INVITED ESSAY

Situating Human Sexual Conditioning

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Abstract Conditioning is often thought of as a basic, automatic learning process that has limited applicability to higher-level human behavior. In addition, conditioning is seen as separable from, and even secondary to, "innate" processes. These ideas involve some misconceptions. The aim of this article is to provide a clearer, more refined sense of human sexual conditioning. After providing some background information and reviewing what is known from laboratory conditioning studies, human sexual conditioning is compared to sexual conditioning in nonhumans, to "innate" sexual responding, and to other types of human learning processes. Recommendations for moving forward in human sexual conditioning research are included.

Keywords Human classical conditioning · Sexual preferences · Partner preference · Learning · Sexual orientation

Introduction

Conditioning is often thought of as a basic, automatic learning process that has limited applicability to higher-level human behavior. In addition, conditioning is seen as separable from, and even secondary to, "innate" processes. For example, sex of partner preference is commonly attributed to genetic or prenatal physiological, as opposed to postnatal experiential, fac-

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tors (see Bailey et al., 2016). Further, sexual conditioning can bring to mind the mostly unsuccessful traditional behavior therapy approaches (e.g., masturbatory conditioning and aversion therapy) for altering "deviant" sexual arousal patterns (for review, see Bancroft, 1974; Beckstead, 2012). The aim of this article is to provide a clearer, more refined sense of human sexual conditioning. After reviewing the human sexual conditioning literature, I will situate or frame such learning in three ways: relative to sexual conditioning in nonhumans, relative to "innate" processes, and relative to other types of human learning processes. I conclude with suggestions for future human sexual conditioning research.

Definitions and Concepts

Broadly, conditioning is a process by which organisms, including humans, learn about the relationships between events. Through conditioning, we can learn to predict events, we can learn signals for biologically significant stimuli, we can learn the value of stimuli, and we can learn the consequences of our actions. Hence, sexual conditioning can prepare us to respond sexually and can contribute to our erotic preferences and to how we behave sexually.

Conditioning procedures—which are used in the laboratory but are assumed to have real-world correlates—tend to be broken down into two types: classical and operant conditioning. Although these processes share properties and they intimately interact, they involve different procedures, result in different outcomes, and most likely involve some different mechanisms (e.g., Lorenzetti, Mozzachiodi, Baxter, & Byrne, 2006). Classical (Pavlovian or respondent) conditioning involves the association between two stimuli (e.g., a bell and food per Pavlov), whereas in operant (instrumental or Skinnerian) conditioning the association formed is between a response and a reinforcer (e.g., lever pressing and food per Skinner). Clas-



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sical conditioning can impact our physiological and/or emotional responsiveness to (sexual) stimuli, our (erotic) preferences, and basic approach/avoidance tendencies. Operant conditioning, on the other hand, can more directly influence what we do sexually, whether that consists of altering physiological responses, changing overt behavior or altering mental processes (e.g., thoughts or fantasies). An example of appetitive classical conditioning of sexual arousal in the laboratory would be pairing a neutral stimulus (e.g., the picture of a penny jar or a cartoon sketch of a male face) with erotic pictures or film, with the intent of demonstrating conditioned genital and subjective arousal to the neutral stimulus. Examples of appetitive operant sexual conditioning in the laboratory would include (1) rewarding (e.g., with money) increased penile tumescence, with the intent of demonstrating enhanced genital responding and (2) rewarding the watching of explicit sexual stimuli, with the intent of demonstrating increased viewing of sexual images.

The main focus of this article will be on classical conditioning, as it is my area of expertise, and also because the human conditioning literature has many more classical-than operantbased conditioning studies. The cues being associated in such learning are called the conditioned (or conditional) stimulus (CS) and unconditioned stimulus (US). The main difference between these cues is in the strength and duration of response they elicit. The CS has been referred to as a neutral or innocuous stimulus, at least prior to conditioning, whereas the US is said to elicit a strong(er) behavior response. The behavioral response elicited by the US is called the unconditioned response (UR), and the response elicited by the CS (after training) is the conditioned response (CR). The CR can be similar to the UR, but it need not be. Whether the CR approximates the UR depends on a number of factors, including the nature of the CS and US, the temporal relationship between the CS and US, contextual conditions as well as the measure used to assess learning (e.g., Akins, Domjan, & Gutiérrez, 1994; Burns & Domjan, 2001; Silva, Timberlake, & Gont, 1998). For example, when pairing a model of a bird (CS) with access to a sexually receptive female (US), Akins (2000) found that male quail who were exposed to a short (1 min) CS-US interval showed conditioned approach to the model, whereas those trained with a long (20 min) CS-US interval showed a conditioned increase in activity in the presence of the model but not conditioned approach. In fact, Pavlovian training can yield conditioned compensatory responses, which oppose the UR (Newlin, 1985, 1986; Siegel, Hinson, Krank, & McCully, 1982). For example, in social drinkers, alcohol increases pulse transit time (a measure of the speed of arterial blood flow) and finger temperature, whereas cues that predict alcohol are associated with opposing physiological responses.

Classical conditioning may result it two different outcomessignal or expectancy and evaluative or affective learning (De Houwer, Thomas, & Baeyens, 2001). The former prepares us for interaction with biologically significant cues or events, and the latter can alter our preferences/attitudes about stimuli associated with such cues or events. Signal learning is the common interpretation for the outcome of classical conditioning, meaning that the CS comes to predict and hence to prepare us for encountering the US (Rescorla, 1988). Evaluative conditioning is proposed to be a form of classical conditioning that involves an associative transfer of affective valence from US to CS as a result of experiencing the pairing of these cues. That is, conditioning can change how much a stimulus is liked or disliked. While this signal versus evaluative distinction makes sense conceptually, it is sometimes difficult to illustrate concretely. However, the phenomenon of sign tracking is helpful in this respect. Sign tracking is a maladaptive outcome of classical conditioning (Brown & Jenkins, 1968; Costa & Broakes, 2007; Williams & Williams, 1969). The effect seems to occur in certain individuals (e.g., Flagel, Watson, Robinson, & Akhil, 2007) and/or under certain conditions (e.g., Versaggi, King, & Meyer, 2016) and has been used to model addiction (Flagel, Akil, & Robinson, 2009; Saunders & Robinson, 2013). One measure of sign tracking that clearly demonstrates its maladaptive nature is the continued conditioned approach to a CS that previously predicted an appetitive US, even when such approach delays or eliminates the presentation of the US. In male quail, it has been found that some birds would approach, stay close and, in some instances, sexually interact with a CS (a wooden block or a terry cloth model) that predicted access to a female, even when the female was present (Burns & Domjan, 1996, 2000; Cetinkaya & Domjan, 2006; Köksal et al., 2004). These cues did not seem to simply signal the US but rather they acquired arousing properties. Fetish object learning could result from sexual evaluative conditioning. One study has directly examined and found evidence for, sign tracking in human sexual behavior (Kimura, Fukui, & Inaki, 1990). In a nonsexual human conditioning study, signal and evaluative conditioning were dissociated within the same paradigm (e.g., Hermans, Crombez, Vansteenwegen, Baeyens, & Eelen, 2002), suggesting that they are (mechanistically) distinct, although not necessarily independent outcomes. That is, Baeyens, Vansteenwegen, Hermans, and Eelen (2001) proposed that signal learning is governed by an expectancy system that requires more cognitive resources to process or translate complex information resulting in anticipation of an object or event. On the other hand, they suggest that evaluative conditioning is mediated by a more "primitive" referential system that employs more rudimentary learning or performance rules resulting in changes in affective value that can influence the direction of behavior (approach/avoid) and modulate (facilitate/suppress) responses generated by the expectancy system. Hence, classical conditioning may incorporate two different functional systems that may employ distinct algorithms for forming, modifying, and/or expressing associations. These different processes could also have different, but also concurrent, impacts on behavior.

What Do We Know About Human Sexual Conditioning?

Although laboratory studies of human sexual conditioning began in the late 1960s (for review, see O'Donohue & Plaud, 1994), it was not until the 1990s that the first methodologically sound studies (Lalumière & Quinsey, 1998; Plaud & Martini, 1999) were published. The vast majority of early human sexual conditioning research has employed male participants and that was also the case for these studies. The first study showing sexual conditioning in women (Hoffmann, Janssen, & Turner, 2004) did not appear until five years later. There are approximately 20 published studies showing convincing evidence of human sexual conditioning. Table 1 lists these studies since 1997 and compares them on participants, conditioning and testing procedures, and findings. I discuss aspects of these, and other, comparisons below.

Most studies have been conducted using a nonclinical population, although there are some exceptions (e.g., Banca et al., 2016; Both, Braun, Weijenborg, & Laan, 2017; Klucken et al., 2016). Across these studies, a differential conditioning paradigm that employs a CS+ (a cue paired with the US) and a CS- (a cue presented during training but not paired with the US) is the most commonly used training procedure. In some instances, a between-subjects control group (unpaired, random, and/or backwards) has been employed. Conditioning tends to be brief (occurring in a single session) and testing occurs soon after training, although there are some exceptions (e.g., Hoffmann, Peterson, & Garner, 2012).

It is not clear which stimuli and measures are most effective for sexual conditioning. Acquisition trials most often involve a delay conditioning procedure, in which there is an overlap between the CS and the US, with 100% reinforcement (i.e., when the CS is always presented with the US). Erotic pictures, short erotic film clips, and brief genital vibrostimulation are the most commonly used USs. More rarely, active sexual participation (e.g., masturbation or partnered sexual interaction) has been employed (e.g., Hoffmann et al., 2012; Kantorowitz, 1978). Although it would seem that actual sexual interaction would be a more salient US, we lack direct comparisons of US effectiveness. Visual cues, which range from simple (e.g., geometric figures) to the complex (e.g., photographs) and from arbitrary to prepared (i.e., evolutionary pre-tuned or reproductively relevant), are common CSs. A few studies have used ambiently and/or discretely presented olfactory cues (Hoffmann, 2007; Hoffmann, Goodrich, Wilson, & Janssen, 2014; Hoffmann & Janssen, 2006; Hoffmann et al., 2012). Prepared (sexually relevant) CSs would seem to be more effective CSs. However, only one study provides direct evidence for this, and the results were not uniform, i.e., women showed stronger CRs to a photograph of a gun relative to a photograph of a naked male torso, at least when these cues were presented liminally (Hoffmann et al., 2004).

Conditioning is typically assessed via genital (plethysmographic) response as well as with measures of subjective arousal to and affective preference (measured explicitly but sometimes implicitly) for the CS. Explicit measures employ Likert or visual analog scales, and implicit measures have involved priming tasks or assessment of approach/avoidance tendencies. Less commonly, measures of US expectancy/contingency awareness (e.g., asking participants, when presented with the CS, to rate to what extent they expect the US), skin conductance, and neural responses have been used. Genital CRs and measures of subjective arousal to and affective preference for the CS, often but not always, yield evidence of learning, but it is usually not robust. In a few studies, the strength of genital CRs has been comparable to the strength of genital responses to the US (i.e., the UR; Brom, personal communication, February 24, 2016; Plaud & Martini, 1999), but it is usually far less robust. US expectation has yielded some of the strongest CRs but has not been consistently used.

In addition to demonstrating conditioned acquisition, evidence has been found for several other basic classical conditioning effects. Specifically, extinction (Brom, Laan, Everaerd, Spinhoven, & Both, 2014, 2015a; Brom et al., 2015c), renewal (Brom et al., 2014, 2015c), conditioned inhibition (Hoffmann et al., 2012), and aversive sexual conditioning (Both et al., 2008a; Brom et al., 2015a) have been documented.

There may be individual differences in conditionability. Although some have suggested that men/males may more readily show conditioned sexual arousal (Pfaus, Kippin, & Centeno, 2001), only a handful of studies have attempted a direct comparison and they have not yielded a clear answer (Brom, 2016). In fact, women may more readily show some types (e.g., aversive) of sexual conditioning (Brom et al., 2015a). Sexually compulsive men may show stronger conditioning than nonsexually compulsive men (Banca et al., 2016; Hoffmann et al., 2014; Klucken et al., 2016), and men high rather than low in extraversion may show stronger conditioned arousal, while those higher compared to those lower in introversion may show stronger conditioned detumescence (Kantorowitz, 1978). For women, those low rather than high in sexual inhibition (Hoffmann, 2011) and those high rather than low in sexual functioning (Both et al., 2008a) may show stronger sexual conditioning.

Conditioning is also moderated by situation. One factor that has been shown to affect conditioning is awareness. There is controversy regarding defining and measuring awareness in the laboratory (Lovibond & Shanks, 2002), and the measures of awareness in sexual conditioning studies have been crude measures, assessed post-training via self-report. There is evidence for sexual conditioning without awareness, particularly with overlap in CS/US presentation, when sexually relevant

Citation	Participants (nonclinical unless denoted*)	Conditioned stimuli (CSs) Unconditioned stimuli (USs)	Conditioned responses	Conditioning procedure	Test procedure	Main conditioning outcome
					Time of test (extinction trials unless denoted*)	Other findings
Appetitive						
Letournea & O'Donohue (1997)	25 women	Short and intermediate neutral visual	Genital arousal	10 single CS trials/day	3 probe trials*/day	No conditioning
		Intermediate erotic film clips	Subjective sexual arousal	5 sessions, one per day		
				Delay conditioning		
				70% reinforcement		
				Explicitly unpaired control group		
Lalumiere & Quinsey	20 men	Short sexual visual	Genital arousal	11 single CS trials	2 single CS trials	Conditioned genital arousal
(1998)		Short erotic film		1 session	Immediate	
		clips		Delay conditioning 100% reinforcement		
				CS-only control group		
Plaud & Martini	9 men	Short neutral visual	Genital arousal	15 single CS trials/ week	5 probe trials*/ week	Conditioned genital arousal
(1999)		Short erotic pictures		3 sessions, one per week		
				Delay conditioning		
				67% reinforcement		
				Random and backwards control groups		
Hoffmann et al. (2004)	27 women	Subliminal and short	Genital arousal	11 differential trials	2 differential trials	Conditioned genital arousal for:
	29 men	men Nonsexual and sexual visual Short erotic film clips	Skin conductance	1 session	Immediate	Subliminal sexual CS
				Trace conditioning		Short sexual CS (men only) Short nonsexual CS (women
				100% reinforcement		
				Explicitly unpaired control group		only)
Both et al. (2008a)	17 women	17 women Short neutral visual	Genital arousal	10 differential trials	4 differential trials	Conditioned genital arousal that extinguished
		Brief genital vibrostimulation	Affective value	1 session	Immediate	Weak conditioned affective value-no extinction
				Delay conditioning		
Poth at al	18 women	Culture in 1	Conital array	100% reinforcement	12 differenti-1	Conditionad ganital arguest the
(2008b)	18 women	visual	Genital arousal		trials	extinguished
		Brief genital vibrostimulation	arousal	1 session	Immediate	
			Affective value	Delay conditioning		
			Skin conductance	100% reinforcement		

 Table 1
 Published studies of human sexual conditioning studies 1997–2017

Table 1 continued

Citation	Participants (nonclinical	Conditioned stimuli (CSs)	Conditioned responses	Conditioning procedure	Test procedure	Main conditioning outcome
	unless denoted*)	Unconditioned stimuli (USs)		Freedow	Time of test (extinction trials unless denoted*)	Other findings
Klucken et al. (2009)	20 women	Short neutral visual	Neural response (fMRI)	21 differential trials	11 differential trials	Conditioned fMRI (reward structures and occipital cortex; CA only)
	20 men	Brief erotic pictures	Subjective sexual arousal	1 session	Immediate	Conditioned subjective sexual arousal (CA only)
		Non-US	Affective value	Trace conditioning		Conditioned affective value (CA only)
			Subjective arousal	100% reinforcement		Conditioned subjective arousal (CA only)
			Subjective disgust			Men > women
			Skin conductance			
			Contingency awareness			
Both et al. (2011)	32 women	Short neutral visual	Genital arousal	8 differential trials	6 differential trials	Conditioned genital arousal-no extinction
		Brief genital vibrostimulation	Subjective sexual arousal	1 session	Immediate	Conditioned subjective sexual arousal that extinguished
			Affective value	Delay conditioning		Weak conditioned affective
			Skin conductance	100% reinforcement		value-no extinction
Hoffmann et al. (2012)	14 men	Long neutral olfactory	Genital arousal	3 differential trials	3 differential trials	Conditioned genital arousal-no extinction
		Partnered sexual interaction	Affective value	1 two-week session	3- to 11-day retention	Conditioned affective value; conditioned inhibition
		Non-US	Contingency awareness	Delay conditioning	interval	
				100% reinforcement		
				Explicitly unpaired control group		
Klucken et al. (2013)	86 men	Short neutral visual	Neural response (fMRI)	21 differential trials	fMRI and SC during acquisition*	Conditioned fMRI (reward structures)
		Brief erotic pictures	Subjective arousal	1 session	Other measures-1 differential trial	Conditioned subjective arousal
			Affective value	Trace conditioning	Immediate	Conditioned affective value
			Skin conductance	100% reinforcement		Conditioned skin conductance
			US expectancy			Conditioned US expectancy
						Genetics (5-HTTLPR) affect conditioning

Table 1 continued

Citation	Participants (nonclinical	Conditioned stimuli (CSs)	Conditioned responses	Conditioning procedure	Test procedure	Main conditioning outcome
_	unless denoted*)	Unconditioned stimuli (USs)		Freedow	Time of test (extinction trials unless denoted*)	Other findings
Brom et al. (2014)	62 women	Short neutral visual	Genital arousal	10 differential trials	10 differential trials	Conditioned genital arousal-no extinction (women only)
	40 men	Brief genital vibrostimulation	Subjective sexual arousal	1 session	Immediate	Conditioned subjective sexual arousal (extinguished in women only)
			Affective value	Delay conditioning	Immediate renewal assessment	Conditioned affective value that extinguished (women only)
			Approach behavior	100% reinforcement		Conditioned US expectancy that extinguished
			US expectancy			Renewal-US expectancy
						Renewal-subjective sexual arousal and affective value (women only)
Hoffmann et al. (2014)	56 men	Short neutral olfactory	Genital arousal	18 differential trials	3 differential trials	Conditioned genital arousal
		Short erotic film clips	Affective value	1 session	Immediate	Conditioned affective value
			Risk taking behavior	Delay conditioning		Increased risk taking in the presence of CS
			Contingency	100% reinforcement		High sexual compulsivity > low
			awareness	Explicitly unpaired control group		sexual compulsivity
Brom et al. (2015b)	53 women	Short sexual visual	Genital arousal	10 differential trials	4 differential trials	Conditioned genital arousal that extinguished (men only)
	40 men	Brief genital vibrostimulation	Subjective sexual arousal	1 session	Immediate	Conditioned subjective sexual arousal-no extinction
			Affective value	Delay conditioning		Conditioned affective value-no extinction
			Approach behavior	100% reinforcement		Conditioned approach behavior (women only)
			US expectancy			Conditioned US expectancy-no extinction
						Down regulation enhances extinction for:
						Subjective sexual arousal (men only)
						Affective value (men only)
						Approach behavior (women only)
Brom et al. (2015c)	62 women	omen Short sexual visual	Genital arousal	10 differential trials	10 differential trials	Conditioned genital arousal that extinguished
		Brief genital vibrostimulation	Subjective sexual arousal	2 sessions	2 sessions (Day 1)	Conditioned subjective sexual arousal that extinguished
			Affective value	Delay conditioning	Renewal assessment	Conditioned affective value that extinguished
			US expectancy	80% reinforcement	(Day 2)	Conditioned US expectancy that extinguished
						Renewal-genital and subjective sexual arousal and affective value
						D-Cycloserine prevents renewal

Table 1 continued

Citation	Participants (nonclinical	Conditioned stimuli (CSs)	Conditioned	Conditioning procedure	Test procedure	Main conditioning outcome
	unless denoted*)	Unconditioned stimuli (USs)		Freedow	Time of test (extinction trials unless denoted*)	Other findings
Banca et al. (2016)	62 men	Brief neutral visual	Affective value/ approach	30 differential trials	20 differential trials	Conditioned preference (CSB only)
Study 1	22 with CSB*	Brief erotic pictures		1 session	Paired associates learning task*	
				Trace conditioning	Immediate	
Study 2	40 men	Brief neutral visual	Neural response (fMRI)	20 differential trials	15 differential trials	Conditioned neural response (occipital cortex)
	20 with CSB*	Brief erotic	()	1 session	Immediate	Decreased ventral striatal
		pictures		Delay conditioning		activity in extinction
				100% reinforcement		
Brom et al. (2016a)	53 women	Short sexual visual	Genital arousal	10 differential trials	4 differential trials	Conditioned genital arousal that extinguished (women only)
	40 men	Brief genital vibrostimulation	Subjective sexual arousal	1 session	Immediate	Conditioned subjective sexual arousal-no extinction
			Affective value	Delay conditioning		Conditioned affective value-no extinction
			Approach behavior	100% reinforcement		Conditioned US expectancy-no extinction
			US expectancy			Conditioned approach (women only)
						Up regulation enhances:
						Resistance to extinction for genital response (women only) conditioning of affective value (men only)
Brom et al. (2016b)	58 women	men Short neutral visual Brief genital vibrostimulation	Genital arousal	8 differential trials	6 differential trials	Weak conditioned genital arousal-no extinction
			Subjective sexual arousal	1 session	Immediate	Weak conditioned subjective sexual arousal-no extinction
			Affective value	Delay conditioning 100% reinforcement		No effect of dopamine antagonism on conditioning
Klucken et al. (2016)	40 men	Short neutral visual	Neural response (fMRI)	21 differential trials	fMRI and SC during acquisition*	Conditioned fMRI (reward structures and occipital cortex)
	20 with CSB*	Brief erotic pictures	Subjective sexual arousal	1 session	Other measures-1 differential trial	Conditioned subjective sexual arousal
			Affective value	Trace conditioning	Immediate	Conditioned affective value
			Subjective arousal	100% reinforcement		Conditioned subjective arousal
			Skin conductance			Conditioned skin conductance
			US expectancy			Conditioned US expectancy
						CSB>non-CSB fMRI (amygdala)
Aversive						

Table 1 continued

Citation	Participants (nonclinical unless denoted*)	Conditioned stimuli (CSs) Unconditioned stimuli (USs)	Conditioned responses	Conditioning procedure	Test procedure	Main conditioning outcome
					Time of test (extinction trials unless denoted*)	Other findings
Both et al. (2008a)	17 women	Short sexual picture	Genital arousal	10 differential trails	4 differential trials	Conditioned decreased genital arousal-no extinction
		Brief wrist shock	Subjective sexual arousal	1 session	Immediate	Conditioned affective value-no extinction
			Affective value	Delay conditioning		
			Skin conductance	100% reinforcement		
Brom et al. (2015a)	34 women	Short sexual picture	Genital arousal	10 differential trials	24 differential trials	Conditioned decreased genital arousal-no extinction (women only)
	38 men	Brief wrist shock	Subjective sexual arousal	1 session	Immediate	Conditioned subjective sexual arousal-no extinction (women only)
			Affective value	Delay conditioning		Conditioned affective value-no extinction
			Avoidance behavior	100% reinforcement		
Both et al. (2017)	71 women	Short sexual picture	Genital arousal	10 differential trials	4 differential trials	No conditioned genital responding
	36 with dyspareunia*	Brief wrist shock	Subjective sexual arousal	1 session	Immediate	Conditioned subjective sexual arousal
			Affective value	Delay conditioning		Conditioned affective value
			US expectancy	100% reinforcement		Conditioned US expectancy
			Skin conductance			Nondyspareunia > dyspareunia; more generalization to CS in dyspareunia

CSB = Compulsive sexual behavior; brief = 50-4000 ms; short = 8-40 s; Intermediate = 120-130 s; long = over 5 min; fMRI—functional magnetic resonance imaging; single CS = only a CS+ was used; differential = CS+ and CS- were used; CS+ = stimulus paired with the US; CS- = stimulus presented during conditioning but not paired with the US; Non-US = stimulus paired with CS-; delay conditioning = CS overlaps with US; trace conditioning = CS does not overlap with US; Immediate = no delay between conditioning and testing; SC = skin conductance; CA = contingency aware; 5HTTLPR = serotonin transporter-linked polymorphic region; renewal = recovery of conditioned responding after context change; >show stronger learning than

cues have been used as CSs and when genital response has been used as a CR, yet awareness seems to enhance conditioning (Both et al., 2008b; Hoffmann, 2010; Hoffmann et al., 2004; Klucken et al., 2009). This is consistent with what has been found in other human conditioning experiments, particularly conditioned fear (Lovibond & Shanks, 2002). Relatedly, regulation strategies, including top-down regulation of physical arousal and pharmacological manipulations, have been shown to affect the acquisition and extinction of sexual CRs in both men and women, although effects differ by sex and by measure (Brom et al., 2015a, 5b, 2016a). Finally, some evidence shows that anxiety may promote sexual conditioning. That is, in Hoffmann et al. (2004), women more readily showed conditioned sexual arousal to a gun compared to a male abdomen CS. The gun-arousal associations may have been facilitated by excitation transfer, considering that women showed a greater skin conductance response to the gun versus the abdomen.

Although it is still unclear how to differentially measure signal versus affective conditioning, it has been suggested that measures of affective preference for the CS and approach/avoidance tendencies (better) map onto evaluative conditioning. As noted in Brom (2016), these measures are slower to extinguish than genital and subjective arousal measures, an effect consistent with other evaluative conditioning literature outside the sexual realm (De Houwer et al., 2001).

Several laboratories have begun to investigate the neural correlates of human sexual conditioning. From this early research, it appears that there is some overlap with animal findings (Pfaus, Ismail, & Coria-Avila, 2010). For example, it has been shown that glutamatergic (Brom et al., 2015c) and dopaminergic (Brom et al., 2016b) signalings are involved, and Klucken et al. (2013) provided indirect evidence that serotonergic signaling is implicated. In addition, imaging studies show involvement of a range of neural structures, particularly those involved

in reward learning—the nucleus accumbens, the amygdala, the orbitofrontal cortex, and the anterior cingulate cortex (Banca et al., 2016; Klucken et al., 2009, 2013).

In summary, some progress has been made in understanding the role of conditioning in human sexual behavior using laboratory studies: Sexual conditioning has been demonstrated in men and women, such conditioning has been replicated in different laboratories, and such learning appears to follow Pavlovian rules. However, the nonhuman sexual conditioning literature is considerably richer (for review, see Akins, 2004; Pfaus et al., 2012).

Comparison to Nonhuman Sexual Conditioning

While there is disagreement over how applicable animal conditioning studies are to human behavior (e.g., Brewer, 1974; Shanks, 2010), integration is possible and desirable as it provides a useful bridge for the applicability of nonhuman (conditioning) work to human laboratory and real-world experience (Kirsh, Lynn, Vigorito, & Miller, 2004; Schactman & Reilly, 2011). Conditioning processes can function in similar ways in humans and other animals. However, it may be that humans differ in the diversity and sophistication of sources of information that are involved in or that can impact the acquisition and/or expression of conditioning. For example, verbal descriptions can serve as stimuli for humans and extra-situational factors (i.e., things outside training context) may more readily impact human learning (see Brewer, 1974; Phelps et al., 2001).

A key difference between human and animal studies is the relative strength of sexual CRs or, more broadly, the seeming relative impact of conditioning on sexual behavior. Nonhumans consistently show learning (i.e., almost all subjects exposed to training show a response), they readily learn (i.e., in just a few trials), and their CRs are robust; this is not the case for human sexual conditioning. A number of factors may explain this discrepancy. It could result from differences in dependent measure. Most animal studies employ measures of appetitive behaviors (e.g., conditioned approach, conditioned place preference, conditioning partner preference), which are not commonly used in human research. Approach, compared to consummatory, responses may be more readily impacted by conditioning (Craig, 1912, 1918). Further, most of the animal work has been done with sexually naïve subjects (but see Snowdon, Tannenbaum, Shultz-Darken, Zielger, & Ferris, 2011 who found no difference in sexual conditioning between sexually naïve and experienced marmosets). Studies using humans, however, have been conducted using adults with masturbatory and/or partnered sexual experience. Also, in addition to these US pre-exposure effects, latent inhibition (or CS pre-exposure) may be more difficult to avoid in humans. Importantly, most animal research involves direct sexual interaction. Not only is such a US more salient but the multidimensionality and participatory nature of this type of stimulation may provide more opportunities for forming associations. Further, the contrived nature of the laboratory environment, which is probably more evident to humans, may be less evocative and/or may only precipitate shallow versus deeper types of processing or learning (Öhman & Mineka, 2001). Finally, humans are probably better able to regulate the expression of conditioning.

Although a direct comparison is complicated, human fear learning as well as appetitive conditioning involving drug cues in the laboratory also pales (is weaker and less reliable) in comparison with such learning in nonhumans (Mayo, 2015; Mayo & de Wit, 2015; Öhman & Mineka, 2001). Yet many believe conditioning processes play a significant role in human fears and substance use and abuse (e.g., Berridge & Robinson, 2003; Robinson & Berridge, 1993, 2000, 2003; Mineka & Öhman, 2002; Mineka & Zinbarg, 2006). And although behavior therapy has had mixed effects in treating anxiety disorders and substance abuse, a more nuanced understanding of conditioning processes in humans has yielded more effective conditionedbased interventions for these conditions (Bouton, Mineka, & Barlow, 2001; Cox, Hogan, Kristian, & Race, 2002; Havermans, Mulkens, Nederkoorn, & Jansen, 2007; Mineka & Zinbarg, 2006; Wiers et al., 2006). Perhaps our expectations for the strength of sexual conditioning are too high, particularly considering the procedures we have used. Nonetheless, the importance of and specific role for classical conditioning in human sexual behavior remains an open question.

Comparison to Innate or Evolutionary Processes

Historically, conditioning processes were subsumed under behaviorism, which is a framework associated with Locke's idea of a tabula rasa and which was focused on proximal rather than distal or evolutionary explanations for behavior. However, that was not how Pavlov (1927) conceptualized the role of classical conditioning. He proposed that it was a process that worked within, and enhanced the efficiency of, physiological systems. Signaling biological events (USs) allows organisms to adopt adaptive responses to those events. Smelling the odor of food that you have previously consumed prepares you to digest that food. Similarly, perhaps smelling the body odor of a previous sex partner prepares you to sexually interact with them. Conditioning not only leads to anticipatory CRs, but it also increases the efficiency of the UR. The modern conceptualization of this functional perspective on classical conditioning is behavior systems theory (Timberlake, 1994). A behavior system is a set of perceptual, central nervous system, and motor mechanisms organized around an important biological function, in this case procurement of a mate and reproduction. Studies in nonhumans have demonstrated the functional role of classical conditioning in sexual behavior (e.g., Domjan, 2005; Domjan & Akins, 2011; Domja, Mahometa, & Matthews, 2012; Hollis, 1997). A common training paradigm consists of pairing some predictive cue with access to a mate. Testing involves comparing the effect of introducing the CS in a mating situation between conditioned and control subjects. Effects of (prior) conditioning include decreased latency to contact and interact with mates, decreased latency to ejaculate, and increases in the number of fertilized eggs (i.e., conditioned fertility). Effects are strongest when both partners have been conditioned but are also evident when only one partner has been conditioned.

Behavior systems theory is not a framework that has been explicitly used in human sexual conditioning research, but it could be instructive for the development of hypotheses and study design (Domjan & Akins, 2011). Further, a key assumption of the theory is that the CS and US have a preexisting relationship. This is similar to the idea of preparedness, yet it takes it a step further. The idea is that the CS and the US are proposed to be part of the same object. A CS is conceptualized as a feature of the US that does not initially elicit the UR. Hence, another way to frame what sexual classical conditioning might afford is that experiencing sexual interaction allows us to associate the many features of our mates-their smell, their voice, aspects of their physical appearance, with the sexual reward we obtain from them. The object of our mate is assembled and integrated in pairing features that are initially nonsexual with those that are sexually arousing, and these associations prepare us to engage with them sexually in the future.

A good, but nonsexual, illustration of this type of object conditioning comes from Zitovitch (Pavlov, 1927). He found that the smell and the sight of meat did not initially produce salivation in infant dogs. They needed experience consuming meat before this response developed. This is a process that Pavlov called *signalization*. Pavlov believed that the response to the sight and the smell of food were not innate but rather was acquired during the course of the organism's experiences. Hence, even though Pavlov used the term unconditioned stimulus, he believed that US properties were acquired and that the motivational aspects were linked with sensory features during experience (Balleine, 2011).

On one level, signalization can explain why we might have trouble distinguishing between what constitutes a US versus a CS. On another level, it suggests that it is difficult to differentiate inborn from learned processes. More recent studies have shown that conditioning plays an important role in seemingly unlearned aspects of eating and drinking. Hall, Arnold, and Myers (2000) found that young rats needed to learn that drinking water alleviates dehydration. Recent research also documents a similar effect in humans. Children who had feeding tubes early in life did not show an interest in eating, and even once the tube was removed, they were uninterested in eating and struggled to enjoy food (Wilken, Cremer, Berry, & Bartmann, 2013).

Seemingly inborn aspects of sexual behavior may be learned as well. For example, we tend to think of species and sex of partner preference as inherent. However, some impressive experimental work using nonhumans illustrates the important role of conditioning in these preferences. Kendrick, Haupt, Hinton, Broad, and Skinner (2001) showed that cross-fostered male and female sheep and goats preferred a mate from their foster versus their biological species. Further, conditioned cross-strain and same-sex partner preferences have been demonstrated in male and female rats, and male quail and drosophila in the laboratory (Cibrian-Llanderal et al., 2012, 2014; Coria-Avila, 2012; Coria-Avila et al., 2006; Griffith & Ejima, 2009; Nash & Domjan, 1991; Nash, Domjan, & Askins, 1989; Triana-Del Rio et al., 2011, 2015). These studies do not necessarily challenge the idea of a predisposition for partner preference, and in fact, some also show evidence of a predisposition. However, the main point is that these studies show that these behaviors are not fixed action patterns; even seemingly hard-wired aspects of behavior can be influenced by experience. Moreover, epigenetic research has further muddied the inborn versus acquired distinction. Dias and Ressler (2014) have shown transgenerational inheritance of learned sensitivities to environmental cues. That is, olfactory fear conditioning in parents made their offspring more responsive to the conditioned odors, despite a lack of direct experience or learning on the part of the offspring. Further, the mechanism behind these epigenetic effects may involve processes similar to those that underlie the synaptic plasticity involved in learning and memory (Sweatt, 2016). Hence, in modeling the development of sexual preferences and behaviors, we need theories (e.g., behavior systems theory or dynamical systems theory; Diamond, 2007; Fausto-Sterling, 2012), which have moved beyond simplistic nature/nurture distinctions.

Comparison to Other Types of Human Learning

Classical conditioning is not a mechanism; it is a procedure or an effect (Rescorla, 1988). To say that someone or some organism has been classically conditioned can mean that they have been exposed to a particular paradigm in which a CS and a US have been paired. It can also refer to the outcome of that procedure, that a CR has developed. These definitions are distinct from how this behavioral change occurs, that is, how the CS and US become associated. Further, mechanism itself can be addressed from different levels of analysis (e.g., Marr, 1982). It is not yet clear how classical conditioning occurs. One way that competing mechanistic explanations for human conditioning have been organized is into implicit and explicit models.

Implicit models view conditioning as an automatic processes and posit mechanisms that use basic associative principles. For example, simple contiguity or co-occurrence leads to link formation or pathway strengthening, potentially via Hebbian rules. Implicit processes are assumed to be rigid, effortless, to pertain to procedural memory, and also assumed to employ lower level (sub-cortical) neural circuits. Associated computational models include traditional animal learning theory and connectionist models.

Traditional animal learning theory explanations (Mackintosh, 1975; Pearce & Hall, 1980; Rescorla & Wagner, 1972) offer simple mathematical models that quantify the strength of learning (see Fig. 1). While such models clearly have their limitations when it comes to explaining (human) behavior (e.g., Miller, 2006), a strength is that their predictions map onto midbrain dopamine signaling that occurs during learning (Montague, Dayan, & Sejnowski, 1996; Schultz, Dayan, & Montague, 1997). Connectionist models derive from machine learning theory and many derive from neural nets, which are simulated systems for how interactions among a cluster of neurons might change based on experience. In other words, connectionist models simulate long-term potentiation and/or long-term depression processes. At the basic level, these models describe learning as strengthening or weakening of connections between nodes which can represent CSs and USs and their interconnections. Combining the computational formulas derived from animal learning experiments with connectionist models increases the complexity of learning to which animal learning theory can be applied (Schmajuk, 2010). For example, the Rescorla-Wagner model can provide the algorithm to determine the weight or the strength of the connection between nodes (see Fig. 2). Increasing the connective architecture of the model, for example, by increasing the number of input nodes, hidden layers, and connections allows for increased sophistication in the type of learning that can be predicted.

Explicit models, on the other hand, view conditioning as a controlled, conscious, or cognitively mediated process in which propositional- or inference-based reasoning leads to changes in expectancies. Such processes are assumed to be slow, flexible, effortful, to pertain to declarative memory, and are also assumed to employ upper-level (e.g., cortico-hippocampal) neural circuits. Associated computational models include Bayesian models, which are more computationally sophisticated than animal learning theory models. One difference is that they allow for uncertainty or noise in prediction. Hence, for such models, the anticipated outcome is probabilistic. Instead of representing associative strength as a single, punctate weight, the Bayesian representation is in the form of a frequency distribution that has a mean of a particular weight. What this distribution represents is a series of beliefs about the likelihood that CS predicts the

$$\Delta V_{A(n)} = \alpha_A \beta \left[\lambda - V_{A(n-1)}\right]$$

Fig. 1 Rescorla–Wagner model. V = associative strength, A = the conditioned stimulus A, α and $\beta =$ constants which represent the salience of the CS and the US, respectively. $\lambda =$ the maximal or asymptotic learning and n = trial number

US, with the mean of the (normal) distribution as the most likely belief about the strength of the relationship. Learning is seen as a shift in beliefs. Subsequent CS–US pairing makes higher values more believable and the distribution narrows, reflecting an increase in certainty about the relationship between the CS and US (Kruschke, 2008).

Some human learning researchers espouse a dual process theory of classical conditioning, meaning that they believe both explicit and implicit processes are involved, potentially under different conditions. Perhaps these different mechanisms map onto signal versus affective learning, respectively (Baeyens et al., 2001), but this idea is far from established. However, a dominant view in the human conditioning literature proposes a single (explicit) process model (Mitchell, De Houwer, & Lovibond, 2009). While this position has support, it has also been challenged (see open peer commentary, which immediately follows the article). A more basic problem with such a proposition is the confounded nature of the implicit versus explicit distinction (Gawronski & Bodenhauen, 2009). For example, these models contrast on a number of different variables, and these variables seem to be dissociable. More precisely, a number of different confounds illustrate this point. One is a species by mechanism confound. Most animal learning theorists agree that conditioning is a cognitive process that yields changes in expectancies. Even simple organisms can learn when the CS and US do not overlap and when CS-US contingency is far from perfect. Contiguity is not what contributes to learning, at least in some instances, even in nonhumans (Rescorla, 1988). Although there is limited cross talk between animal and human learning researchers, principles used to explain basic animal conditioning can explain sophisticated learning in humans. Rescorla-Wagner-like and connectionist models have been used to account for aspects of linguistic processing, episodic memory, causal judgments, categorical learning, even complex probabilistic category learning in which there is no clear-cut rule for membership such as distinguishing wines, diagnosing diseases, and predicting the weather (e.g., Baeyens, Milin, Đurđević, Hendrix, & Marelli, 2011; Gluck, 2008; Kruschke & Johansen, 1999). Similarly, there is a sophistication of learning task with sophistication of mechanism confound. In humans and other animals, real-life conditioning situations are multifaceted and multidimensional; CSs and USs are often quite complex objects or events. Extensions of the Rescorla-Wagner model, for example Wagner's affective extension of sometimes opponent process (AESOP; Wagner & Brandon, 1989) and componential sometimes opponent process (C-SOP; Wagner & Brandon, 2001) models, capture the multicomponential nature of CSs and US, and these models can be used to explain aspects of human contingency learning, for example multicue probability learning and multiattribute judgments (Enkvist, Newell, Juslin, & Olsson, 2006; Juslin, Olsson, & Olsson, 2003).

Fig. 2 Simple computational model in which two CSs predict a US. The Rescorla–Wagner model has been used as the algorithm to determine weights. CS_A is a better predictor than CS_B perhaps because it is more salient and/or because it has been more consistently paired with the US



In addition, awareness seems confounded with mechanism. Awareness does not perfectly align with complexity or flexibility. Humans can distinguish between and can engage in unconscious cross-modal matching of the sound and sight of letters (Faivre et al., 2014), we can lip-read without awareness (Plass, Guzman-Martinez, Ortega, Grabowecky, & Suzuki, 2014), we actively maintain and integrate perceptual information over time without awareness (Atas, Faivre, Timmermans, Cleeremans, & Kouider, 2014), and we can learn longlasting preference without conscious awareness (Pine, Mendelsohn, & Dudai, 2014). Humans engage in unconscious goal pursuit (Aarts & Custers, 2012), and this and other research (Farooqi & Manly, 2015) have shown that nonconscious processing can be highly flexible. More specific to conditioning, Gawronski and Bodenhausen's (2006) associative-propositional evaluation (APE) model proposes that attitude formation and change can occur via evaluative conditioning. Further, Hahn, Judd, Hirsh, and Blair (2013) found that people have insight into their implicit attitudes, even when they differ from explicit ones and even when their feelings may reflect badly on them.

Neural circuit is also confounded with mechanism. There are integrative models of human learning and memory that combine incremental associative learning models and rapid formation of declarative memory models that seem helpful for integrating across the implicit—explicit divide. Although these models were proposed in the late 1980s through the 1990s (Ashby, Alfonso-Reese, Turken, & Waldron, 1998; Gluck & Bowers, 1988; McClelland, McNaughton, & O'Reilly, 1995), they remain viable (Gluck, 2008; Gluck, Myers, & Meeter, 2005; O'Reilly, Bhattacharyya, Howard, & Ketz, 2014). Finally, there is a computational model by mechanism interaction. With the advent of deep learning networks which can accommodate an increased number of hidden layers, connectionist models can account for even more sophisticated human learning (Mnih et al., 2015; Yamins & DiCarlo, 2016). On the other hand, Bayesian models are not only applicable to complex human learning, they have been integrated with animal learning theory (e.g., Courville, Daw, & Touretzky, 2006; Kruschke, 2008) to explain basic associative learning and they have been used to explain functioning at the level of the neuron (O'Reilly, Jbabdi, & Behrens, 2012). In fact, Baluška and Levin (2016) showed that similar mechanisms mediating sensory and memory processes can function in nonneural cells as well as at the organismal level. That is, similar mechanisms can explain "cognition" in single-celled organisms, in plants and in tissues of animal bodies, include the mammalian brain.

We need to think more precisely but also more comprehensively about mechanism in human sexual conditioning. Multiple mechanisms most likely contribute and convergence and divergence among these mechanisms and other types of human learning also exist. Processes behind conditioning can be just as complicated or as simple as other types of learning in which we engage. Classical conditioning can be impactful in human sexual behavior, yet it is unclear at what level conditioning functions and precisely how it works.

Conclusion

At a minimum, human sexual conditioning studies are important in translational research. Such work holds the potential for helping to understand human learning processes more broadly, for explaining aspects of human sexual behavior, and for improving sexual functioning. For example, recent research has shown conditioning processes might play a role in the establishment of compulsive sexual behavior (Banca et al., 2016; Hoffmann et al., 2014; Klucken et al., 2016) and dyspareunia (Both et al., 2017), as well as in the treatment of these disorders.

Although sexual conditioning has been demonstrated in men and women in the laboratory, conditioned responses are often not robust. Creating laboratory procedures for yielding stronger, more consistent CRs would help with investigation of the contributions and limitations of conditioning processes in explaining how cues come to signal sexual arousal or opportunity as well as how they might acquire erotic competence. Work with prepared CSs (e.g., body odors), more immersive USs (e.g., actual sexual behavior and potentially occurring outside the laboratory; Hoffmann et al., 2012), and other CRs (e.g., conditioned place preference and alpha asymmetry to assess approach; Prause, Staley, & Roberts, 2014) would seem in order. Complimentary nonexperimental research seeking more information about the relationship between early or peak sexual experiences and sexual preferences should also be performed. In addition, we should expand but also refine our theoretical approaches, and we should acknowledge that learning can affect the most fundamental aspects of sexual behavior.

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Compliance with Ethical Standards

Conflict of interest The author declares that she has no conflict of interests.

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