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The behavior system for sexual learning☆

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ABSTRACT

In this paper we review and update evidence relevant to formulating a behavior system for sexual learning. We emphasize behavioral rather than neurobiological evidence and mechanisms. Our analysis focuses on three types of responses or response modes: general search, focal search, and consummatory or copulatory behavior. We consider how these response modes are influenced by three categories of stimuli: spatially distributed contextual cues, arbitrary localized stimuli, and species-typical cues provided by the sexual partner. We characterize behavior control by these types of stimuli before and after various Pavlovian conditioning procedures in which the unconditioned stimulus is provided by copulation with a sexual partner. The results document extensive Pavlovian modifications of sexual behavior. These conditioning effects reflect new conditioned responses that come to be elicited by various categories of stimuli. In addition, the conditioning of contextual cues and localized stimuli facilitate sexual responding to species-typical cues. Thus, learning experiences enhance how the species-typical cues of a sexual partner stimulate sexual behavior. These modulatory conditioning effects not only produce significant behavioral changes but also increase rates of fertilization of eggs and numbers of offspring produced. These latter findings suggest that sexual learning can lead to differential reproductive success, which in turn can contribute to evolutionary change.

1. Introduction

Consideration of behavior systems was a response to classic learning theories that attempted to be general theories of behavior, applicable to all responses and stimuli. General process learning theory was challenged by the discovery of a number of phenomena that showed that generality principles were not always empirically supported, especially when researchers attempted to provide functional and adaptive explanations for learning (Domjan, 1997; Shettleworth, 1998). A behavior systems approach seeks to integrate the strengths of laboratory learning theory with ethological observations, and emphasizes the organization of behavior (unlearned and learned) in a framework that reflects functional requirements and adaptive benefits for the organism.

Sexual behavior and sexual learning are ideal for analysis from a behavior systems perspective, as described by Timberlake (1983, 1994, 2001). Such an approach is encouraged because sexual behavior consists of a number of different types of responses, each of which is controlled by a different set or category of stimuli. Sexual behavior is more successful in promoting genetic transmission when all of these responses are coordinated in a systematic and functional manner. Hence the major challenge is to characterize how this coordination is achieved, or, to use Timberlake's language, to characterize how the behavior system is organized.

An important implication of the behavior systems perspective on learning is that the effectiveness and outcome of a conditioning procedure depends on how that procedure activates evolved behavioral structures that enable the species to cope effectively with major biological challenges such as feeding, defense, and reproduction (Burghardt and Bowers, 2017). Pavlov provided the core concept that motivates the behavior systems approach in his claim that conditioned responses are based on unconditioned behavior (Pavlov, 1927). In Pavlovian conditioning, a conditioned stimulus (CS) is paired with an unconditioned stimulus (US), with the result that the CS comes to elicit a response related to the responses that previously were only elicited by the US. How conditioned behavior is built on the structure of unconditioned behavior is analyzed in greater detail in the behavior

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systems approach to learning. Instead of regarding unconditioned behavior as just an unconditioned response to an unconditioned stimulus, the behavior systems approach views the substrate for learning as consisting of an integrated complex of behavioral units or response modes that a species brings to a learning situation.

The purpose of this paper is to describe the primary components of the behavior system for sexual learning. We think about sexual learning as much more than the development of a conditioned response. Rather, sexual learning is manifest in many different ways. We adopt Timberlake's perspective in thinking about sexual behavior as a system that is organized to achieve a major biological function, reproduction and genetic transmission from one generation to the next. We assume that the numerous ways in which sexual behavior can be altered by experience are part of an organized system that operates in a coordinated fashion to better achieve the reproductive function of sexual behavior. In this paper, we characterize the sexual learning system based on the evidence that is currently available. We do not claim that our characterization is complete or definitive but we hope that it provides a useful starting point for organizing research on sexual learning.

Our approach differs from Timberlake's in that he discussed the structure of behavior systems, not systems of learning. Behavior systems were introduced by classic ethologists in their efforts to characterize the behavior of animals from an ecological and biological perspective. Timberlake extended the behavior systems approach to better understand the impact of instrumental and Pavlovian conditioning procedures. Our approach builds on this progression by using numerous sexual learning effects and phenomena to characterize a learning system. (For reviews of research on sexual learning from other perspectives, see Akins, 2004; Brom et al., 2014; Krause, 2003; Pfaus et al., 2012; Woodson, 2002).

Our treatment substantially expands on previous descriptions of the sexual learning system by Domjan (1994), and Akins and Cusato (2015). We follow the approach of those earlier accounts in focusing on research with domesticated quail (*Coturnix coturnix japonica*) because we are most familiar with that species and because studies with quail have explored a much broader range of learning phenomena than studies of sexual learning with any other species. Although quail are not common research subjects in psychology, they are studied extensively in poultry science (Mills et al., 1997). They are relatively small birds and easily accommodated in laboratory settings. Sex hormones in quail (and the readiness of quail to engage in sexual behavior) are controlled by the photoperiod, which makes it easier to schedule sexual interactions with quail than with laboratory rats.

Although our discussion will be anchored on research with quail, we will also describe research with laboratory rats and other animals when relevant. We agree that behavior systems are more precisely described for an individual species, but we believe that some common phenomena and mechanisms exists among related species and identifying those commonalities may promote understanding how sexual behavior is modified by experience. Therefore, we describe what we consider to be a generally applicable system for organizing data on sexual learning. However, we look forward to modifications of our model as new data emerge that do not readily fit our current framework.

We begin with a description of the sexual behavior system prior to the introduction of a learning manipulation. We then describe various learning effects and show how these are superimposed on the unconditioned response profile. Much of the research on sexual learning has employed male participants; therefore, we begin with a review of sexual learning in males. We then turn our attention to how the sexual behavior of females may be modified by learning and how female sexual learning is different from learning in males. In the next section we discuss how Pavlovian signaling serves to fine tune the sexual interactions of males and females, with the consequence that copulatory behavior becomes more effective in producing offspring. In this section, we review the growing experimental literature on how conditioned fertility effects contribute to the outcome of sperm competition and sperm allocation. Finally, we discuss major issues that have yet to be adequately addressed in studies of the sexual learning system.

2. Organization of unconditioned sexual behavior

The ultimate function of sexual behavior is reproduction. However, the fertilization of eggs to produce offspring is often the end point of an intricate and long behavior sequence that begins with search for a potential sexual partner, followed by approach and courtship behavior. If the courtship is successful, the couple may move on to the various responses that are involved in copulation and then care of the embryo and the offspring.

Timberlake characterized behavior systems as consisting of a hierarchy of control units. The top of the hierarchy consisted of response modes, each of which may have several response modules. In characterizing the feeding or food capture system, for example, Timberlake identified three major response modes: general search, focal search, and food handling and ingestion. Since sexual behavior also involves approach to an attractive goal (in this case a sexual partner), we followed Timberlake's lead in characterizing the response modes involved in sexual behavior.

Fig. 1 summarizes the response modes that we have examined. General search behavior is manifest in increased locomotion and exploratory behavior that is not directed at a specific location. Focal search, in contrast, is more spatially restricted, being limited to particular area or spatially localized stimulus, such as the location of a potential sexual partner. The general and focal search response modes make up what ethologists previously referred to as appetitive behavior.

In the presence of a sexual partner, copulatory responses may occur. In male quail, copulation involves the male grabbing the back of the female's neck, mounting on top of her, and then making a series of cloacal thrusts. The grab, mount, and cloacal contact responses correspond to consummatory behavior in the ethological literature (see Gutiérrez, 2018). Fig. 1 shows the response modules associated with copulation (grab, mount, and cloacal contact response). We do not show response modules associated with the general and focal search modes because we have not identified or measured these empirically.

The response modes presented in Fig. 1 are adequate for the evidence that is available for male quail and rats. However, additional response modes will have to be considered for species that engage in elaborate courtship rituals or form pair bonds as a result of courtship.

Fig. 1 suggests that the activation of successive response modes is a

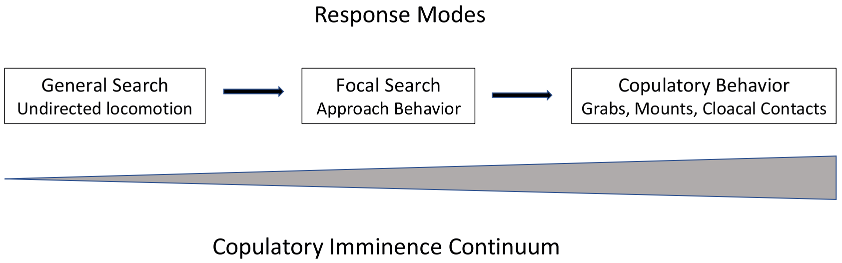

Fig. 1. Response modes of the sexual behavior system organized by copulatory imminence.

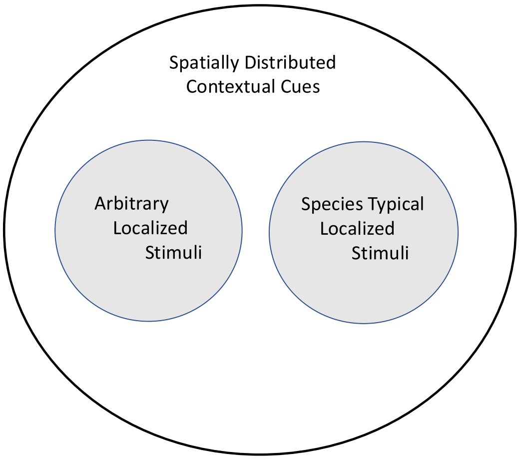

Fig. 2. Major stimulus categories in the sexual behavior system.

function of the imminence of encountering a potential sexual partner. When a sexual partner is not available, copulatory imminence is low and general search or focal search behavior is more likely than copulatory behavior. The concept of "copulatory imminence" was inspired by the "predatory imminence" continuum proposed by Fanselow for the defensive behavior system (e.g., Fanselow and Lester, 1988). The term "imminence" suggests that time is important in organizing the behavior system. However, as we will show, copulatory imminence also depends on stimuli that are encountered and the sexual significance of those stimuli.

We have considered three categories of stimuli in analyzing the sexual learning system. These are illustrated in Fig. 2. Consummatory or copulatory responses are initially elicited only by cues provided by a sexual partner. Since these cues are unique to a particular species, we refer to these as species-typical cues. Depending on the type of animal, species-typical cues for sexual responding may be visual, tactile, olfactory, or auditory cues. We used taxidermic models to identify the species-typical cues for quail sexual behavior. We found that a taxidermic female head with limited neck feathers is sufficient to elicit strong sexual responses in sexually experienced males (Domjan and Nash, 1988; Domjan, 1998). Thus, for male quail, species-typical cues for sexual behavior consist of visual features of a female's head and neck.

Species-typical cues occur in the presence of background or contextual cues. Contextual cues are not spatially localized and include stimuli such as overall levels of illumination, temperature, and background levels of noise. A third category of stimuli that we have been interested in are localized cues that are not inherently a part of the sexual behavior system, such as turning on a small light or tone. These are the types of stimuli that Pavlov used in his initial studies of conditioning. We refer to these types of cues as *arbitrary localized stimuli.*

The organization of the sexual behavior system prior to any form of conditioning or learning is illustrated in Fig. 3. The various response modes are presented on the horizonal axis and the different categories of stimuli are presented on the vertical axis. The darkness of the shading in each square represents the degree of control of a particular type of behavior by a particular category of stimuli. Prior to conditioning, general search behavior occurs primarily in response to spatially distributed contextual cues. Arbitrary localized stimuli have no particular significance prior to conditioning and are not likely to elicit strong orientation or approach responses. Therefore, in the unconditioned response profile, arbitrary local cues function as just features of the context and may elicit some general search behavior.

Species-typical cues are features of a female that generate strong approach and social proximity behavior. These responses bring the male closer to the female until physical contact and copulation occur. Thus, species-typical cues elicit strong focal search and copulatory responses in the unconditioned sexual response profile. We assume that general search is not elicited by species-typical cues because the presence of these cues serves to identify the location of the potential sexual partner, making general search responses unnecessary.

As we will show (see below), general search and focal search behavior can be measured in the laboratory, and which of these responses predominates depends on the temporal imminence of a sexual encounter with a female. In natural habitats, the sexual behavior sequence probably starts with general search responses that bring a male in the proximity of a female, at which point focal search responses take over. Once the female is encountered, the male may initiate courtship and copulatory responses.

3. Organization of the male sexual behavior system after conditioning

In studies of sexual learning, conditioning episodes or trials involve the presentation of a conditioned stimulus followed by access to a live female that typically results in copulatory behavior. Visual exposure to a female is an effective unconditioned stimulus for the sexual conditioning of male quail. However, stronger conditioned responses develop if exposure to the female also includes copulation (Holloway and Domjan, 1993b). We assume that sensory aspects of copulation are critical for these conditioning effects, but that has not been empirically verified. The conditioned stimulus in studies of sexual conditioning may consist of contextual cues, arbitrary local stimuli, or species-typical cues. Each of these three categories of stimuli can become readily associated with copulatory reinforcement in male quail. In some cases, the learning is directly evident in increased responding to the conditioned stimuli. However, often the most important consequence of learning is that the conditioned stimulus increases the effectiveness of species-typical cues in eliciting sexual behavior. These learning effects are summarized in Fig. 4.

3.1. Conditioning general search behavior

We measure general search behavior in the laboratory as an increase in non-directed locomotor behavior (line crossings on a grid on the floor of the test chamber). We assume that increased general search behavior occurs unconditionally in response to contextual cues when the sexual behavior system is activated (see Fig. 3). General search behavior can be also sexually conditioned, as indicated by the symbols in the left column of Fig. 4. Contextual cues may become conditioned to elicit general search behavior if exposure to a distinctive context becomes associated with sexual reinforcement. Akins (1998) found that the pairing of a distinctive context with sexual reinforcement in male quail results in increased locomotor behavior in that context. Thus, sexual conditioning can increase general search behavior elicited unconditionally by contextual cues.

Laboratory rats also show an increase in locomotor behavior in response to sexually conditioned contextual cues. In this species, a bi-level chamber is used to provide the contextual cues. The chamber has two levels, with transit from one level to the other made possible by connecting ramps. When exposure to the bi-level chamber for male rats is associated with sexual reinforcement, increased locomotor behavior develops as the conditioned response. The increased locomotion is measured in terms of more frequent changes from one level of the chamber to the other (e.g., Mendelson and Pfaus, 1989).

General search behavior also occurs as a conditioned response to a localized arbitrary cue. However, an important boundary condition for this effect is that the CS be presented for a relatively long duration (20 min rather than 1 min) (Akins, 2000; Akins et al., 1994).

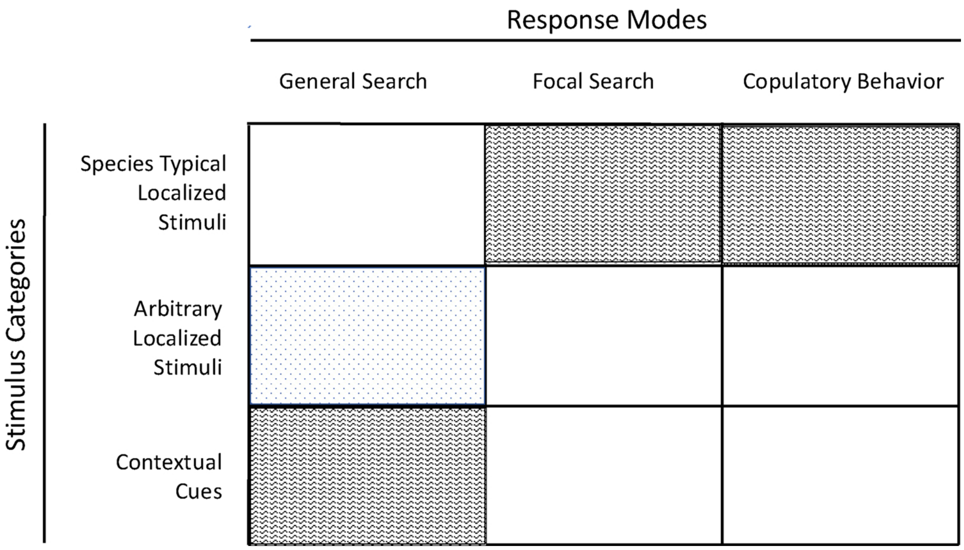

Fig. 3. The unconditioned response profile of the sexual behavior system. Degree of shading represents strength of control of a particular response mode by a particular stimulus category.

3.2. Conditioning focal search or approach responses

Learned responses that consist of approaching the conditioned stimulus can be conditioned with contextual cues, local cues, and species-typical cues. Conditioning of focal search or approach behavior is represented by the symbols in the middle column of Fig. 4.

3.2.1. Conditioned approach to contextual cues

Conditioning of sexual approach behavior to contextual cues is investigated using the place preference procedure (Tzschentke, 2007). In one application of the procedure with male quail, Akins (1998) employed two distinctive contexts differentiated by the texture of the floor (sand vs. wire mesh) and the color of the walls and ceiling (orange vs green). Placement of a male quail in one of the contexts was paired with access to a female in that context whereas placement of the male in the alternate context was not paired with a female quail. After every fifth conditioning trial, the birds were given a choice between the two contexts. The conditioning trials resulted in a strong preference for the conditioned context, indicating approach to that context.

Evidence of place preferences conditioned with sexual reinforcement has been also obtained in studies with female quail (Gutiérrez and Domjan, 2011), and both male and female rats (see Pfaus et al., 2001, for a review). A significant finding in this area of research is that the preference of female rats for a context associated with copulation is greater if the females are allowed to pace their copulatory interactions with the male (Paredes and Alonso, 1997; Paredes and Vazquez, 1999).

3.2.2. Conditioned approach to localized arbitrary cues

The most common measure of sexual conditioning in male quail is conditioned approach to an arbitrary localized stimulus. A variety of localized stimuli have been used successfully to conditioned approach behavior in male quail. These have included a small light, a block of foam or wood, and a terrycloth object that the males could mount and copulate with. In fact, every localized arbitrary cue that we have tried was effective as a CS in conditioning sexual approach behavior in male quail. Furthermore, the conditioned approach behavior developed even if an omission contingency was used in which presentation of the sexual US was cancelled when the subject made the approach response (Crawford and Domjan, 1993).

With the use of arbitrary localized conditioned stimuli we have been able to demonstrate many major features of Pavlovian conditioning, including acquisition (e.g., Domjan et al., 1986), extinction (Domjan et al., 1986; Krause et al., 2003), stimulus discrimination, conditional discrimination, and trace conditioning (Akins and Domjan, 1996; Burns

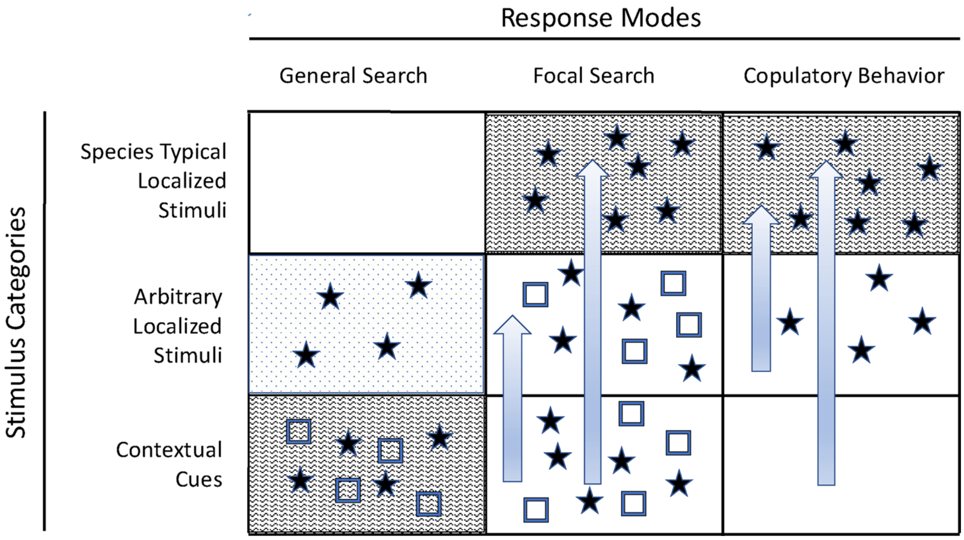

Fig. 4. Modification of the sexual behavior system for males by Palovian conditioning. Symbols in each quadrant represent conditioning effects. Stars represent data from studies with quail. Small squares represent data from studies with rats. Arrows indicate how conditioning enables certain cues to modulate responding to other types of stimuli. The origin of each arrow represents the modulating stimulus and the tip of the arrow represents the target of the modulation. The shading of the background is the same as in Fig. 2 and represent strength of control of each response component unconditionally.

and Domjan, 1996, 2000), blocking (Köksal et al., 1994), conditioned inhibition (Crawford and Domjan, 1996), US devaluation effects (Hilliard and Domjan, 1995; Holloway and Domjan, 1993a), second-order conditioning (Crawford and Domjan, 1995), and relative waiting time effects (Burns and Domjan, 2001).

Sexual conditioned approach behavior is also evident if the conditioned stimulus is a feature of the sexual partner rather than a feature of the inanimate environment in which copulation takes place. In an early study of this effect, Domjan et al. (1988) adorned a female quail with a large bright orange feather on each side of her back. During conditioning trials, the adorned female was presented behind a wire screen as the CS. Following exposure to the adorned female, a normal female was released into the chamber to provide the copulatory unconditioned stimulus for birds in the paired group. Birds in a control group received exposures to the adorned female unpaired with copulation. The conditioning procedure significantly increased how much time males spent with the adorned female. Conditioned males also became more likely to copulate with the adorned female when the wire screen separating the adorned female was removed.

Sexually conditioned approach behavior is also evident in the studies of conditioned partner preference in rats (see review by Coria-Avila et al., 2016). In a foundational demonstration of this effect (Kippin et al., 1998), a distinctive odor (almond extract) applied to a female rat was used as the CS. During conditioning trials, males were permitted to interact with either sexually receptive or nonreceptive females. For males in the paired group, the CS scent was always applied to the sexually receptive female. Following nine paired trials, the participants received a choice between two sexually receptive females, one scented with the almond odor and the other not scented. Males for whom the scent was previously paired with access to a sexually receptive female ejaculated first and more often with the scented female (see also Kippin and Pfaus, 2001; Kippin et al., 2001). Although conditioned approach behavior was not directly measured in these experiments, ejaculatory preference no doubt involved approaching one female more often than another.

3.2.3. Conditioned approach to species-typical cues

Unlike arbitrary localized stimuli, species-typical cues provided by a potential sexual partner elicit approach behavior unconditionally (see Fig. 3). However, such cues can also gain additional behavioral control through Pavlovian conditioning. This conditioning effect is evident when the species-typical cues are limited so as to avoid a behavioral ceiling effect. Köksal et al. (1994) used a conditioned stimulus object that was made mostly of terrycloth stuffed with cotton. One portion of the terrycloth object was a horizontal pad the quail could mount. This was positioned behind a vertical section that they could grab. The top of the vertical section had limited species-typical cues provided by the taxidermically prepared head and some neck feathers of a female quail (see Fig. 5).

Two groups of sexually naïve male quail served in the experiment. For birds in the paired group, a 30-sec presentation of the CS object was followed by the release of a female into the experimental chamber for 5 min. For birds in the unpaired group, the opportunity to copulate with a female was provided 25–35 min before exposure to the CS object. For both groups, every third trial was a CS-alone test trial. Approach to the CS object across trials is presented in Fig. 5. The males did not approach the CS object on the first trial. However, a robust approach response developed quickly in the paired group, with asymptotic behavior evident after just four conditioning trials. A much lower level of approach responding was evident among birds in the unpaired group throughout the experiment. These results show that limited species-typical cues that do not elicit much approach behavior unconditionally can become conditioned rapidly to elicit vigorous responding.

The fact that species-typical cues can become conditioned with sexual reinforcement does not prove that these types of cues operate differently than arbitrary localized stimuli. However, systematic comparisons of conditioning with species-typical cues vs. arbitrary local cues indicates that species-typical cues support more robust conditioned behavior in a number of respects. A conditioned stimulus object that includes limited species-typical cues can be conditioned more rapidly than a comparable object that lacks species-typical features. Including species-typical cues in a CS object facilitates the conditioning of copulatory responses and also facilitates second-order sexual conditioning. Further evidence of more robust conditioning with species-typical cues is evident in insensitivity to increases in the CS-US interval, resistance to extinction, and resistance to the blocking effect (see reviews by Akins and Cusato, 2015; Domjan et al., 2004).

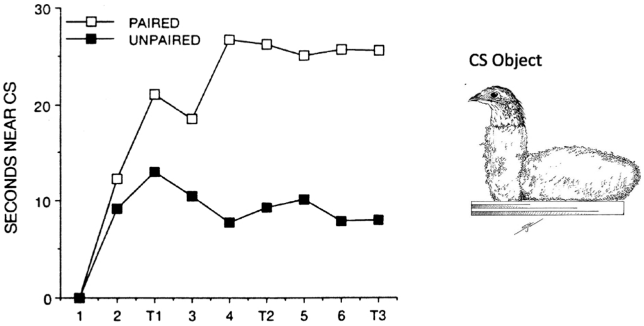

Fig. 5. Conditioned approach to a CS object that consists of limited female cues on a terrycloth object. For the Paired group, the CS object was presented just before copulation with a female during conditioning trials. “T” represents unreinforced test trials with the CS. (Based on Köksal et al., 1994).

What makes species-typical cues especially effective in sexual conditioning is not fully understood. Adding limited female cues to a CS object makes that object more similar to the unconditioned stimulus (which is access to a live female). CS-US similarity is no doubt one of the factors that makes CS objects with female features especially effective in sexual conditioning (Cusato and Domjan, 2012). However, CS-US similarity cannot account for all of the results (Cusato and Domjan, 2000), suggesting that other factors also may be involved.

3.3. Conditioning copulatory responses

Copulation in male quail consists of the male grabbing the rear of the female’s head, mounting on her back, and then making a series of cloacal contact movements, which serve to transfer sperm to the female. The grab (G), mount (M), and cloacal contact movement (CCM) responses are elicited unconditionally by the species-typical cues provided by a female. These responses can also come to be directed toward conditioned stimuli that have become associated with sexual reinforcement. Conditioned copulatory responses are represented by the stars in the right column of Fig. 4.

A critical factor determining whether or not conditioned copulatory responses develop is the nature of the CS. Copulatory responses involve coordinated interactions with the eliciting stimulus (grabbing and mounting the CS). Conditioned stimuli that do not support such behaviors will not come to elicit conditioned copulation. Thus, conditioned copulatory responses do not occur in response to contextual cues or tones or lights. Three-dimensional objects are more likely to provide the required supporting stimulation but not all objects are equally effective. We have not observed the development of conditioned copulatory responses to a block of wood or hard foam, or a small stuffed toy. However, male quail can be readily conditioned to grab, mount, and make cloacal contact movements to a CS that consists of a terrycloth object with a taxidermic female head and some neck feathers (Cusato and Domjan, 1998). Interestingly, less conditioned responding occurs to the same type of terrycloth object if the object lacks the female head.

We have found two ways to promote conditioned copulation with a terrycloth object that is entirely lacking species-typical features. One method involves first establishing copulatory responses to a CS object that includes substantial taxidermic female features. At this point, the female cues can be gradually covered with terrycloth across trials without loss of the conditioned copulatory behavior. Fading out female cues in this fashion results in a transfer of conditioned copulatory behavior from the species-typical cues to the arbitrary terrycloth object (Domjan et al., 1992b). However, even with the fading strategy only about half of the males exhibit conditioned copulatory behavior. Thus, unlike conditioned approach, which occurs in all birds, conditioned copulatory behavior is not inevitable even if a fading procedure is used.

The experiments on fading out female cues employed 15 conditioning trials. In subsequent research, a terrycloth model without species-typical cues was used as the CS from the start of a training sequence that extended to 30 conditioning trials (Çetinkaya and Domjan, 2006; Köksal et al., 2004), which is a large number of trials for a quail sexual conditioning protocol. The probability of males grabbing and mounting the CS object increased with the extended sexual conditioning protocol. However, even with so many conditioning trials, only about half of the male birds came to make conditioned copulatory responses. Interestingly, the males that showed conditioned copulatory responses to the terrycloth CS also showed greater resistance to extinction when the terrycloth CS was repeatedly presented without sexual reinforcement in an extinction procedure (Köksal et al., 2004). In a subsequent experiment (Köksal et al., 2017), males that developed conditioned copulation with the terrycloth CS also showed more second-order conditioning when the terrycloth CS was subsequently paired with a new CS (a flashing light or a cylindrical object). These results suggest that for birds that show conditioned copulatory responses to a terrycloth object, this object comes to function somewhat like a US.

3.4. Conditioned modulatory influences between stimulus categories

As previously reported, Pavlovian conditioning results in the emergence of conditioned responses to a CS associated with sexual reinforcement. In addition to these direct effects, a Pavlovian CS may also alter or modulate how the participants respond to other cues. Such modulatory effects have been most often observed with conditioned context cues. Conditioned context cues may modulate sexual conditioned responding both to arbitrary localized conditioned stimuli and to species-typical cues. Modulatory effects in sexual conditioning are illustrated by the arrows in Fig. 4. The origin of each arrow represents the modulating stimulus and the end of the arrow represents the target of the modulation.

3.4.1. Modulatory effects of context on responding to a localized arbitrary CS

The study of contextual cues as modulators of responding to localized conditioned stimuli has a long history in studies of conditioning and learning (see Schmajuk and Holland, 1998; Swartzentruber, 1995). Such studies typically involve a conditional discrimination. In the first demonstration of context modulation of conditioned responding in sexual conditioning, Domjan et al. (1992a, Experiment 2), used a small wood box as the localized CS. The CS was presented equally often in each of two different contexts. The two experimental contexts were differentiated in height, type of flooring (wire-mesh or sand), color of the walls, background noise, ambient lighting, and the presence (or absence) of wood branches.

The male quail received 20 conditioning trials in each context. In one of the contexts, presentation of the localized CS was paired with the release of a female and consequent sexual reinforcement. This was designated as the “sexual” context. Exposure to the CS in the alternate context (the “nonsexual” context) was never followed by access to a female. The conditional discrimination procedure produced much more conditioned approach behavior to the CS in the sexual context than in the alternate context, indicating that the contextual cues came to control conditioned approach to a localized arbitrary CS (See also Akins, 1998).

3.4.2. Modulatory effects of context on responding to species-typical cues

Contextual cues that have been paired with sexual reinforcement also increase responding to species-typical cues. In fact, this is one of the most robust effects in the sexual conditioning literature, although it is not always characterized in these terms. As we will discuss in later sections, context modulation of responding to species-typical cues results in enhanced sexual performance. In an early demonstration of this effect, Domjan et al. (1989) housed male quail in a large experimental chamber or in a smaller wire mesh home cage on alternate days. One group of males received access to a female on 15 occasions when they were in the experimental chambers. For another group, the mating trials were conducted in the home cages. The response of both groups to limited female cues was then tested in the experimental chambers. For this test, a terrycloth object that included the taxidermic head and neck of a female quail was introduced into the experimental chamber for the first time.

Responding to the limited female cues was measured by counting the number of grabs, mounts, and cloacal contact responses the males directed at the head + neck terrycloth model. Birds for whom the prior copulatory episodes occurred in the experimental chamber were much more likely to make copulatory responses to the head + neck model than birds in the control group that had equal prior sexual experience but in the home cages. Copulatory responses to the limited female cues occurred in 72% of the birds that received context conditioning. In contrast, only 18% of the subjects in the control group made any grabs, mounts, or cloacal contact responses to the head + neck model.

In the above experiment, 15 context conditioning trials were conducted before the test for enhanced responding to limited species-typical cues. In subsequent research, Hilliard et al. (1997) found the context modulation of responding to female cues is such a robust phenomenon that a single context conditioning trial is sufficient to obtain the effect. Males in these experiments were exposed to a novel experimental context for 0–4 min and were then allowed to copulate with a female in that context. Birds in the control group also received exposure to the experimental context but their copulatory access to a female was provided in the home cages unpaired with the context exposure. One day after the single context conditioning trial, subjects were tested for their response to a female head + neck model presented in the experimental chamber. On average, birds that received context conditioning spent more than four times as much time near the model than birds in the control group. The single context conditioning trial also significantly increased the likelihood that the male quail would attempt to mount and copulate with the head + neck model.

A subsequent experiment also employed a context conditioning procedure, followed by a probe test of responding to a head + neck model in the conditioned context (Domjan et al., 1998). However, in addition to measuring time spent near the probe stimulus, we also measured and analyzed the semen males released as a consequence of interactions with the head + neck model. As in earlier experiments, context conditioning increased the effectiveness of female head + neck cues in eliciting approach and copulatory responses. This context modulation of responses to female cues also resulted in the release of greater quantities of semen and sperm.

In the above experiments, the effects of a sexually conditioned context were measured by introducing a probe stimulus with just limited female features because of concern that additional female cues might elicit unconditioned sexual responses that would obscure clear evidence of conditioning. The approach employed in these experiments followed the common strategy of using CS-alone test trials to measure conditioning effects so as to preclude unconditioned responding during testing. Although most of the Pavlovian conditioning literature is based on this CS-alone test trial methodology, a growing body of evidence suggests that the adaptive significance of Pavlovian conditioning does not depend on how subjects respond to the CS but how a CS alters responding to the unconditioned stimulus (see review by Domjan, 2005).

Species-typical cues are essentially components of a US. In our program of research, the sexual US for a male bird is copulatory access to a female. Female head + neck cues presented in a terrycloth model are components of the stimuli that are provided by a live female sexual partner. Therefore, the increased responding to species-typical cues documented in the above experiments are examples of conditioned modifications of responding to an unconditioned stimulus. These results suggest that conditioned contextual cues may also alter how males interact with a live female. That prediction has been confirmed in studies with both quail and rats.

In an early study of sexual conditioning in male rats, the CS consisted of contextual cues provided by placing the rats in a plastic tub before carrying them to a test room for exposure to a female (Zamble et al., 1985). Conditioned sexual arousal was measured by a decrease in the latency of the males to ejaculate when they were given access to a sexually receptive female following exposure to the CS during a post-conditioning test trial. No change in ejaculatory latency was observed among males that had CS exposures presented unpaired with exposure to a female. However, the latency to ejaculate was substantially lower for male rats that previously received paired presentations of the CS context with exposure to a female rat. The shorter latency to ejaculate among the paired subjects reflects enhanced responding to the species-typical cues of a sexually receptive female.

In a subsequent study, Domjan et al. (1988) found that conditioned contextual cues increase social proximity behavior in male quail. Social proximity behavior was measured by how much time males spent near a window through which they could see a female. Males spent significantly more time near the window in a context that had been sexually conditioned than in a control context.

3.4.3. Modulatory effects of localized stimuli on responding to species-typical cues

Conditioned localized stimuli can also enhance the effectiveness of species-typical cues in eliciting sexual behavior. This phenomenon was observed in the initial demonstration of the sexual conditioning of approach behavior to a small red light (Domjan et al., 1986). In addition to approaching the light, conditioned males also had shorter latencies to grab and copulate with the female US that was presented after the light. Grabbing the female to initiate sexual contact was a response to cues provided by the female and not a response to the red-light CS. Therefore, this is an example of conditioned facilitation of responding to species-typical cues.

Working with a species of fish, the blue gourami, Hollis et al. (1997) conducted conditioning trials in which a light was presented for 10 s, followed by exposure to a female behind a barrier for 5 min. Fish in a control group received these stimulus presentations in an unpaired fashion. After 18 conditioning trials, the barrier separating the male and female was removed after presentation of the 10-sec CS and the two fish were permitted to interact continuously for the next six days. During these interactions, conditioned males made fewer aggressive responses (bites) towards the female, engaged in more nest building, made more clasp and copulatory responses, and produced many more offspring. The facilitated courtship and sexual behavior of the conditioned males was a response to the cues provided by the female since the CS was not present during these interactions. Thus, this study provides additional evidence of the facilitation of responding to species-typical cues by the presentation of a sexually conditioned localized stimulus.

4. Organization of the female sexual behavior system

Much of what we have discussed so far involved the behavior of male participants. How about females? An important assumption of the behavior systems approach is that the outcome of conditioning procedures is best understood in terms of how those procedures interact with the behavioral organization that organisms bring to a learning situation. Males and females differ in fundamental ways in their sexual behavior and those preexisting differences may significantly influence the outcomes of sexual conditioning procedures.

In a landmark paper, Trivers (1972) argued that differences in gamete size (anisogamy) between males and females reflect differences in parental investment, and these differences have far reaching consequences for many aspects of the sexual behavior of males and females. Because eggs are typically much larger than sperm (and energetically more costly to produce), females invest more in their offspring than do males. As a consequence, males tend to compete more among each other for access to females whereas females tend to choose among available males. This yields significant differences in the mechanisms of mate choice for males and females.

Extending Trivers' differential parental investment theory, Domjan and Hollis (1988) argued that male-female differences in parental investment should be reflected in corresponding differences in sexual learning. Because of their lower parental investment, males should take advantage of every opportunity to mate and should have lower thresholds for sexual arousal. As a consequence, sexual arousal (and related proceptive responses) should be more easily conditioned in males than in females, conditioned to a wider range of cues, and perhaps be evident in more proactive forms of behavior.

The evidence reviewed in the preceding section confirms that sexual conditioning readily occurs in males and sexual learning occurs with a wide range of different types of stimuli. However, the above studies did not directly compare how sexual conditioning occurs in male and female participants. In many species, male courtship and proceptive responses are more prominent and easier to observe than female responses. For example, sexually active male Japanese quail exposed to a female conspecific quickly approach, grab, and mount the female. In contrast, female quail do not show immediate proceptive responses when placed in the presence of a male (Mills et al., 1997). It is mostly when the male approaches and grabs the female that she may show signs of receptivity in the form of squatting.

4.1. Sex differences in approach or focal search behavior

The first evidence we obtained indicating that male and female quail differ substantially in how they manifest sexual interest came from a study of social proximity behavior (Domjan and Hall, 1986). Male/female pairs of quail were housed together in a large arena. For a test session, one of the birds was placed under a clear plastic hood and we measured how much time the unrestrained bird spent near its partner. In a control condition, the plastic hood was empty. If the female was under the hood and the male was free to roam the experimental chamber, the male spent most of its time near the restrained female. In fact, the male spent much more time close to the clear plastic hood when it contained a female than when it was empty. Comparable results did not occur with the female quail. Having a male under the clear plastic hood did not change how much time females spent near the hood. Thus, females did not show a tendency to approach the location of a male or the species-typical cues provided by a male.

Consistent with the failure of female quail to approach and spend time near a male cage mate, females also fail to show conditioned approach behavior to a CS object that has been paired with access to a male. Whereas conditioned approach is a prominent aspect of sexual conditioning of male quail, this type of behavior is absent in female quail (Gutiérrez and Domjan, 1997, Experiment 1).

4.2. Conditioned modulation of female responses to male species-typical cues

Although female quail do not show sexually conditioned approach responses, sexual conditioning is evident in how females interact with a

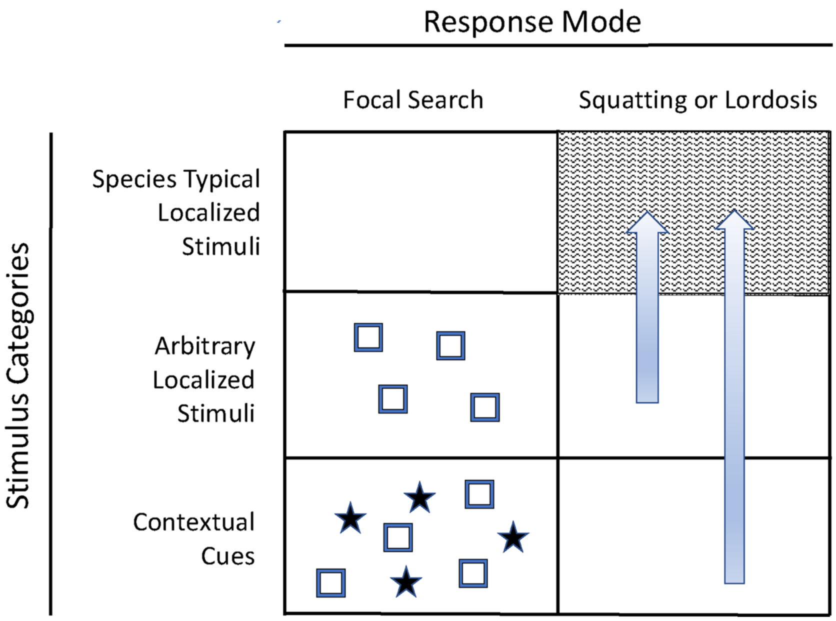

Fig. 6. Female response profile. Shading represents unconditioned control of behavior. Stars represent conditioning effects with quail. Open squares represent conditioning effects with rats. Arrows represent conditioned modulation of the effectiveness of species typical cues in eliciting sexual behavior in both quail and rats.

male following exposure to the CS. Sexually conditioned females are more likely to squat when a male is released and show longer durations of squatting behavior in response to the male. These effects are related to the ability to predict the release of the male. Longer durations of squatting occur if the male is released after exposure to a localized CS that was previously paired with access to a male. Exposure to an unpaired CS does not yield increased squatting behavior (Gutiérrez and Domjan, 1997, Experiments 2 and 3).

It is important to note that the increased squatting behavior that was observed as a conditioned response among female quail by Gutiérrez and Domjan (1997) was not a response to the CS that was paired with access to a male. Rather, it was a response to the male bird (US) that was presented after the CS. Thus, this conditioning effect is an example of conditioning increasing the effectiveness of the species-typical cues provided by a male in eliciting squatting behavior on the part of the female. This result is represented by the shorter arrow in Fig. 6.

Increased reactivity to the species-typical cues that are provided by a male is also produced by conditioned contextual cues. This is represented by the longer arrow in Fig. 6. Evidence for modulation of reactivity to species-typical cues by conditioning contextual cues in female quail may be inferred from data on conditioned fertility effects in female quail (Adkins-Regan and MacKillop, 2003). As explained below (Section 5), increases in fertilization success reflect increased efficiency of copulation by the male, which is controlled primarily by female squatting and immobility.

4.3. *Conditioned place preference or approach to contextual cues*

In addition to modulation of how females respond to the cues provided by a male, sexual conditioning of females can also produce a preference for the place or context where males were previously located (Gutiérrez and Domjan, 2011). In these experiments, male/female pairs of quail were housed in two distinctive compartments separated by a wire-mesh screen. After three days, a spatial preference test was conducted with the wire screen removed. The male was also removed for the test trial so that the female's behavior would only reflect her spatial preference. Using both a between-subjects design and a within-subjects design, females showed increased preference for the area where the male was previously housed. In contrast, having a female housed in the target area had no effect on spatial preference. Thus, the increased spatial preference was a sexual conditioning effect rather than a more general social learning phenomenon. This phenomenon is represented by the stars in the left column of Fig. 6.

It is important to note that the female context conditioning effect reported by Gutiérrez and Domjan (2011) was produced by having the presence of a male associated with distinctive spatial cues. No copulation was involved during the conditioning phase. This may have been an important aspect of the procedure used. Copulation with a male may sometimes have aversive components for a female, which might work against the conditioning of a preference for the context where the male was encountered. Evidence consistent with that prediction has been obtained in studies of sexual conditioning of female rats.

Female rats show a preference for a spatial context in which they previously copulated with a male but their preference is even greater if they were exposed to a male in that area behind a barrier in the absence of copulation (Oldenburger et al., 1992). Because of this effect, spatial preference conditioning in female rats is typically conducted by permitting the females to pace their copulation with a male during the conditioning trials (Paredes and Alonso, 1997). Paced copulation is achieved with the use of an apparatus that allows the female to enter an area housing a male, without the male being able to enter the female's area. Using the paced copulation method, female rats have shown sexual conditioning to contextual cues as well an arbitrary odor applied to the male (Coria-Avila and Pfaus, 2007). These results are represented by the open squares in Fig. 6.

5. Putting it all together: interactions between males and females and fertilization success

So far, we discussed how the sexual behavior of males and females can be modified by learning. In most of that research, only the behavior of the target animal was observed and conditioned. The behavior of a male or a female is easy to observe independent of a sexual partner if the focus is on general search or focal search responses or place preferences because these behaviors can be measured in test trials that exclude the sexual partner. Consummatory or copulatory responses can be measured for one sex independent of the other if the behavior occurs in response to an inanimate model (e.g., Çetinkaya and Domjan, 1998).

The effects of learning on copulatory efficiency can also be measured in the context of sexual competition, which is more complex because it includes not only a mating pair, but also a male competitor. Gutiérrez and Domjan (1996) evaluated the idea that a CS would improve copulatory efficiency in a competition situation by facilitating a male's approach to the female. Male quail were conditioned individually with an auditory cue (CS) that signaled the availability of a female in a large test arena (12 m × 6 m). Following the conditioning phase, two males were introduced to the arena at the same time for the opportunity to copulate with a single female. During this test, the cue that signaled the female was presented for one of the males but not for the other. The males for whom the CS signaled the presence of a female copulated with her first in the competition test.

The Pavlovian signaling effect just described was extended subsequently to competition between males of different social or dominance status. At the outset of the experiment, Montoya et al. (2016) evaluated the copulatory efficiency of each of three males in a group. As expected, winner (dominant) males showed higher copulatory efficiency than middle or loser males. Loser males were then trained in a Pavlovian situation in which a CS signaled access to a female. Winner and middle males received an unpaired training procedure. During post-conditioning tests, all three males were allowed again to compete for access to a female quail. When the CS was presented, the conditioned males copulated faster than the middle or dominant males. This shows that Pavlovian learning improved copulation efficiency and turned previously loser males into winners in competing with two other males for access to a female.

Copulation or other form of sexual interaction with a live sexual partner typically involves behavioral contributions by both the male and the female. Parsing the relative contributions of the two participants can be methodologically challenging. When domesticated quail (*Coturnix japonica*) are permitted to copulate in a laboratory test chamber (which is usually about a square meter), the male approaches, grabs, and mounts the female so aggressively that it is difficulty to observe or measure what is the behavioral contribution of the female to the copulatory sequence. Domjan et al. (2003) used a behavior genetics approach to assess the relative contribution of males and females in the copulatory behavior sequence. The quail in this study had undergone 24 generations of genetic selection for either high sociality or low fearfulness based on behavioral testing during the first 10 days post-hatch. In adulthood, the quail in the high sociality line showed more vigorous sexual behavior than those in the low fear line (Burns et al., 1998).

Domjan et al. (2003) tested the copulatory behavior of male-female pairs that had the same genetic history as compared to pairs in which the male and female were from different genetic lines. Interestingly, the latency of the male to grab, mount, and make cloacal thrusts on the female were determined primarily by the female's genetic history. If the female was from the high sociality line, the male initiated copulation more quickly. The male's own genetic history did not influence its latency to copulate with the female. The frequency of grabs, mounts, and cloacal contact responses was not influenced by the genetic history of either the male or the female. However, the efficiency of the male's copulatory behavior was strongly influenced by the genetic line of the female. Copulatory efficiency was measured in terms of how often a grab response ended in a cloacal contact response. A male that is unable to mount and make cloacal contact after grabbing the female is likely to return and try again. Thus, inefficient copulations are characterized by numerous grabs and mounts but few cloacal contacts. As with the male's latency to initiate copulation, the copulatory efficiency of the male was determined primarily by the genetic history of the female. These results show that measures of copulatory latency and efficiency reflect the female's contribution to copulatory interactions between a male and a female. Females may facilitate shorter copulatory latencies and more efficient copulations by the male by squatting and not running away when the male grabs and mounts the female.

Another measure of sexual behavior, the most important measure from an evolutionary perspective, is the rate of successful fertilizations or numbers of offspring that are produced as a result of the copulation. Domjan et al. (2003) made detailed observations of the copulatory behavior of male-female pairs of quail from an unselected genetic line of quail. In addition to measuring copulatory latency and efficiency, this experiment included measures of female immobility or squatting in the presence of the male. After the copulation test, the eggs produced by the females were collected and incubated to see how many of them were fertilized.

Female quail produce about one egg per day and store sperm so that 6–8 eggs can become fertilized following a single copulatory episode. Domjan et al. (2003) found that longer durations of female immobility were associated with shorter latencies of the male to initiate copulation and greater efficiencies in male copulatory behavior. These behavioral parameters were in turn strongly associated with greater numbers of fertilized eggs produced. Fertilization rates were positively correlated with female immobility and male copulatory efficiency and negatively correlated with male copulatory latency. These results suggest that fertilization rates are determined by the joint behavioral contributions of the male and the female. The results also indicate that the rate of fertilization can be used as a simple proxy for the behavioral contributions of both the male and the female to a copulatory interaction.

5.1. *Conditioned increases in fertility and reproductive success*

As we have seen, fertilization rates are related to the duration of squatting or immobility on the part of the female during a copulation episode (Domjan et al., 2003), and squatting in the presence of a female can be conditioned to cues predictive of a copulatory encounter (Gutiérrez and Domjan, 1997). These results imply that a sexual conditioning procedure should also increase how many fertilized eggs result from a copulatory interaction. This prediction has been confirmed in a growing number of studies.

In our initial experiment on conditioned fertility (Mahometa and Domjan, 2005), male-female pairs of quail were housed on opposite sides of an opaque barrier. The conditioned stimulus was the presentation of a small light near the doorway separating the two compartments. The CS was presented to both the male and the female bird for 30 s on each conditioning trial, followed by opening of the door to allow the male and female to copulate. All of the male-female pairs received the identical conditioning procedure. After 15 conditioning trials, a copulatory test trial was conducted during which the door separating the male and female compartments was opened. For independent groups, this copulatory period was preceded by presentation of the CS signal to both the male and female subject, just the male bird, just the female bird, or neither of the two birds. The eggs produced during the next 10 days were then collected and checked for the presence of a chick embryo.

Presentation of the sexually conditioned CS to both the male and female of a given pair increased the efficiency of the copulatory interaction and also significantly increased the rate of fertilized eggs that resulted from the copulation. Interestingly, presenting the CS to just the male or just the female bird of a pair had no effect. These results show that sexual conditioning increases fertilization success and confirm that fertilization success is facilitated by the behavioral contributions of both the male and the female bird.

The findings of Mahometa and Domjan (2005) are similar to demonstrations of increased fertility produced by sexual conditioning in the blue gourami fish (Hollis et al., 1997) and the Japanese quail (Adkins-Regan and MacKillop, 2003). In the experiment with the blue gourami, only the male received the sexual conditioning procedure. Thus, in the gourami, sexual conditioning of the male appears to be sufficient to yield increased fertilization success. Adkins-Regan and MacKillop (2003) tested for conditioned fertility in quail under circumstances in which only the male or only the female received the sexual conditioning procedure and found increased rates of fertilization in both cases. In contrast to these results, Mahometa and Domjan

(2005) observed increased fertility only when both the male and female were signaled during the postconditioning test for copulation.

Why conditioned increase in fertilization seems to require signaling both the male and the female in some cases but not in others remains to be investigated. The species tested is no doubt critical. In the blue gourami, the female contributes the eggs but the male is responsible for nest building and caring for the eggs after they have been deposited in the nest. That is very different from quail, which fits the more common pattern of greater parental investment by females than males.

5.2. Conditioned fertility and sexual competition between males

The fact that exposure to a sexually conditioned CS increases fertilization success demonstrates that Pavlovian conditioning contributes directly to reproductive fitness. The discovery of conditioned fertility effects shows that Pavlovian conditioning processes are directly involved in how evolution shapes the distribution of phenotypic traits in future generations. But, the course of evolution is determined not only by the absolute rate of reproduction of certain individuals but also their relative rates of reproduction in comparison to other members of the species. The importance of relative rates of reproduction are highlighted in situations involving sexual competition. Sexual competition occurs when two males copulate with the same female or when one male copulates with several females.

As we noted earlier, Pavlovian signaling enables a male to copulate with a female first in sexual competition situations in which two or three males compete to copulate with a single female. Does Pavlovian signaling also enable a male to fertilize more of the eggs that a female produces in a situation where two males copulate with a single female? This question was addressed by Matthews et al. (2007). Contextual cues were used as the CS. Male and female quail were placed in one of two distinctive experimental chambers. Placements in one of the chambers (the sexual context) was paired with copulatory access to a sexual partner. Placements in the alternate context (the nonsexual context) occurred without copulatory opportunity. During the critical test for sexual competition, two males were permitted to copulate with the same female in succession. These copulations occurred in a conditioned context for the female. For one of the males the test context was sexually conditioned whereas for the other male the test context was not conditioned. Whether the signaled male copulated first or second with the female was counterbalanced across females.

Which of the males fertilized more of the eggs that were laid by the female during the next 10 days was then determined using a microsatellite-based DNA fingerprinting procedure. Significantly more of the eggs produced (72%) were fertilized by the males for whom the copulation occurred in the sexual context as compared to the males that copulated in the nonsexual context (28%). The order in which the two types of males copulated with the female did not make a significant difference. A control experiment showed that in the absence of Pavlovian conditioning, the first and second male fertilized about equal numbers of eggs. These results show that in a sexual competition situation, paternity is biased in favor of males who expect the copulatory interaction because of their prior conditioning history. Thus, the conditioned fertility effect is evident not only in isolated copulations but also in situations where a female copulates with multiple males.

In the above experiment, 15 min separated the two copulatory periods that each female received. If the interval between the two copulatory periods is much longer (5 h rather than 15 min), the second male has a substantial advantage in fertilizing the eggs that are subsequently produced. In the absence of a Pavlovian signal for either male, the first male is responsible for just 26% of the fertilized eggs that are produced whereas the second male is responsible for 74% of the fertilized eggs (Domjan et al., 2012). Matthews (reported in Domjan et al., 2012) examined what would happen to the first-male disadvantage if copulation with the first male was signaled by a Pavlovian conditioned CS whereas copulation with the second male was not signaled. Under those circumstances, the first-male disadvantage was substantially attenuated. Now the first male was responsible for 43% of all fertilized eggs, with the second male responsible for the remaining 57%. This experiment demonstrates that the paternity advantage provided by a Pavlovian CS associated with copulation is also evident when competing males copulate with the same female separated by a substantial time interval.

5.3. Conditioned fertility and sperm allocation between females

Another form of sexual competition involves a given male attempting copulations with multiple females so as to produce more offspring. A male can increase its genetic representation in future generations by copulating with two (or more) females in succession. If the interval between successive copulations is short, the typical outcome is that more sperm are allocated to the first female than the second. Matthews studied sperm allocation when the same male quail copulated with two females in succession separated by 15 min (reported in Domjan et al., 2012). In the absence of a Pavlovian signal for either copulation, the first female produced more fertilized eggs (24%) than the second female (6%). However, this marked second-female disadvantage was substantially reduced if copulation with the second female was preceded by a CS. When the CS was presented before the second copulation (and not before the first), the rates of fertilization were similar for the two females (23% and 27%).

It is unlikely that the altered sperm allocation effect was due to growth of new sperm stimulated by the Pavlovian CS, since the CS was presented for just 1 min prior to copulation with the second female. A more likely explanation is that the Pavlovian signal stimulated increased cloacal contractions (Holloway et al., 2005), which in turn increased the amount of sperm that was released (Domjan et al., 1988) and transferred during the copulation with the second female.

6. Areas for future investigation

Although numerous features of the behavior system for sexual learning have been examined, much remains to be explored. All of the studies with quail were conducted using visual and tactile cues as conditioned stimuli. The potential function of auditory cues in sexual learning remains to be examined. Given that quail are vocal animals and vocalizations are socially controlled (see Mills et al., 1997), auditory cues could be a major part of their behavior system for sexual learning. One could pursue the analysis of auditory cues in sexual learning with a distinction between arbitrary and species-typical auditory stimuli, in a manner analogous to our analysis of visual cues.

The distinction between arbitrary and species-typical stimuli could also be extended to contextual cues. Contextual cues could be species-typical if they involve the unique ecological niche where sexual behavior occurs in the wild. For example, for species that only copulate at night or in a burrow, stimuli characteristic of those unique environments would be species-typical.

Of the three major response modes included in the behavior system for sexual learning, we know the least about the nature of general search behavior. How might we begin to characterize the microstructure of general search? If search behavior is guided by specific localized stimuli, shouldn't we characterize it as focal search rather than general search? At the level of the microstructure of behavior, how do we distinguish general search from focal search?

The behavior system for sexual learning that we developed is based primarily on excitatory Pavlovian conditioning. Although there is also evidence of inhibitory sexual conditioning (Crawford and Domjan, 1996), we have not explored phenomena of inhibitory conditioning in as great detail as excitatory conditioning. The issue of inhibitory sexual conditioning may be especially relevant in developing treatment procedures for some forms of sexual dysfunction such as pedophilia or premature ejaculation.

Another aspect of sexual learning in quail that remains to be further examined is the conditioning of female sexual behavior. For example, we do not know what is the best US for conditioning of female quail. In one of our studies the US was copulation with a male (Gutiérrez and Domjan, 1997) whereas in other studies, the US was exposure to a male behind a wire screen barrier (Adkins-Regan and MacKillop, 2003; Gutiérrez and Domjan, 2011). However, the two techniques have not been compared directly. In sexual conditioning of female rats, the best US is exposure to a male under circumstances that permit the female to pace its contact with the male (Coria-Avila and Pfaus, 2007). A paced copulation procedure has been recently developed for female quail, using tethered males (de Bournonville et al., 2016), allowing females to effectively avoid or approach a male. This technique has not been used to study sexual learning, but offers new possibilities for the comparison of the modulatory effects of contextual and local cues on appetitive and consummatory female sexual behavior.

All of the studies that we reviewed involved Pavlovian conditioning. Although experiments have demonstrated that sexual reinforcement can be used in instrumental conditioning procedures as well, a behavior system for sexual learning that combines Pavlovian and instrumental components has not been developed. We do not know whether different types of sexual reinforcers (e.g., visual access vs. physical access to a sexual partner) operate over similar spatial and temporal domains. We also don't know whether or how sexual reinforcers determine or limit the types of instrumental responses that can be easily conditioned Another major area of investigation is the interaction of Pavlovian and instrumental conditioning using Pavlovian-instrumental transfer experiments. Pavlovian-instrumental transfer effects would no doubt depend on whether the Pavlovian CS involved contextual cues, arbitrary local cues or species-typical cues.

An important part of the behavior system that we developed based on research with quail is that sexual conditioning serves to modify the copulatory interactions of the male and female in a way that significantly increases reproductive fitness. Other than the one experiment with the blue gourami (Hollis et al., 1997), a fish species, measures of reproductive fitness have only been obtained in studies with quail. Given the substantial body of research on sexual learning in rats, it would be interesting to examine whether and how sexual conditioning may increase reproductive fitness in that species.

As observed by Montoya et al. (2016), the sexual behavior system is likely to interact with the social dominance system. Sexual behaviors may also depend on concurrent demands of foraging and predatory defense systems. Interactions between different systems of behavior have not been systematically studied. The understanding of such interactions is likely to provide an increasingly complex account on how animals integrate various aspects of their behavior in solving adaptive problems in their natural environment.

One of the strengths of the evidence reviewed in this paper is that the data were obtained under carefully controlled laboratory conditions. However, this is also a weakness, in that the data fail to show how sexual learning can influence behavior and reproductive outcomes under natural conditions in the ecological niche of the species. Studies of sexual learning under more natural conditions in the laboratory or in the ecological niche of a species would be very exciting. *Coturnix japonica* is probably not the ideal species for such studies, since quail tend to hide in grass and bushes and are difficult to locate unless they take flight when they are disturbed. Laboratory rats are probably also not suitable for such investigations since they are nocturnal and live in underground burrows.

As information about sexual conditioning becomes available from a growing number of species, it would be informative to examine how the sexual learning systems of various species are related to how their sexual behavior has evolved. In addition to the studies with quail and rats that we discussed in this paper, sexual learning has been also investigated in gerbils (Villarreal and Domjan, 1998), fish (Hollis et al., 1989, 1997), and humans (Brom et al., 2014). However, studies with various species have employed different conditioned and unconditioned stimuli and different ways of arranging these in a conditioning procedure. These methodological variations make direct comparisons between species difficult. Early in the conceptualization of the field of sexual learning, Domjan and Hollis (1988) suggested that sexual learning systems may differ among species as a function of differences in their mating systems. For example, the sexual learning system of monogamous species might be different from the sexual learning system of polygynous and polyandrous species. The goal of obtaining such information has yet to be realized.

7. Summary and conclusion

Since the work of Pavlov, psychologists have recognized that the nature of conditioned behavior depends on the unconditioned responses that organisms bring to a learning situation. However, Pavlov's concepts of an unconditioned stimulus and an unconditioned response are too simplistic to characterize all of the ways in which the evolutionary history of an organism influences how that organism is modified by a conditioning procedure. The behavior systems approach advocated by William Timberlake provides a much more comprehensive and complex characterization of the role of preexisting behavioral structures in determine the outcome of new learning experiences.

Timberlake's behavior systems approach encourages investigators to consider three dimensions of a learning situation that will determine the outcome of a conditioning procedure: a response dimension, a stimulus dimension, and a temporal dimension. The response dimension in behavior systems is typically organized in what are referred to as response modes. Our analysis of the behavior system for sexual learning has focused on three major response modes, general search, focal search, and consummatory or copulatory responses. Each of these response modes presumably evolved to achieve a particular goal. The function of the general search mode is to approach and identify an area where a sexual partner may be found. The focal search mode operates in a more restricted spatial domain since it involves approach to a potential mate. Consummatory or copulatory responses occur when the mate has been located and involves direct interactions with that mate.

The three response modes vary in topographical specificity, although that feature has not been the focus of experimental research. General search behavior has the least topographical specificity, focal search is intermediate, and copulatory behavior has the greatest degree of topographical specificity. The degree of topographical specificity is related to the stimulus dimension of behavior systems to some degree. Our characterization of the behavior system for sexual learning emphasized three types of stimuli. The first of these are contextual cues which are spatially distributed and distinguish different areas of considerable extent (such as one type of experimental chamber rather than another). The second category of cues are spatially localized stimuli that serve to identify a specific location within a larger environmental context. Finally, the sexual learning system also includes species-typical cues provided by a sexual partner. These are sometimes treated as unconditioned stimuli for sexual activity but our research has shown that responses to species- typical cues also can be substantially modified by conditioning procedures.

There is some correspondence between response modes and categories of stimuli. Contextual cues often elicit general search responses. Localized stimuli are more apt to elicit approach or focal search responses, and species-typical cues usually elicit both focal search and copulatory behaviors. However, the correspondence between response and stimulus categories is far from perfect. Localized stimuli can elicit general search behavior if there is a long delay between the CS and US. Localized stimuli that do not include species-typical cues can also elicit copulatory responses given the right conditioning parameters.

Another reason that stimulus categories do not map directly onto response categories is the existence of powerful interactions between stimulus categories in eliciting various categories or modes of

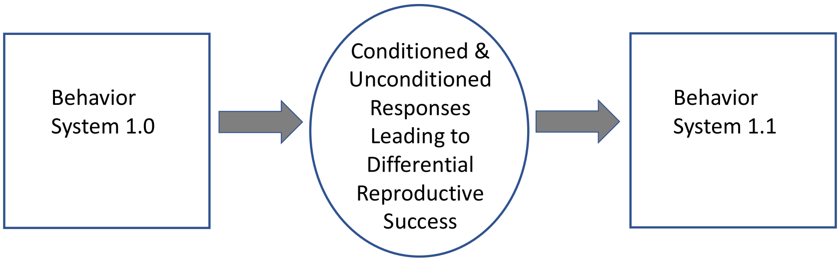

Fig. 7. Model of how a behavior system may evolve through differential reproductive success generated by the outputs of the system.

conditioned sexual behavior. Conditioned contextual cues, for example, can facilitate the effectiveness of localized CSs in eliciting conditioned approach responses. Even more importantly, both conditioned contextual cues and conditioned local stimuli can facilitate the effectiveness of species-typical cues in eliciting or regulating the occurrence of copulatory behavior.

The third major variable in Timberlake's behavior systems approach is time to consummation of the behavior sequence under investigation. In common Pavlovian procedures, presentation of the US permits consummation of the behavior sequence. Delay to the US is represented by the CS-US interval in the conditioning procedure. The sexual behavior system has provided evidence that short CS-US intervals produce conditioned approach or focal search behavior whereas long CS-US intervals produce conditioned general search behavior (Akins, 2000; Akins et al., 1994). A similar shift in the response mode that becomes conditioned with CS-US intervals of different durations has been observed in the feeding system (e.g., Silva and Timberlake, 1997) and the defensive behavior system (e.g., Waddell et al., 2006).

Behavior systems improve how organisms achieve major biological goals (feeding, defense, reproduction). Behavior systems also influence how learning is manifest in behavior, presumably because such influences are evolutionarily adaptive. Adaptive value can be measured by proxies of reproductive success, such as good health and longevity. However, the most direct measure of adaptation is increased reproductive success or increased numbers of offspring produced. As far as we know, the effects of learning on reproductive success have been directly measured to date only in the sexual behavior system. This presents a challenge for students of other behavior systems who have argued for adaptive significance without empirically documenting contributions to reproductive fitness.

Studies of the fertility consequences of sexual conditioning have provided extensive and powerful evidence that the behavior system for sexual learning has evolved because it is highly adaptive. The feature of the behavior system for sexual learning that is primarily responsible for increased reproductive success is the mechanism whereby conditioned context cues and conditioned localized stimuli enhance the effectiveness of species-typical cues in eliciting effective copulation. Signaling a sexual encounter by a localized or context CS, decreases the latency of the initiation of copulatory behavior, increases the efficiency of that behavior, and these behavioral changes are associated with increased fertility. The conditioned increase in fertility is evident not only with isolated copulations but also situations involving sexual competition and sperm allocation where more than one male copulates with a female or more than one female is inseminated by a given male.

Behavior systems are typically considered to reflect the outcome of evolutionary history or past evolutionary change. Evidence that the operation of a behavior system can itself produce differential reproductive success and differential genetic transmission suggests that how a behavior system governs phenotypic learned behaviors can shape the future structure of that behavior system. This process is illustrated in Fig. 7, in which Behavior System 1.0 leads to behaviors associated with differential reproductive success, which in turn leads to the evolution of Behavior System 1.1. To date we do not have documented examples of the evolution of a behavior system as conceptualized in Fig. 7. However, the existing evidence suggests that sexual conditioning could be a strong epigenetic influence in the evolution of the behavior system of future generations.

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