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Resistance to Extinction and Psychopathology, With New Evidence of How a CS Can Act Like a US in The Sexual conditioning of Male Japanese Quail (*Coturnix Coturnix Japonica*)

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This paper is organized in three sections. In the first section, we discuss the relevance of comparative psychology to clinical issues by relating resistance to extinction to psychological disorders involving anxiety, addiction, and fetishism. In the second section, we review areas of comparative psychology that deal in one way or another with the general problem of treating an insignificant event as it were significant. We describe research on supernormal stimuli, evaluative conditioning, acquired drives, incentive sensitization, and consummatory response theory. In the third section of the paper, we present new research on second-order sexual conditioning of male Japanese quail related to the consummatory response theory. First-order condiioning was conducted by pairing the presentation of a terrycloth object (CS1 or conditioned stimulus 1) with copulation with a female (the US or unconditioned stimulus). The male quail came to approach the terrycloth object during the first-order conditioning phase. In addition, about half of the quail also showed conditioned consummatory responses directed towards the terrycloth object. During the second-order conditioning phase, the terrycloth object was used to condition responding to a light (CS2) in the absence of further exposures to the unconditioned stimulus. Birds that showed conditioned consummatory behavior towards CS1 persisted in this behavior during the second-order phase and showed successful second-order conditioning of the light. In contrast, birds that failed to develop conditioned consummatory responses to CS1 showed rapid extinction and minimal second-order conditioning. The implications of these finding for learning theory and for psychopathology are discussed.

When a conditioned stimulus or CS (e.g., a light) is presented with an unconditioned stimulus or US (e.g., food), a conditioned response or CR (salivation) comes to be elicited by the CS. Because initially the salivary response was only elicited by the US, the gradual transfer of the response to the CS is called acquisition. Following acquisition, if the CS is presented repeatedly without the US, the common result is that the CR declines, a process that is called extinction. However under certain conditions, a CS can show strong resistance to extinction. Even though the CS is no longer followed by a US, it can continue to elicit the CR almost indefinitely (Köksal et al., 2004; Sidman, 1955; Soloman, Kamin, & Wynne, 1953; Vansteenwegen, Francken, Vervliet, Clercq, & Eelen, 2006; Wessa & Flor, 2007). Such resistance to extinction may be also observed in instrumental conditioning situations. For example, a secondary reinforcer or punisher (a light paired with food or shock) may continue to reinforce instrumental behavior even though the primary reinforcer or punisher is no longer presented (Knoll, 2003, 2005; Mowrer, 1956).

Persistence of conditioned responding in extinction is highly relevant to psychopathology. Certain forms of psychopathology are characterized by responding to biologically unimportant stimuli as if they were biologically significant, or pursuing seemingly unimportant stimuli as if they were primary reinforcers. In a sense, this is a form of distortion of reality, which is a common feature of psychopathology. Pursuing conditioned stimuli as if they were primary reinforcers can move the organism away from biologically significant events, causing it to spend its valuable time and energy in vain. In many psychological disorders, certain CSs gain strong emotional valence (appetitive or aversive) and this valence is not lost it in the face of

repeated and prolonged CS-alone presentations (e.g., Weiss et al., 2001; Wessa & Flor, 2007). Such persistence of maladaptive behavior is especially relevant in phobias, obsessive compulsive disorder, paraphilias (especially fetishism), and addiction.

Our aim in this paper is to discuss the relationship between comparative psychology and various forms of psychopathology that involve resistance to extinction. We begin by discussing issues related to resistance to extinction as they relate to anxiety disorders, addiction, and paraphilias. In the next section, we discuss various phenomena in comparative psychology that may be considered to be examples of distortions of reality in the sense that humans and other animals treat insignificant events as if they were important. Phenomena reviewed in this section include supernormal stimuli, and the persistent responding in extinction that is observed with evaluative conditioning, acquired drives, incentive sensitization, and conditioned consummatory responding. In the last section of the paper, we present a novel example of a distortion of reality in the second-order conditioning of sexual behavior in domesticated quail. In this experiment, male quail came to copulate with an artificial object as if it were a live female, and this copulatory behavior supported significant and persistent second-order sexual conditioning. We end with a discussion of the mechanisms of this second-order conditioning effect and its implications for psychopathology and psychotherapy.

Resistance to Extinction in Psychological Disorders

Persistence of maladaptive behavior occurs in many psychological disorders. We think that the issue is particularly important for anxiety disorders, addiction, and paraphilias (especially fetishism).

Anxiety disorders. Fear is an important survival-enhancing emotion, helping organisms move away from potentially life-threatening situations or objects. However, when excessive fear is elicited by an object or situation in the absence of danger, the life-saving emotion becomes a disorder, called an anxiety disorder. Rather than showing fear to an aversive US, the individual shows anxiety to a CS which was associated with the US. Phobias (social phobia, agoraphobia, simple phobia), panic attacks, generalized anxiety disorders (GAD) and Post Traumatic Stress Disorder (PTSD) all involve aversive learning. Although genetic and neurobiological mechanisms also have an important role, associative learning is definitely involved (Lissek et al., 2005, 2014; Mineka & Oehlberg, 2008).

Psychotherapy for anxiety disorders involves extinction of an aversive CS in one way or another. A conditioned aversive CS may survive for a long time in the absence of further pairings of the CS with the US because of inadequate CS-alone exposures. Since the CS activates an aversive affective state (anxiety), the individual is motivated to terminate this noxious emotion by moving away from the CS or quickly terminating the CS. Individuals try to avoid the conditioned fear or employ safety behaviors when exposed such conditions (Graham & Milad, 2011). These tactics employed by an anxious individual prevent appropriate exposure and extinction of the CS (Lovibond, Mitchell, Minard, Brady, & Menzies, 2009). Typically, an individual suffering from anxiety disorders aborts exposure trials prematurely. Short exposure to an aversive CS may be ineffective in activating the extinction process. Such brief CS exposures may even lead to escalation of anxiety rather than attenuation, a phenomenon called incubation (Eysenck, 1979). Most successful treatments aimed at reducing anxiety include a form of extinction (gradual exposure) or counterconditioning with exposure (desensitization), along with other cognitive or pharmacological interventions. The basic strategy is to promote CS exposure to help the person realize that the CS is no longer followed by an aversive US (Foa & Kozak, 1986; McNally, 2007; Olatunji, Cisler, & Deacon, 2010; Powers & Emmelkamp, 2008). Application of these procedures in multiple contexts reduces relapse (recovery from extinction) by preventing renewal (Bouton, 2002).

Addiction. Drug addiction involves an irresistible urge to take a drug and loss of control over drug taking (DSM-V, 2013). Drug addiction involves conditioned stimuli that are resistant to extinction and have strong motivational power, leading to high rates of relapse (or recovery from extinction). However, the associative structure of addiction is more complex. Most researchers agree that drug addiction involves both appetitive and aversive conditioning processes (Koob, 1996, 2013; Wikler, 1973). Appetitive qualities of drug conditioning are critical for establishment of drug self-administration, which may lead, in time, to dependence. However, aversive conditioning may play an important role in the maintenance of dependence after the hedonic effect of drug is lost due to neuroadaptation (habituation). Thus, initial drug administration may be established by the positive affective state created by drug intake, whereas sustained drug use may be controlled by elimination of aversive affective states (withdrawal symptoms). Another important aspect of drug addiction is relapse after long periods of abstinence. Negative or positive affective states can get associated with a cue during the course of drug taking and can instigate craving and drug taking responses after abstinence (O'Brien, 1975; Skinner & Aubin, 2010). Therapies for drug addiction basically involve application of different methods to eliminate craving and relapse (Xue et al., 2012).

Paraphilias. A paraphilia is an atypical sexual behavior. DSM-V (2013) defines paraphilias as recurrent intense sexually-arousing fantasies that occur over at least six months. These sexual urges, or behaviors generally involving nonhuman objects, the suffering or humiliation of oneself or one's partner, or children or other nonconsenting persons. Sexual urges have a very compelling nature. Paraphilias involving nonhuman objects are characterized by a fixation on a nonliving object such as shoes, underwear, or other garment. Usually, the fetish object is necessary or desired for normal sexual functioning. Many different things can become objects of a sexual fetish. The associative structure of paraphilias is thought to be basically appetitive conditioning. Stimuli (CS) present during initial sexual experiences (appetitive US) become associated with sexual arousal (UR).

The classical conditioning account of the etiology of paraphilias is generally accepted (Hall 2000; Laws & Marshal, 1991; Marshal & Eccles, 1993; Rachman, 1961). The problematic association between the inappropriate stimulus (CS) and sexual arousal (CR) is strengthened through repetition during an individual's life time. Therefore, the CS (or inappropriate sexual object) becomes highly effective in eliciting sexual arousal. Treatment procedures target this association. However, presentation of the CS alone has little effect in reducing the sexual arousing capacity of the stimulus, probably due to the nature of sexual reinforcement system and presence of conditioned consummatory responses (Crawford, Holloway, & Domjan, 1992; Köksal et al., 2004; Pfaus, 1996). That is probably why treatment of paraphilias often involves aversive conditioning (covert sensitization or aversive training; Cautela, 1967; Kelly, 1982; Krueger & Kaplan, 2002; Marshal & Lippens 1977; Quinsey & Earls, 1990).

Treating Insignificant Events as if They Were Significant

In general, organisms seek proximity to appetitive USs and move away from aversive USs. Such behaviors are not acquired or learned, otherwise they would not fit the definition of a US. This holds true for primary reinforcers and punishers of instrumental behavior as well. However, if an organism moves towards an aversive event (e.g., masochisms) or moves away from an appetitive US (e.g., anorexia), the behavior may be maladaptive. As we will discuss below, maladaptive responses can be the result of learning. One of the most important shortcomings of the evolution of learning is the possibility of inappropriate or maladaptive learning (or conditioning). Treating a nonsignificant event as if it were significant can beviewed as learning that has

gone awry or is maladapted. However, such maladaptive responses can be observed not only as a result of learning but also in biologically pre-programmed behaviors.

Pre-Preprogramed Responses: Supernormal Stimuli

The concept of supernormal stimuli, first developed by Tinbergen (1948, 1951), shows that even in the absence of any learning, under certain conditions the nervous system makes an error and prefers an artificial stimulus over a biologically significant one. In the classic Tinbergen experiment on food soliciting by herring gull chicks, the chicks showed more pecking responses to an artificial model with a red dot than to the head of a herring gull with a red dot on the tip of its beak.

Responses to a supernormal stimulus may be considered maladaptive because the organism shows a stronger response to the supernormal stimulus than to the natural one. Exaggerated responses to supernormal stimuli have been investigated in various species, including birds (Baerends, 1959; Grim & Honza, 2001; Tanaka, Morimoto, Stevens, & Ueda, 2011), insects (Jaffe, Miras & Cabrera, 2007; Kral, 2016; Shermer, 2015), baboons (Bielert & Anderson, 1985), and even humans (Doyle & Pazhoohi, 2012; Morris, White, Morrison, & Fisher, 2013). The critical element is that the supernormal stimulus contains features of the natural releasing stimulus in an exaggerated form that is not encountered in nature and therefore has to be fabricated artificially.

In her books, *Waistland* (2007) and *Supernormal Stimuli* (2010), Barrett writes about how artificially created stimuli appeal to human instincts more than the natural objects they mimic. Our natural instincts overrun their evolutionary purpose in the world of supernormal stimuli and we end up making responses that are detrimental to our physical and psychological health. Barrett provides examples of responding to supernormal stimuli from a variety of aspects of life, ranging from eating and drinking, to sexual behavior, and even internet use. Modern life includes a flood of supernormal stimuli. Unless one actively resists reacting to these artificial cues, one is destined to make maladaptive responses to many contemporary environmental stimuli.

An important feature of supernormal stimuli is that the organism shows a response to a unnatural and insignificant stimulus, ignoring the natural and significant cues, and this response persists despite it being maladaptive. The persistent and repetitive nature of responses to biologically inappropriate cues makes them relevant to psychological disorders. However, many instances of continued responding to biologically inappropriate stimuli are the results of some type of learning rather than being instinctive. We discuss such cases next.

Learned Responses and Mechanisms of Resistance to Extinction

In this section we discuss examples of persistent learned responding to cues that are not biologically significant. We discuss evaluative conditioning, acquired drives, incentive sensitization, and conditioned consummatory responses.

Evaluative conditioning. Various investigators have proposed that classical or Pavlovian conditioning involves two types of learning (e.g., Hermans, Vansteenwegen, Crombez, Baeyens, & Eelen, 2002). One is expectancy or signal learning in which a previously ineffective stimulus (CS) becomes a signal

for a biologically significant event like food or water (US) as a result of the CS being paired with the US. Once this type of learning has taken place, the CS activates an expectancy that the US will occur. The second type of learning involves a change in the valence of the CS. As a result of the CS being paired with the US, the valence of the US is transferred to the previously ineffective stimulus. Because of this valence transfer, the CS comes to function as a second-order US (De Houwer, Thomas, Baeyens, 2001). For example, a picture or melody that is paired with an appetitive US also becomes pleasant. This type of conditioning is called evaluative conditioning or referential learning (Levey & Martin, 1975; Razran, 1954; Staats & Staats, 1957). Evaluative conditioning has been studied in diverse areas of psychology including attitude formation (Herring et al., 2013), marketing (Walther & Grigoriadis, 2004), emotion research (Mallan & Lipp, 2007; Niedenthal, 1990), and clinical psychology (Blessing Zölling, Weierstall, Dammann, & Martin 2013; Klucken, Wehrum-Osinsky, Schweckendiek, Kruse, & Stark, 2016; Olatunji, 2006).

In expectancy learning, presentation of a CS activates both the memory of the US and an expectancy for its occurrence. In contrast, in evaluative conditioning presentation of a CS activates only the memory of the US, without any expectancy that the US will occur. Evaluative conditioning is prevalent in the learning of preferences and likes and dislikes. Basically it involves acquired emotional responses to stimuli, and choices based on those emotions.

The existence of two types of conditioning, though sometimes questioned (Davey, 1994; Lipp & Purkis, 2005), has been generally accepted in the learning literature (Baeyens, Crombez, Van den Berg, & Elen, 1988; Baeyens, & De Houwer, 1995; Baeyens, Elen, Van den Bergh, & Crombez, 1989; De Houwer, Baeyens, & Field, 2005; Diaz, Ruiz, & Baeyens, 2005; Hermans, et al., 2002; Martin & Levey, 1994). Separating the effects of classical conditioning into expectancy and evaluative learning also has major implications for extinction. Much of the evidence for extinction in Pavlovian conditioning appears to involve the expectancy learning component. Omission of the US during extinction trials violates what the CS previously signaled and hence produces a change signal value. Proponents of evaluative conditioning claim that extinction of evaluative responses to a CS is either weak or non-existent (Baeyens, et al., 1988; Dwyer, Jarratt, & Dick 2007; Vansteenwegen et al., 2006). The extraordinary resistance of evaluative conditioning to extinction is considered to be one of its distinctive features.

Evaluative learning is defined by the transfer of the valence of one stimulus to another due to pairing of the two stimuli close in time. In a typical extinction trial, presentation of the CS by itself activates a US memory, which in turn activates a US expectancy but no US is presented. Extinction is explained as involving the learning of a new relationship between the CS and the US (Bouton, 2004). The organism now learns that the CS predicts the absence of the US, and this new learning supercedes the previous learning that the CS predicts the US, leading to a reduction of the CR, and hence extinction. For this extinction process to operate, the CS has to activate a US expectancy so that the absence of the US can create a violation of that expectancy. The absence of an expected US in extinction, apart from establishing a new CS-noUS association, also leads to the emergence of different emotional state. For example, if the US is an appetitive stimulus, the omission of the US in extinction will lead to the aversive emotional state of frustration. The violation of the expected US, with its attendant frustration, leads to a reduction of the CR in extinction.

In evaluative conditioning, since the CS activates only a US memory (without US expectancy), there is no violation of expectancy in extinction to produce a new emotion (frustration) or a new association between the CS and US (CS predicts no US; Hermans, et al., 2002). Therefore, the association between the CS and the memory of the US memory can continue indefinitely, resulting great resistance to extinction.

A different but related factor leading to resistance to extinction in evaluative conditioning can be procedural. Evaluative conditioning studies are typically conducted with human participants, using mostly verbal reports of liking to measure the conditioned response. That a CS retains its association with a US is indicated by continued liking for the CS in the absence of predicting that the US will occur. For example, whenever a person approaches his home on Friday evening, he hears a specific song coming from his house indicating that his girlfriend has arrived. However, a couple of times he hears this song on a Friday evening but to his disappointment there is no one there. The song is just playing on the radio that he left on. Surely, he will experience frustration, and the song will lose its power to predict her presence. However, when he has no expectation of meeting her, he may continue to like the song whenever he hears it, and the song will continue to activate the memory of the girl friend. His liking for the song may continue for an indefinite time. If liking is used to measure extinction, little extinction may be evident. The basic prediction is that the referential system is more resistant to extinction than the expectancy system (Hermans, et al., 2002).

Acquired drive. The concept of drives became prominent in learning theory with C. Hull's theorizing. His explanation of reinforcement was based on drive reduction. Responses followed by the reduction of a drive (like hunger) were reinforced. This relatively simple idea was later elaborated by postulating two different types of drives, primary and secondary. Primary drives were unlearned and based on biological needs. Secondary drives, in contrast, were acquired through Pavlovian conditioning (in association with a primary drive). A prominent example of an acquired drive is conditioned fear that results when a CS is paired with a shock (US) in a shuttle avoidance task (Mowrer, 1947). Animals make an instrumental response to terminate the conditioned fear produced by the CS, which signals that shock is about to occur. The avoidance response reduces the acquired drive of fear and is therefore reinforced.

Interestingly, avoidance responses acquired under these circumstances are remarkably resistant to extinction (Solomon, Kamin, & Wynne, 1953). The acquired fear that motivates avoidance responding seems to be remarkably resistant to extinction despite the fact that the shock US is no longer presented during extinction trials. Because each presentation of the CS activates a US memory and expectancy and hence a state of fear, the animal emits the avoidance response, which terminates the CS and the aversive emotional state of fear. Thus, secondary drive reduction continues to occur on extinction trials. In this way the animal never learns that the expectancy elicited by the CS is violated, even though the CS is no longer followed by the US (Lovibond, et al., 2009).

In contrast to conditioned fear, strong resistance to extinction is not observed with conditioned appetitive drives. In fact, even the establishment of conditioned appetitive drives (hunger) appears to be much more difficult (Brozovich, Malony, & Wright, 1963; Calvin, Bicknell, & Sperling, 1953; Novin & Miller, 1962). Calvin, Bicknel, and Sperling (1953) and Wright (1965) reported positive results with hunger. However, in their experiments the learned drive was assessed through amount of food eaten. The animals consumed more food in a box where they were previously placed while experiencing strong hunger. Such results were probably transient, and the investigators did not measure resistance to extinction. Later similar experiments conducted by Wike and his colleagues (Wike, Cour, & Mellgren, 1967; Wike, & Knutson, 1966) failed to replicate these results.

As the concept of drives and drive reduction theory of reinforcement lost their popularity in the field of learning, fewer experiments on acquired drives were conducted. More recently, in a book published in 2005 by a Hungarian psychopharmacologist, J. Knoll, the importance of acquired drives in human behavior and culture has been resurrected. Knoll divides vertebrates into three groups according to "the mode of operations of their brain," a) those that operate with innate drives only (the majority), b) those with an ability to acquire

drives (a minority), and c) *Homo sapiens* that operate almost exclusively on the basis of acquired drives. Knoll suggests that innate drives operate in the service of a limited number of vital goals, whereas acquired drives operate in the service of an unlimited number of unimportant goals.

After conducting a series of experiments with rats, Knoll concluded that his rats developed a glass cylinder seeking drive. The training procedure for this acquired drive was very similar to standard shuttle avoidance training. The rats were presented a bell (CS) and an aversive US, a 60 C° hot plate. The rats escaped from the aversive hot plate by jumping to the top of a glass cylinder. After training, the rats persisted with the jumping response to the CS through 100 extinction trials in the absence of the hot plate US. Resistance to extinction of this response can be explained in the same manner as persistence of shuttle avoidance responding. Since the rats never experienced the absence of the US during extinction, they did not experience a violation of the US expectancy.

Incentive sensitization. A more recent explanation for why a CS may continue to elicit a CR despite prolonged extinction is provided by incentive sensitization theory (Berridge & Robinson, 1993). This theory, which was formulated to account for drug addiction and relapse, uses two different process: sensitization and Pavlovian conditioning. Repeated exposure to addictive drugs sensitizes brain circuits involved in the attribution of incentive salience to drugs and drug-related cues. This hypersensitivity of neural circuits leads to a high level of wanting (incentive motivation) for the drug. Pavlovian conditioning in turn defines which object will be wanted. Sensitization and Pavlovian conditioning jointly explain why pathological wanting is expressed in the environment where the drug was previously taken. The emergence of motivation to take the drug is explained by sensitized neural circuits and the direction and place of the motivated behavior is explained by Pavlovian conditioning (Robinson & Berridge, 2008).

Berridge (2001) claimed that stimuli acquire incentive properties when paired with a biologically significant stimulus (a US). Stimuli that have gained incentive salience will display three qualities. First, incentive stimuli will elicit approach behavior. As a result, an individual's probability of getting into contact with the associated reward increases. Second, incentive stimuli are desired. They are motivational magnets and can reinforce new instrumental responses (acting like secondary reinforces). Third, incentive stimuli can lead to the emergence of a new motivational state that can generate seeking the original reinforcer (drug). This quality of incentive stimuli may lead to craving and relapse even though one tries to steer clear of the drug. These three properties of incentive stimuli can be investigated using well known conditioning procedures such as Pavlovian excitatory conditioning, conditioned reinforcement, and Pavlovian-instrumental transfer procedures.

Tests of the incentive sensitization theory with laboratory rats have led to the discovery of strong individual differences incentive learning. When a Pavlovian appetitive conditioning procedure was applied, some of the rats showed strong approach to the CS (sign tracking), whereas other rats approached the cup where food (the US) was delivered (goal tracking). Of particular interest was the fact the animals that showed sign tracking were those whose behavior was more strongly controlled and motivated by drug cues (Flagel, Akil, & Robinson, 2009; Robinson & Flagel, 2009).

Conditioned consummatory responding. Hull's drive reduction theory of reinforcement was criticized by Sheffield and his colleagues (Sheffield & Roby, 1950; Sheffield, Roby, & Campbell, 1954) who conducted a series of experiments to show that responses can be reinforced in the absence of drive reduction (primary reinforcement like food). In one study, the reinforcer was the opportunity to drink a saccharin solution which was non-nutritive and therefore could not reduce the hunger drive (Sheffield, et al., 1954). Even though

the saccharin solution did not provide any nutrition, it nevertheless served as an effective reinforce for instrumental behavior. Subsequent studies conducted by Foster (1968) showed that saccharin is an effective primary reinforcer for new-born pigs (1 to 3 hours old), indicating that the reinforcing properties of saccharin did not depend on post-partum learning. Based on these observations, Sheffield argued that consummatory responding can be the basis for reinforcement in the absence of drive reduction.

The saccharin experiments demonstrated the consummatory responding is sufficient for a substance to be reinforcing. In a related experiment involving sexual conditioning, Sheffield, Wulff, and Backer (1951) showed that exposure to a female is an effective reinforcer for male rats even if the males are not permitted to intromit or ejaculate. This shows that consummatory responding is not always necessary. However, consummatory responding increases reinforcer efficacy. In studies of sexual conditioning with male quail, Holloway and Domjan (1993) showed that males that were permitted to consummate their copulation with a female showed stronger conditioned approach to an arbitrary CS than males that were exposed to a female without cloacal contact.

Consummatory responding has been also shown to enhance resistance to extinction. Köksal et al. (2004) examined the sexual conditioning and extinction of male quail using two different conditioned stimuli. One conditioned stimulus was a light and the other was a terrycloth object that the males could copulate with. Acquisition trials consisted of pairing each CS type with copulatory access to a female quail. Both CS types generated conditioned approach responses. Because the light could not support copulatory behavior, no conditioned copulatory responses were observed to the light CS. However, conditioned copulatory responses developed in about half of the male quail that received the terrycloth object as the CS. Most interestingly, the quail that came copulated with the CS object showed virtually no extinction when the CS was no longer paired with a female. In contrast, significant decreases in conditioned responding occurred with the CS light and in quail that did not develop conditioned consummatory responses to the CS. These results indicate that consummatory behavior serves to protect a CS from extinction. Evidently conditioned consummatory responding enables a CS to functionvery much like a US. In the next section we report the results of new experiments that test this hypothesis in the context of second-order conditioning.

The Role of Conditioned Consummatory Responses in Second-Order Conditioning: Can a CS Act Like a US?

Second-order conditioning was originally developed by Pavlov (1927) and is commonly used to explain the spread of associative power to previously ineffective stimuli in the absence of any further pairings with a US. As the term implies, second-order conditioning involves two stages. In the first stage, an ineffective stimulus such as a localized light (CS1) is paired with a US (e.g., food or shock). Through such pairings, CS1 gains the capacity to elicit conditioned responses. Once acquisition of responding to CS1 is well established, CS1 is used to condition responding to a new stimulus CS2 (e.g., a tone) without the presentation of the original US. Second-order conditioning is said to have occurred if the pairings of CS2 with CS1 result in the development of conditioned responding to CS2.

Higher order conditioning has been very important in understanding how the associative properties of a given CS can be transferred to other unrelated stimuli in the absence of presentations of the US. Second-order conditioning has been investigated as a topic not only for conditioning theory (Rescorla, 1980) but also for social psychology and consumer research (Alexomanolaki, Kennett, & Loveday, 2010; Blair & Shimp, 1992) and clinical psychology (Davey & Arulampalam, 1982; Wessa & Flor, 2007; Wolpe & Rowan, 1988).

In social psychology, second-order conditioning has been implicated in the acquisition of affective meaning by cultural signs and symbols. Studies of attitude formation have also shown the importance of first- and second-order conditioning. In clinical psychology, second-order associations have been implicated to explain the transfer of fears and anxieties from one situation (or object) to another.

Second-order conditioning has been examined in various species, including rhesus monkeys (Cook & Mineka, 1987), pigeons (Rashotte, Griffin, & Sisk, 1977), honeybees (Hussaini, Komischke, Menzel, & Lachnit, 2007), Drosophiia (Tabone & De Belle, 2011), and fish (Topal & Csanyi, 1999). Studies of factors that influence second-order conditioning have focused on the inter-stimulus interval (Kehoe, Feyer, & Moses, 1981), similarity of CS1 to CS2 (Rescorla & Furrow, 1977), US magnitude (O'Connell & Rashotte, 1982), and number of training trials (Yin, Barnet, & Miller, 1994). For our current research, US magnitude and number of training trials were important variables.

There is clear evidence that an increase in US magnitude results in increased strength of second-order conditioning (O'Connell & Rashotte, 1982). The effects of the number of trials of second-order conditioning is more complex. The basic procedure for second-order conditioning is similar to the procedure for inhibitory conditioning. In both cases, CS1 is paired with a US and CS2 is paired with CS1 in the absence of the US. The primary difference is that in second-order conditioning CS1-US pairings precede CS2-CS1 pairings. In contrast, in inhibitory conditioning, the two types of trials are intermixed or presented in a random order. Yin et al. (1994) showed that irrespective of order of phases, second order-conditioning is sensitive to the number of CS2-CS1 trials. With a small number of trials, CS2 gains positive associative value and second-order conditioning is observed. As the number of CS2-CS1 trials is increased beyond that, CS2 starts to gain conditioned inhibitory properties, as CS2 becomes a signal for the omission of the US.

Another relevant factor is whether or not CS1 undergoes extinction during the course of second-order conditioning. Wessa and Flor (2007) showed that in patients with post-traumatic stress disorder, not only the trauma itself but trauma-relevant cues (CS1) acted as USs, and CS1 was very slow to undergo extinction when presented without a US. Under these circumstances, CS1 led to the transfer of fear responses to previously neutral stimuli (CS2).

A similar retardation of extinction was observed in sexual conditioning of male Japanese quail (Köksal et al., 2004). In these experiments, a terrycloth object was used as the CS that was paired with the opportunity to copulate with a female. Sexual conditioning resulted in the males approaching the CS object. In addition, about half of the quail also came to make conditioned consummatory sexual responses to the terrycloth object. Birds that manifested conditioned consummatory responses (grab, mount and cloacal responses) showed great resistance to extinction when the CS was subsequently presented without the US. These birds behaved to the CS as if it was a US (a female quail).

In the present experiment we investigated the effect of the presence of conditioned consummatory sexual behavior on the effectiveness of a CS1 to produce second-order conditioning. If the presence of consummatory behavior can turn a CS1 into a US, then participants that acquired conditioned consummatory responses during the course of first-order conditioning (group Cons-R) should show stronger second-order conditioning than participants that just came to approach CS1 during first-order conditioning (group App-R). Another prediction was that participants that showed conditioned consummatory responses to CS1 would not show extinction of responding to CS1 during the course of second-order conditioning. This was expected to facilitate second-order conditioning even if numerous second-order trials were conducted.

Method

Experiment 1

  Subjects. 63 experimentally naïve male Japanese quail, about 3 months of age, served as research participants. The quail were raised in a colony kept in the Boğaziçi University animal learning laboratory according to the guidelines set by the Center of Life Sciences. After hatching, the birds were group-housed in brooders. When the birds were about one month of age, males were placed in individual cages. Females continued to be housed in groups. 63 females served as copulation partners to provide the sexual unconditional stimulus. Lights in the colony were on from 6 am to 10 pm, to maintain the birds in reproductive condition. Food and water were freely available both in the home cages and in the experimental chambers. The experimental groups were run in 5 replications (5, 8, 9, 9, 8 subjects in each), with a total of 39 subjects. Each of the two control groups had 12 subjects.

  Apparatus. Six experimental chambers, positioned adjacent to one another, were used to house male quail individually during treatment trials. Each chamber was 115 cm wide, 71 cm high, and 121 cm deep. The floor and the front were made of wire mesh, and the remaining walls were made of 1.5 cm plywood. The fronts were hinged and could be swung open to service the chambers. A cage for a female quail, 30 cm wide x 29 cm high x 60 cm deep, was centered on one side of each male experimental chamber. A sliding opaque door controlled the male's access to the female side cage.

  CS1 was a terrycloth object that consisted of a vertical cylinder at the end of a horizontal mounting pad (similar to object 6 in Fig. 1 of Domjan, Huber-McDonald, & Holloway, 1992). The vertical section was 8 cm tall and about 2.5 cm in diameter; the horizontal pad was 5.0 cm high, 5.5 cm wide, and 11.5 cm long. The shape of the terrycloth object allowed males to make grab, mount, and cloacal contact responses. The terrycloth CS was located 15 cm in front of the door to the female's cage. When not in use, the CS was hidden under a wooden hood (15 cm wide x 15 cm high x 15 cm deep). Presentation of the CS was achieved by raising the covering hood with a string and pulley arrangement. To measure conditioned approach to the CS, a rectangular area, 43 cm wide x 45 cm long, was marked on the floor of the experimental chamber around the terrycloth object. Time spent in this zone before and during the CS1 presentations was recorded.

  CS2 was a flashing light provided by a rectangular prism (12 cm wide x 5 cm high x 8 cm deep) for four replications of the experimental groups, and a cylindrical object (6 cm in diameter and 12 cm high) for the rest of the groups. The light was placed on the floor, on the wall opposite the door that was used to release the female on first-order trials. Only one side of the rectangular prism was lit, the other sides were covered with opaque plastic. An area identical to that around CS1 was marked around the CS2 light to measure conditioned approach response to CS2. The distance between CS1 and C2 was 69 cm.

  Procedure. Three groups of participants were tested, experimental, control-1, and control-2. The basic procedure was identical for each group except for the relationship between CS1, US, and CS2, as explained below. In each group, the participants were run in two squads (A and B; except for the first replication of the experimental group which was run in a single squad because it involved only 5 participants). The number of participants in each squad varied between 4 and 6. Each squad was housed in the experimental chambers during alternate 24 hr periods. While the subjects of one squad were in the test cages, the subjects of the other squad were housed in the colony cages. The birds were exchanged around the noon each day. This housing procedure was started 8 days before the experimental manipulations, to habituate the animals to the experimental chamber and to being handled. During this habituation period, each male bird received one 5-min period of access to a female quail. For this presentation, the female was put in the experimental chamber through the service door.

  Following the habituation phase, sexual conditioning started. For birds in the Experimental group (see Table 1), acquisition (first-order conditioning) consisted of a total of 30 trials, with one or two trials conducted each day. On each conditioning trial, the participants received exposure to the conditioned stimulus (CS1, terrycloth object) presented for 30 s shortly before a female was released from the side cage for 5 min of copulatory opportunity. In the second-order conditioning phase, the terrycloth object (CS1) was paired with the flashing light (CS2) on each of 30 trials for birds in the Experimental group. On these second-order trials, CS2 was presented for 30 s, immediately followed by presentation of CS1 for 30 s, and no access to a female (US) was provided.

  Participants in the Control-1 group received CS1 paired with the US in the same manner as the Experimental group during the first-order conditioning phase (see Table 1). However, during the second-order conditioning phase, CS2 (light) was presented with the CS1 (terrycloth) in an explicitly unpaired fashion with a temporal separation of 35-65 min. During these unpaired trials, sometimes CS2 came first followed by CS1, or CS1 came first followed by CS2, with the order randomly varied across days.

During the first phase of the experiment, participants in the Control-2 group received CS1 and US presented in an explicitly unpaired fashion with a temporal separation of 35-65 min. On these unpaired trials, sometimes CS1 came first followed by the US, or the US came first then followed by CS1, with the order randomly varied across trials. Following these unpaired trials during the first phase of the experiment, Control-2 received paired presentations of CS2 with CS1 during the second-order phase, as the Experimental group.

Table 1
*Summary of Groups and Procedures for Experiment 1*

Groups	First Order	Second Order	N
Experimental Group	CS1-US paired	CS2-CS1 paired	39
Control-1 group	CS1-US paired	CS2/CS1 unpaired	12
Control-2 group	CS1/US unpaired	CS1-CS2 paired	12

Approach responses to both CS2 and CS1 were assessed as time spent in the designated areas near each stimulus during the 30 s of stimulus presentation. The number of conditioned consummatory responses to CS1 was also counted. Video recordings of trials were made every fifth day (Trials 1, 5, 10, 15, 20, 25 and 30) during the experiment. These recordings were later scored in a separate room by a research asistant. A random sample of 56 trials for approach and 45 trials for cloacal contact responses were scored twice by 5 undergrad students who were uninformed about group assignments, to obtain inter-rater reliability scores, which were satisfactory, $r = 0.98$ and $r = .95$, respectively.

Results

As a result of the pairings of CS1 (terrycloth object) with a live female (US), all of the birds in the experimental group came to spend more time in the area that was designated around the CS1 object to measure CS approach behavior. In addition, some of the male quail also executed conditioned sexual consummatory responses to the CS1. Copulation in quail begins with the male grabbing the back of the female's head, mounting on her back with both feet, and then bringing its cloaca in contact with the female's by arching its back and making the cloacal contact response. Males that made cloacal thrusts on the CS1 object were designated as consummatory responders (Cons-R). Because second-order conditioning developed differently in males that made cloacal contacts with CS1 as compared to those that only approached CS1, the data were grouped by this factor. Thirteen of the male birds showed cloacal contact responses during the acquisition phase (between trials 10 and 30), and seven additional birds copulated with terrycloth object in the early trials of the second-order phase (between trials 1 and 10). These subjects constituted group Cons-R ($n = 20$). The remaining participants that approached the terrycloth object but did not make conditioned consummatory responses were designated as the approach responder group (App-R, $n = 19$).

The left side of Figure 1 shows the mean time spent near the CS1 object on trials 1, 5, 10, 15, 25, and 30 of the original acquisition phase (first-order conditioning) for groups Cons-R and App-R. The approach data for both CS1 and CS2 during second-order conditioning phase is presented on the right side of Figure 1. During first-order conditioning, both groups Cons-R and App-R showed increases in time spent near CS1, but the increase was a bit greater for group Cons-R. A repeated-measure analysis of variance was conducted on the first-order acquisition data, with groups (Cons-R and App-R), and trials (1, 5, 10, 15, 20, 25, and 30) as variables. The results showed a significant main effect of groups, $F(1,37) = 7.123$, $p < 0.050$, $\eta_p^2 = 0.161$, trials $F(6,222) = 52.55$ $p < 0.010$, $\eta_p^2 = 0.587$, and a significant group × trials interaction $F(1,222) = 4.173$, $p < 0.010$, $\eta_p^2 = 0.101$. The difference in approach responding between groups Cons-R and App-R was not clearly evident until trials 25 and 30.
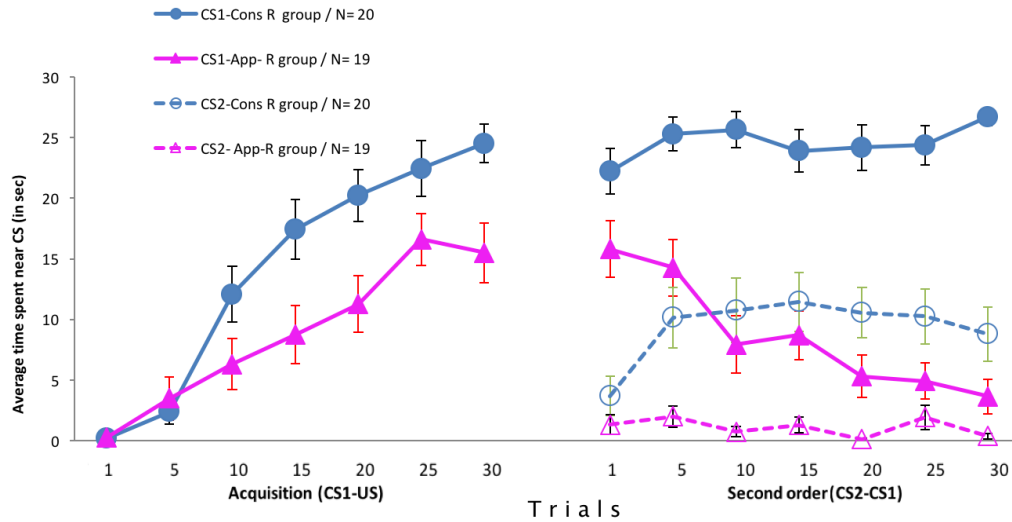
Figure 1. **Mean approach responses to CS1 and CS2 for groups Cons-R and App-R in Experiment 1.** First-order acquisition is shown on the left side and second-order conditioning is shown on the right. Filled symbols represent responding to CS1 and open symbols represent responding to CS2. Circles represent data for group Cons-R and triangles represent data for group App-R. Error bars represent standard error of the mean.

During the second-order conditioning phase, conditioned approach to CS1 declined substantially among the birds in group App-R but did not decrease among the quail in group Cons-R. This impression was substantiated by a groups x trials analysis of approach to CS1, which showed a significant main effect of groups, $F(1,37) = 64.377$, $p < 0.001$, $\eta_p^2 = 0.635$, trials $F(6,222) = 5.95$ $p < 0.001$, $\eta_p^2 = 0.231$, and a groups × trials interaction, $F(6,222) = 11.67$ $p < 0.001$, $\eta_p^2 = 0.139$.

Conditioned approach responses to CS2 also differed substantially between groups Cons-R and App-R. Group Cons-R showed substantially more responding to CS2 than Group App-R, and the second-order responding was much more persistent in Group Cons-R. An analysis of the approach scores for CS2 showed a significant effect of group, $F(1,37) = 17.32$, $p < 0.010$, $\eta_p^2 = 0.319$, trial $F(6,222) = 3.25$ $p < 0.010$, $\eta_p^2 = 0.081$, and a significant group × trial interaction, $F(6,222) = 3.49$, $p < 0.010$, $\eta_p^2 = 0.086$.

The finding that conditioned approach responding to CS1 was much more persistent in the second-order conditioning phase for group Cons-R than group App-R is consistent with the finding reported by Köksal et al. (2004) that conditioned consummatory responding leads to persistence in extinction. The fact that conditioned consummatory responding failed to extinguish when CS1 was no longer paired with a sexual US in the second-order phase turned out to have major implications for second-order conditioning. Evidently, the persistence of responding to CS1 permitted CS1 to function more effectively in conditioning CS2.
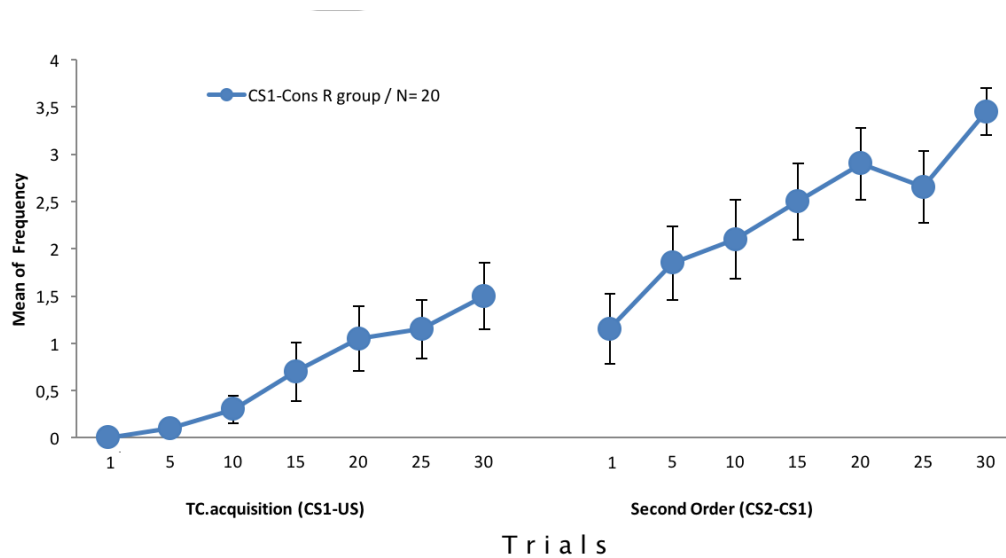
Figure 2. **Mean number of cloacal contact responses to the terrycloth (CS1) in Cons-R group subjects in Experiment 1.** Responding during the first-order phase is shown on the left and responding during the second-order phase is shown on the right. Error bars represent standard error of the mean.

We also calculated number of conditioned consummatory responses (cloacal contacts) made to CS1 during both original acquisition (first-order conditioning) and in the second-order conditioning phase. These data are presented in Figure 2 for group Cons-R. (All of the data points were zero for group App-R, which did not make cloacal contacts with CS1.) Cloacal contacts with CS1 increased substantially in group Cons-R during both first-order and second-order conditioning. An analysis of variance showed a significant effect of trials during both first-order conditioning, $F(6,19) = 8.69$, $p < 0.001$, $\eta_p^2 = 0.314$, and second-order conditioning, $F(6,19) = 8.74$, $p < 0.010$, $\eta_p^2 = 0.315$. The increase in cloacal contacts with CS1 during the second-order conditioning phase is particularly noteworthy, since CS1 was no longer paired with the original US (sexual access to a live female) during the second-order conditioning phase. Copulation with the CS1 object appears to have become self-maintained in subjects in group Cons-R.

Approach responses to CS1 and CS2 for the two control groups are displayed in Figure 3 for both the first-order and second-order phases of Experiment 1. Quail in group Control-1 received pairings of CS1 with the US in the first-order phase but CS2 was presented unpaired with CS1 in the second-order phase. As with the males in the experimental group, pairings of the terrycloth object with sexual reinforcement resulted in the development of copulatory responses to CS1 in about half of the subjects. However, whether or not conditioned consummatory responding developed, pairings of CS1 with the US resulted in approach responses to CS1. No such approach responses developed in the quail in group control-2, which received unpaired presentations of CS1s with the US during the first-order phase. This confirms the common finding in our laboratory that for approach and copulatory responses to develop to a terrycloth object (CS1), that object has to be paired with copulatory access to a female (the US).
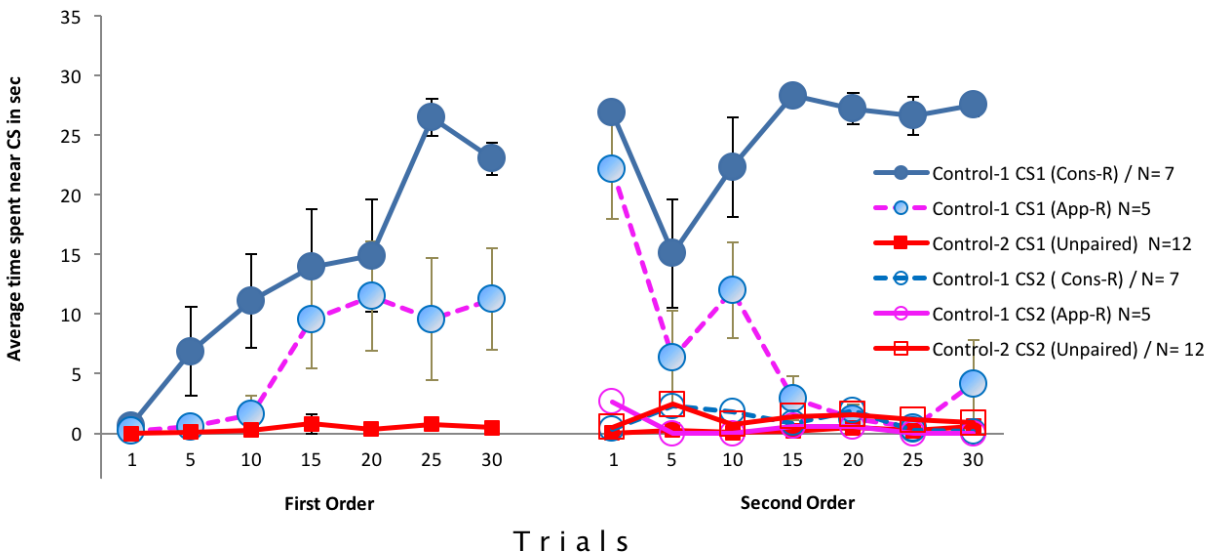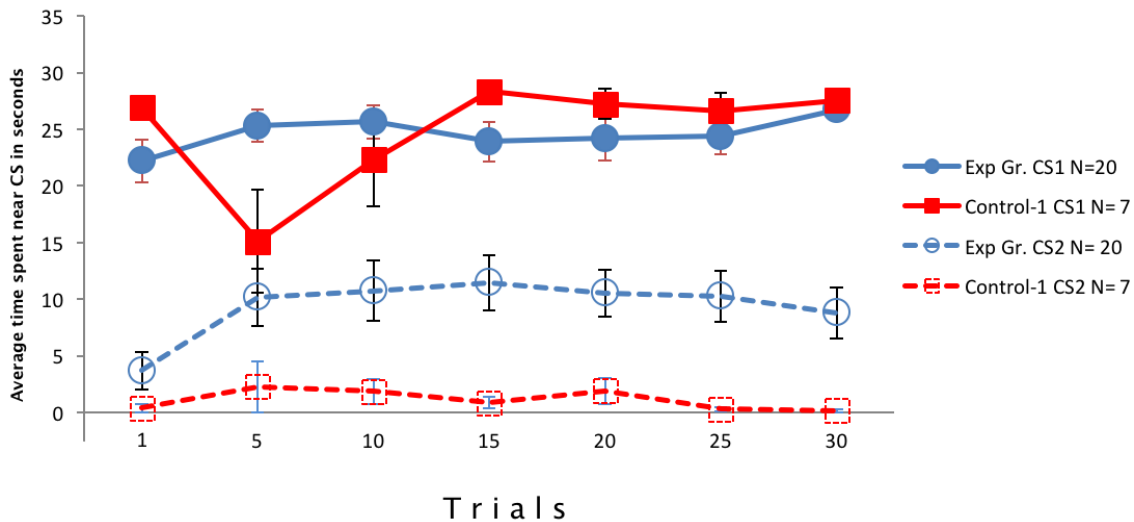
Figure 3. **Mean approach responses to CS1 and CS2 for the two control groups in Experiment 1.** Data for the first-order phase is shown on the left side and data for the second-order phase is shown on the right. Circles represent data for group Control-1 (CS1-US paired; CS2/CS1 unpaired). Squares represent data for group Control-2 (CS1/US unpaired; CS2-CS1 paired). Data for group Control-1 are shown separately for males that copulated with CS1 (Cons-R) and those that did not copulate with CS1 (No Cons-R). Error bars indicate standard error of the mean.

In the second-order phase, responding to CS1 persisted in subjects that copulated with CS1 as a result of the CS1-US pairings in the first-order phase (Cons-R). This replicates a similar result that was obtained in the Experimental group (see Figure 1). Also, consistent with the results shown by the Experimental group (and prior research by Köksal et al., 2004), persistence in approach to CS1 did not occur in the second-order phase among birds that did not copulate with CS1 (No Cons-R). Birds that received CS1 unpaired with the US in the first phase (Control-2) continued to show near-zero approach to CS1 in the second-order phase. This provides further evidence that responding to CS1 does not develop if CS1 is not paired with the US.

Minimal responding to CS2 was observed in the second phase of the experiment in both groups control-1 and control-2. No significant effects of either trials or groups were observed in responding to CS2, group $F(2,21) < 1.00$, trial $F(86,126) < 1.00$, and trial × group interaction $F(12,126) < 1.00$. This was the case even for birds in group control-1 that copulated with the terrycloth object (CS2, Cons-R). This outcome demonstrates that responding to CS2 does not occur if CS2 is not paired with CS1 (Control-1) or if CS1 is not paired with the US (Control-2).

We also compared the approach responses to CS1 and CS2 in the Cons-R birds in the Experimental and Control-1 groups during the second-order phase of the experiment (see Figure 4). This is an important comparison because the birds of both of these groups received CS1-US pairings in the first phase. However, in the second-order phase the experimental group received pairing of CS2 and CS1 whereas Control-1 subjects were exposed to unpaired presentations of CS1 and CS2. A repeated-measures ANOVA showed no significant group effect in responding to CS1, $F(1,25) < 1.00$. However, there was a significant difference between groups in responding to CS2, $F(1,25)=6.40$, $p < 0.05$, $\eta_p^2 = 0.204$. Thus, the subjects in the two groups showed similar responding to the terrycloth object, but significantly different responding to CS2 (see Figure 4). These observations substantiate our claim that the responding to CS2 that was observed in the experimental group (Figure 1) is a genuine second-order conditioning effect and not due to mere exposure to CS1, CS2, and the US.

Figure 4. **Mean approach responses of Cons-R subjects in the experimental group and group Control-1 during second-order conditioning in Experiment 1.** Responses to CS1 (terrycloth) are shown by the filled symbols and responses to CS2 (light) are shown by the open symbols. Circles represent data for the experiment group. Squares represent data for group control-l. Error bars indicate standard error of the mean.

Experiment 2

Experiment 1 provided strong evidence of second-order conditioning of approach to a light conditioned stimulus if the first-order conditioned stimulus (CS1) came to elicit conditioned consummatory behavior as a result of its pairings with the sexual US. The goal of Experiment 2 was to see if the strength of the second-order conditioning observed in Experiment 1 is comparable to the strength of first-order conditioning of a light CS using similar conditioning parameters.

Subjects. Seventeen experimentally naive male subjects were used. Their age and housing conditions were the same as in Experiment 1. Same number of experimental naive female birds served in the study.

The same apparatus and methods were used as in Experiment 1. However, only first-order conditioning was conducted. The CS used during the first-order conditioning trials was the light that had served as CS2 in Experiment 1; 30 conditioning trials were conducted, with approach to the CS measured in the same manner as in Experiment 1.

Results

The acquisition of responding to the light CS is shown in Figure 5. Since we were interested in seeing whether copulation with a female US would condition as strong approach responses to the light as copulating with a terrycloth object, we replotted the second-order conditioning data obtained from the Cons-R birds in the experimental group in Experiment 1. Acquisition of approach to the light was very similar in the two condition. A repeated-measures ANOVA yielded no significant effect groups and no groups x trials interaction, F<1. However, the effect of trials was found to be significant, $F(6,35) = 6.87$, $p < 0.001$, $\eta_p^2 = 0.164$. These findings indicate that the second-order conditioned approach to the light that was obtained in birds that copulated with the terrycloth object was as strong as first-order conditioning of the light paired with a sexual US.
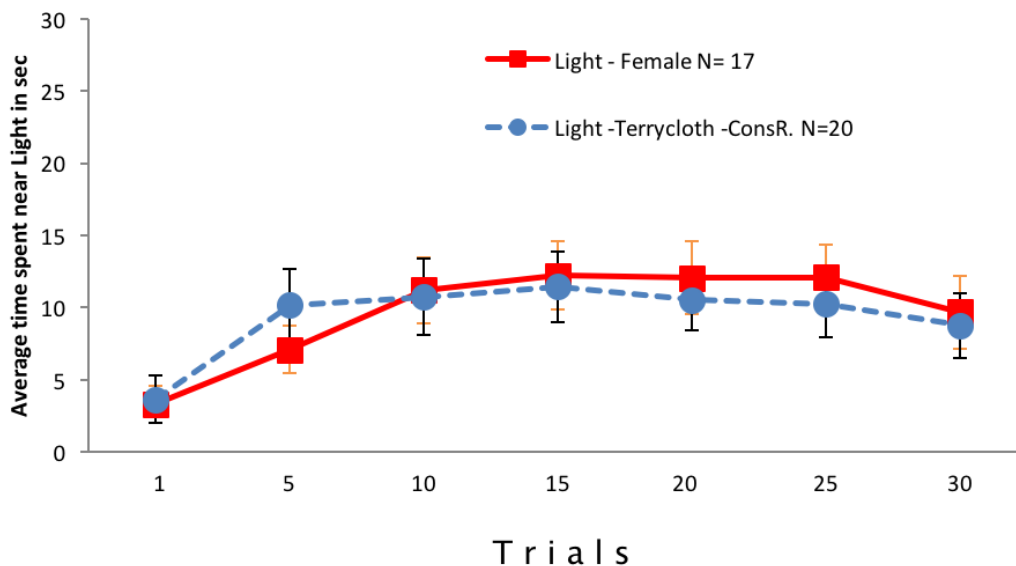
Figure 5. **Comparison of first- and second-order conditioning to the light CS.** Approach responses to the light paired with access to a female (first-order conditioning) is shown by the square symbols connected by a solid line. Approach responses to the light paired with the conditioned terrycloth model (second-order conditioning) is shown by the filled circles connected by dashed lines. Error bars present standard error of the mean.

Discussion

The present study confirms that approaching the CS is a highly reliable index of sexual conditioning in male quail (Domjan & Akins, 2011). Pairing a terrycloth object (CS1) with copulatory access to a female (first-order conditioning) resulted in conditioned approach to the CS whether or not the quail came to copulate with the terrycloth object (Cons-R and App-R). Group Cons-R showed somewhat stronger approach responding than group App-R, but only on trials 25 and 30. The most important novel finding in the experiment occurred during second-order conditioning. During the second-order phase, a novel light (CS2) was paired with the previously conditioned terrycloth object (CS1). Conditioned approach responding to CS2 occurred only among males that showed conditioned consummatory responses to CS1 (group Cons-R).

The acquisition of responding to CS2 was no doubt related to responding to CS1 during the second-order phase. During second-order conditioning, the US is no longer presented, and a common outcome is that responding to CS1 declines as a result. Such extinction was clearly evident among subjects that did not come to copulate with CS1 (group App-R) (see Figure 1). The mean conditioned approach score for group App-R was 9.3 sec during the first second-order trial and 2.2 sec. during the 30th (last) second-order trial. In contrast, extinction of approach responding to CS1 did not occur during the course of second-order conditioning for subjects in group Cons-R. The mean approach response to CS1 for these subjects was 23 seconds during the first trial of second-order conditioning and 26 seconds during the last trial. Thus, in the absence of any further pairings of CS1 with the US (female), male quail in group Cons-R showed no loss of conditioned approach to CS1.

The persistence of conditioned responding in group Cons-R during the course of second-order conditioning was also evident in measures of copulation with CS1 during the second-order phase (Figure 2). In fact, copulatory activity directed towards CS1 continued to increase during the course of second-order conditioning in group Cons-R. The mean frequency of cloacal contact responses increased from 1.2 during the first second-order trial to 3.7 during the last trial of second-order conditioning. These findings indicate that the behavioral efficacy of the terrycloth object increased with repeated trials during which copulation was directed towards the stimulus in the absence of a live female (the US).

Second-order responding (conditioned approach to the light that served as CS2) was similar to the responding to CS1. Subjects that continued to approach and copulate with CS1 (group Cons-R) also came to approach CS2, as CS2 was repeatedly paired with CS1 during the course of second-order conditioning. Since the magnitude of conditioned approach and consummatory responses to CS1 persisted during second-order conditioning for group Cons-R, CS1 was able to support conditioning to CS2 throughout the second-order phase. In contrast, second-order responding to CS2 did not develop among subjects in group App-R. It is reasonable to attribute the lack of second-order conditioning to the fact that group App-R showed rapid extinction of responding to CS1 during the second-order phase. Rapid extinction of responding to CS1 typically makes it difficult produce second-order conditioning. In fact, extended second-order trials can result in the conditioning of inhibition rather than excitation to CS2 (Yin, et al., 1994).

The remarkably robust nature of the second-order responding that developed to CS2 (light) was further substantiated in Experiment 2 by comparing second-order conditioning of the light in group Cons-R to first-order conditioning of the light in an new group of birds. The acquisition of conditioned approach under these contrasting circumstances was not distinguishable. This suggests that the copulatory behavior that was elicited by CS1 in group Cons-R made CS1 function much like copulation with a live female in conditioning approach behavior to CS2. Thus, a CS that comes to elicit consummatory behavior appears to function very much like a US, significantly facilitating second-order conditioning.

General Discussion

The results of the present study support the consummatory response model of reinforcement. The model suggest that what makes a stimulus a reinforcer is presence or absence of consummatory responding. If a stimulus can elicit a consummatory response, then it can act like a reinforcer. Sheffield et al. (1954) conducted a number of experiment with saccharin as a stimulus capable of sustaining consummatory responding. These studies showed that saccharin does act like a reinforcer. However, saccharin may not provide a good test of the consummatory response model because it has many of the same physiological effects as sugar. In addition, prolonged ingestion of saccharin may have negative consequences that undermine the reinforcing efficacy of the consummatory response in this case (Routtenberg & Lindy, 1965).

Sexual reinforcement may provide a better model in which to test the consummatory response model because there are no long-term negative consequences to continued copulation with an arbitrary object such as a terrycloth model. In fact, we have observed sexually conditioned male quail copulating with a terrycloth model even if a live female is present and available (Köksal et al., 2004). This makes the quail sexual behavior system particularly suitable as a model system for studying human sexual fetishes.

The present results suggest that any object that can induce consummatory behavior can become conditioned as a "sexually-relevant" object. If the object comes to elicit consummatory behavior and that behavior is pleasurable, the object can come to function as if it were an unconditioned stimulus. In the present study, sexual conditioned consummatory responses to the terrycloth object occurred in about half of the subjects (Cons-R group). For these quail, the terrycloth object appeared to have gained US-like qualities. This led to highly persistent responding in the absence of further first-order pairings with a female. This persistent responding to the terrycloth object in turn facilitated second-order conditioning. In the absence of this conditioned consummatory responding, the terrycloth object acted as an ordinary CS1 and underwent extinction during the course of second-order CS2-CS1 pairings. That in turn undermined the success of the second-order conditioning trials. A major remaining issue in this line of research is to identify the factors that determine why some quail showed conditioned consummatory responses whereas others did not display such conditioned behavior.

The present findings also suggest that what makes a CS resistant to extinction may be different for aversively and appetitively motivated behavior. With a CS that has been associated with an aversive US (shock or trauma), as soon as the CS is given the organism becomes fearful and responds to terminate or move away

from the situation so as to reduce the conditioned fear. Each time the CS is presented, the organism immediately tries to terminate it, which minimizes expose to the CS during extinction trials. Therefore, increasing CS exposure has been an integral component of treatments for anxiety disorders (Foa & Kozak, 1986; McNally, 2007; Olatunji, Cisler, & Deacon, 2010; Powers & Emmelkamp, 2008; Resick Nishith, Weaver, Astin, & Feuer, 2002). With increased durations of exposure to the CS in the absence of the US, the CS loses its aversive properties and once again becomes an innocuous stimulus.

For appetitively motivated behaviors, the situation may be different. Because the CS is paired with an appetitive US (for example sexual opportunity), each time the CS is presented the organism moves towards the stimulus. If the CS comes to elicit conditioned consummatory responses, each exposure to the CS will act like a further conditioning trial even in the absence of the US, since the consummatory behavior will serve as a reinforcer. Therefore, for appetitively motivated behaviors exposure to the CS by itself will not alleviate the problem behavior (like fetishism). In fact, CS-alone exposures may even lead to a worsening of the problem. Here, treatment programs that include aversive conditioning may be required to reduce the appetitive quality of the CS (Cautela, 1967; Kelly, 1982; Krueger & Kaplan, 2002; Marshal & Lippens 1977; Quinsey & Earls, 1990).

Acknowledgments

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