



Review

The role of conditioning, learning and dopamine in sexual behavior: A narrative review of animal and human studies



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ABSTRACT

Many theories of human sexual behavior assume that sexual stimuli obtain arousing properties through associative learning processes. It is widely accepted that classical conditioning contributes to the etiology of both normal and maladaptive human behaviors. Despite the hypothesized importance of basic learning processes in sexual behavior, research on classical conditioning of the sexual response in humans is scarce. In the present paper, animal studies and studies in humans on the role of pavlovian conditioning on sexual responses are reviewed. Animal research shows robust, direct effects of conditioning processes on partner- and place preference. On the contrast, the empirical research with humans in this area is limited and earlier studies within this field are plagued by methodological confounds. Although recent experimental demonstrations of human sexual conditioning are neither numerous nor robust, sexual arousal showed to be conditionable in both men and women. The present paper serves to highlight the major empirical findings and to renew the insight in how stimuli can acquire sexually arousing value. Hereby also related neurobiological processes in reward learning are discussed. Finally, the connections between animal and human research on the conditionability of sexual responses are discussed, and suggestions for future directions in human research are given.

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1. Introduction

It is widely accepted that associative learning contributes to the etiology of both normal and maladaptive human behaviors (Day and Carelli, 2007). Psychopathology and deviant sexual preferences and behaviors are also thought to develop through conditioning processes (Letourneau and O'Donohue, 1997; Ågmo et al., 2004; Martin-Soelch et al., 2007; Pfaus, 1999a,b; Singer and Toates, 1987; Toates, 2009). Knowledge about basic learning processes involved in sexual behaviors, can help foster potentially critical insights in the etiology of extreme forms of sexual behavior. This may help in the development of clinical treatments for those behaviors, including paraphilias, or deviant sexual preferences, that manifest perturbed motivation, but also for the more prevalent sexual desire and arousal disorders. Because much sexual behavior is thought to be acquired through learning, and given the specific hypothesis that classical conditioning plays an etiological role in the development of sexual dysfunction, research in the area of classical conditioning of human sexual arousal is warranted. Despite the hypothesized importance of basic learning processes in sexual behavior, research of classical conditioning of sexual response in humans is scarce (Akins, 2004; Pfaus et al., 2001). Sexual conditioning studies with women are even scarcer in the literature. In the present paper, we will discuss the studies that provide evidence for basic sexual learning and conditioning processes in sexual arousal, desire and behavior, and focus especially on how stimuli can acquire sexually arousing properties.

According to incentive motivation models, sexual motivation is the result of the interplay of a sensitive internal sexual system with external motivational stimuli. External stimuli that can promote motivation are called incentive stimuli (Ågmo, 1999; Bindra, 1968, 1974; Both et al., 2007; Singer and Toates, 1987). Sexual incentives are generally positive, and likely to illicit approach behavior. The motivational valence can be unconditioned (primary) or conditioned (secondary) as a result of associative learning (Di Chiara, 1995). Some stimuli, e.g. stroking or kissing may be innately sexually competent, but many sexual stimuli are not intrinsically sexually competent. The attractiveness of those stimuli depends on their history of positive or negative consequences and the resulting meaning that is stored in memory. Specific cues of sexually competent stimuli may gain learned incentive value through their association with the stimulus. While conditioned learning is not the only way in which humans acquire certain sexual behaviors, these processes represent an essential link between stimulus and response (Toates, 1998), and can be point of intervention in the treatment of disorders in sexual behavior. Therefore, it seems highly valuable to gain insight in the processes through which stimuli may acquire sexual motivational value. Despite the overall consensus that learning plays an essential role in sexual development and the expression of sexual activity, sexual learning has only recently been tied into a more general framework of incentive motivation theory. Over the last decade, clinical and empirical support

for the incentive-motivation model of desire has accumulated and the model is now incorporated into the current operational definition of sexual desire disorder in the DSM-5 (Brotto, 2010). This, combined with the fact that the model of incentive motivation was developed primarily with reference to research in nonhumans (Toates, 2009; Pfaus et al., 2001) makes clear that there is a need for an overview of the integration and extension of this theory with a focus on recent human sex research. Thereby, an attempt is made to form links between the processes described in the incentive motivation model and the proposed human brain regions involved.

First, we briefly discuss the different forms of conditioning and the associated neural systems. Further insights in associative learning by looking closely at the neural pathways involved in these processes have identified different brain regions and neurotransmitter systems involved in conditioned learning. Especially, dopaminergic terminations in the basal forebrain foster sexual arousal and sexual motivation and seem to play a major role in reward learning (Di Chiara, 1999; Dominguez and Hull, 2005; Hull et al., 2004). Gaining knowledge about the functional neurobiology underlying human sexual behavior is important, as this may lead to understanding of functions that apply to the most primitive aspects of human mental functioning. Thereby, it may also offer an opportunity for intervention. Although the involvement of other neurotransmitter systems such as the serotonergic, endorphin, and glutamate system in sexual behavior have been reported, the current article primarily focuses on the dopaminergic system. Further on, we briefly review the literature on appetitive and aversive conditioning of the sexual response in animal studies. Mainly results from rat studies will be discussed, but when relevant, studies with other rodents, avian species, nonhuman primates and even fish will be discussed. Subsequently, the literature of sexual conditioning in humans is reviewed. In that section we will first discuss literature on the conditioning of the male sexual response, after which we will discuss the research conducted so far on the conditioning of the female sexual response. We will conclude with a discussion and suggestions for future directions. But first, for a thorough understanding, we will outline the different forms of conditioning and the related basic learning phenomena in the following section.

2. Basic learning processes

Why include basic learning mechanisms in an understanding of the neurobiology of sexual behavior? From an evolutionary perspective, the development of sexual learning mechanisms is thought to offer some reproductive advantage and modulate reproductive fitness. This has indeed been shown by several animal studies. For instance, classical-conditioned male quail subjects released greater volume of semen and greater numbers of spermatozoa than control subjects (Domjan et al., 1998). Second, in blue gourami fish, classical conditioning provides the means to enhance territorial defence and yields large reproductive benefits

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