquisition of approach behavior than the CS that did not contain species typical female cues. Results of the latter finding are in agreement with previous studies that demonstrated that female species typical cues are very effective in eliciting sexual approach and copulatory responses (Cusato & Domjan, 2012; Domjan, 1998; Domjan et al., 2004). Further, the head and neck cues of the female quail have also been shown to facilitate conditioning to a food US (Cusato & Domjan, 1998) and to disrupt traditional blocking and extinction effects (Köksal et al., 1994; Krause et al., 2003).

From a behavior systems and ecological perspective, the presence of species typical cues may activate a more focal or consummatory module along the continuum. In nature, a male quail might see a female's head and neck sticking out above the grass from a distance. These female head and neck cues may facilitate approach behavior that later becomes conditioned by either Pavlovian conditioning and/or approach to the cues being instrumentally reinforced by the copulatory event. Because female head and neck cues are encountered reliably before a copulatory event, these cues may become strong predictors of the copulatory event, thereby making conditioned copulatory responding more likely to occur.

Manipulation of the C/T ratio

The research previously described indicates that the features of the CS and the length of the CS-US interval may be major determinants of the topography of conditioned behavior. However, both the CS and the CS-US interval occur within a temporal context. The temporal context is the interval between successive trials or the intertrial interval. Numerous theories predict that conditioned responding is determined by the duration of the intertrial interval (I) relative to the duration of the conditioning trial (T), the I/T ratio (Gallistel & Gibbon, 2000; Gibbon & Balsam, 1981; Jenkins et al., 1981). The findings of several previous studies have demonstrated that increasing the I/T ratio increases sign tracking behavior in pigeons (Gibbon & Balsam, 1981) and goal tracking behavior in rats (Holland, 2000; Lattal, 1999).

Burns and Domjan (2001) conducted experiments that involved varying the exposure to the experimental context prior to each trial rather than varying the intertrial interval per se, and as such they investigated the C/T rather than I/T. In their experiments, an arbitrary CS (a wood block) was presented to male quail followed by an opportunity to copulate with a female quail (US). The location of the CS was separate from the location of the female US for the purpose of distinguishing between conditioned approach toward the CS (sign tracking) and conditioned approach toward the female (goal tracking). The amount of time subjects spent in the experimental context before presentation of the CS (C) relative to the duration of the CS (T) was manipulated. CS presentation was always 30 s whereas exposure to the experimental context ranged from 45 to 5,400 s. Therefore, the C/T ratios tested were 1.5, 4.5, 45, and 180 s.

Figure 7 illustrates the amount of time male quail spent near the CS (sign tracking; top panel) and near the US (goal tracking; bottom panel) for groups that received the C/T ratio for 1.5, 4.5, 45, or 180 s during trials 1, 5, 10, and 15.

Results showed that sign tracking increased with increasing C/T ratios whereas goal tracking decreased as a function of increasing C/T ratios. As the time spent in the experimental context was increased relative to the duration of the

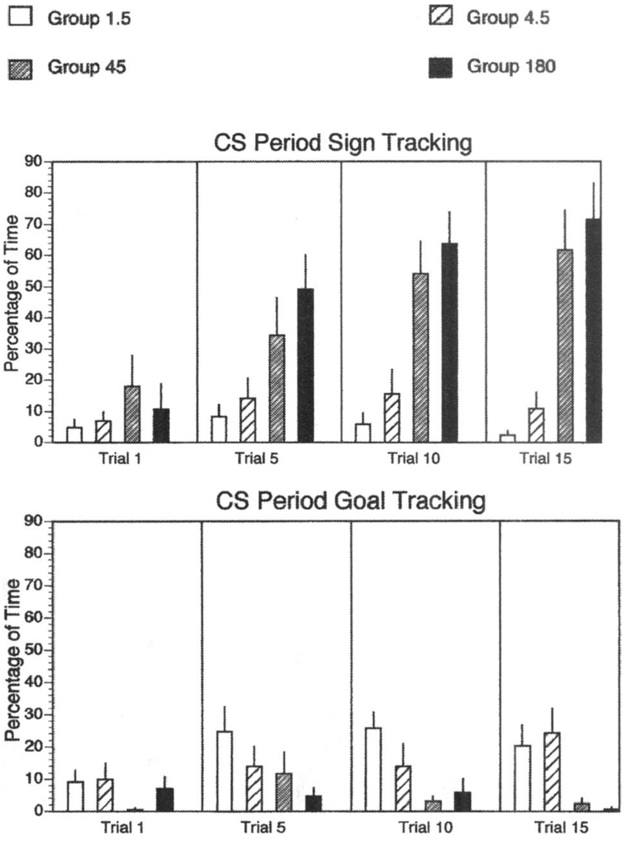

Fig. 7 Mean (+SEM) percent time spent near the conditioned stimulus (CS) (**top panel**) and unconditioned stimulus (US) (**bottom panel**) during trials 1, 5, 10, and 15 (from Burns & Domjan, 2001)

CS, male quail spent more time near the CS and less time near the US across trials. Thus, sign tracking developed when the exposure to the experimental context was longer and when the CS was present. In contrast, goal tracking developed when context exposure was shorter than the CS and it did not appear to be controlled by the CS. The findings are contradictory to previous findings that showed an increase in goal tracking with increasing C/T ratios (Holland, 2000; Lattal, 1999). Burns and Domjan (2001) point out numerous differences between the studies such as differences in species, experimental preparations, number of trials per day, and amount of context exposure. Regardless of the different findings between the studies, one of the key findings of Burns and Domjan (2001) as it relates to the behavior systems approach is that, by measuring both sign-tracking and goal-tracking responses in the same experiment, a change in the topography of the conditioned response was evident rather than an all-or-none outcome as a function of varying the C/T.

Manipulation of a delayed versus trace interval

All of the previously described sexual conditioning research utilized a delayed conditioning procedure in which the CS was presented until the start of the US, without a gap in time between the two stimuli. In a trace-conditioning procedure, the CS is presented before the US but is removed before the delivery of the US such that there is a gap in time or “trace interval” between the end of the CS and the start of the US. The majority of previous research on trace conditioning suggests that weaker conditioning occurs with a trace-conditioning procedure than with a delayed procedure (e.g., Kamin, 1965; Newlin & LoLordo, 1976; Schneiderman, 1966). General process theory would likely assume that general principles of learning were contributing to these findings.

Akins and Domjan (1996) investigated delayed versus trace conditioning procedures in a sexual conditioning experiment. For the delayed group, male quail had visual access to an arbitrary localized CS for 60 s and this was immediately followed by an opportunity to copulate with a female quail (US). In contrast, Group Trace received visual access to the CS for 30 s, followed by 30 s of no CS and subsequent copulatory opportunity. Group Control received an explicitly unpaired procedure. Large size test chambers with three Zones (Zones 0, 1, and 2) were used as in previous long-delay experiments (e.g., Akins et al., 1994).

The percentage of time spent in Zone 0, near the CS for trace, delayed, and control groups across blocks of trials is shown in Fig. 8.

During the first 30 s when the CS was present for all groups, delayed and trace groups had similar levels of conditioned approach and both had greater overall approach and a stronger acquisition of approach to the CS compared to the control group. During the second 30 s, the CS remained present for the delayed and control group but was absent for the trace group. Group Delayed displayed greater conditioned approach to the CS across trial blocks compared to both Group Trace and Group Control. Group Trace showed more conditioned approach than Group Control. Therefore, based on using Zone 0 as a measure of conditioned approach behavior, the presence of the trace interval reduced learning.

Interestingly, when the data were analyzed for time spent in Zones 0+1, the CS zone plus the large chamber next to the CS zone, both delayed and trace groups spent similar and significantly greater time near the CS than the unpaired control group (see Fig. 9).

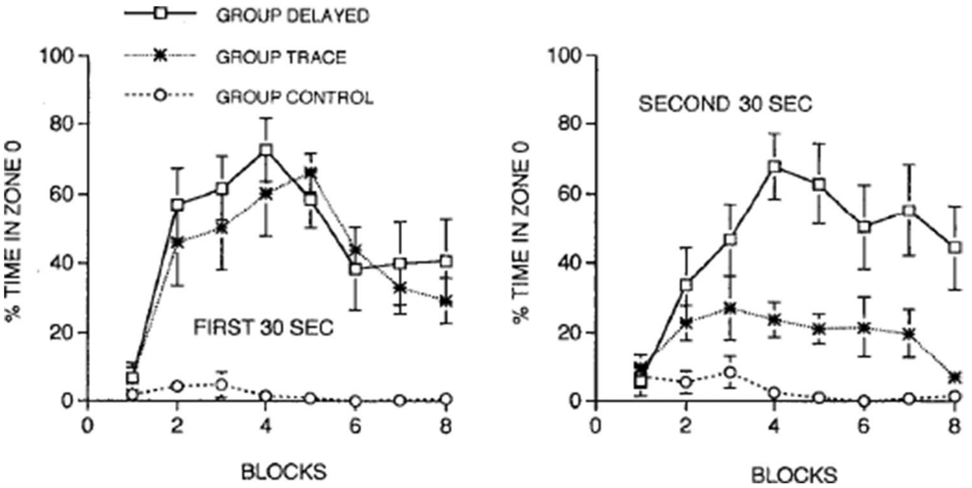

Fig. 8 Mean percentage of time (+SEM) spent in Zone 0, the zone closest to the conditioned stimulus (CS), for the first 30 s across two-trial blocks (**left panel**) and for the second 30 s across two-trial blocks (**right panel**) (from Akins & Domjan, 1996)

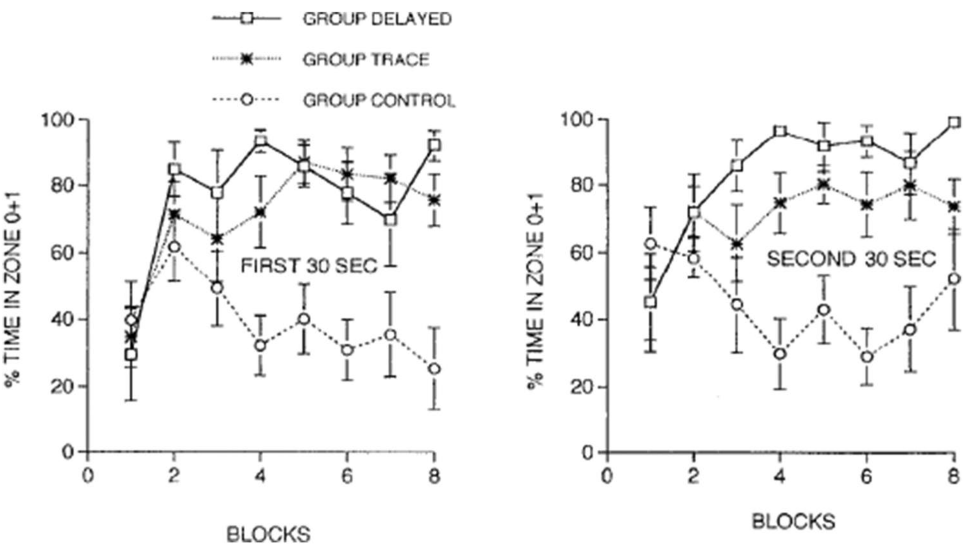

Fig. 9 Mean percentage of time spent in Zone 0+1, the zone closest to the conditioned stimulus (CS) and the adjacent larger zone (Zone 1) for the first 30 s across two-trial blocks (**left panel**) and for the second 30 s across two-trial blocks (**right panel**)

The initial interpretation, when only the small zone near the CS was included, was that the group that received trace conditioning had a reduction in conditioned-approach behavior once the CS was removed during the trace interval. However, Group Trace spent as much time in the CS half of the chamber during the trace interval as Group Delayed in the second 30 s of when the larger area was included. Thus, it appears that the trace interval did not produce a decrement in conditioned responding but rather a change in the spatial topography of the conditioned response.

The change in the spatial specificity of conditioned approach during the trace interval may also be interpreted from a behavior systems perspective. The group that received the trace interval after the CS demonstrated focal search behavior toward the CS when it was present. During the trace interval, their focal search area was further removed from the location where the CS had been presented. The absence of the CS may have resulted in movement from a more localized area to a more general area and possibly closer to the general search mode.

The above findings are consistent with previous sign-tracking experiments conducted with male Japanese quail. In these studies, male quail continued to approach and remain near a CS paired with a copulatory event when the CS was located 25, 61, 91, 112 cm (Burns & Domjan, 1996), and 233 cm (Burns & Domjan, 2001) from the US. In the trace experiment described above, the exact distance quail spent near the CS was not quantified. However, since the length of the entire chamber was 182.6 cm and mid-way between the two furthest zones, Zones 1 and 2) was approximately 91.3 cm, delayed and trace group quail were spending a significant amount of time near the CS within the zone range observed in previous sign-tracking studies (Burns & Domjan, 1996; Burns & Domjan, 2001).

General discussion

In summary, this paper has presented and reviewed several experiments that provide evidence for the role of temporal factors in determining the topography of sexual conditioned responding. The findings of these studies also highlight the importance of taking into consideration the stimuli and responses involved and linking it to the ethology of the species. For example, using CSs with species typical female cues may dramatically change the nature of the CR compared to using arbitrary cues. Another highlight of these sexual conditioning studies is with the use of various behavioral measures used to quantify conditioned responding. In some cases, a CR may not have been identified if the experiment was not designed to capture a different CR than the original targeted CR. Finally, one of the main findings suggests that it may be that, in some cases, a decline or absence in conditioned responding observed may be an artifact of the use of a limited range of behavioral measures.

The general process theory of learning could not have predicted the outcome of these sexual conditioning studies. The theory would have predicted that the outcome of these studies would have been the same as in other preparations regardless of the stimuli and responses involved. Specifically, it would have predicted that the conditioned approach behavior observed with an arbitrary stimulus would not have changed with the use of species typical cues. Similarly, it would have predicted that the conditioned response would have declined with a long CS-US interval or the inclusion of a trace interval, without taking into account that the CR might change as a function of the CS-US interval or trace interval.

While the general process theory cannot account for many of the findings of sexual conditioning, the behavior systems approach accounts for these findings exceptionally well. Behavior systems were first described by Timberlake (Timberlake & Lucas, 1989; Timberlake, 1994; Timberlake 2001). Borrowing from Timberlake's terminology and conceptualization, Domjan developed a behavior system for sexual conditioning (Domjan, 1994). In it, he provides a data-driven elaborate account of how the sexual responding of male quail is modulated by the presence of certain types of stimuli and their temporal and spatial integration along the behavior system response continuum. Years later, the behavior system of sexual learning continues to be expanded upon to include additional findings (Akins & Cusato, 2015; Domjan & Gutierrez, 2019).

The research on sexual conditioning is predominantly with male quail. However, Domjan and Gutiérrez (2019) describe the organization of the female sexual behavior system and sex differences in sexual conditioning. For example, a conditioned approach appears to be prominent in male quail but not female quail. Rather female quail are more likely to demonstrate conditioned squatting behavior (Gutiérrez & Domjan, 1997) and conditioned approach to contextual cues where a male was housed (Gutiérrez & Domjan, 2011). From an evolutionary perspective, approaching the territory of a potential mate and squatting behavior during a mating encounter may be important for the reproductive success of the female quail. Thus, the sexual conditioning of female quail has also been explored as part of the behavior systems approach.

In conclusion, research conducted on sexual conditioning of male and female quail provides strong support for the integration of ethology and learning in accordance with the behavior systems approach. This integration of ethology and learning provides a more comprehensive understanding of sexual behavior relative to relying solely on traditional learning approaches.

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